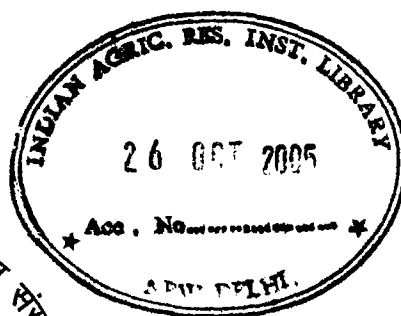


CHARACTERIZATION OF THE RESPONSE OF RICE CULTIVARS (*Oryza sativa* L.) TO THE INTERACTION OF ELEVATED CO₂ AND TEMPERATURE

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2005

T- 7456

CHARACTERIZATION OF THE RESPONSE OF RICE CULTIVARS (*Oryza sativa* L.) TO THE INTERACTION OF ELEVATED CO₂ AND TEMPERATURE

By

K.B. SUJATHA

A Thesis

submitted to the Post Graduate School,
Indian Agricultural Research Institute, New Delhi,
in partial fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

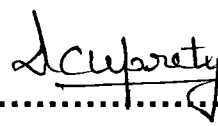
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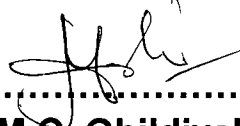
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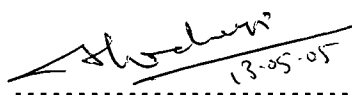
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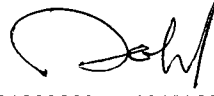
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CERTIFICATE

This is to certify that the thesis entitled “**Characterization of the response of rice cultivars (*Oryza sativa* L.) to the interaction of elevated CO₂ and temperature**” submitted in partial fulfilment of the requirements for the award of the degree of **DOCTOR OF PHILOSOPHY in PLANT PHYSIOLOGY** to the Post Graduate School, Indian Agricultural Research Institute, New Delhi, is a record of *bona fide* research work carried out by **Ms. K.B. SUJATHA** under my guidance and supervision.

No part of the thesis has been submitted for any other degree or diploma. All the help and assistance received during the course of this investigation have been duly acknowledged by her.

Place : New Delhi
Date : Feb. 21, 2005


(D.C. UPRETY)
Chairman
Advisory Committee

Dedicated

to

❖ ***My beloved Dad (K.R. Bhaskaran Nair)***

&

Mom (K.K. Kalyanikutty)

❖ ***Brother (Hari Kumar)***

❖ ***Husband (Rajesh)***

and

❖ ***Son (Ananth)***

ACKNOWLEDGEMENTS

First of all, I thank the Almighty and express my deep sense of dedication to my beloved parents, brother, husband and son for their love, zeal, devotion, support and encouragement in fulfilling my task of completing the work successfully.

With great privilege, I express my heartfelt gratitude to my chairman Dr. D.C. Uprety, National Fellow and Principal Scientist, Division of Plant Physiology for his meticulous guidance, kind and fatherly treatment, enthusiastic encouragement and critical appraisal throughout the course of this investigation.

My sincere and heartfelt thanks are due to the members of the advisory committee, Dr. M.C. Ghildiyal, Division of Plant Physiology, Mr. Anil Dahuja, Division of Biochemistry and Dr. H.C. Joshi, Division of Environmental Science for their dexterous guidance and useful criticism during the period of research work.

I express my special thanks to Dr. G.C. Sivasana, Head, Dr. P.S. Deshmukh, Professor, Dr. R.K. Sairam, Principal Scientist, Dr. Renu Pandey, Scientist, Division of Plant Physiology for their care and attention rendered throughout the course of study.

The amity and unabated support received from my mother-in-law and father-in-law, Ranjini Edathi, Mukunda and Harsha Mal will be ever cherished.

I am ineffable to express my profound and personal indebtedness to my beloved friends Nagewari, Selai, Usha, Vinu, Prabhu, Ramakrishna, Selaamani and Muthu Subramanian for their fervored guidance, great care and constant encouragement. Their attention and untiring help rendered essence to my work.

I am also grateful to extend my deep gratitude to my beloved madam Dr. M.K. Katarani and Sivakumar for their love, care and continuous help.

I feel immense pleasure in extending my thanks to my affectionate and caring junior friends, Thasni, Suma, Panki, Devi, Priya, Baby, Pushpalatha and Sumesh for their good company, kind cooperation and profound help provided during my stay at Indian Agricultural Research Institute.

I am delighted to express my heartfelt thanks to my classmates Eshilmathi, Linga Srinivasa Rao and Vijay for their timely help and support.

I also extend my heartfelt thanks to Dr. D.C. Saxena, Dr. Sita Ram, Dr. Tej Pal Singh, Dr. Neeta, Sh. Bhagwan Das, Mr. Moed and Mr. Ganesh for their help during the period of my study at Indian Agricultural Research Institute.

I gratefully acknowledge the assiduous moral support extended by Mrs. Uprety madam.

I extend my sincere thanks to Dr. A.K. Singh, Scientist (SS), Division of Genetics and Dr. Hari Prasad, Scientist (SS), Division of Genetics for providing me the plant material for my study.

I owe my thanks to the team of M/s Shiva Computers who typed the thesis with patience, cheerfulness and precision.

Last, but not the least, I gratefully acknowledge the financial support provided by IARI, National Fellow Project, ICAR and NATCOM Project from Ministry of Environment for carrying out this study.

There are many others who have helped me in various ways and supported me. I sincerely thank all of them and their forgiveness for not monitoring them here by name.

New Delhi- 110 012⁵
Dated: Feb. 21, 2004

K. B. Sujatha
(K.B. SUJATHA)

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1. INTRODUCTION

The environment is constantly changing as a result of man's activities and the present challenge is to predict, how agriculture will respond to the changing environment of tomorrow.

One of the major driving forces for global climate change is the rapid increase in the green house gas concentration in the atmosphere. The human activities have led to the build-up of green house gases such as water vapour, carbon dioxide, methane, nitrous oxide and chlorofluorocarbons. The dramatic increase in human population since the pre-industrial period, raised concentration of these gases due to large-scale use of fossil fuels, deforestation, industrialization and urbanization. The carbon dioxide content of earth's atmosphere had been amazingly constant for several centuries, striking at an average concentration of approximately $280 \mu\text{mol mol}^{-1}$. With the beginning of industrial revolution (1874) the equilibrium was perturbed and the carbon dioxide content of the air began to rise subsequently to unprecedented economic growth.

Measurement of atmospheric carbon dioxide concentration began at South Pole, Antarctica, as early as 1957, and at Mauna Loa (Hawaii) in march 1958, by using the analysis of air trapped in bubbles in ice cores. Mauna Loa studies observed an increase of $1.0 \mu\text{mol mol}^{-1}$ of CO_2 per year from 1958 to 1982 (Keeling *et al.*, 1995). The current atmospheric concentration of CO_2 is $372 \mu\text{mol mol}^{-1}$ (Uprety *et al.*, 2003a), which is approximately 33 % more



since the industrial revolution (Fig. 1). It is currently increasing at the rate of $1.5\text{--}1.8\ \mu\text{mol mol}^{-1}$ per year. This exponential rise of CO_2 in the atmosphere if continued at the present rate, the concentration of CO_2 may be doubled by the end of 21st Century (Houghton *et al.*, 1996). Measurements in Delhi region also showed similar increase in CO_2 concentration (Upreti *et al.*, 2004) (Fig. 2).

The potential consequence of the rise in CO_2 concentration with respect to plant biology is its effect on plant process of photosynthesis- **Biological Effect**. The higher level of atmospheric CO_2 affects C_3 , C_4 and CAM plants differentially (Poorter, 1993). It enhances the growth rate of almost all plants (Kimball, 1983) but the enhancement was very significant in C_3 species. C_3 plants (rice, wheat, oil seeds, pulses etc.) respond to elevated CO_2 by reducing the oxygenase activity of RuBP carboxylase/oxygenase enzyme resulting in the suppression of photorespiration (Long and Drake, 1992). C_4 plants (maize, sorghum, sugarcane etc.) show little or no photosynthetic response to elevated CO_2 , because they are CO_2 saturated and not competitively inhibited by O_2 . The increase in CO_2 is expected to cause global warming by absorbing the long wave heat radiations from the earth's surface and altering the precipitation (Moya *et al.*, 1998)- **Climatic Effect**. According to global circulation models (GCMs), the temperature changes may not be uniform. At Polar Regions it may increase by $4\text{--}5^\circ\text{C}$ and at equator by less than 1°C . Over the last 140 years from 1860 to 2000, the global average surface temperature has increased by $0.6^\circ\text{C} \pm 0.2^\circ\text{C}$ (Fig. 3). The Third Assessment Report (TAR) of IPCC projects a global average warming of 1.4 to 5.8°C by the year 2100 (Fig. 4).

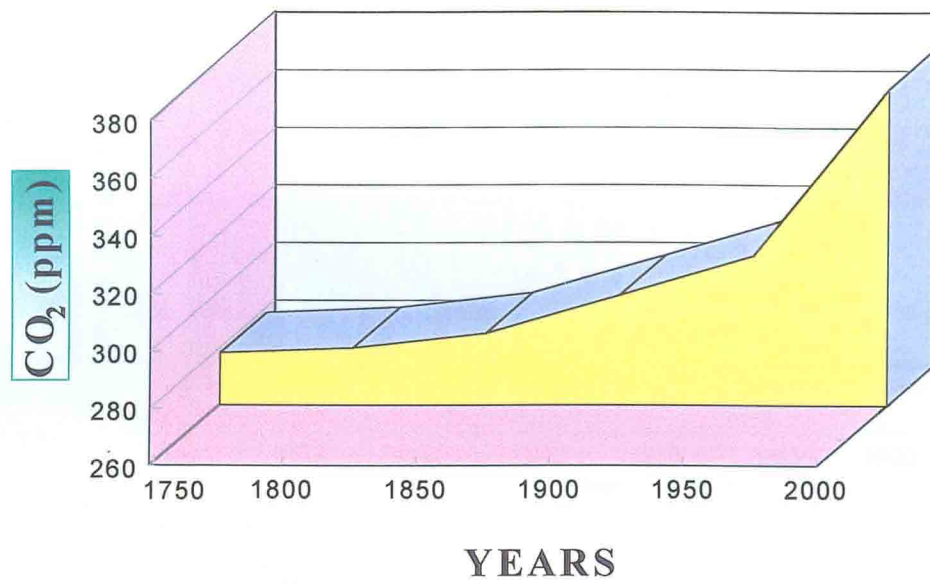


Fig. 1. Exponential rise of atmospheric CO₂ concentration (Uprety *et al.*, 2003a)

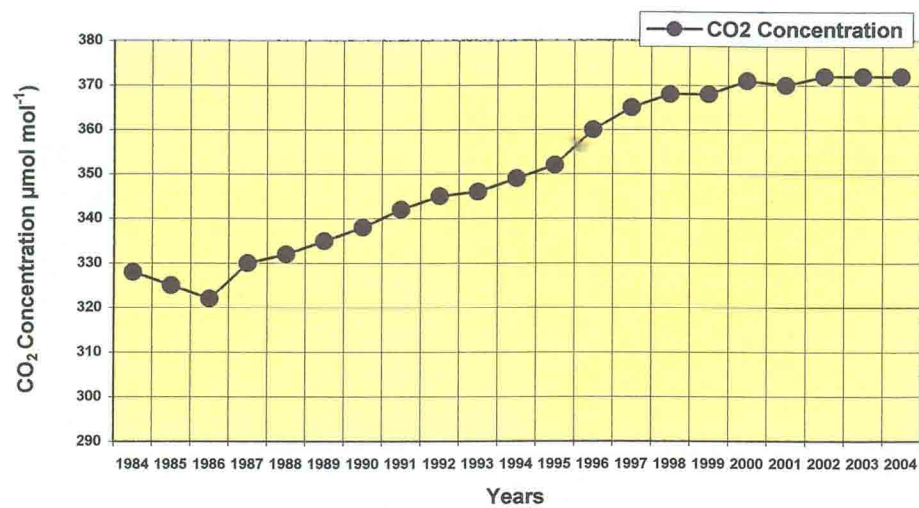


Fig. 2. The rise in atmospheric CO₂ at Indian Agricultural Research Institute, New Delhi from 1984 to 2004 (Uprety *et al.*, 2004)

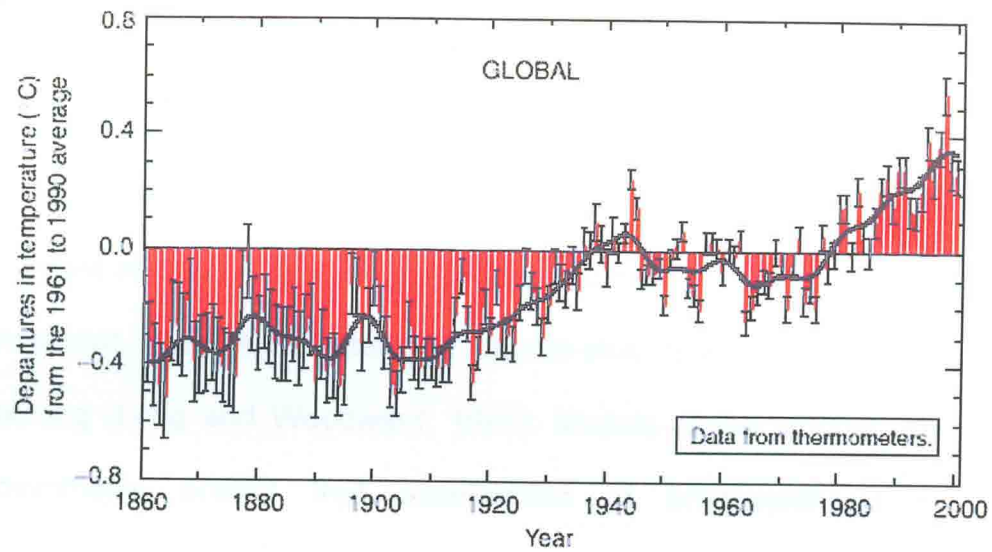


Fig. 3. Variations of the earth's surface temperature for the past 140 years (Source : IPCC Third Assessment Report, 2001)

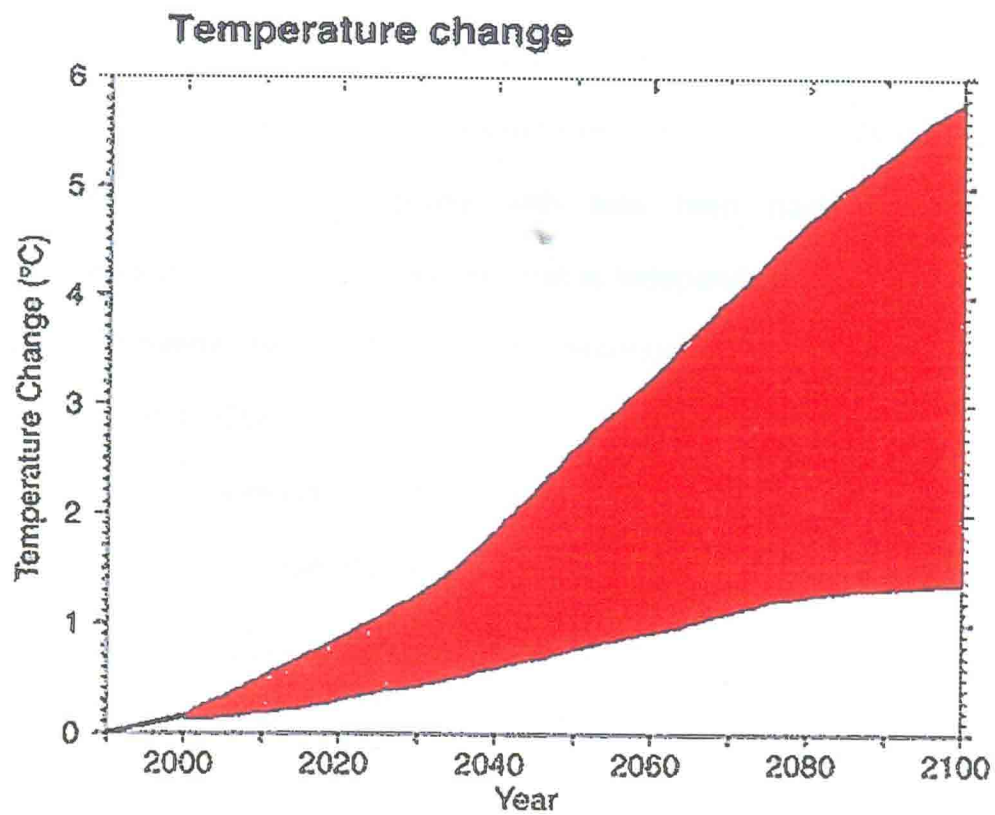


Fig. 4. Temperature change (Source : IPCC Third Assessment Report, 2001)

Investigations on global climate change have been mostly done on plant response to high CO₂ level. To understand the responses of the plant system to global climate change, a careful examination of the combined effect of temperature and CO₂ on plants was required. The warming that is predicted to occur will affect numerous physiological and morphological aspects of plant development and would alter the source-sink relationship and biomass partitioning (Long and Woodward, 1988). Models of the biochemistry of C₃ photosynthesis predict that acceleration of photosynthesis by CO₂ enhancement could be further increased with rise in temperature (Long, 1991, Kirschbaum, 1994) because photorespiratory losses will be reduced by elevated CO₂ levels. Idso and Idso (1994) showed that plant growth enhancement due to elevated CO₂ was highly significant at higher temperature. Moreover, the increased supply of assimilates caused by higher CO₂ could be combined with the increased sink metabolism resulting from the warming to produce larger plants with less feed back inhibition of photosynthesis and a carbohydrate flux that is independent of the pool sizes (Farrar and Williams, 1991). Therefore, it is essential to observe the effects of temperature and CO₂ levels on plant carbon balance, growth and development, and biomass accumulation (Morison and Lawlor, 1999). In the present study the response of rice crop to the changed CO₂ and temperature conditions was studied.

The crop selected for the present study was rice, mainly because rice is a major food crop of the world in general and Asia in particular. Nearly 90 % of the world's rice is produced and consumed in Asia (Table A), wherein it is a staple food for nearly 2.4 billion people. Rice provides two third of the calories

**Table A. Production, import and export of rice during the triennium ending 1995
(million tons)**

Country/Continents	Production	Export	Import	Net trade	Consumption	Self-sufficiency ratio (%)
ASIA	329.4	12.6	9.1	3.4	326	101
South Asia						
India	80.9	2.0	0.1	1.9	79	102
Bangladesh	17.5		0.5	-0.5	18	97
Pakistan	3.8	1.3	0.0	1.3	2	152
Sri Lanka	1.5		0.1	-0.1	2	94
China	121.1	1.1	1.0	0.1	121	100
East Asia						
Indonesia	31.8	0.2	1.3	-1.1	33	97
Vietnam	16.4	2.1		2.1	14	115
Thailand	13.5	5.1		5.1	8	161
Myanmar	12.1	0.0	0.4	-0.4	12	97
Japan	8.5	0.1	0.9	-0.7	9	92
Philippines	7.0	-	0.2	-0.2	7	98
Korea, Rep. of	4.4	-	0.0	0.0	4	100
Korea, DPR	2.0	0.0		0.0	2	100
AFRICA	9.2	0.3	3.7	-3.4	13	73
North Africa	3.0		0.2	-0.2	3	94
Egypt	3.0	0.2	0.0	0.2	3	108
Sub-Saharan Africa	6.1	-	3.5	-3.5	10	64
Western Africa	3.5	-	-	0.0	3	100
Central +Eastern & Southern Africa	2.6	-	-	0.0	3	100
CENTRAL AMERICA	1.2	0.0	1.2	-1.2	2	49
SOUTH AMERICA	12.0	1.1	1.3	-0.2	12	98
Brazil	7.0		0.9	-0.9	8	89
NORTH AMERICA	5.3	2.5	0.4	2.4	3	182
United States	5.3	2.5		2.8	2	214
EUROPE	1.4	0.3	1.1	-0.8	2	64
CIS	1.0	0.0	0.3	-0.3	1	16
OCEANIA (Australia)	0.7	0.5	0.3	0.2	0	148
WORLD	360.2	17.6	17.4	0.1	360	100
Asia	329.4	12.6	9.1	3.4	326	101
Rest of the world	30.9	5.0	8.3	-3.3	33	-1.0
Developing Countries	343.3	13.8	14.1	-0.3	344	100
Developed Countries	17.0	3.8	3.3	0.5	17	103

Source: FAO Food Outlook. Various Issues

for most Asians with cereal based-diets (Anonymous, 2002). Following the introduction of IR-8 rice during the 1960's its production in Asia grew at unprecedented rate of 3% during 1967–85 (Fig. 5). Similar growth in world rice production also occurred during this period (Fig. 6). Further to keep pace with rapidly increasing world population, an increase in the production of rice by at least 46% by the year 2025 was required (Horie *et al.*, 2000). Potential future climatic change resulting from increased atmospheric carbon dioxide (CO₂) concentration and other green house gases, especially the rise in temperature, hampers our ability to predict global rice production and raises serious questions concerning food security for the near future. An accurate prediction of the impact of climatic change on rice productivity is essential for the estimation of the rice production potential. Several rice crop simulation models like ORYZA 1 (Kropff *et al.*, 1993) and SIMRIW (simulation model for rice-weather relation) (Horie, 1987) were used to study the effects of increasing CO₂ level and temperature on potential yield of rice. The two crop simulation models predicted that at different CO₂ levels, an increase in temperature would cause decline in yields and at all temperature increments, an increase in CO₂ would increase yield in rice (Mathews *et al.*, 1995). However, these modeling studies, point to the need for further research in order to test and improve our understanding of elevated CO₂ and temperature effect of rice growth, development and productivity.

An effort has been made to study the interactive effect of elevated CO₂ and temperature on rice varieties in the present investigation. Open top chamber (OTC) and free air carbon dioxide enrichment (FACE) facilities were used for studying the responses of rice varieties to the elevated CO₂. The

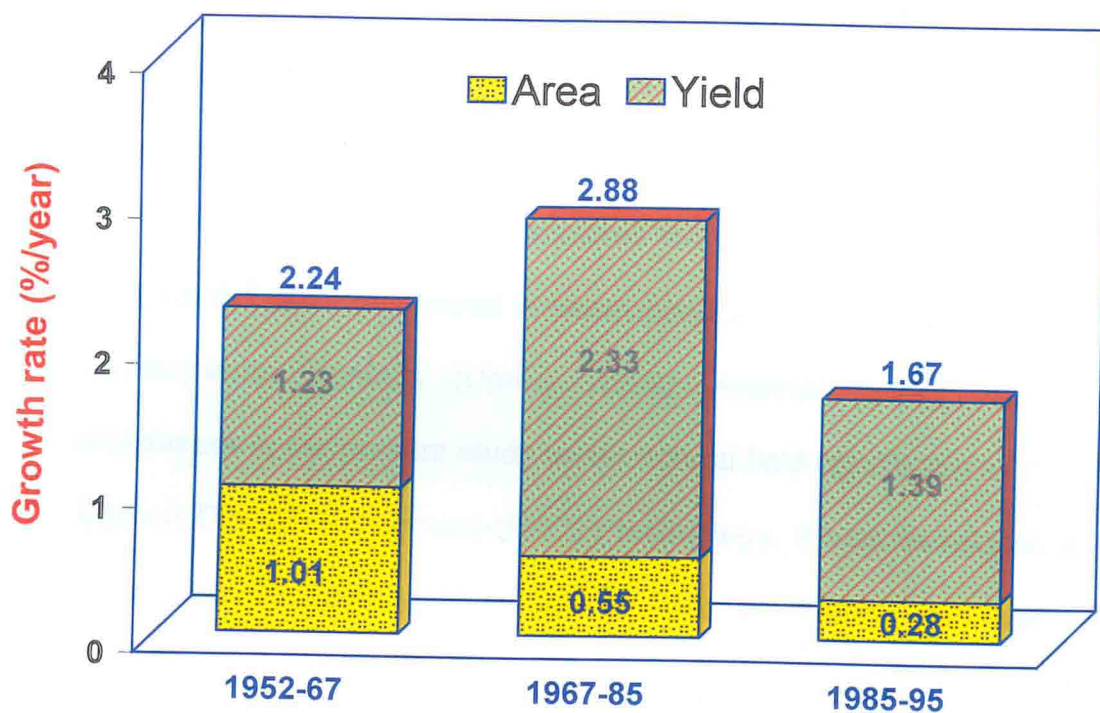


Fig. 5. Percentage growth in rice production and productivity : Pre- and Post-Green Revolution (Asia)

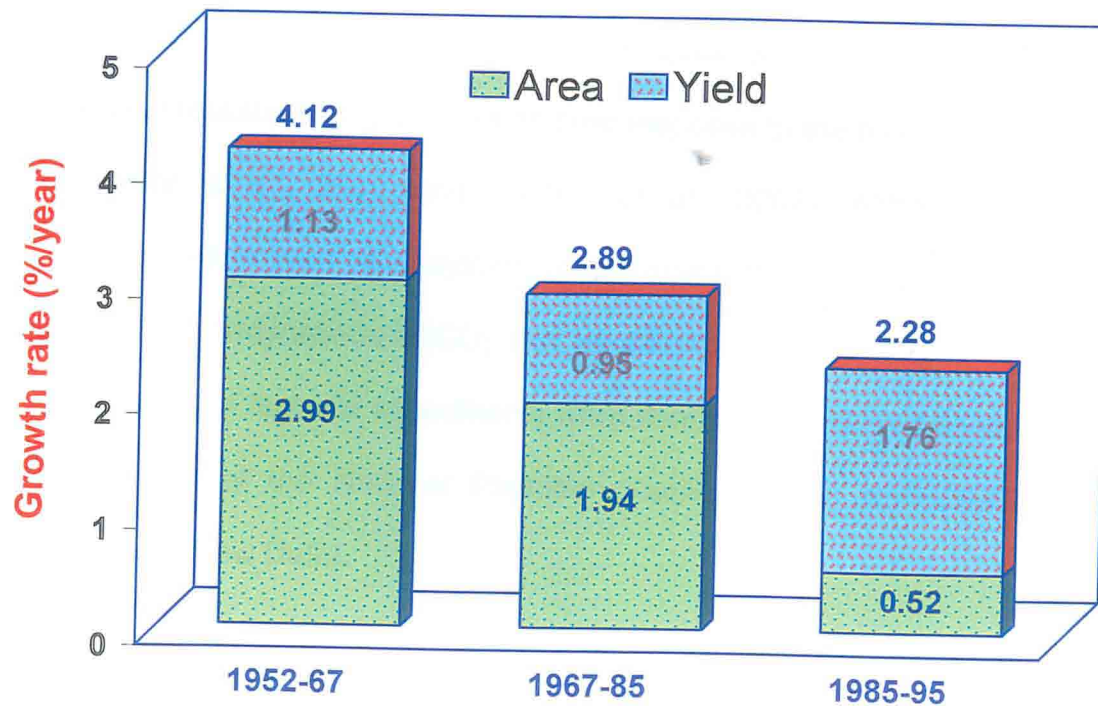


Fig. 6. Percentage growth in rice production and productivity : Pre- and Post Green Revolution (Rest of world) Source: FAO

temperature and CO₂ interaction studies were done using the phytotron controlled growth chambers. Open top chamber was one of the most widely used techniques for studying the response of crops and crop ecosystems to the elevated CO₂. OTC also measures the dynamic changes in temperature, light, rainfall etc experienced in unenclosed area without costly and complex environmental controls (Upreti, 1998). Another facility used for CO₂ enrichment in the present study under natural field condition was the Free Air Carbon Dioxide Enrichment (FACE) technology. It was developed at Indian Agricultural Research Institute, New Delhi for the South Asian region (Upreti *et al.*, 2000 and Maini *et al.*, 2002). This technology has many advantages over open and closed chamber systems used by earlier scientist (Upreti, 1998). FACE could enrich a larger area of vegetation with CO₂, without confounding effect of growth chamber, for extended period of time and lower cost per unit area than any other techniques. Both OTC and FACE provides almost realistic biological data on crop response to the rising atmospheric CO₂ (Upreti *et al.*, 2000 and Kimball *et al.*, 2002). Although, experiments conducted using FACE system utilize true field grown conditions, however factorial combinations of CO₂ and temperature treatment was difficult. Thus, the required factorial experiments were conducted in closed controlled growth chambers at the National Phytotron Facility, Indian Agricultural Research Institute, New Delhi.

The identification of cultivars for the optimal response to CO₂ and / or temperature has not been analysed under tropical conditions (Moya *et al.*, 1998). Two varieties of rice viz., Pusa RH-10, the first aromatic, super fine grained hybrid and Pusa Sugandh-2, an aromatic, pure line variety released in

the year 2001, were selected. The hybrid rice was selected because it was considered as the practically feasible and adoptable option to increase the rice production, as has been amply demonstrated in People's Republic of China, the first largest country in the world in rice production (Ahmed *et al.*, 2003). To meet the requirement and to fill the gap of productivity for future, it was imperative to simulate conditions of high CO₂ and temperature to study the response of these rice varieties under the following objectives.

1. To study the response of rice varieties to elevated CO₂, using Open Top Chambers (OTC) and Free Air Carbon Dioxide Enrichment (FACE) facilities for CO₂ enrichment.
2. Physiological and biochemical characterization of these responses.
3. To find out the interactive effect of elevated CO₂ and temperature on photosynthetic parameters of rice cultivars.
4. To determine the effect of elevated CO₂ on the temperature induced morphological changes in rice cultivars.

The database generated on various morphological, physiological and biochemical parameters will help in developing plant type and model for future climatic condition. This study will help in tailoring suitable rice plants and identifying nutrient management practices and cultivation of such cultivars for future.

2. REVIEW OF LITERATURE

Global climate changes are unique challenges to the agriculture. Following changes that affect agroecosystem are:

1. Change in land use and land cover
2. Decline in biodiversity
3. Accumulation of green house gases in the atmosphere
4. Change in climate

One of the major driving forces of global climate change in the rapid increase in the green house gases including water vapour, carbon dioxide, methane, nitrous oxide and chlorofluoro carbons.

One of the most important green house gas which profoundly affects the agricultural productivity and food security is the carbon dioxide. Plants have been directly affected by rising atmospheric CO₂ concentration because it is the first molecular link from atmosphere to biosphere. The drastic increase in human population, since the pre industrial revolution increased the concentration of CO₂ due to large scale use of fossil fuels, deforestation, industrialization and urbanization. Gifford (1994) showed that burning of fossil fuel puts 5.8-6.2 Gt C year⁻¹ into the atmosphere and tropical deforestation adds another 1.5-3.0 Gt C year⁻¹ accumulating about 8.0 Gt C year⁻¹ with atmospheric level. Of this 4.7 Gt C is being absorbed by the oceanic and terrestrial biota per year and 3.3 Gt C year⁻¹ remains in the atmosphere

accounting to the rise in its concentration (Tans *et al.* 1995). Among the countries, the major contribution of the total CO₂ emissions of the world is from USA (41%), followed by Germany (22%) and Japan (21%) and India contributes only 2% of the total CO₂ emissions of the world (WB, 2001, Fig. 7).

The measurement of atmospheric CO₂ concentration at Antarctica as early as 1957 and Mauna Loa (Hawaii) in 1958 using the analysis of air trapped in bubbles in polar ice core, showed that it was about 205 $\mu\text{mol mol}^{-1}$, 20000 years ago. Pre industrial value was 280 $\mu\text{mol mol}^{-1}$ which remained stagnant for 10,000 years Mauna Loa studies observed an increase of 1.0 $\mu\text{mol mol}^{-1} \text{ yr}^{-1}$ from 1958 to 1982. The 1958 value of atmospheric CO₂ was 316 $\mu\text{mol mol}^{-1}$ (Keeling *et al.*, 1995) and in 1995-2000, it was recorded as high as 360 $\mu\text{mol mol}^{-1}$ (Collette, 1995) and today it is 372 $\mu\text{mol mol}^{-1}$ (Upreti *et al.*, 2004) (Fig. 1), which is approximately 33% more, since the beginning of the industrial revolution. It is currently increasing at the rate of 1.5-1.8 $\mu\text{mol mol}^{-1} \text{ yr}^{-1}$ (Keeling *et al.*, 1995) and is likely to be doubled by the end of the 21st century (Houghton *et al.*, 1996).

The atmospheric concentration of methane (CH₄) had increased by 1060 ppb (151%) since 1750 (Fig. 8) and continues to increase. More than half of the current CH₄ emissions are anthropogenic (e.g. use of fossil fuels, cattle, rice agriculture and landfills). In addition, carbon monoxide (CO) emissions have recently been identified as a cause of increasing CH₄ concentration.

The atmospheric concentration of nitrous oxide (N₂O) has increased by 46 ppb (17%) since 1750 (Fig. 5) and continues to increase. The present N₂O

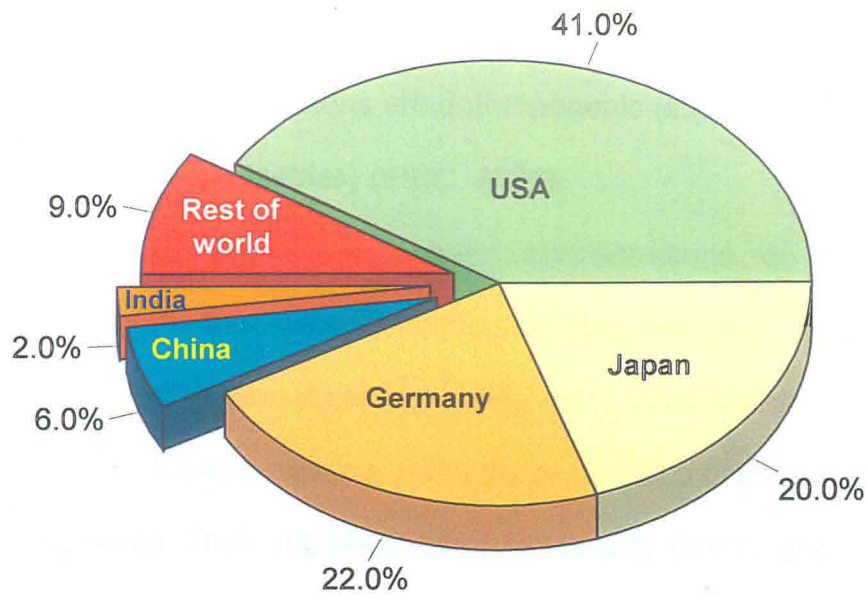


Fig. 7 Per cent contribution of CO₂ emission from different countries
(Source : WB, 2001)

Indicators of the human influence on the atmosphere during the Industrial Era

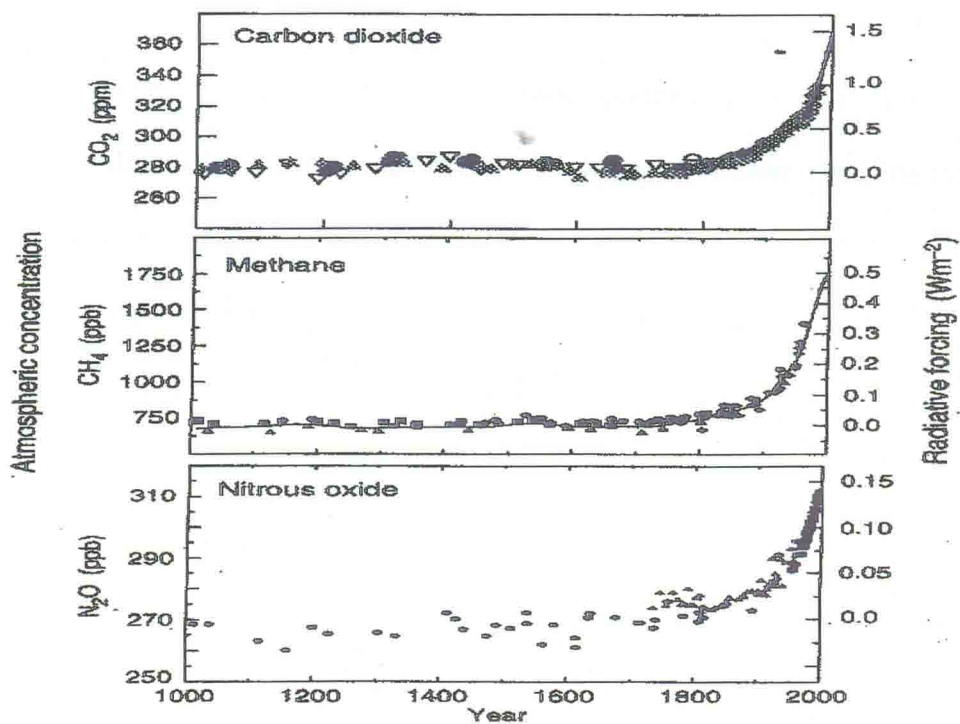


Fig. 8. Global atmospheric concentration and radiative forcing of three well mixed greenhouse gases.

concentration has not been exceeded during the past 1000 years. About a third of current N_2O emissions are anthropogenic (e.g. agricultural soils, cattle feed and chemical industries) (IPCC, 2001).

Since 1995, the atmospheric concentrations of many of those halocarbon gases that are both ozone depleting and green house gases (e.g. CFCl_3 and CF_2Cl_2), are either increasing more slowly or decreasing, both in response to reduced emissions under the regulations of montreal protocol and its amendments. Their substitute compounds (e.g. CHFCl and $\text{CF}_3\text{CH}_2\text{F}$) and some other synthetic compounds (e.g. perfluorocarbons (PFCs) and sulphur hexafluoride (SF_6)) are also green house gases, and their concentrations are currently increasing (IPCC, 2001).

The influence of green house gases (GHGs) on climate can be broadly compared using the concept of radiative forcing. Radiative forcing is a measure of the influence, a factor has, in altering the balance of incoming and outgoing energy in the earth atmosphere system. It is an index of the importance of the factor in potential climate change mechanism. The radiative forcing due to increase of the well mixed GHGs from 1750 to 2000 is estimated to be 2.43 Wm^{-2} : 1.46 from CO_2 ; 0.48 Wm^{-2} from CH_4 ; 0.34 Wm^{-2} from the halocarbons; and 0.15 Wm^{-2} from N_2O (Fig. 8).

The increase in CO_2 concentration in the atmosphere caused global warming by absorbing long wave heat radiations from earth's surface. This is referred as **climatic effect**. However, according to GCM models, the temperature changes will not be uniform. The temperature rise in Polar region may range from $4\text{-}5^\circ\text{C}$ and near equator less than 1°C .

The cumulative value of surface temperature change without feed back for the period 1850-1980 was 0.56°C . Carbon dioxide increase contribute a 0.4°C and the contributions of other trace gases was approximately 0.16°C . Several theoretical models have predicted that near global temperature will increase $3-4^{\circ}\text{C}$ with doubling of CO_2 concentration (IPCC, 2001). Long term temperature records have concluded that global temperature have increased about 0.5°C about the last 100 years (Hurrell, 1998). Warmer spring summer air temperature might be beneficial to crop yield at north (Jones *et al.*, 1985). However, more recent experiments indicate that the temperature rise will be less than 0.26°C for a doubling of CO_2 concentration in temperate latitude (Bazzaz, 1990) where length of growing season could increase. The increased temperature may have negative effect in Mediterranean type of environment, where high summer temperature and water stress already limiting production of crops. Adaptation of climate change exist in some cropping systems to maintain or even increase crop yield under future climate change compared to current conditions. Farmers may be able to use these changes in environmental conditions by choosing the most favourable crops, cultivars and cropping systems.

Plants have been directly affected by rising atmospheric CO_2 as it serves as a main substrate of the photosynthetic carbon assimilation. There is concomitant decline in photorespiratory activity and alternation in stomatal behaviour (**Biological effect**). C_3 plants (wheat, rice, oilseed, pulses etc.) respond to elevated CO_2 since it reduces the oxygenase activity of RuBP carboxylase-oxygenase enzyme in plants. C_4 plants (sorghum, maize, sugarcane etc.) showed little or no photosynthetic response to elevated CO_2

because C_4 pathway is not competitively inhibited by O_2 and is completely CO_2 saturated. The differing responses of C_3 and C_4 species to CO_2 will likely to change the competitiveness and C_3 weeds may become problem in C_4 crops whereas C_3 crops may get advantage over C_4 weeds. This could affect the complexion of agro-ecosystem (Drake, 1992). However, there is no consensus on the quantitative effects of increased CO_2 on plant processes and growth due to differences in response at different stages of growth, species of crops and because of growth limiting environmental factors.

History of carbondioxide and crop response study

The first recorded observation of the effect of CO_2 on plant growth is attributed to de Sussure (1804) who noted that pea plants grew faster when exposed to an atmosphere enriched with CO_2 . The first description of the CO_2 green house effect was reported by John Tindal (1861). Swedish Nobel prize winner Svante Arrhenius (1896) and American geologist T.C. Chamberlin (1899) first published an account on green house effect. However, CO_2 fertilization was practiced by green house grower over the last 200 years using the decomposition of organic material as a source of CO_2 . The first CO_2 experiment in the field was carried out in 1920-23 by Lundegardh on sugarbeet and oat. He observed 16 per cent increase in sugarbeet root production with 15 per cent increase in CO_2 concentration (from 284-328 $\mu\text{mol mol}^{-1}$), whereas oat production was 30 per cent more for doubling of CO_2 concentration from 282-594 $\mu\text{mol mol}^{-1}$. By 1961, about 400 acres of green house crops were being grown with CO_2 enrichment in the Netherlands. Kimball (1983) reviewed 430 observations and reported 33 per cent increase

in average yield of various crops due to doubling of CO₂ above ambient level (Table B).

Table B. Historical observations on CO₂ enrichment in plants (modified version of Wittwer, 1986) in chronological order		
Year	Observations	Observer
1948	Major increase in mass of a willow came from the atmosphere	Van Helmont
1804	First observation of CO ₂ enrichment on plant growth	de Sassure
1894-1902	Positive effects of CO ₂ enrichment on plant growth	Demoussy
1902	Negative effects of CO ₂ enhancement of plant growth	Brown & Escombe
1918	Positive effects of CO ₂ on plant growth (U.S.A.)	Cummings & Jones
1931	600 nurseries reported using CO ₂ in Germany	Reinau
1959	Basic studies on CO ₂ and light responses in plants	Gaastra
1961	Dutch growers add CO ₂ for improving yields of 400 acres lettuce	Anon
1962	Response of cucumber reported to the complimentary effect of CO ₂ and light	Hopes & Ries
1996-1966	Response of flower crops reported	Goldberry & Holly
1964	Comprehensive studies on tomato & cucumber	Wittwer & Robh
1976	Positive effects noted for the growth of tree seedling	Hannover <i>et al.</i>
1987	Reduction in transpiration cooling in leaves of cotton	Idso <i>et al.</i>
1983-1986	Observed 31 per cent increase in agricultural plant productivity	Kimball
1983-1987	64 per cent increase in cotton yield both (lint + seed at 650 $\mu\text{mol mol}^{-1}$ CO ₂)	Kimball <i>et al.</i>
1995-2004	Elevated CO ₂ ameliorated the adverse moisture stress effect in <i>Brassica</i> plants. Demonstrated the possibilities of transferring the CO ₂ responsive characters from the parent <i>B. campestris</i> to the hybrid <i>B. oxycamp.</i> Study of response of rice cultivars to elevated CO ₂	Uprety <i>et al.</i>

The response of plants to the elevated CO₂ has been documented in numerous paper and review articles ranging from detailed biochemical to broad co-physiological studies (Johnson *et al.*, 1993, Kimball *et al.*, 2002 and Long *et al.*, 2004). It must, however, be emphasized that most of the findings on physiological and allocation response to CO₂ were first discovered in agricultural crops. However, most of the earlier studies on plant responses to

the rising atmospheric CO₂ were done on temperate crops using closed chambers and controlled facilities or short-term responses. These do not represent the response of crops to rising atmospheric CO₂ under natural conditions.

Thus, a programme was started on impact assessment analysis of crop responses to rising atmospheric CO₂ at Indian agricultural Research Institute through a National Fellow Project (Upreti, 1998) with the following objectives:

- (A) To develop facilities for CO₂ enrichment technology
- (B) Study the responses of crop plants to elevated CO₂
- (C) Characterize the responses of crops to tailor plants for higher CO₂ environment and
- (D) Identifying the crop cultivation and nutrient management technology for them.
- (E) Application of crops response data in preparing the model and developing plant types for further CO₂ enrichment

2.1 CARBON DIOXIDE AND TEMPERATURE ENRICHMENT TECHNOLOGIES

Most of the research on plant responses to high CO₂ concentration have been conducted in the past under laboratory, greenhouse or controlled field conditions (Bazzaz and Garbutt, 1988). With the development of temperature control in greenhouse, the studies on interactive effect of CO₂ and temperature became possible (Mitchell *et al.*, 1995). Agricultural scientists have used controlled environments and field based facilities to study the crop responses to individual factors such as radiation, temperature, humidity and water availability. Technologies earlier used were based on

single component approach, have been successfully applied to study the responses of plant to increased CO₂. Although this single component approach is highly effective way of discovering how one atmospheric factor influences crops, in practice several interactions will influence the responses. Thus innovative approaches have been developed for conducting long-term experiments to investigate the impact of rising atmospheric CO₂ and temperature interactions on crop plants.

Several systems are used to study the responses of plant communities to elevated CO₂. Before 1980, most studies on the effects of elevated CO₂ were carried out in controlled environmental facility including leaf cuvettes, whole-plant growth chambers and greenhouses. There are intensive precisely controlled closed system now that continuously recondition and re-circulate the air in controlled environment of growth cabinets, phytotron, growth chambers etc. and open field exposures systems such as open top chambers (OTC) and free air carbon dioxide enrichment (FACE) which are moderately more expensive and less precise than closed systems (Allen *et al.*, 1992). Each of these research system has its advantages and disadvantages. New methods and facilities have been devised and field exposure techniques that do not modify micro-climate are being developed and improved for exposure of large area of plants to elevated CO₂. Though the cost and difficulties of CO₂ and temperature effects in the field are considerable, but such research must be done to give confidence in the conclusions arising from the simpler controlled environmental study. During the current decade, there have been new approaches to CO₂ and temperature enrichment technology under FACE condition which has reduced the cost. Further the computer models which

make predictions for field condition should at least be based on the data collected at field (Lawlor and Mitchell, 1991).

The long-term experiments to investigate the influence of rising CO₂ in plants include:

1. Control of gas concentration, composition and environment around the leaf and whole plant
2. Measurements of various physical parameters such as changes in gas contacts.
3. Collection and evaluation of data

In the current study OTC's and FACE technologies were used for studying the crop responses to the CO₂ enrichment. The temperature and CO₂ interaction studies were done in the phytotron.

2.1.1 Open top chambers (OTC)

OTCs as described by Heagal *et al.* (1973) were extensively used as plant exposure units both in air pollution and in CO₂ response studies in the field. These systems have been used to expose potted plants, annual crops and trees to a variety of air pollutants and CO₂. They are currently in use at a number of laboratories in North America, Europe and South-Asian countries. Hardy and Hevelka (1975) first used a square wall open top enclosure to expose soybean plants to atmosphere enriched with CO₂ for the purpose of studying the effect on photosynthetic production and symbiotic nitrogen fixation. Rogers *et al.* (1983) adapted the basic cylindrical open top chamber system to generate large scale CO₂ test atmospheres in the field. Nakayama and Kimball (1988) used a square wall open top chamber with 0.2 m diameter perforated polythene rolls in cotton. Drake *et al.* (1989) developed an OTC

system for CO₂ enrichment of salt marsh vegetation that re-circulated part of input air. Upreti (1998) designed and developed OTC for South Asian climatic conditions. These chambers with frustum are being used by South Asian research network for multi-country, multi-disciplinary CO₂ response experiments.

OTC is one of the most widely used techniques for studying the responses of crops and crop ecosystems to the elevated CO₂. Climate in OTC tracks the dynamic change in temperature, light, rainfall etc. experience in un-enclosed area without costly and complex environmental controls. OTC's subjects the whole plant to the treatment without restricting the root growth. The principle advantage of OTC is the ability to provide control over the atmospheric variations, to which plants are exposed while maintaining more or less edaphic conditions of the field study (Hendry *et al.*, 1992).

2.1.2 Free Air Carbon dioxide Enrichment (FACE) Technology

Further progress required experimental techniques to maintain elevated CO₂ concentration with natural systems for long period of time at cost that are reasonable. Free air CO₂ enrichment approach is one of the successful new technologies for achieving these objective. The data on C fixation under ambient and elevated CO₂ levels without any confounding effects of growth chambers such as decreased light intensity, unnatural wind flow, elevated temperature and disturbed soil water patterns, will become available. It provides an approach for enriching relatively larger areas for vegetation with CO₂ for extended period of time of less cost per unit experimental area than any other known techniques. Engineered and developed by Brookhaven National Laboratory, New York, USA, FACE

experimental system takes advantage of micro-scale meteorological condition to maintain desired CO₂ concentration over larger area. The FACE system is an example of the application of modern technology to field experimentation to enable detailed observations and experiments with crop and ecological systems that previously were beyond the reach of agronomists, plant physiologist and ecologists.

It provides experimental means for addressing sophisticated questions about CO₂ effects on outdoor environments including transpiration, plant-water relation, photosynthesis and carbon metabolism, molecular control of plant biochemistry, plant-insect and plant-disease interactions' and the relationship between direct CO₂ effects and other changing environmental influences such as light, temperature, water and nutrient availability. The FACE system could open new opportunity to address questions to the frontiers of biological sciences raising from molecular biology to plant community dynamics to global carbon balance. The FACE experiments can provide data with which to build and evaluate models that can reliably predict, plant responses to environmental changes

Advantages of FACE technology

1. No observable effect of ambient environment
2. Stable control of CO₂ concentration
3. Large plot size
4. Sufficient plant material for extensive sampling
5. Initial capital cost similar to other systems
6. Low cost per sample unit
7. Low cost per sample investigator

The FACE system consist of a circular array of independently valved vent pipes from which CO₂ is injected into treatment plot through a mass-flow controller regulated by algorithm that can account for wind direction, wind velocity and running average gas concentration measured in the centre of the treatment plots. It consists of four subsystems.

- a) CO₂ storage and vaporization system
- b) CO₂ flow and distribution system
- c) CO₂ regulation and control system
- d) Performance monitoring and data logging system

Various types of FACE systems were developed in recent years which include, **Arizona FACE system** which includes vertical vent pipes and around 22 m diameter FACE ring located in Maricopa, Arizona, USA (Hendrey, 1993).

Mini FACE system which was developed by the Institute of Agro-meteorology and Environmental analysis, Firenze, Italy. The FACE ring is less than 2 m diameter and the system is portable. It was used in Europe during mid-nineties.

Mid-FACE is another type of FACE technology that was developed by Japanese group of scientists under the leadership of Kobayashi at the National Institute of Agro-environmental Sciences, Ibaraki, Japan. It is octagonal in shape with a vertical FACE ring. In this case, use of plastic irrigation tube gives good mixing of CO₂ and air without confounding blower effect.

The present experiment was done in the South Asian mid-FACE designed and developed at Indian Agricultural Research Institute, New Delhi (Upreti *et al.*, 2000). The FACE ring in this case are of 8 m diameter,

octagon-shaped. This facility is also being used by the South Asian countries viz., Bangladesh, Nepal, Pakistan and Sri Lanka at Indian Agricultural Research Institute, New Delhi for multi-country rice experiments.

2.1.3 Carbon dioxide and temperature interaction technology

Plant response to CO₂ are quite different for plants grown under isolated conditions (e.g in pots) compared with those measured under field conditions.

Although experiments conducted using the FACE system utilize true field-grown conditions however, factorial combinations of CO₂ and air temperature treatments is difficult. Thus the required factorial experiments was conducted in closed-chamber systems. Controlled environments allows the investigation to create any environment or environmental gradient. Because each environmental factor of interest is established and varied at will, one may administer a desired environmental treatment and be assured that the results are the product of treatment alone. Most experiments on the effects of increase in temperature or CO₂ on crops have been conducted in closed chambers. Hofstra and Hesketh (1975) studied the interactive effect of CO₂ and temperature on photosynthesis in soybean plants under the controlled environmental conditions at the Duke University Phytotron. The first interaction study at the Duke University Phytotron environments was carried out in C₄ weeds by Potwin and Strain (1985). Further studies in controlled chamber were carried out in rice at IRRI, Philippines (Baker and Allen, 1993 and Baker *et al.*, 1994). Further rice research under these controlled conditions were done by Allen *et al.* (1995).

2.2 CROP

Rice crop was selected for the present study, mainly because, rice is a staple food crop of Asia. Over 90 per cent of the world's rice is produced and consumed in Asia (Table 1) where the monsoonal climates dominate. Rice is not only the staple food of South Asian region but also provides the livelihood of most of Asian inhabitants. It is produced mainly by subsistence farmers in developing countries.

Cultivated rice consists of two distinct species of *Oryza*: *Oryza sativa* L. and *Oryza glaberrima*. The dominant species in the world rice production is *O. sativa* whereas, *O. glaberrima* is limited mainly to west Africa. *Oryza sativa* consist of three subspecies viz., *indica*, *japonica* and *javanica*, which are genetically distinct from each other. Crosses among these subspecies generally result in extensive or partial spikelet sterility.

World rice production increased at higher rate due to high yielding varieties in the past three decades. However, total rice production will need to increase by 46 per cent by the year 2025 (Horie *et al.*, 2000) to keep pace with the projected population growth, especially in Asia.

Rice is a staple food of India, providing 43 per cent of calorie requirement for more than 70 per cent of Indian population (Ahmed *et al.*, 2003). Rice occupies largest area among all the crops grown in India. The area under rice in India (44 million hectares), is the largest in the world among all rice growing countries. Annual production of rice in the country is around 90 million tons second largest in the world after China.

During the post independence period of 55 years there has been remarkable achievement in the production of rice. The area under rice

increased 1.5 times, from 30 million hectares to approximately 45 million hectares, while the production increased four times from 22 million tons to 90 million tons (Mishra, 2004). The productivity has increased three times from 0.7 tons per hectare to 2.0 tons per hectare. This spectacular progress helped India to achieve self sufficiency in rice production during early 80s.

To meet the demands of increasing population and maintain this self sufficiency, the present production level of around 90 million tons, need to be increased up to 140 million tons by the year 2025 (Mishra, 2004). Achievement of these production goals is likely to be very difficult because of the predicted future climate changes. The production of hybrid and high yielding responsive cultivars will be imperative to meet the challenges of rising atmospheric CO₂ and temperature.

2.3 PHOTOSYNTHESIS AND PHOTOSYNTHETIC ACCLIMATION

The present atmospheric CO₂ is an important limiting factor for the photosynthesis, growth and productivity of many crops species. In a leaf, the photosynthetic rate is a direct result of the activity of ribulose biphosphate carboxylase-oxygenase (Rubisco), which in turn is influenced by various environmental factors, including CO₂, temperature, and light. The current atmospheric CO₂ is insufficient to saturate Rubisco in C₃ plants. Consequently, in short-term measurements an increase in the availability of this substrate results in a rise in leaf photosynthetic rates, partly because high CO₂ inhibits the oxygenase reaction of Rubisco and the subsequent loss of CO₂ through photorespiration (Bowes, 1993). However, for some species, longer exposure to elevated CO₂ results in acclimation of photosynthesis with down-regulation of the amount of Rubisco protein (Rowland-Bamford *et al.*,

1991), although other species show minimal down-regulation (Campbell *et al.*, 1998, Sage *et al.* 1989 and Socias *et al.*, 1993). This coarse control of the amount of Rubisco protein serves to optimize CO₂ acquisition with utilization of the fixed carbon (Woodrow 1994). In addition to coarse control of Rubisco protein, there are fine controls, which respond more rapidly to changes in environmental conditions. In this regard, two major mechanisms are known to regulate Rubisco activity. One involves the reversible carbamylation of lysine residue in the active site to activate the enzyme, while the other operates by the reversible binding of 2-carboxyarabinitol-1 phosphate (CA1P), the Rubisco dark inhibitor, to the carbamylates site (Vu *et al.*, 1983 and Sage & Reid 1994). The carbamylation of Rubisco is dependent on RuBP, CA1P and other inhibitory phosphorylated compound from the catalytic sites (Servaites 1990 and Portis 1992). Rubisco activation responds to relatively rapid changes in irradiance and CO₂ or O₂, while the regulation by CA1P seems to occur only in response to irradiance, predominantly low light and most obviously darkness (Salvucci 1989 and Sage and Reid 1994). There are number of reports which show that long-term growth at elevated CO₂ can cause a reduction in Rubisco activation, but it is unclear whether rising CO₂ also influences the fine control of Rubisco exercised by CA1P (Bowes 1993). In addition to CO₂, the photosynthetic rates of C₃ plants are affected by temperature, and this effect is also primarily exerted through Rubisco (Long 1991). An increase in temperature reduces the activation state of enzyme (Kobza and Edwards, 1987 and Holaday *et al.*, 1992), and decreases both the specificity for CO₂ and the solubility of CO₂, relative to O₂ (Jordan and Ogren 1984). The latter two effects result in greater losses of CO₂ to photorespiration

as the temperature rises. Consequently, a doubling of atmospheric CO₂, and the concomitant inhibition of the Rubisco oxygenase reaction, should moderate the adverse effects of high temperature on C₃ photosynthesis, and result in even greater enhancement of net photosynthesis by elevated CO₂ as the temperature during the growth increases (Long, 1991).

Even though, all C₃ plants showed positive response to elevated CO₂, the enhancement effects were different among the C₃ crops. Soybean photosynthesis, biomass and yield increased with increasing CO₂ up to 900 $\mu\text{mol mol}^{-1}$, whereas with rice, the greatest increase occurred below 500 $\mu\text{mol mol}^{-1}$ CO₂, which is much below the predicted CO₂ value for the 21st century (Jones *et al.*, 1984 and Rowland-Bamford *et al.*, 1991). The carbon exchange rates were higher in CO₂ enriched tomato plants throughout the growing season (Yelle *et al.*, 1989). A substantial increase in cotton canopy photosynthesis was observed by Ramachandra Reddy *et al.* (1993) and Reddy *et al.* (1997).

Pospisilova *et al.* (1999) studied the effect of elevated CO₂ in *Nicotiana tabaccum* L. plants. Plants were grown *in vitro* and transferred to *ex vitro* conditions for a period of 28 days in a greenhouse under normal CO₂ concentration (330 $\mu\text{mol mol}^{-1}$) and elevated CO₂ concentration (1000 $\mu\text{mol mol}^{-1}$). It was observed that leaf photosynthetic rate (A) of elevated CO₂ plants was similar to that of control plants when both were measured under normal CO₂, but higher when both were measured under elevated CO₂. The A of elevated CO₂ plants was much higher than the A of control plants. Chlorophyll a and b content, and activities of whole electron transport chain and of photo system (PS) II were not markedly affected under elevated CO₂. There was an

increase in the maximum efficiency of PS II measured as the ratio of variable to maximum fluorescence. No down-regulation of photosynthesis occurred in transplanted plants grown for 4 week under elevated CO₂. Upreti *et al.* (2002) studied the protein profile of two basmati rice cultivars grown under elevated CO₂. A decrease in the low molecular mass proteins including rubisco and an increase in high molecular mass photosystem-II proteins were observed in both the cultivars. The reduction in the larger and smaller subunits of Rubisco did not affect the CO₂ induced enhancement in the photosynthetic rate.

Though photosynthetic rates increased at elevated CO₂, Wullshleger *et al.* (1992) observed a reduction in chlorophyll and accessory pigments under elevated CO₂ conditions in yellow poplar and white oak seedlings. The reduction in chlorophyll in yellow poplar was 27 per cent and in white oak seedling was 55 per cent. Van Oosten *et al.* (1994) observed in tomato plants that the chl. a/b ratio decreased significantly over nine days of exposure to CO₂. This implies that the total chlorophyll at elevated CO₂ decreased significantly on dry weight basis as a result of decrease in SLA (Faria *et al.*, 1996).

The response of crops were different when elevated temperature condition was given with high CO₂. Ziska and Bunce (1995) exposed three soybean cultivars (Maple Glen, Clark and CNS) to three CO₂ concentrations. (370,555, and 740 $\mu\text{mol mol}^{-1}$) and three growth temperature 20/15°C, 25/20°C and 31/26°C day/night). They showed that increasing CO₂ concentration resulted in stimulation of single leaf photosynthesis for 40-60 d after emergence at 20/15°C in all cultivars and for Maple Glen and CNS at all temperatures.

Delgado *et al.* (1994) studied the response of winter wheat (*Triticum aestivum* L. cv. Mercia) grown at two different atmospheric CO₂ concentrations (350 and 700 $\mu\text{mol mol}^{-1}$), two temperatures, ambient and ambient +4°C with two rates of nitrogen supply (high and low). Leaves grown at 700 $\mu\text{mol mol}^{-1}$ CO₂ had slightly greater photosynthetic capacity (10% mean increase) than those grown at ambient CO₂ concentration but there were no differences in carboxylation efficiency or apparent quantum yield. The amounts of chlorophyll, soluble protein and ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) per unit leaf area did not change with long term exposure to elevated CO₂ concentration. Thus winter wheat, grown under simulated field conditions, for which total biomass was large compared to normal field production, did not experience loss of components of the photosynthetic system or loss of photosynthetic competence with elevated CO₂ concentration. However, nitrogen supply and temperature had large effects on photosynthetic characteristics but did not interact with elevated CO₂ concentration. Nitrogen deficiency resulted in the decrease in the content of protein, including rubisco, and chlorophyll, and reduction in photosynthetic capacity and carboxylation efficiency. An increase in temperature also reduced these components and shortened the effective life of the leaves, reducing the duration of high photosynthetic capacity.

Vu *et al.* (1997) observed that the interactive effect of elevated CO₂ and temperature showed a different response in soybean and rice. The CO₂ enhancement of leaf photosynthetic assimilation rates in soybean increased in a linear manner by 32-95 per cent with increasing growth temperatures from 28-40°C, whereas with rice the degree of enhancement was relatively

constant at about 60 per cent, from 32 to 38°C. Both elevated CO₂ and temperature exerted down-regulation of the amount of rubisco protein, but the two species differed in the degree of responsiveness. CO₂ enrichment and high growth temperatures reduced the Rubisco content of rice by 22 and 23 per cent, respectively, but only by 8 and 17 per cent for soybean. The maximum degree of Rubisco down-regulation appeared to be limited, as in rice the substantial individual effects of these two variables, when combined, were less than additive. In rice, total activity and activation were reduced, but in soybean only activation was lowered. The apparent catalytic turnover rate (K_{cat}) of rice Rubisco was unaffected by these variables, but in soybean elevated CO₂ and temperature increase the apparent K_{cat} by 8 and 22 per cent, respectively.

Takeuchi *et al.* (2001) studied the relationship between leaf photosynthesis (Ps), nitrogen (N) and light environment on *Populus tremuloides* trees in a developing canopy under free-air CO₂ enrichment. Elevated CO₂ significantly decreased leaf N on a mass, but not on an area, basis. N per unit leaf area was related linearly to PPFD throughout the canopies, and elevated CO₂ did not affect that relationship. Elevated CO₂ increased photosynthesis only in the upper (unshaded) canopy, whereas characteristics that would favour photosynthesis in shade were unaffected by elevated CO₂. The lack of CO₂ stimulation at the mid and lower canopy was probably related to significant down-regulation of photosynthetic capacity, there was no down regulation of photosynthesis in the upper canopy. The relationship between photosynthesis and leaf N indicated that N was not optimally allocated within the canopy in a manner that would maximize whole-

canopy photosynthesis or photosynthetic N use efficiency. Thus, elevated CO₂ had no effect on the optimization of canopy N allocation.

As plants acclimate to growth in elevated $p\text{CO}_2$ they often fail to sustain the initial, maximal stimulation of net CO₂ uptake rate under optimal microclimatic conditions (Drake *et al.*, 1997). Rogers and Humphries (2000) demonstrated that this phenomenon could be attributed almost entirely to a decrease in the carboxylation capacity of Rubisco. This decrease in carboxylation capacity with growth in elevated $p\text{CO}_2$ is well documented and most commonly associated with a reduction in the amount of Rubisco (Stitt and Krapp, 1999). A reduction in the amount of Rubisco following growth in elevated $p\text{CO}_2$ could have different causes and the mode by which this occurs is uncertain. There are two basic mechanisms by which Rubisco acclimation is thought to occur. The first mechanism hypothesizes that the reduction in Rubisco content occurs via selective reduction in Rubisco resulting from a sugar mediated feedback control on the amount of enzyme. Elevated CO₂ induced increased levels of hexose sugars lead, via a hexokinase-related signal, to the repression of Rubisco gene expression and a subsequent decrease in the levels of Rubisco protein (Moore *et al.*, 1999). There are problems with this proposed mechanism, not least of which is the uncertainty as to the nature of the sugar signal and even whether acclimation is a uniquely sugar-mediated phenomenon (Stitt and Krapp, 1999). An alternative concept is that Rubisco acclimation is the result of a non selective reduction in leaf nitrogen content (Curtis *et al.*, 2000). Under this hypothesis, decreases observed in Rubisco may reflect a general reduction of leaf protein, due to reallocation of nitrogen within the plant (Nakano *et al.*, 1997 and Makino *et al.*,

1997) or earlier leaf senescence in nitrogen limited plants (Miller *et al.*, 1997). Under conditions of nitrogen limitation, acclimation may be accelerated in elevated $p\text{CO}_2$ because the plants are larger and therefore, experience acute nitrogen limitation sooner, or to a greater extent. Farage *et al.* (1998) demonstrated that even when growth was restricted by a low-N relative addition rate, photosynthetic acclimation in elevated $p\text{CO}_2$ could be ameliorated if nitrogen was added in direct proportion to plant growth, supporting the concept that N dilution is the cause of Rubisco acclimation.

Sicher and Bunce (1997) observed that the photosynthetic rates of barley penultimate leaves and wheat flag leaves decreased with leaf age in all three CO_2 treatments (350, 525 and 700 $\mu\text{mol mol}^{-1}$). Initial Rubisco activity, total soluble protein and Rubisco protein in these leaves of barley and wheat decreased with leaf age. This indicated that photosynthetic acclimation was positively correlated with changes of initial Rubisco activity in both the crops.

Adam *et al.* (2000) reported that elevated CO_2 did not alter *in vivo* carboxylation capacity, $[V_{\text{Cmax}}]$ in the flag leaf of wheat at either low or high N. In the older shaded leaves lower in the canopy, acclimatory decline in V_{Cmax} was observed and was found to correlate with reduced Rubisco activity and content. The dependency of acclimation on N supply was different at each developmental stage. With adequate N supply, acclimation to elevated CO_2 was also accompanied by an increased LHC II/Rubisco ratio. At low N supply, contents of Rubisco and LHC II were reduced in all leaves, although an increased LHC II/Rubisco ratio under elevated CO_2 was still observed. These results showed the importance of leaf position, leaf age and crop

developmental stage in understanding the acclimation of photosynthesis to elevated CO₂ and nutrient stress.

Mitchell *et al.* (2000) studied the carboxylation and RuBP-regeneration capacities, which determine light saturated photosynthetic rate, in the leaves of spring wheat (*Triticum aestivum* L. cv. Minaret) grown under different atmospheric CO₂ partial pressure (pC_a) and N supply regimes. Acclimation of the balance between the two capacities to growth at elevated pC_a in wheat was only partial and appears to occur mostly in older flag leaves and at low nitrogen. This observed balance between carboxylation and RuBP regeneration capacities in young wheat leaves could be consistent with adaptation to the current, or even the preindustrial pC_a .

Photosynthetic acclimation as manifested by a decrease in Rubisco activity of *Pinus faeda* (loblolly pine) to long term growth in elevated CO₂ (FACE) was observed by Rogers and Ellsworth (2002). They observed this acclimation in one-year old needles but not in current year needles. Needles exhibiting acclimation had reduced levels of *Lsu* Rubisco and an increased foliar carbohydrate content but showed no evidence of decrease in needle nitrogen or total protein content, which in turn support the concept that photosynthetic acclimation in elevated CO₂ is caused by selective down regulation of Rubisco.

Seneweera *et al.* (2002) observed leaf CO₂ assimilation rates (A) and biochemical parameters in rice (*Oryza sativa* L. cv. Akitakomachi) at 32-36 (eight leaf) and 76-80 (flag leaf) days after transplanting, in ambient CO₂ and FACE with low, medium or high N supplies. Acclimation due to FACE was pronounced in flag leaves at each N supply. This was not fully accounted for

by reductions in leaf N concentrations, because A/N and V_{cmax}/N were lower in FACE grown flag leaves. Acclimation did not occur in the eighth leaf and A/N and V_{cmax}/N was not significantly increased in FACE grown leaves. Soluble protein/sucrose and amino acid/sucrose concentrations decreased under FACE, whereas sucrose phosphate synthase protein levels increased. At flag leaf stage, there was a discrepancy between the demand and supply of N, which was resolved by enhanced leaf N remobilization, associated with the lower Rubisco concentrations under FACE. In contrast to the early growth stage, enhanced growth of rice plants was accompanied by increased plant N uptake in FACE. It was concluded that photosynthetic acclimation in flag leaves occurs under FACE because there is a large demand for N for reproductive development, relative to supply of N from root uptake and remobilization from leaves.

2.4 STOMATAL SENSITIVITY

Stomatal conductance (g_s) is generally expected to decline in plants with an increase in atmospheric CO_2 above the current level (Wand *et al.* (1999). There are many important physiological and ecological implications of such a decline. For example, lower g_s may alter ecosystem hydrology by reducing transpiration and could increase the surface temperature through reduced evaporative cooling (Bounoua *et al.*, 1999). Reduced g_s , coupled with increased photosynthesis may also improve the water use efficiency (WUE) of many plants, which is of particular importance for productivity in arid and semi-arid regions (Smith *et al.*, 2000).

A major factor that could alter stomatal responses to CO_2 is the degree to which stomata acclimate to higher CO_2 concentration. Stomatal acclimation

to CO₂ would be ecologically important if it either tempered or enhanced the reduction in g_s with rising CO₂ (Santrucek and Sage, 1996 and Morison, 1998). Stomatal acclimation to CO₂ may occur in several ways, including changes in maximum g_s and stomatal sensitivity to CO₂. Other responses to CO₂ such as changes in stomatal morphology (density and size) may also influence g_s independently of physiological acclimation. Despite its potential importance for regulating plant water loss at high CO₂, stomatal acclimation has only been regulating the water use efficiency in plants (Drake *et al.*, 1997 and Morison, 1998). According to Maherali *et al.* (2002), incorporating stomatal acclimation into modeling studies could improve the ability to predict changes in ecosystem water fluxes and water availability with rising CO₂ and to understand their magnitudes relative to the past.

High temperature, on the other hand, has received less attention, presumably because consequences for transpiration seem straight forward to predict (higher water loss at higher leaf temperature T_L) (Njis *et al.*, 1997). Stomata may partially close to compensate for an increase in leaf to air vapour pressure difference (Δ_L), arising from higher T_L . Reduced stomatal conductance has been observed by Morgan *et al.* (1994), in *Pascopyrum smithii* leaves. Jones *et al.* (1985) who found no difference in soybean canopy conductance between temperature treatments. However, changes in conductance need not be of a functional nature, as anatomical development may also adapt to higher temperature, for example by altering stomatal density (Beerling and Chaloner, 1994). Leaf area development is another factor which may accelerate and enhance transpiration at increased temperature (e.g. in carrot, Wheeler *et al.*, 1994), but the opposite may also

occur if climate warming leads to more frequent supra-optimal conditions (e.g. in *Lolium perenne* during summer (Ferris *et al.*, 1996).

Upreti *et al.* (1995) observed that *Brassica* species responded to elevated CO₂ significantly under moisture stress conditions mitigating the adverse effect on photosynthesis and growth. The water status of plant significantly improved under elevated CO₂ concentration possibly by increasing stomatal resistance and increased root growth.

Wilson and Bunce (1997) studied the response of soybean cultivars at three CO₂ concentrations in outdoor growth chambers and at two concentrations in controlled environment growth chambers to the interactive effects of CO₂, temperature and leaf to air vapour pressure difference (LAVPD) on stomatal conductance. The decline in stomatal conductance with CO₂ was a function of both leaf temperature and LAVPD. In the field measurements, stomatal conductance was more sensitive to LAVPD at low CO₂ at 30⁰C but not at 35⁰C. There was also a direct increase in conductance with temperature, which was greater at the two elevated carbon dioxide concentrations. Environmental growth chamber results showed that the relative stomatal sensitivity to LAVPD decreased with both leaf temperature and CO₂.

Hans *et al.* (1999) studied the response of *Pinus sylvestriformis* var. *Sylvestriformis* in response to increased CO₂ concentration (500±100 µmol mol⁻¹). They observed that increased CO₂ concentration reduced average stomatal opening, stomatal conductance and stomatal density to 78, 80 and 87 per cent, respectively, compared with their values under ambient CO₂ condition.

Upreti *et al.* (2002) observed that elevated CO₂ brought about a reduction in stomatal conductance and increase in stomatal index, size of stomatal guard cells, stroma and epidermal cell in rice cultivars and demonstrated that such acclimation helped in the regulation of photosynthesis under the higher CO₂. According to them, these changes in stomatal characters made rice cultivars adjustable to higher CO₂ environment.

Wullschleger *et al.* (2002) in a study on *Liquidambar styraciflua* (Sweetgum) observed 44 per cent reduction in stomatal conductance for leaves exposed to free air CO₂ enrichment, whereas canopy conductance, averaged over the growing season, was only 14 per cent lower in plants exposed to CO₂ enrichment. The magnitude of this response was dependent on vapour pressure deficit and soil water potential. Annual estimates of evapotranspiration showed relatively small reductions due to atmospheric CO₂ enrichment.

Woodward *et al.* (2002) observed that flower production was related to stomatal density under elevated CO₂ condition in 48 accessions of *Arabidopsis thaliana*. They demonstrated that the flowering was benefited from a small reduction in stomatal density with CO₂ enrichment under well watered conditions, however a large reduction in stomatal density under drought did not show any effect.

Conley *et al.* (2001) observed that elevated CO₂ reduced cumulative ET by 10 per cent when Sorghum (*Sorghum bicolor*) plants were given ample water, and by 4 per cent under severe drought stress. Water use efficiency (WUE) based on grain yield increased, due to CO₂ enrichment, by 9 and 19 per cent in wet and dry plots, respectively, based on total biomass, WUE

increased by 16 and 17 per cent in wet and dry plots, respectively. They suggested that in the future high CO₂ environment, water requirements for irrigated sorghum will be lower than at present, while dry land productivity will increase, provided global warming is minimum.

Bethenod (2001) studied the effect of elevated CO₂ concentration on plant transpiration and water use efficiency in maize (*Zea mays*). They observed that the daily transpiration of plants increased with leaf growth. Doubling CO₂ induced a decrease in daily plant transpiration. The daily mean transpiration decrease was 17 per cent during the whole crop growth period. Doubling CO₂ induced a 23 per cent increase in water use efficiency (dry weight per cumulated transpiration).

Sebastiani *et al.* (2002) exposed one year old olive (*Olea europaea*) cuttings of two cultivars (Frantoio and Moraiolo) for five months to ambient ($360 \pm 16 \mu\text{mol mol}^{-1}$) and elevated ($560 \pm 52 \mu\text{mol mol}^{-1}$) CO₂ concentration in a free air CO₂ enrichment facility. The exposure to elevated CO₂ enhanced the rate of net photosynthesis and decreased stomatal conductance, leading to higher water use efficiency. Chlorophyll concentrations (chlorophyll content per unit leaf area) decreased only in Frantoio leaves of plants grown in elevated CO₂. Stomatal density and leaf nutrients did not differ between treatments and cultivars.

Gunderson *et al.* (2002) reported that there was no interaction effect of high temperature and CO₂ on photosynthetic carbon assimilation and stomatal conductance in the canopy of sweetgum (*Liquidambar styraciflua* L.) plantation during 3 years of CO₂ enrichment.

Susanna *et al.* (2004) analysed the variation in stomatal density, leaf conductance and leaf water relations in semi natural grassland communities in three different experiment setups (natural CO₂ springs, plastic tunnels and mini FACE systems). Natural degassing vents continuously expose the surrounding vegetation to truly long term elevated CO₂ and can complement short term manipulative experiments. Elevated CO₂ concentration effects on stomata persist in the long term, though different species growing in the same environment show species specific responses. The general decrease in stomatal conductance after exposure to elevated CO₂ was not associated with clear changes in the stomata number on leaf surfaces. The hypothesis of long term adaptive modifications to stomatal number and distribution of plants exposed to elevated CO₂ was not supported by these experiments on grassland communities. Elastic cell wall properties were affected to some extent by elevated CO₂. Above ground biomass did not vary between CO₂ treatments, leaf area index did not compensate for reduced stomatal conductance, and the root system had potentially greater soil exploration capacity. Variation in response to elevated CO₂ may provide a mechanism for changing competitive interactions among plant species.

2.5 RESPIRATION

Global increase of atmospheric CO₂ concentration (C_a) affects the dark respiration in plants (Jhanke, 2001). Doubling of C_a was said to reduce respiration rates by 15-20 per cent (Drake *et al.*, 1999 and Gonzalez- Meler and Siedow 1999), and the direct (short-term) effects of elevated CO₂ on respiration are assumed to be greater than the indirect (long-term) ones (Amthor 1997). A doubling of CO₂ has been reported to cause a reduction of

respiration rate, an absence of any effect, and even an enhancement of respiration (Amthor, 1997). Possible explanations of the inhibitory effect of CO₂ are the inhibition of enzymes involved in respiration (re)fixation of CO₂ (Wullshleger *et al.*, 1994).

DuCloux *et al.* (1989) studied the effect of doubling of atmospheric CO₂ concentration on photosynthesis of wheat, and observed that O₂ uptake was reduced by 40 per cent due to high CO₂. Bunce and Caulfield (1991) observed a 30-40 per cent reduction in CO₂ efflux rates in *Lolium perenne* and *Medicago sativa*, grown under elevated CO₂. Wullshleger and Norby (1992) have noted that growth respiration decreased by 12-31 per cent and maintenance respiration decreased by 45 to 54 per cent for > sapling leaves of oak grown at elevated CO₂.

Baker *et al.* (1992) subjected rice plants (*Oryza sativa* cv. IR-30) in naturally sunlit plant growth chamber of entire season in sub-ambient (160 and 250 $\mu\text{mol mol}^{-1}$), ambient (330 $\mu\text{mol mol}^{-1}$) or super-ambient (500,660 and 900 $\mu\text{mol mol}^{-1}$) CO₂ treatments. They reported that specific respiration rate decreased with time during the growing season and was higher in sub-ambient CO₂ treatments. This greater specific respiration rate in sub-ambient condition was attributed to a higher specific maintenance respiration rate and was associated with higher plant tissue N content. Azicon-Bieto *et al.* (1994) observed that elevated CO₂ decreased the O₂ uptake in stem of *S. olneyi* and leaves of *Lindera benzoin* when expressed on either dry weight or area basis.

Gonzalez-Meler *et al.* (1996) found *in vitro* cytochrome C oxidase (COX) activity was reduced to 19 per cent by an increase in CO₂ (360 $\mu\text{mol mol}^{-1}$) concentration. However, more recently, Gonzalez-Meler and Siedow

(1999) and Bunce (2001) suggested that the primary effect of CO₂ is not on COX. This is because typical *in vivo* flux control coefficient of COX (in absence of ADP) are near zero and because of elevated CO₂ inhibits respiration to a greater extent in substrate availability. Bruhn *et al.* (2002) observed in *Plantago* species that the relative difference between rates of respiration at two atmospheric CO₂ values increased with decreasing temperature. Uprety *et al.* (2003) showed a decrease in the dark respiration rate in basmati rice cultivars at elevated CO₂. Davey *et al.* (2004) determined the leaf O₂ uptake in response to instantaneous elevation of CO₂ in nine contrasting species and to long-term elevation in seven species from four field experiments. Over six hundred separate measurements of respiration failed to reveal any decrease in respiratory O₂ uptake with an instantaneous increase in CO₂. Respiration was found insensitive not only to doubling CO₂, but also to a 5-fold increase. Using a wide range of species and conditions, it was confirmed that inhibition of respiration by instantaneous elevation of CO₂ is likely an experimental artifact. Instead of the expected decrease in respiration per unit leaf area in response to long term growth in the field at elevated CO₂. There was a significant increase of 11% and 7% on an area and mass basis, respectively averaged across all experiments. The findings suggest that leaf dark respiration will increase and not decrease as atmospheric CO₂ rises.

2.6 CARBOHYDRATE PARTITIONING

Species with C₃ photosynthesis exhibit up to a 50 per cent increase in photosynthesis rate when exposed to twice ambient CO₂, but this initial enhancement often declines as the plant acclimates to the high (CO₂). A plausible rationale for the down regulation is that it optimizes carbon gain with

respect to the capacity of the plant for carbon utilization (Bowes, 1996). In this regard, both N and carbohydrates play important roles, as the down regulation of photosynthesis at elevated (CO_2) becomes more evident when N supply or carbohydrate sink capacity is limited (Drake *et al.*, 1997). If optimization processes are involved in photosynthetic regulation and N utilization by the plant, then we might expect that in addition to down-regulation of the capacity for carbon gain, to also have up-regulation of the capacity for carbon utilization and export. The findings with rice that canopy photosynthesis, growth and yield increased with (CO_2) suggest that the capacity for carbon utilization and transport must also have increased (Baker *et al.*, 1990 and Baker and Allen, 1993). In this respect, SPS is a key regulatory enzyme involved in the partitioning of photo assimilate between sucrose and starch in leaves (Stitt and Sonnewald, 1995, Huber and Huber, 1996 and Koch, 1996). It catalyzes the penultimate step in the synthesis of sucrose and shares control of this pathway with the first committed step catalyzed by cytosolic fructose-1, 6-bisphosphatase (Stitt and Sonnewald, 1995). There is diversity among species as to how recently fixed carbon is stored in the leaves, with temperate Gramineae accumulating sucrose and fructose in preference to starch (Pollock and Farrar, 1996). The potential to up-regulate leaf SPS activity in response to growth at elevated CO_2 might be particularly important in species that accumulate sucrose. A body of evidence indicates that SPS activity is responsive to various factors. Thus, the expression of SPS genes is affected by sugars availability, particularly glucose and sucrose, source to sink transitions, irradiance and N nutrition (Huber and Huber, 1996, Koch, 1996). Enzyme activity can change in response to light/dark transitions as a

result of reversible protein phosphorylation, which reduces activation and alters the affinity for substrates and effectors (Huber and Huber, 1996). Metabolites may influence enzyme activity, particularly Glc-6-P and P_i , which act as an allosteric activator and inhibitor, respectively (Stitt *et al.*, 1987).

Vu *et al.* (1989) observed that soybean grown under $800 \mu\text{mol mol}^{-1}$ CO_2 showed increases of 37, 205, 108, 33, 22 and 31 per cent in SLW, starch, sucrose, reducing sugars, chlorophyll and soluble proteins respectively, over control plants at $330 \mu\text{mol mol}^{-1}$ CO_2 . Carbon dioxide enrichment caused an increase in leaf thickness due to an increased number of palisade cells but no major alterations in chloroplast ultra structures. The extra starch formed under CO_2 enrichment was attributed to slightly larger starch grains, among more and larger chloroplasts and more mesophyll cells, rather than as more starch grain per chloroplast. The increase in starch storage sites, together with the maintenance of rubisco activity enabled soybean to continue to exhibit high photosynthetic rates out through the growth period.

Rowland-Bamford *et al.* (1990) studied the response of the leaf blades of rice plants exposed to outdoor, naturally sunlit, environmentally controlled growth chambers with CO_2 concentrations of 160, 250, 330, 500, 660 and $900 \mu\text{mol mol}^{-1}$. They observed that the priority between the partitioning of carbon into storage carbohydrates or into export changed with developmental stage and CO_2 concentration. During vegetative growth, leaf sucrose and starch concentrations increased with increasing CO_2 concentrations but tended to level off above $500 \mu\text{mol mol}^{-1}$ CO_2 . Similarly, photosynthesis also increased with CO_2 concentrations up to $500 \mu\text{mol mol}^{-1}$ and then reached a plateau at

higher concentrations. The ratio of starch to sucrose concentration was positively correlated with the CO₂ concentration. At maturity, increasing CO₂ concentration resulted in an increase in total non-structural carbohydrate (TNC) concentration in leaf blades, leaf sheaths and culms. Carbohydrates that were stored in vegetative plant parts before heading made a smaller contribution to grain dry weight at CO₂ concentrations below 330 $\mu\text{mol mol}^{-1}$ than for treatments at concentrations above ambient. Increasing CO₂ concentration had no effect on the carbohydrate concentration in the grain at maturity.

Wang and Nobel (1996) observed that after exposure to a doubled CO₂ concentrations, glucose and starch in the chlorenchyma of basal cladodes of *Opuntia ficus-indica* increased 175 and 57 per cent, respectively compared with the current CO₂ concentration of 370 $\mu\text{mol mol}^{-1}$, but sucrose content was virtually unaffected. Doubling CO₂ concentration increased the nocturnal malate production in basal cladodes by 75 per cent, Pi by 32 per cent, soluble starch synthase activity by 30 per cent sucrose Pi synthase activity by 146 per cent, but did not affect the activity of hexokinase. Doubled CO₂ accelerated phloem transport of sucrose out of the basal cladodes, resulting in a 73 per cent higher dry weight for the daughter cladodes. Doubling CO₂ increased the glucose content in 14 d daughter cladode by 167 per cent.

Hussain *et al.* (1999) studied the effect of elevated CO₂ and temperature on photosynthetic transfer in rice plants while analysing the regulation of sucrose phosphate synthase (SPS) activities. Leaf SPS activities were up-regulated in the CO₂ enriched plants, averaging 20 per cent higher than in ambient CO₂ grown plants. Similarly, SPS activities increased 2.4 per

cent for each 1°C rise in growth temperature from 25 to 34°C , but decreased 11.5 per cent at 37°C . Leaf sucrose content was higher and mirrored SPS activity better, than starch, although starch was more responsive to CO_2 treatment. Leaf sucrose and starch contents were significantly higher throughout the season in plants at elevated CO_2 , but the N content averaged 6.5 per cent lower. Increasing growth temperatures from 25 to 37°C caused a linear decrease (62%) in leaf starch content, but not in sucrose. Consequently, the starch : sucrose ratio declined with growth temperature. This was due to the up regulation of leaf SPS which may be an acclimation response of rice to optimize the utilization and export of organic C with the increased rates of inorganic C fixation in elevated CO_2 or temperature growth regimes.

Plant responses to elevated CO_2 concentrations (CO_2) may be regulated by both accelerated ontogeny and allocational changes as plants grow. Lewis *et al.* (2002) observed that the growth of *Xanthium strumarium* L. at elevated (CO_2) increased net photosynthetic rates by approximately 30 per cent throughout vegetative growth (i.e. active carbohydrate sinks), approximately 10 per cent during flowering (i.e. minimal sink activity), and approximately 20 per cent during fruit production (i.e. active sinks). At the harvest, the ratio of source to sink tissue significantly decreased with increasing plant age and was correlated with leaf soluble sugar concentration. Leaf soluble sugar concentration was negatively correlated with the relative photosynthetic response to elevated (CO_2). These results suggest that age and ontogeny independently affect photosynthetic responses to elevated

(CO₂) and the effects are mediated by reversible changes in source : sink balance.

In tropical epiphytic CAM orchid (Mokaro yellow), Li *et al.* (2002) suggested that the down regulation of Rubisco and upregulation of SPS and SS are two important acclimation processes that are beneficial because it enhanced both photosynthetic capacity at high CO₂ and reduced resource investment in excessive Rubisco capacity.

Prasad *et al.* (2004) studied the responses of kidney bean (*Phaseolus vulgaris* L. cv. Montcalm) plants grown under day time maximum/night time minimum temperatures of 28/18, 34/24 and 40/30⁰C at ambient carbon dioxide concentration (CO₂: 350 $\mu\text{mol mol}^{-1}$) and 28/18, 31/21, 34/24, 37/27 and 40/30⁰C at elevated (twice ambient) CO₂, to characterize how increases in growth CO₂ and temperature affected kidney bean leaf photosynthesis and carbohydrate metabolism. Elevated CO₂ enhanced leaf photosynthetic rates by about 57% across the temperature regimes, compared with plants grown at ambient CO₂. Growth at either elevated temperature or CO₂ decreased activity, protein content and activation of the primary photosynthetic enzyme ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco). Elevated CO₂ increased activities of sucrose phosphate synthase (SPS) and adenosine-5'-diphosphoglucose pyrophosphorylase (AGP) and accumulation of soluble sugars and starch across all temperatures, compared with plants grown at ambient CO₂. At elevated CO₂, growth temperatures above 34/24⁰C significantly increased leaf carbohydrates (total soluble sugars and starch) and activity of AGP. The upregulation of leaf carbohydrate metabolism

enzymes under elevated CO₂ plus temperature would be beneficial for growth and productivity of kidney bean in future climate.

2.7 NITROGEN UPTAKE KINETICS

Higher rates of nitrate assimilation are required to support faster growth in enhanced carbon dioxide. Although nitrogen decreases on weight basis in enhanced CO₂, this is partly due to a decrease in nitrate (Hocking and Meyer, 1991). Sugars stimulate the expression of *nir* ((Geiger *et al.*, 1998) and the post translational activation of NR (Bachmann and Huber, 1996). The subsequent synthesis of amino acids depend on carbon skeletons produced by photosynthesis and sugar catabolism, and sucrose also drives the export of amino acids in the phloem and their utilization in sink organs.

Enhanced activity of CO₂ led to a small increase of NR activity in mustard (Maevskaya *et al.*, 1990) and *Vigna radiata* (Sharma and Sengupta, 1990), but in case of wheat, NR activity was decreased by 2-fold (Hocking and Meyer, 1991).

Conroy (1992) reported that high CO₂ alters nutrient requirement and N concentration of foliage, roots and grains are consistently lower in plants grown at elevated CO₂ irrespective of availability of N in soil. According to him changes in nutrient uptake from the soil, remobilization in the plant of efficiency of utilization at elevated CO₂ will influence fertilizer management in agricultural and forest ecosystems and nutrient cycling in natural ecosystem.

The C-N ratio of plants grown in elevated atmospheric CO₂ was increased (Curtis *et al.*, 1989 and Baker *et al.*, 1992). Conroy and Hocking (1993) suggested that stomatal closure resulting in decreased transpiration rates in CO₂ enriched atmosphere is in part responsible for the decrease in N

content of plant grown in these conditions. Nitrogen mineralization could increase response of labile C inputs for root production and this carbon becomes key regulator for soil dynamics (Clarton, 1995). Bunce and Ziska (1996) observed that at doubled CO₂ concentration, the N content of soybean was lowered by 24 per cent.

Fonseca *et al.* (1997) grew vegetative plants of an inbred line, A4, of *Plantago major* ssp. *Pleiosperma* (L.) Pilger at 350 $\mu\text{mol mol}^{-1}$ or at elevated (700 $\mu\text{mol mol}^{-1}$) CO₂ in non-limiting nutrient solution with nitrates. In the roots soluble sugar concentration increased during the transient period of RGR stimulation (up to 23%), as did the root respiration rate. Changes in nitrogen metabolism were also restricted to this period and consisted of an increase in (1) *in vivo* and *in vitro* root nitrate reductase (EC 1.6.6.1) activity, (2) *in vitro* leaf nitrate reductase activity, (3) leaf and root nitrate reductase mRNA and (4) reduced nitrogen concentration in the roots. The elevated CO₂ related signal for the increase in nitrate reductase transcript levels in the roots is due to the increase in the availability of soluble sugars. The results suggest that the short-term enhancement of root carbon and nitrogen metabolism may be responsible for the transient effect of elevated CO₂ on whole plant RGR.

Geiger *et al.* (1998) observed in young tobacco plants that enhanced carbon dioxide led to larger increases of NR activity and NR activation, a 2–3 fold increase of glutamine, a 50 per cent increase of glutamate, and a 2–3-fold increase in minor amino acids. It also led to a higher nitrate level. Thus enhanced carbon dioxide leads to a very effective stimulation of nitrate uptake, nitrate assimilation and amino acid synthesis in seedlings. This will

play an important role in allowing faster growth rates in enhanced carbon dioxide at this stage.

Wand *et al.* (1999) performed a meta-analysis on observations reported for wild C₃ and C₄ grasses species. When there were no stresses, elevated CO₂ reduced leaf nitrogen concentration by 11 and 3% for C₃ and C₄ species.

Upreti and Mahalakshmi (2000) reported that elevated CO₂ increased carbon sequestration in leaf, stem and roots of *Brassica* plants through increased photosynthesis and decreased respiration. According to them application of additional nitrogen nutrition sustain the positive effect of CO₂ enrichment by utilizing additional carbohydrates for the development of new sinks. Excess carbohydrate, make plant flexible and responsive to additional nitrogen application for sustaining this CO₂ enrichment.

Kimball *et al.* (2001) showed that the N concentration of wheat grains grown in FACE, decreased by about 3% under ample N and water, 4% under low water and 9% under low soil N.

Yamakawa *et al.* (2004) reported that the nitrogen (N), phosphorus (P), potassium (K) and magnesium (Mg) concentrations of rice were significantly 21, 6, 14 and 9% lower, respectively, in rice grown with FACE than the concentrations in ambient grown rice at panicle initiation, and the N and K concentrations were significantly lower with FACE at harvest.

2.8 PLANT GROWTH, BIOMASS AND YIELD

Tropical plants show alterations in morphology and biomass distribution due to growth in an elevated CO₂ environment. Upreti *et al.*

(2003) observed an increase in plant height and tillering under elevated CO₂ concentration in rice cultivars.

Baker *et al.* (1990) showed an increase in tillering when rice plants were exposed to ambient super CO₂ (500, 600, 900 $\mu\text{mol mol}^{-1}$ CO₂) concentration. The increased tillering resulted in more number of panicles per plant under elevated CO₂ concentrations. Imai (1995) reported that increased tiller number in rice resulted in a greater leaf area per plant. Large differences in leaf area index (LAI) have been reported among the various FACE experiments in the response of rice cultivars to elevated CO₂. Among the C₃ members of gramineae family like wheat, ryegrass and rice, the mean increase of leaf area index was about 11% at ample water and ample and very high N (Kimball *et al.*, 2002). In case of C₄ sorghum, Ottman *et al.* (2001) reported no response of leaf area index to elevated CO₂.

Hoddinott and Jolliffe (1988) in their investigation with *Phaseolus vulgaris* at 380, 800 and 1400 $\mu\text{mol mol}^{-1}$ CO₂ of carbon dioxide observed that elevated CO₂ increased the specific leaf weight (SLW) significantly, indicating a denser leaf structure. Similarly in soybean, Vu *et al.* (1989) reported a 37 per cent increase in SLW at elevated CO₂ (800 $\mu\text{mol mol}^{-1}$ CO₂) compared to the control plants at 330 $\mu\text{mol mol}^{-1}$ CO₂). The net assimilation rate (NAR) and SLW were always higher in CO₂ enriched plants, suggesting that assimilates were preferentially accumulated in the leaves as reserves rather than contributing to leaf expansion (Yelle *et al.*, 1990). The increase in NAR at high CO₂ was due to the increase in relative growth rate (RGR) because RGR was highly correlated with NAR than that of leaf area ratio (LAR) (Bunce, 1995). According to Wand *et al.* (2001), net carbon dioxide assimilation rate is an

important indicator of plant growth, which was evident from, the study made in a C₄ South African grass exposed to elevated CO₂.

Faria *et al.* (1996) reported that the concentration of total chlorophyll showed a small increase in elevated CO₂ plant on leaf area basis, but it decreased significantly on dry weight basis as a result of the reduction in (SLA). The changes in SLA may result from effects on leaf thickness (mass/area) or changes in tissue density (dry weight/fresh weight). Tognetti and Johnson (1999) also showed that elevated CO₂ significantly decreased the specific leaf area (SLA) and leaf area ratio (LAR) in leaves of *Quercus ilex* L. Ziska (2002) showed that CO₂ enrichment significantly increased the biomass accumulation and the relative ratio of biomass increase to leaf area expansion in *Cirsium arvense*. The LAR and SLA were, however, significantly reduced at elevated CO₂ compared to ambient.

Rogers *et al.* (1986) reported an increase in dry matter accumulation in soybean by about 78.1 per cent at 700 $\mu\text{mol mol}^{-1}$ CO₂ compared to 334 $\mu\text{mol mol}^{-1}$ CO₂. Studies in cotton (Idso *et al.*, 1987) at elevated CO₂ conditions showed that the cotton biomass increased by 82 per cent and at the same time the grain yield was increased by 87 per cent. Baker *et al.* (1990) reported that rice plants when exposed to elevated CO₂ increased the total shoot biomass, root biomass and final grain yield. The harvest index (HI) of the rice crop also showed an increase at elevated CO₂. According to Ziska *et al.* (1997) and Moya *et al.* (1998), the additional tillers produced in rice increased the number of panicles leading to a grain yield increases from 5 to 60 per cent. Polle *et al.* (2001) reported an increase in whole plant biomass and stem diameter in holm oak (*Quercus ilex* L.) seedlings under elevated CO₂

condition. Upreti *et al.* (2003) also showed an increase in rice grain yield at elevated CO₂ condition which was mainly attributed to increased tillering, increased number of panicle per plant and an increased grain mass.

Processes involved in plant growth at a wide range of scales were affected by both temperature and CO₂ and their potential interactions (Centritto *et al.*, 1999a). The warming effect (even a few tenths of a degree) acting cumulatively over long periods of time may significantly affect the rates of both ontogenetic development and growth in leaf area and biomass (Pinter *et al.*, 1996). Warmer temperature increases the rate of ontogenetic development in determinate crops like wheat and resulting substantial shortening of the growth period. This shortening of growth period further shortens the duration of carbon fixation and biomass accumulation to seed set (Morison 1996). However, Van *et al.* (1999) reported increase in photosynthetic rate, stimulation in grain yield and slight decrease in crop light interception capacity due to the interactive effect of elevated CO₂ and temperature in spring wheat cultivars.

Ferris *et al.* (1996) reported that at high temperature, the leaf extension, segmental elongation rates, cell wall extensibility and final leaf size in *Lolium perennae* L. cv. Vigor were reduced, whereas in elevated CO₂ x temperature condition, all these factors increased. The increased leaf area was mainly due to the increase in the leaf cell wall extensibility and an increase in the activity of cell wall loosening enzyme, xyloglucan endotransglycosylase (Ferris *et al.*, 2001). However, when the N supply to the plants was limited, as in cork oak (*Quercus suber* L.), the effects of CO₂ enrichment over leaf area and biomass accumulation are lost, suggesting that

in native ecosystem with low N availability, the effect of CO₂ enrichment may be insignificant (Maroco *et al.*, 2002).

The response of root systems to CO₂ and temperature is also highly significant because of their role in mining water and nutrients and manipulating the plants ability to withstand water and nutrient stress. Changes in root growth also affect carbon partitioning by the plant, as well as the role of the soil as a sink in the global carbon budget and its potential to modify soil characteristics and water-holding capacity. The interactive effect of CO₂ and temperature on cotton showed that root weight was significantly greater in 700 $\mu\text{mol mol}^{-1}$ CO₂ treatment at all depths and at all temperatures. Number of roots increased with increasing temperature up to 25/17°C but was not affected by CO₂ treatments. Roots in the 350 $\mu\text{mol mol}^{-1}$ CO₂ treatment were longer and penetrated the soil profile faster at lower temperatures. In the 700 $\mu\text{mol mol}^{-1}$ CO₂ treatment, roots were more evenly distributed down the soil profile than in the ambient CO₂ treatment (Reddy *et al.*, 1994).

Elevated mean annual temperature increased net photosynthetic rates by an average of 33 per cent across high CO₂ concentration in trees (Lewis *et al.*, 2001). This positive interactive effect of increased CO₂ and temperature increased the net assimilation rates (NAR) in oak saplings (*Quercus myrsinaefolia*). Thus, the interaction of CO₂ enrichment and warming enhanced the NAR in spring season and also completely compensated the negative effect of warming during summer (Usami *et al.*, 2001).

The considerable variation in the magnitude of the response to elevated CO₂ can be attributed to different factors such as air temperature, nutrient supply and cultivars. Higher temperature in combination with CO₂

enhancement appears to enhance vegetative biomass accumulation in CO₂ plants (Long, 1991). Alberto *et al.* (1996) studied the responses of rice to two different CO₂ concentration (393 and 594 $\mu\text{mol mol}^{-1}$) at two different day/night temp, of 27/21 and 37/29°C. At 27/21°C, increasing the CO₂ concentration resulted in a significant increase in above ground biomass (+47%) and seed yield (+55%) rice. However, at higher growth temperature (37/29°C), growth and reproductive stimulation of rice by elevated CO₂ was reduced compared to the lower growth temperature.

2.9 ANTIOXIDANT ENZYMES

Plants grown under elevated CO₂ might be better protected from environmental stress by an increased capacity for detoxification and repair (Carlson and Bazzaz, 1982). Higher temperature reported to cause oxidative stress and reduce membrane stability in plants. In several herbaceous plant species antioxidative systems were induced in response to drought stress (Smirnoff, 1993). Possibly plant grown at an elevated CO₂ concentration contained increased metabolic reserves and thus, might have an enhanced metabolic flexibility to respond to oxidative stress compared with plants grown at ambient CO₂ concentrations (Schwanz *et al.*, 1996). Production of reactive oxygen species (ROS), including superoxide (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radical (OH^-), is an inevitable consequence of life in an oxygen rich environment under several stress condition (Polle *et al.*, 1990). ROS damage plant cell by oxidizing membrane lipids including photosynthetic apparatus and also damage the proteins, chlorophyll and nucleic acids (Foyer *et al.*, 1994). H_2O_2 is generated as metabolite of enzymatic reaction and during photosynthesis (Salin, 1987). The antioxidant ascorbate and

glutathione participate in both enzymatic and non-enzymatic H_2O_2 degradation (Smith *et al.*, 1990). Peroxidase decompose H_2O_2 by oxidation of co-substrate such as phenolic compounds or antioxidant (Polle *et al.*, 1990),

According to Salin (1987) the Cu, Zn, Fe-SOD in higher plants are mostly associated with the chloroplast, where they scavenge super oxide anions originating from "leakage" of photosynthetic transport chain, PS I (Mehler's reaction) and reduced ferridoxin, especially under conditions which favors NADPH accumulation (Halliwal and Gutteridge, 1989). It could be expected that increasing atmospheric CO_2 enhance the demand for photo-reducing power and this could reduce risk of oxy-radical formation. Badiani *et al.* (1993) showed that the chloroplast SOD activity was reduced under elevated CO_2 conditions.

Schwanz *et al.* (1996) investigated antioxidative systems and the malondialdehyde and carbohydrate in sun and shade acclimated leaves of sour orange (*Citrus aurantium*) trees that had grown for 7.5 year under ambient and elevated ($+300 \mu\text{mol mol}^{-1}$) atmospheric CO_2 concentrations. Sun-acclimated leaves contained higher ascorbate, glutathione and soluble carbohydrate contents and higher catalase activities than shade-acclimated leaves. The activities of superoxide dismutases, which belonged to the family of Cu/Zn-isozymes, were similar in sun and shade acclimated leaves and decreased in response to enhanced CO_2 .

Polle *et al.* (1997) studied the responses of antioxidant enzymes and malondialdehyde content in beech (*Fagus sylvatica* L.) seedlings to elevated CO_2 and nitrogen. Guaiacol peroxidase activities did not respond to either CO_2 or nutrient treatment. Catalase activity decreased with decreasing

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nutrient supply rate and also in response to elevated CO₂. Superoxide dismutase activity was affected by both nutrient supply and CO₂ concentration. In leaves from trees grown with the high-nutrient treatment, superoxide dismutase activity was low irrespective of CO₂ concentration. In chlorotic leaves, SOD activity was increased, suggesting an enhanced need for detoxification of reactive oxygen species. Leaves from plants grown under elevated CO₂ with medium nutrient supply rates showed decreased malondialdehyde contents and superoxide dismutase activities. This suggests that the intrinsic oxidative stress of leaves was decreased under these conditions. These results imply that intrinsic oxidative stress is modulated by the balance between N and C assimilation.

Sgherri *et al.* (2000) observed in alfalfa (*Medicago sativa* L.) that ascorbate was more affected than glutathione by CO₂ enrichment and an interaction between CO₂ and drought prevented the decrease in ascorbate/dehydroascorbate ratio and increased the reduced glutathione/oxidized glutathione ratio as compared with ambient CO₂ plants. The interaction between CO₂ and drought increased the alfalfa plants capacity to overcome oxidative stress as compared with plants grown at elevated CO₂.

Toppi *et al.* (2002) observed in leaves of *Dactylis glomerata* L. and *Trifolium repens* L., no differences between ambient and elevated CO₂ were detected for their protein content, activity of oxidant-scavenging enzymes (catalase, superoxide dismutase, ascorbate peroxidase and guaiacal peroxidase), and lipid peroxidation. The activity of antioxidant-regenerating enzymes (monodehydroascorbate reductase, dehydroascorbate reductase and glutathione disulfide reductase) and the content of antioxidants (ascorbic

acid, dehydroascorbic acid, reduced glutathione and glutathione disulfide) showed remarkable variability between leaves from plants grown in ambient and CO₂ enriched mini FACE rings. Thus, in general it can be concluded that the effects of elevated CO₂ at environmentally relevant concentrations on the leaf antioxidant status of a grassland community are extremely variable, species-specific and rather limited

2.10 INTERACTION OF TEMPERATURE AND CO₂

The effects of increasing CO₂ and temperature on plant productivity have been considered separately, but consequences of their interaction have received scant attention. Cure (1985) proposed relative increases in plant growth due to elevated CO₂ to be greater at higher temperatures. Cure and Acock (1986) distinguished between C₃ plants grown at high and low irradiance, where, in the latter case effects of all temperatures on the CO₂ response of plants were less pronounced. A study on the growth of *Azolla pinnata*, *Daucus carota*, *Eichhornia crassipes* and *Raphanus sativa* revealed a marked temperature dependence for the increase in biomass due to elevated CO₂ (Idso *et al.*, 1987). It was observed that elevated CO₂ may reduce plant productivity at temperatures below 18.5°C. Although finite values for this temperature threshold were arbitrary, it raises the possibility that plant adapted to low temperatures may show little or no change in growth parameters when subjected to elevated CO₂. This change in growth pattern did not occur for plants grown under combined elevated CO₂ and temperature (4°C above ambient). The rate of carbon assimilation in barley leaves measured at ≤10°C was unaffected by elevated CO₂, whilst accumulation of pools of phosphorylated intermediates in both control and CO₂-enriched

leaves reflects the recycling of phosphate as the major limiting factor on carbon assimilation (Labate *et al.*, 1990). From the model of Farrar and Willams (1991), stimulation of sucrose (synthesis with temperature would be expected) to increase the degree of phosphate recycling to the chloroplast and hence permit enhanced rates of assimilate production for CO₂ enriched leaves. Indeed, under conditions of high CO₂ and temperature, photosynthesis is limited not by phosphate regeneration but by RuBP regeneration capacity (Sage *et al.*, 1990 and Labate *et al.*, 1990).

Idso *et al.* (1987a) have shown that the stimulatory effect of elevated CO₂ upon the growth of *Daucus carota*, *Raphnus sativa* and *Gossypium hirsutum* was linearly related to air temperature. According to them, a 3°C increase in air temperature at a CO₂ concentration of 640 µmol mol⁻¹ increased the average growth enhancement factor from 1.3 to 1.56. If the vapour pressure difference between leaf and air remained the same, and stomatal conductance was decreased by 30-40 per cent, it can be concluded that WUE was substantially increased and that this increase was also temperature dependent. Lin *et al.* (1997) observed in rice that increasing CO₂ and temperature resulted in a greater stimulation of photosynthesis compared to increasing CO₂ at ambient temperature prior to the onset of flowering.

2.11 SEED QUALITY

Much less, however, is known about the effects of elevated concentration of atmospheric CO₂ on the nutritive value of food (Lawlor and Mitchell, 1991). Decline in wheat ear N or grain N was detected by Hocking and Meyer (1991) and Conroy (1992). Conroy *et al.* (1994) studied the grain quality changes in wheat and rice at elevated CO₂. Reduction in N

concentration and hence protein occurred in wheat flour which reduced its baking quality. Rice grain also showed similar reduction in N concentration which had only little effect on grain quality. The amylose content also increased which was correlated with high glucose concentration in both the leaf and grain. Increase in seed oil content in *Brassica* species was accompanied by a decrease in seed protein. The reduced transpiration could be responsible for reduction in nitrogen uptake resulting in lower protein content in harvested *Brassica* grain as reported by Uprety *et al.* (1995).

Williams *et al.* (1995) studied the qualitative and quantitative changes in both non-starch and starch lipid fractions in wheat at elevated CO₂ and temperature at two levels of nitrogen (high and low). Temperature was by far the most influential growth factors, although interactions between all three growth conditions occurred, as confirmed by analysis of variance. Growth at elevated temperatures had the general effect of reducing the amounts of accumulated lipids, particularly non-polar lipids (1322 mg fatty acids per 100 g fresh weight at ambient temperatures as opposed to 777 mg fatty acids for 100 g fresh weight at 4°C above ambient temperatures). There were changes in the proportions of the major non-starch as well as the starch lipids. In the non polar lipids (principally triacylglycerols), the membrane glycosylglycerides and phosphatidylcholine were the main constituents, whereas in the starch lipids, lysophosphatidylcholine and lysophosphatidyl ethanolamine represented over 70% of the total. Depending on the growth conditions, the percentages of lipids such as monogalactosyldiacylglycerol, digalactosyldiacylglycerol and phosphatidylcholine (non-starch) or the starch lysophosphatidyl ethanolamine varied 2-fold or more. Significant changes in

the acyl composition of individual lipids were also observed, most often in the proportions of palmitate, oleate and linoleate. The observed alterations in wheat lipids are likely to affect the properties of any flours derived from grain grown under climate change conditions.

Upreti *et al.* (1997) observed that elevated CO₂ brought about a significant increase in carbohydrate component in the *Brassica* seed. The increase was starch content (37.5%), reducing sugars (28%), total sugars (24%) and non-reducing sugars (22%). The elevated CO₂ significantly reduced protein content (10.3%) in the seeds. CO₂ enrichment also increased the oil content (10.4%). The accumulation of carbohydrates may possibly lead to reduction in protein content due to dilution effect. Idso *et al.* (2002) reported that elevated CO₂ not only increase fruit production but also increase the vitamin C concentration by 7 per cent in juice of sour orange.

3. MATERIALS AND METHODS

The response of basmati rice varieties to elevated CO₂ was studied using Open Top Chambers (OTC) and Free Air Carbon dioxide Enrichment (FACE) facilities in the present investigation. The interactive effect of elevated CO₂ and temperature on this crop was investigated in controlled plant growth chambers at National Phytotron Facility of Indian Agricultural Research Institute, New Delhi. This study was conducted in the *kharif* crop seasons of 2002 and 2003 (Appendix I & II). The details of the materials used and the methodologies adopted during the course of this study are furnished below.

3.1 PLANT MATERIAL

Basmati rice varieties viz., Pusa RH-10 (PRH-10) and Pusa Sugandh-2 (PS-2) were used to study their response to the elevated CO₂ and to its, interaction with higher temperature.

3.1.1 Pusa RH-10

Pusa RH-10 is the first aromatic, super fine grained hybrid with desirable grain and cooking quality traits. It is a semi-dwarf, medium early duration (115-125 days) variety which has recorded an yield advantage of 40% over the check variety Pusa Basmati-1. It has a wider adaptation to the abiotic stresses. The hybrid completes its lifecycle 15-20 days earlier and escapes infestation of major pests and diseases. It also saves at least 1-2 irrigation at the terminal growth. The parents of the hybrid

are Pusa 6A (female parent) and PRR-78 (male parent). This hybrid was released in the year 2001 by the Indian Agricultural Research Institute, New Delhi-12. It was derived by a three line hybrid breeding using cytoplasmic genetic male sterility system (Zaman *et al.*, 2004).

3.1.2 Pusa Sugandh-2

Pusa Sugandh-2 is an aromatic, pure line variety derived from the parents, Pusa 1238-1 and Pusa 1238-81-6. Pusa Sugandh-2 was developed through relative inter-mating in F_2 and subsequent generations of a partially restored basmati quality F_1 hybrid following pedigree selection. This variety was also released in the year 2001 by the Indian Agricultural Research Institute, New Delhi. It is a semi-dwarf, medium early duration variety (120-130 days) with an yield advantage of 17% over Pusa Basmati-1 (PB-1). It is resistant to brown spot and moderately resistant to blast and shows wider adaptations to abiotic stress compared to PB-1 (Zaman *et al.*, 2004).

3.2 TECHNOLOGY

3.2.1 Open top chambers (OTCs)

The open top chambers developed at Indian Agricultural Research Institute (Upreti, 1998) were used in the CO_2 enrichment study. These chambers were comprised of five sub-systems (Fig. 9 & 12).

- (a) Supply of pure and high concentration of CO_2 ,
- (b) System of valves, regulators and flow meters,
- (c) Chambers or area to be CO_2 controlled,
- (d) Appropriate gas analyzer with feed back control, and
- (e) Computed data acquisition and programming.



Fig. 9. Open top chambers with rice crop

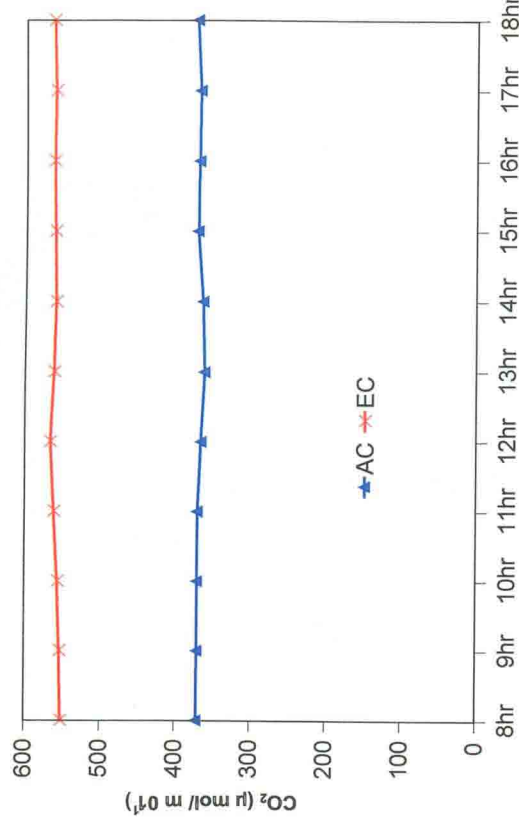


Fig. 10. Diurnal variation of CO₂ concentration within the OTC

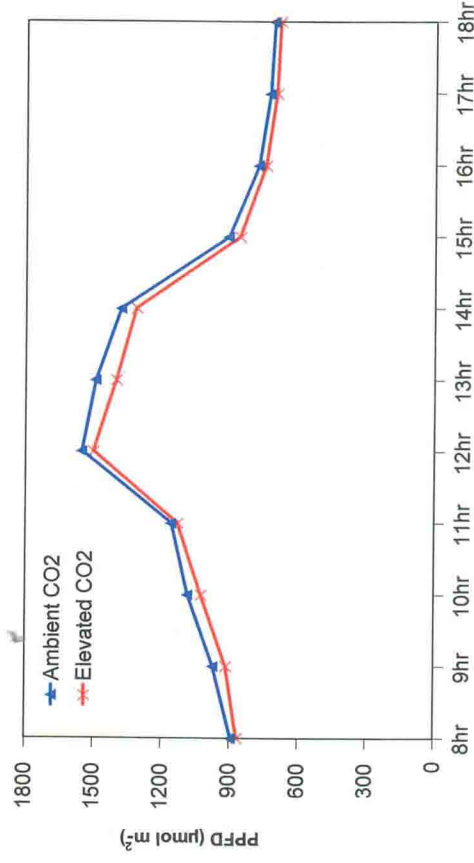
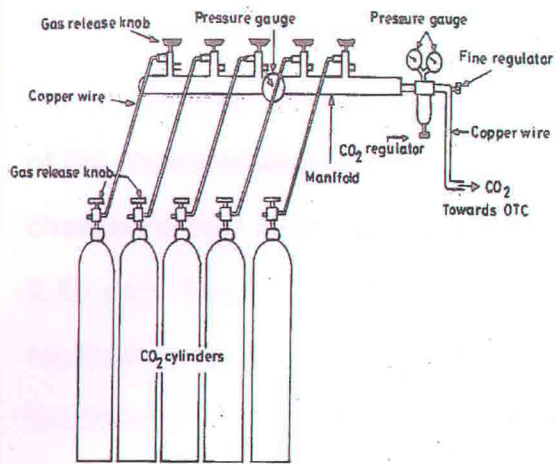
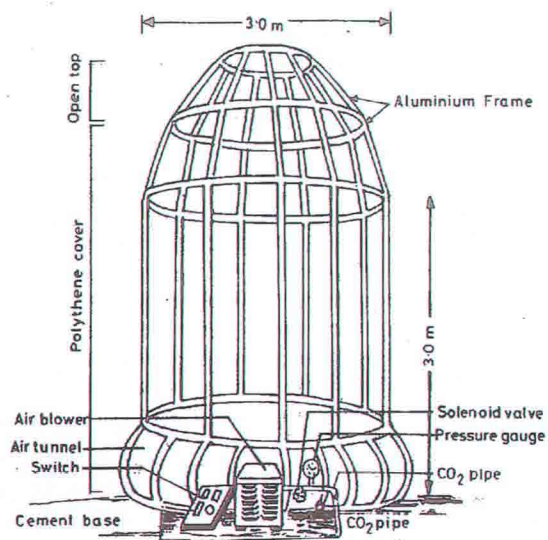


Fig. 11. Diurnal variation of photosynthetic photon flux density (PPFD) (μmol m⁻²) within the OTC



CO₂ cylinders



Representative diagram of an OTC

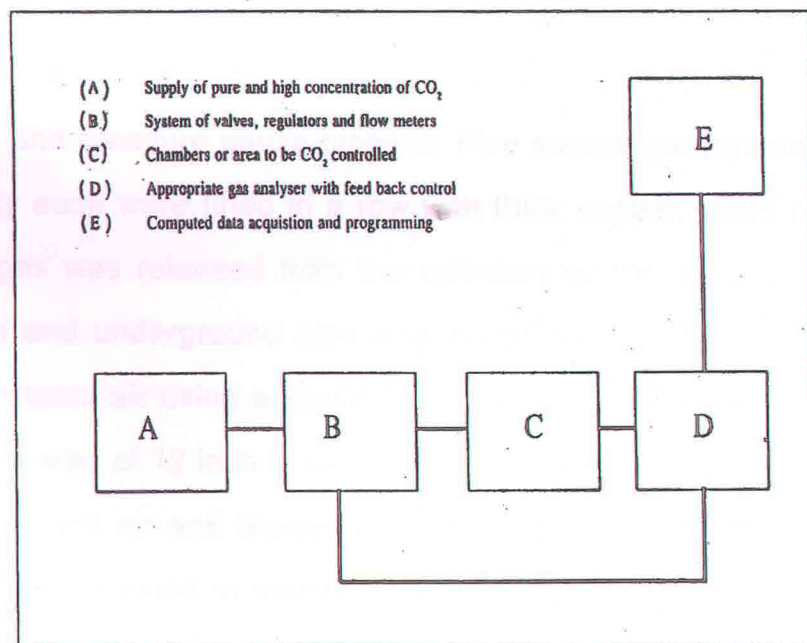


Fig. 12. Basic scheme of measurement and control system for CO₂ enhancement

These open top chambers were made of an aluminium frame installed on the ground. Each chamber covered a circular area of three meter diameter. The vertical sidewall was three meter in height and top of the chamber was kept open to provide the near natural condition. These chambers had a characteristic slender shape and were covered with a 0.15 mm thick transparent polyvinyl chloride (PVC) sheet. Chambers equipped with a frustum at the top to deflect air and prevent dilution of the desired CO₂ concentrations within the chamber. There was a cylindrical double walled plenum around the base for uniform CO₂ circulation. The inner side of the plenum was having numerous gas outlets of different sizes, the smaller being nearest to the gas inlet pipe. Commercial CO₂ was added in the upstream of the frame to ensure adequate mixing and to create the desired concentration. Blowers were used to distribute CO₂ enriched air uniformly throughout the plant canopy. The CO₂ gas was supplied to the chamber from gas cylinders using a manifold, gas regulators and pressure gauge pipeline. Five source gas cylinders of 45 kg capacity each were fitted in a row with thick copper outlet pipe (Fig. 12). CO₂ gas was released from the cylinders to the chamber through a manifold and underground pipe and injected into the chamber along with the ambient air using a blower. The air blower fitted at the base of the chamber was of 12 inch in diameter, which thoroughly mixed the CO₂ with atmospheric air and blowed the gas mixer to the chamber tunnel. The blower also helped in maintaining the inside air temperature closer to that of outside ambient atmosphere. The relative photosynthetic photon flux density (PPFD) in the chambers was maintained about 95 per cent of full sunlight by frequent and gentle washing of the transparent polythene sheet. The daily observation on temperature and RH were monitored in

the chambers and recorded in thermohygrograph (Lawrence and Mayo, India model: w/l712/z). The diurnal variation in temperature and CO₂ inside the chamber was recorded (Fig. 10). The hourly value of light intensity inside the chambers were also recorded (Fig. 11):

The concentration of CO₂ in the OTC was regulated by four-step operation:

- (a) Standardizing the gas release from the source to the manifold with the help of a pressure gauge,
- (b) Opening two successive finer metered valves for controlled release of gas from manifold to the under ground pipe,
- (c) Adjusting the solenoid valve at the end of the pipe with the help of pressure meter, and
- (d) The monitoring of CO₂ concentration was done by Infra Red gas analyzer (IRGA) by drawing air from different positions of crop canopy.

3.2.2 Free-air CO₂ enrichment (FACE) technology

South Asian Mid-FACE used in this study was designed, developed and established at Indian Agricultural Research Institute, New Delhi (Upreti *et al.*, 2000) (Fig. 13). The Free Air CO₂ Enrichment (FACE) technology was based on the principle of injecting additional CO₂ gas in open field suitably so as to attain a predetermined elevated level of gas concentration with uniform distribution in the field under varying meteorological conditions of wind, temperature and humidity. The main components of a FACE facility were:



FACE with rice crop

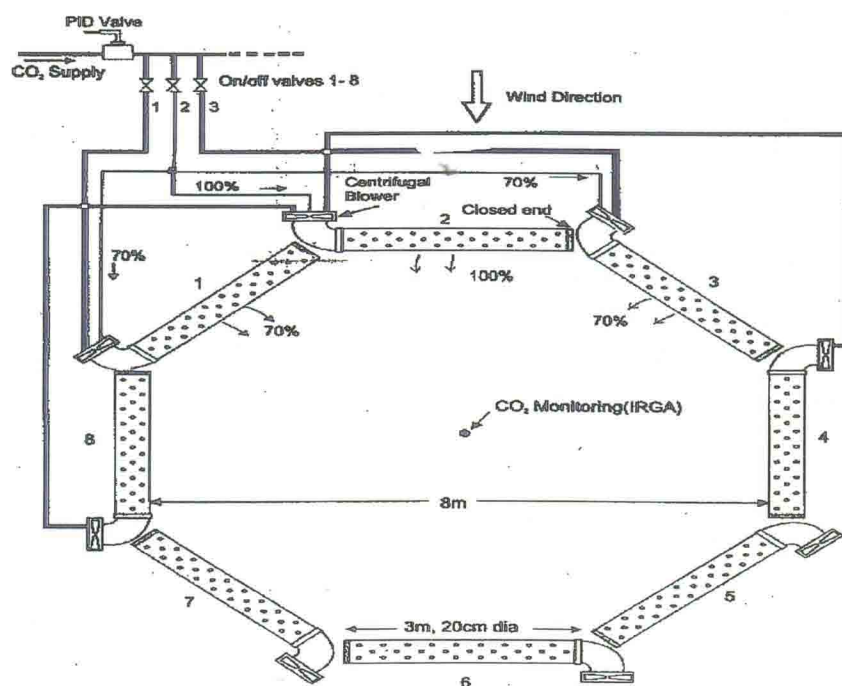


Fig. 13. Layout schematic of Mid-FACE facility

- i. CO₂ gas storage and distribution system.
- ii. The FACE ring, generally known as plenum, through which CO₂ enriched air was injected into the open field.
- iii. Different sensors and actuators used for monitoring the environment and controlling the operations.
- iv. An electronic system for controlling these operations.

System design

The mid-FACE ring was octagonal in shape having a diameter of 8 m as shown in the block schematic diagram (Fig. 14). The eight arms of the FACE ring were made of rigid PVC pipes of 200 mm diameter and wall thickness of 4.5 mm. Each arm of the octagon was fitted with a centrifugal air blower at one end for blowing air into the pipe and was closed at the other end. Four rows of holes (4 mm diameter) were drilled on each arm for the outlet of CO₂ enriched air. The CO₂ was injected at the input of each arm blower for pre-mixing with air within the pipe before its injection in the fields. The air blower pressure and holes on the pipe were arranged in such a way that the air outlet from the holes along the whole length of pipe remained at uniform pressure. All the eight arms of the octagon had independent supply of CO₂ controlled by 8 on/off valves. A common computer controlled proportional integral differential (PID) valve regulate the quantity of CO₂ to be released into the arms.

The CO₂ was released at a time into the field from 3 adjacent arms of the FACE ring. There were three nozzles for CO₂ injection for each arm. Depending on the downward wind direction, the central arm got CO₂ from the nozzle having 1.5 mm diameter and adjacent arms got supply

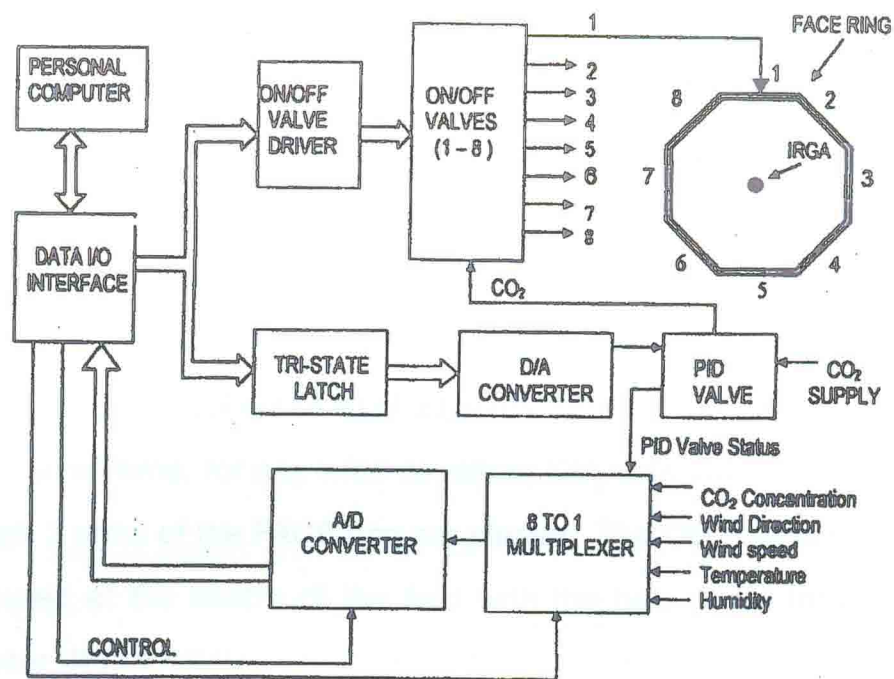


Fig. 14. Block schematic of the system controller for Mid-FACE facility

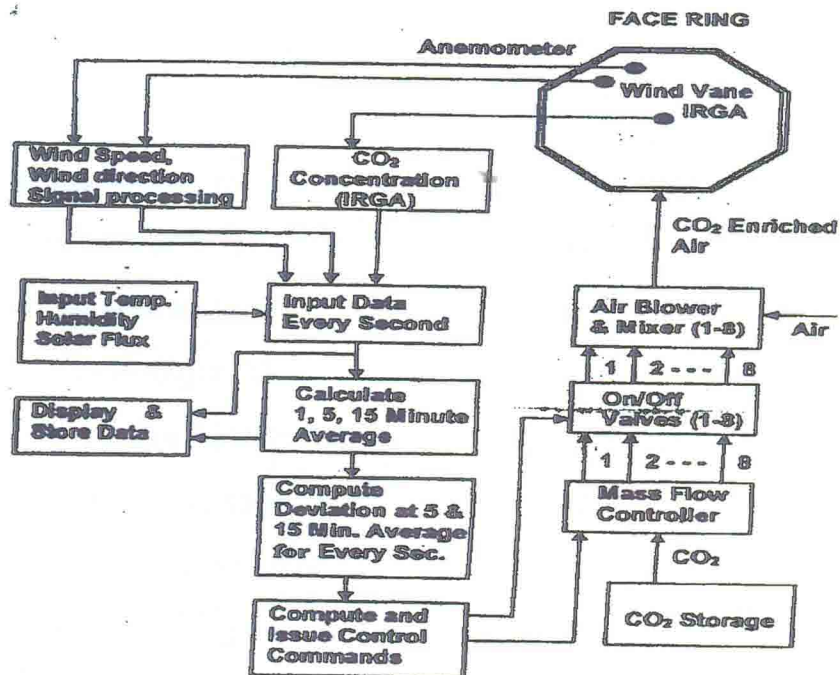


Fig 15. Flow chart for control sequence

from nozzles having 1.0 mm diameter. As shown in Fig. 14, when the downward wind direction was towards the arm 2 side, the on/off valve No. 2 was switched on and CO₂ was released from the arms 1,2 and 3. The CO₂ was injected into the arm 2 through the nozzle of 1.5 mm diameter and into the arms 1 and 3 through the nozzle of 1.0 mm diameter to take care of the effect of tilt of adjacent arms with wind direction. Thus, at any given time, for any wind direction, CO₂ was always released only through 3 arms of the FACE ring per plenum. The CO₂ concentration was measured at the centre of the field with the help of an Infra-Red Gas Analyzer (IRGA WMA-2). Sampling of gas was done continuously through a thin polythene tubing (4.3 mm ID) with the inlet height adjusted at about 5-25 cm above the crop canopy. The output from IRGA was the DC voltage in the range 0.5 V corresponding to 0-2000 ppm of CO₂.

The concentration of CO₂ in open field not only depended on the quantity of CO₂ enriched air released from the plenum, but also on the gas dispersion characteristics controlled by the meteorological factors such as wind speed, wind direction, humidity and temperature within the plenum. The sensors for wind speed (anemometer), wind direction (wind vane) and temperature were located near the centre of the FACE ring at plant canopy height. Their output signals were continuously measured in real time by the system controller. The output from the wind speed sensor was a DC voltage in the range of 0-5 V corresponding to wind velocity of 0-33 m/s and output from the windvane was also a DC voltage in the range of 0-5 V corresponding to wind direction of 0-359° with reference to the north.

The PID valve controlled the quantity of CO₂ to be released into

plenum arms, which depends on the control voltage, applied to it (0-10 V). To evaluate the proper operation of the PID valve, a feedback signal (from PID valve) was also monitored to know the actual status of the valve. This signal was in the range of 0-5 V corresponding to the fully closed and fully open conditions of the PID valve.

The fumigation of CO₂ gas into the field from the plenum was made at the crop canopy height. The height of plenum could be adjusted from time to time to match with the height of the crop canopy by resting the plenum on height-adjustable stands. Plenum could be raised up to 5 feet from the ground level in steps of 2 inches. Two banks of 25 cylinders in parallel were used for CO₂ storage and dissemination under constant pressure. Normally, one bank of cylinders supplied CO₂ to the ring. The second bank was switched on when CO₂ got exhausted in the 1st bank. A buffer tank was installed after the cylinder bank, which took care of the pressure variations in the supply line due to decreasing level of CO₂ in the cylinders during Mid-FACE operation.

Control system

The control process involved monitoring of CO₂ concentration and meteorological parameters inside the FACE ring along with the issue of control signals to a number of devices for their proper operation. A PC-based system controller was designed to control all such operations of the FACE facility. The system had been designed to measure 8 analog input signals in time-multiplexed mode. They were then digitized using a 10-bit analog to digital converter, which was connected, to the parallel port (LPT1) of PC. Thus, digitized signals entered the PC through this parallel port. The control signals required for the on/off valves (0 V-off,

5 V-on) of 8 arms of plenum were generated by the PC in the 8-bit digital form and sent out through a data I/O card. As the on/off valves operate at 24 V and require a current of 1 amp, the digital data were converted into the required analog form using suitable interface, capable of supplying the required voltage and current to the on/off valves. Similarly, the signal for controlling the PID valve was issued by the PC in the form of an 8-bit digital word sent out through another port of the data I/O card. The 8-bit digital to analog converter converted the digital data in to analog form of 0 to 10 V required for the proper operation of PID valve. The operations of all the interfaces such as A/D converter, D/A converter, multiplexer and latches, etc. were synchronized under the control of PC.

Apart from maintaining the CO₂ concentration at the target value, the system controller was also used to record all the data, make computations and display the data in suitable tabular and graphic format. The data were recorded in the form of files.

Operation sequence

The operational sequence of the Mid-FACE facility was shown in the flow chart (Fig. 15). The data from the meteorological sensors (wind speed and wind direction) along with the CO₂ concentration (Fig. 17) were measured in every one-second by the control system. Then, 1, 5 and 15 min. averages, along with their deviations from the instantaneous (every 1 second) values, were computed. Based on these inputs, the control system, through a specially developed PID algorithm, controlled the flow rate of CO₂ gas in the plenum with the help of a PID controller valve. The direction of wind decides which on/off valve was to be opened to release CO₂. In case the wind velocity was less than 0.5 m/s (which is

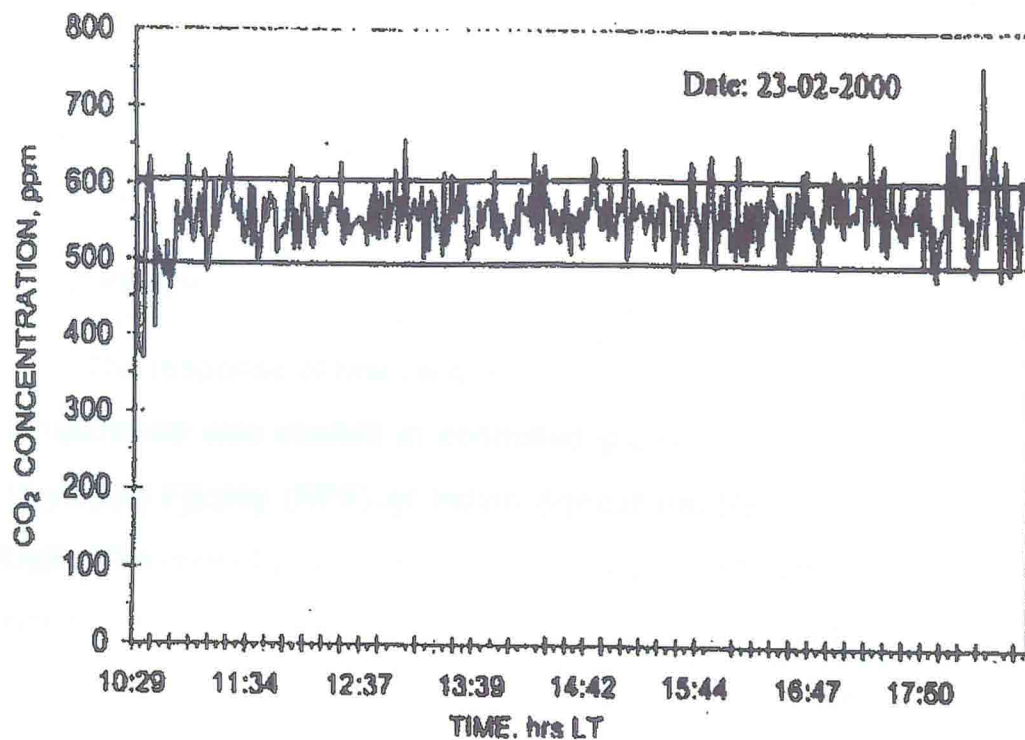


Fig. 16. Daylong CO₂ concentration at the centre of the Mid-FACE

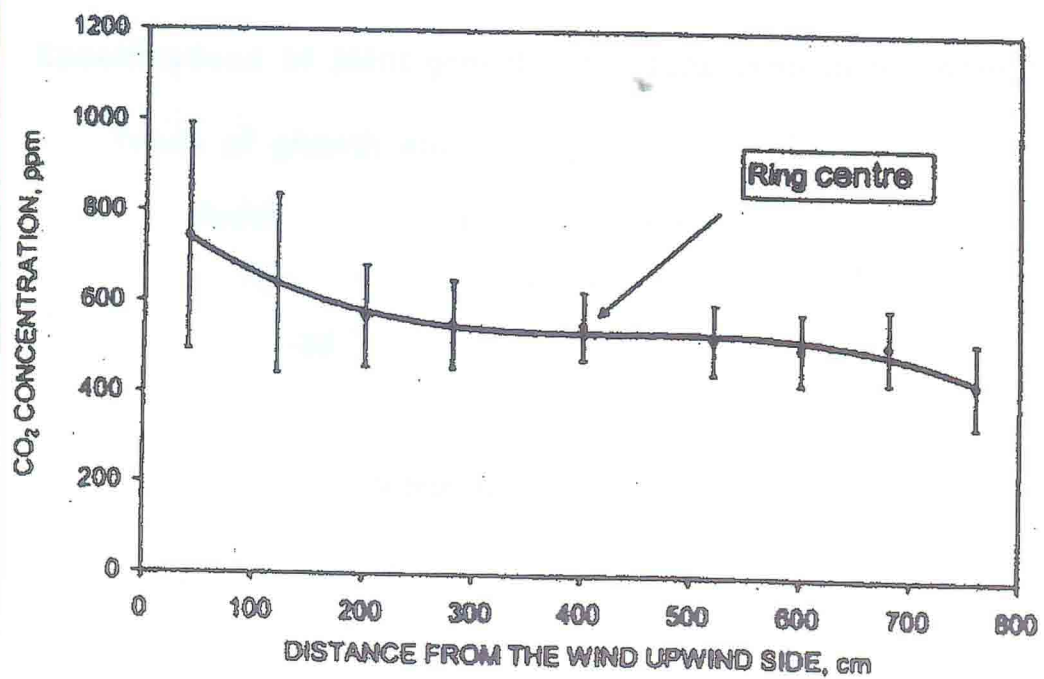


Fig. 17. Horizontal gradient of CO₂ concentration in Mid-FACE

taken as the case of calm air), the valves were opened in a cyclic order as no dispersion of CO₂ occurs in such conditions. Thus, a predetermined constant level of enriched CO₂ was maintained at the centre of plenum (Fig. 16).

3.2.3 Phytotron

The response of rice varieties to the interaction of elevated CO₂ and temperature was studied in controlled growth chamber at the National Phytotron Facility (NPF) of Indian Agricultural Research Institute, New Delhi. The core of this facility is an array of 22 growth chambers of different sizes all equipped with microprocessor controlled gadgetry to provide numerous combinations of precisely controlled and monitored environmental conditions, namely, temperature, humidity, light and photo-period. Few chambers have provision of CO₂ control also. The specifications of the growth chambers installed in the NPF and the environmental parameters that are measured and controlled in them are described below:

Specifications of plant growth chambers used in the phytotron

(i) Types of growth chambers

Model	Floor area (sq. ft.)	Numbers
E -15	15	12
PGW -36	36	8
CG -72	72	2

(ii) Temperature control features

- (a) Display to nearest 0.1 °C
- (b) Control accuracy +/-0.5 °C
- (c) Operating range 4 to 45 °C

- (d) Ramp or step mode change

- (iii) Humidity control features**

- (a) Direct reading in % RH

- (b) Control accuracy + 3%

- (c) Programmable range normal to 99%

- (d) Ramp or step mode change

- (iv) Lighting control features**

- (a) Two channels for independent intensity control

- (b) Channel #1 : Fluorescent lighting 0 to 8 levels

- (c) Channel #2 : Incandescent lighting 0 to 8 levels

- (d) Step change

- (v) Carbon dioxide control**

- (a) Resultant 3000 $\mu\text{mol mol}^{-1}$, additive only.

- (vi) Time lines available**

A time line is the programme time fixed on the controller at which minute, a new value is given to a variable to trigger the change required in the parameter from that time till the next time line is encountered)

- (a) 192 time lines per 24 hour period

- (vii) Other general features**

- (a) A continuous display of chamber operating conditions.

- (b) Access to the operating history of chamber components.

- (c) Alarms for temperature and RH, if drifted above settings

- (d) Keyboard lock through user's code
- (e) Host computer connectivity

The basic construction of a plant growth chamber shown in Fig. 18. includes an enclosure made of insulated walls. The space is divided in two chambers; one for mechanical equipment, and another for placing the plants. The mechanical chamber is fitted with compressor, air circulating fans, evaporator, heaters and sensor box. The compressor operates continuously to circulate refrigerant through the evaporator (cooling coils). The fans circulate air past the evaporator and heater coils to add or remove heat from the plant chamber. Cooling and heating process is controlled through the microprocessor, which transmits commands based on the signal received from the sensors. To monitor temperature and relative humidity (RH), a sample of air from the plant chamber is continuously collected through a tube, called as telensaier, and passed through the sensor box. Two thermometers, one dry bulb and another wet bulb, measure the dry and wet bulb temperatures of the sampled air. The information is transmitted to the microprocessor for determining RH and temperature of the plant chamber and necessary commands are given to the mechanical equipment. The lights are switched off and on through a real time clock depending upon the input data. The amount of CO₂ is added through a separate controller. Elevated levels of CO₂ may be lowered by opening exhaustments provided in the plant chamber for the purpose. Thus, the entire operation to monitor and control of all the pertinent environmental parameters is fully automated.

Environmental parameters

Irradiation (light), temperature, relative humidity, and, carbon dioxide

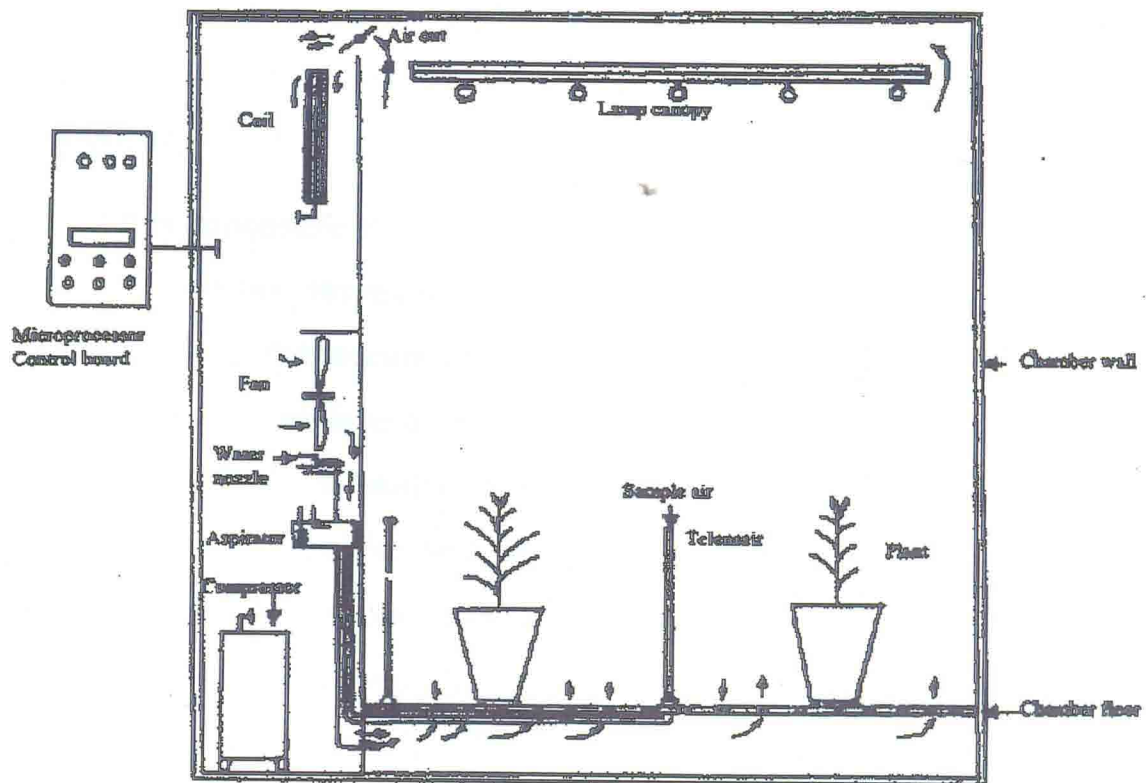


Fig 18. Plant growth chambers with rice crop

are the most important environmental parameters affecting the plant growth. The measurement and control of these parameters in the context of NPF chambers is described below.

Light

Measurement of light is done in either of the following two systems:

- (i) Photometric: It deals specifically with measurement of light as seen by the “human eye”.
- (ii) Radiometric: It describes incident radiation in absolute energy terms.

Both of the above systems of measurements have complex interrelationship, which depend on the sensitivity of various light receptors. Luminance and Irradiation are, respectively, the photometric and radiometric terms that define the flux density. In photometric terms, the units are lux (lumens/m²), while in radiometry the most valuable units are milliwatts/cm² (mW/cm²).

It is impossible to exactly match the spectrum of sunlight in a plant growth chamber. However, most of the chambers create simulated light by combining fluorescent and incandescent lamps to develop various spectra and to achieve a high range of intensity. Incandescence is the light created by a heated body and its spectrum depends on the temperature and the exposed surface of the heated element. Most of the energy from incandescent lamps is emitted as infrared radiation between 600 to 800 nm wavelength which also create heat energy. These lamps exhibit a decrease in radiant output with time of use. Fluorescent lamps have been the primary and most common source of light in the growth

chambers. In a close installed arrangement, these lamps provide fairly uniform distributed light source with high PAR spectrum. Light output from fluorescent lamps decreases approximately 10 per cent during the first 1,000 operating hours of use. These lamps also operate differently under different temperatures. Light output decreases by 12 per cent when the temperature is raised from 25 to 35°C.

The plant growth chambers of NPF employ a standard combination of 75 per cent fluorescent and 25 per cent incandescent lamps by total wattage. The above combination provides a good general spectral distribution as shown in Fig..... The expected life of these lamps is 6000 hours each. As mentioned earlier, the light intensity decreases with the aging of light sources and, so, it is imperative to compensate for this change during an experiment. Implementing a replacement schedule of lights, especially of fluorescent, after certain hours of use. The experimenter needs to be aware that light intensity inside the chamber at any light level is also not uniform on its floor area. While it is not possible to completely eliminate the spatial variation, the compensation for the aging of lights can be provided by replacing old lights in a planned schedule.

The light measurement and control system in the NPF chambers is in photometric units. An approximate conversion of photometric units in radiometric units is as given below:

$$10,000 \text{ Lux} = 123 \text{ } \mu\text{moles/m}^2/\text{sec}.$$

The chambers have 8 levels each of fluorescent and incandescent lamps. Depending on the light requirements of plants during 24 hours cycle / desired levels of lights, in combination of fluorescent and incandescent lamps, are chosen. The experimenter is expected to know the light

quantum requirements at different stages of the crop cycle to simulate the light conditions. As mentioned earlier, the quality and quantity of light emitted depends on the age of lamps. It is thus necessary that due compensation is made by the manager during the experiment to maintain proper light conditions.

Temperature

The NRF chambers are equipped with a microprocessor controlled integrated system comprising of compressors and heaters to maintain predetermined temperature inside the chamber. The air enters into the chamber through the vents provided in the floor. A variable height tube is placed at the centre of the floor through which air sample is drawn and sent to the sensor box where its dry bulb temperature is measured by a resistance type of thermometer. Any change in the temperature generates an electrical signal, which is monitored by the microprocessor continuously. The information is compared with the input data and necessary commands are sent to the mechanical equipment to change the course of action, if required.

The change in temperature is affected in ramp mode which is close to the natural condition. The experiment should predecide the temperature schedule carefully so as to simulate the environmental condition of the crop. Care should be observed in the following two respects.

- (i) The top of the telensair should be positioned at the tip of plants so that the air sample closely represents the temperature of the plant canopy.
- (ii) Safety limits of high and low temperatures must be set for every new temperature program.

Humidity

The humidity gradients across the chamber are proportional to the temperature gradient in the chamber. It also depends on the airflow within the chamber. The unique floor design with a large number of vents ensures uniform airflow through the entire plant canopy. These vents also allow quick disposal of excess irrigation water, which may otherwise add to the RH unnecessarily. As in the case of temperature, the sample of air is collected through the telesair and taken to the sensor box where both, dry and wet bulb temperatures are measured. The values of both the temperatures are compared and converted into RH. It must be remembered that there are low and high limits of RH for the chambers to function satisfactorily. These limits are governed by lower dew point at 7°C and 29°C at the higher end. Any amounts within this restricted domain of psychrometric chart can be accomplished without any measures. High or low humidity may be obtained but the chamber has to be programmed within the specified domain of dry and wet bulb temperatures. It is very important that wet wick is clean and always wrapped around the thermometer bulb, otherwise erroneous indications and control of RH will occur.

Carbon dioxide

For CO₂ specific studies, however, a few chambers of the NPF have been provided with CO₂ additive facility. A separate controller has been installed in such chambers to analyze the air sample taken from within the plant canopy. Whenever gas addition is required, the micro-processor activates a solenoid installed on the CO₂ cylinder to inject required amount of CO₂ into the chamber. Elevated levels of CO₂, especially at night-time, are removed passively by exhausting it to the exterior through vents.

Master control system

In addition to the microprocessor provided on each chamber to control the operation of chamber, a master host computer has also been connected to each chamber for remote control. The host computer contains two types of software. The first type is called the operating system to process signals and transmit necessary commands to the machine. The second type consists of application programs to do works like, spreadsheets word processing, data logging, storing and retrieving the operating history, etc. The software is designed as a multi-tasking and multi-user operating system. Every user can be given a password to access information. The operating histories of all the concurrent experiments can be stored in compressed form and retrieved whenever required.

3.3 PLANT CULTURE

3.3.1 Open top chambers and Free Air Carbon dioxide Enrichment

Seeds of rice varieties were sown in the nursery. Seedlings were hand-transplanted 20 days after sowing in the fields of FACE and OTC. The field was prepared by hoeing. Farm yard manure (FYM) was applied at the rate of 5 tonnes/ha during the time of field preparation. Hills and rows were 20 cm apart respectively. Nitrogen, phosphorus and potassium nutrients were applied at the rate of 100:40:40 kg/ha in the form of urea, single super phosphate and potash respectively. Nitrogen applied in 3 split doses, with the application of 50% as basal dressing, 25 per cent at mid-tillering stage and the remaining 25 per cent at panicle-initiation stage. Fields were flooded to 5 cm above the soil surface throughout the season with the exception of 10 days before harvest. Manual weeding was done to remove the weeds. There were two open top chambers with ambient

concentration of CO₂ and in rest of the two chambers, the level of CO₂ was increased exogenously to 550±15 µmol mol⁻¹.

In the FACE experiment CO₂ was maintained as follows:

- (a) Ambient carbon dioxide condition which was 60 meters away from the FACE ring (370 µmol mol⁻¹)
- (b) Elevated carbon dioxide conditions in the FACE ring (550 µmol mol⁻¹).

The randomized block design was adopted for the OTC and FACE studies.

3.3.2 Phytotron

In the Phytotron experiment, seeds were sown in trays containing 100% peat soil (decomposed coir pith). Deionized watering was done daily in the trays until the emergence of second leaf (i.e., upto 10 days of sowing). For the next 10 days half the strength of Hoagland's solution was given daily as nutrient solution. Seedlings were transplanted after 20 days to the pots (8 inch) containing the peat soil. Area inside the plant growth chamber was 36 sq.ft. and 45 number of 8 inch pots were placed. All the nutrients required by the rice crop were present in trace amounts in the peat soil. The peat soil also had a good water holding capacity and it gave full support for the roots to spread.

Full strength Hoagland's solution containing nutrients were given daily to the transplanted plants upto maturity. Deionized water was used to wash out toxic elements.

The Hoagland's solution used in Phytotron experiment consisted of following chemicals.

Chemicals	mg/litres
$\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$	950
$(\text{NH}_4)_2\text{H}_2\text{PO}_4$	120
KNO_3	610
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	490
H_3BO_3	0.6
$\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$	0.4
$\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$	0.09
$\text{CuSO}_4 \cdot 5\text{H}_2\text{O}^*$	0.05
H_2MoO_4	0.02
$\text{Co}(\text{NO}_3)_2 \cdot 6\text{H}_2\text{O}$	0.025
$\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$	24.8
NaOH	6.6
EDTA	33.2

(*Keeping in view of the deficiency symptom, double the dose. Maintain the pH between 5.3-5.5)

Climatic conditions inside the plant growth chamber was similar to that of the natural environment. The RH maintained in the chamber was 70 per cent with the following light intensity schedule.

Time	Level of light	Light intensity
0800 hrs.	10	5 klux
1000 hrs.	30	15 klux
1200 hrs.	50	27 klux

1400 hrs.	60	33 klux
1500 hrs.	50	27 klux
1600 hrs.	40	21 klux
1800 hrs.	11	5.2 klux
1900 – 0000 hrs.	10	5 klux
0000 – 0800 hrs.	No light	

Thus, a total 16 hour photoperiod was given to the plants. The level of light was maintained with tube lights and incandescent bulbs. Temperature and the carbon dioxide concentrations were maintained in the chamber as follows.

- Ambient CO₂ concentration (370 $\mu\text{mol mol}^{-1}$) with ambient temperature (31/24°C)
- Ambient CO₂ concentration (370 $\mu\text{mol mol}^{-1}$) with elevated temperature (35/28°C)
- Elevated CO₂ concentration (550 $\pm$ 15 $\mu\text{mol mol}^{-1}$) with ambient temperature (31/24°C)
- Elevated CO₂ concentration (550 $\pm$ 15 $\mu\text{mol mol}^{-1}$) with elevated temperature (35/28°C)

The plants were sprayed with 0.2 per cent Metasystox (0.25 EC) or Cascade to control the green aphids. The statistical design adopted for the Phytotron study was completely factorial randomized block design.

3.4 OBSERVATIONS RECORDED

Following observations were recorded at the vegetative, heading and ripening stages of the crop.

Pusa RH-10: Vegetative (45 DAS), heading (70 DAS) & ripening (90 DAS)

Pusa Sugandh-2: Vegetative (50 DAS), heading (75 DAS) & ripening (95 DAS)

All the observations were taken using three replicates for each treatment.

3.4.1 Plant growth

3.4.1.1 Plant height

Height of plant was measured with the help of a meter scale from the base of plant to the apex of main axis and was recorded in centimeters (cms).

3.4.1.2 Number of tillers

Number of tillers for sample plants were counted at the vegetative, heading and ripening stages and average number of tillers per hill was computed.

3.4.1.3 Number of leaves

The number of leaves per plant was recorded at vegetative, heading and ripening stages of growth. Physiologically mature and active leaves were considered for counting.

3.4.1.4 Leaf area

The leaves were separated from the stem and cleaned with tissue paper. The area of fresh green leaves for each treatment was measured using leaf area meter (Model LICOR 3000, USA) and was expressed in $\text{cm}^2 \text{ plant}^{-1}$.

3.4.1.5 Root length

Roots were dug out at different stages of growth according to method of Sirohi *et al.* (1978). Soil was separated from roots by gentle washing. They were further washed over a fine sieve. The length of the root was measured from shoot demarcation point to root tip by meter scale and expressed in cm plant⁻¹.

3.4.2 Growth analysis

3.4.2.1 Leaf Area Index (LAI)

Leaf area index (LAI) was calculated at vegetative, heading and ripening stages using formula suggested by Evans (1972).

Leaf area index expresses the ratio of leaf surface (one side only) to the ground area occupied by the plant.

$$LAI = \frac{\text{Total leaf area}}{\text{Ground area}}$$

3.4.2.2 Specific Leaf Area (SLA)

Specific leaf area was calculated as leaf area per unit of dry matter and was expressed as cm²g⁻¹.

$$SLA = [(A_2/LW_2) + (A_1/LW_1)]/2$$

Where, A₁ and A₂ were leaf area and LW₁ and LW₂ were dry weight of leaf.

3.4.2.3 Specific Leaf Weight (SLW)

SLW denote leaf dry weight per unit leaf area and was expressed as g cm⁻².

$$SLW = [LW_2/A_2 + LW_1/A_1]/2$$

Where, A_1 and A_2 were leaf area and LW_1 and LW_2 were dry weight of leaf.

3.4.2.4 Net Assimilation Rate (NAR)

It is the measurement of average photosynthetic efficiency and calculation was based on increase in dry weight of plant per unit leaf area per unit time and expressed as $gcm^{-2}day^{-1}$. NAR was calculated using following formula.

$$NAR = (W_2 - W_1 / A_2 - A_1) (\ln A_2 - \ln A_1) / t_2 - t_1$$

Where, W_1 and W_2 were total dry weight of plant and A_1 and A_2 were leaf area for time t_1 and t_2 , respectively (Radford, 1967).

3.4.2.5 Crop Growth Rate (CGR)

CGR was measured by harvesting (sampling) a crop community at frequent intervals and calculating the increase in dry weight from one sample to the next. It represented dry weight gained per unit area of crop in a unit time and expressed as $gm^{-2} day^{-1}$.

$$CGR = W_2 - W_1 / (t_2 - t_1) GA$$

Where, W_1 and W_2 were total dry weight of plant for time t_1 and t_2 , respectively and GA was ground area (Radford, 1967).

3.4.3 Total dry matter

Plants were separated into root, stem, leaves and panicles at different stages of growth. Samples were dried in an oven at $70^{\circ}C$ for 48 hrs (Baker *et al.*, 1990) till constant weight was acquired. Dry mass of plant parts was measured subsequently the dry matter distribution was studied (Gardner *et al.*, 1985).

3.4.4 Phenology

Days to maximum tillering and flower initiation were determined on five tagged plants of five separate hills and daily measurements were made (Imai *et al.*, 1985).

3.4.5 Gas-exchange parameters

Fully expanded uppermost leaf of main shoot was used for measuring the gas exchange parameters at different stages of growth. The measurement was done on clear sunny days between 1000 to 1200 hrs, when photosynthetically active radiation (PAR) ranged between 900-1500 $\mu\text{E m}^{-2}\text{s}^{-1}$.

3.4.5.1 Photosynthesis

The rate of photosynthesis was measured on leaves using a portable Infrared Gas Analyzer (IRGA, LI-COR-6200, Lincoln, Nebraska, USA). Infrared gas analysis of CO_2 is the method of determining CO_2 concentration for the measurement of photosynthesis and respiration in plants.

Operation

The target leaf was inserted in the leaf chamber facing the sun. The vapour pressure was monitored on the display board after inserting the leaf, and flow rate was adjusted till a constant rate was obtained. The incident photon flux density was monitored from the quantum sensor mounted on the leaf chamber. Assimilation by the enclosed leaf area caused a depletion of CO_2 concentration inside the chamber and this depletion was measured for three consecutive times of 10 seconds each. Based on the CO_2 depletion and other factors such as temperature, pressure and volume of the enclosure, the rate of photosynthesis was

computed by the inbuilt microcomputer of the IRGA, which was expressed in $\mu\text{mol m}^{-2}\text{s}^{-1}$.

The expression used in calculating photosynthesis in IRGA is:

$$A = \frac{Fd - eC}{100 SP} - \frac{P G V_t}{8.314 (T_a + 273) S} - \frac{\partial C}{\partial t} - CEG$$

T_a = Chamber air temperature (C), C = CO_2 concentration (μLL^{-1}) Fd = Flow through desiccant ($\mu\text{mol s}^{-1}$), e = vapour pressure in chamber (mb), $\partial C / \partial t$ = Rate of CO_2 Change ($\mu\text{LL}^{-1}\text{s}^{-1}$), E = Transpiration rate ($\text{mol}^{-2}\text{s}^{-1}$), A = Photosynthetic rate ($\mu\text{mol m}^{-2}\text{s}^{-1}$), P = Atmospheric pressure (mb), S = Leaf area (cm^2), V_t = Total volume (cm^3).

3.4.5.2 Respiration

The respiration was measured following the method of Amthor (1994) using IRGA (LICOR-6200). The leaf chamber with the target leaf was covered for 10 minutes to avoid any penetration of radiant energy. The rate of respiration in terms of efflux of CO_2 concentration was recorded and expressed as $\mu\text{mol m}^{-2}\text{s}^{-1}$.

3.4.5.3 Stomatal conductance

The stomatal conductance was measured following the method of Centritto *et al.* (1999) using IRGA (LICOR-6200). The stomatal conductance was expressed as $\text{mol m}^{-2}\text{s}^{-1}$.

3.4.6 Chlorophyll content

Leaf chlorophyll was extracted by non-maceration method using Dimethyl Sulphoxide (DMSO) (Hiscox and Israelstam, 1979) and light absorption at 663 nm and 645 nm was read in a spectrophotometer. The amount of chlorophyll content was calculated using absorption coefficients.

The fresh leaf material (0.5 g) in a test tube containing 5 ml of DMSO was kept in an oven at 65°C for about 4 hours. Chlorophyll was extracted in a test tube and the volume was made 10 ml by using DMSO. The OD of the extract was read at 663 nm and 645 nm using spectrophotometer (Model: GS570155, EC India Ltd). The chlorophyll content was determined by the formula as suggested by Arnon (1949) and expressed as mg g⁻¹ leaf fresh weight.

$$\text{Chlorophyll 'a'} = \frac{[12.7(D_{663}) - 2.69 (D_{645})] \times V}{1000 \times W}$$

$$\text{Chlorophyll 'b'} = \frac{[22.9(D_{645}) - 4.68 (D_{663})] \times V}{1000 \times W}$$

$$\text{Total Chlorophyll} = \frac{[22.2(D_{645}) + 8.02 (D_{663})] \times V}{1000 \times W}$$

Where, D = Optical density; V = Final volume of the DMSO; W = Weight of the leaf sample

3.4.7 Carbohydrates

Extraction of sugars

Sample extraction for estimation of sugar was done according to method reported by McCready *et al.* (1950). The sampling was done on sunny day at about 1100 hrs. Fresh samples of leaves (1.0 g), stem (1.5 g) and panicle (1.0 g) were used for the extraction of sugar. Similar samples were oven dried at 80°C to constant weight for dry weight determination. Fresh samples of leaves (1.0 g), stem (1.5 g) and panicle (1.0 g) were boiled in 20 ml of 80 per cent (v/v) ethanol in a water bath

for 5 minutes. The extract was decanted in a beaker. This ethanol extraction was repeated for 3 more times followed by a final boiling with 20 ml of distilled water for the same time and the supernatant was decanted. The combined extract was made up to volume with distilled water in a 100 ml volumetric flask.

Clarification of sugar extract

Fifty milliliter of aliquot of the extract was evaporated in a water bath so that the liquid did not dry out completely. Subsequently, 1 ml of lead acetate was added to precipitate the colloidal substance. It was then filtered into a beaker and 3 ml of disodium hydrogen phosphate was added and made up to required volume. This aliquot was used for determining the reducing sugar by Nelson's arsenomolybdate method (Nelson, 1944).

Reagents

- i. **Arsenomolybdate colour reagent** : Twenty-five grams of ammonium molybdate $[(\text{NH}_4)_6\text{MO}_{24}\cdot 4\text{H}_2\text{O}]$ was dissolved in 45 ml of distilled water and 21 ml of concentrated H_2SO_4 was added to it and mixed. An aqueous solution of sodium arsenate ($\text{Na}_2\text{HASO}_4\cdot 7\text{H}_2\text{O}$; 3 g/25 ml) was added and mixed with the above solution and subsequently placed in an incubator at 37°C for 48 hrs.
- ii. **Alkaline copper tartarate (Somogyi's) reagent** : Twenty-four grams of anhydrous sodium carbonate and 12 g of Rochelle salt (Sodium Potassium tartarate) were dissolved in 250 ml of distilled water in a beaker. To this solution, 40 ml of 10 per cent solution, of copper sulphate was added with continuous stirring. This was

followed by the addition of 16 g of sodium bicarbonate. In another beaker, 18 g of sodium sulphate was dissolved in 500 ml of hot water and boiled to expel air. After cooling, both these solutions were mixed and diluted to make the volume to 1000 ml.

- iii. **Standard stock glucose solution :** Hundred milligram of glucose was dissolved in 100 ml distilled water. Working standards were prepared by diluting the stock solution with distilled water (100 $\mu\text{g/ml}$).

(a) Reducing sugars

One milliliter of the aliquot was taken in test tube and made to a uniform volume of 2 ml with distilled water. It was then mixed with 1.0 ml of Somogyi's copper reagent and heated in boiling water bath for 12 minutes and then cooled in running tap water. One ml of arsenomolybdate reagent was added to it and volume was made upto 10 ml. Absorbance was recorded in a spectrophotometer (Model : GS570155, EC India Ltd.) at a wavelength of 530 nm. A blank and two freshly prepared glucose standards were also included with each set of samples. The sugar content was calculated from a standard curve drawn from freshly prepared glucose solutions and expressed in mg g^{-1} DW.

(b) Total sugar

Five milliliter of extract was hydrolyzed by boiling with half volume of 0.5 N HCl in water bath for 30 min and neutralized at slightly acidic side with NaOH (0.5 N). The neutralized extract was made to 10 ml. This solution was used for determining the total sugar. An aliquot of this was analyzed for sugar following the same procedure as described for reducing sugar and expressed in mg g^{-1} DW.

(c) Non-reducing sugar

The reducing sugar was subtracted from the total sugar to obtain the non-reducing sugar content and was expressed in mg g^{-1} DW.

(d) Starch

Starch content was determined by Anthrone method (Mcready *et al.*, 1950). The dry residue left after sugar extraction was powdered and a known amount of it was hydrolyzed by boiling with 10 ml of 1 N HCl in a glycerin bath at $112\text{--}115^{\circ}\text{C}$ for 30 minutes. The residue was repeatedly washed with distilled water until a negative test of starch by iodine was obtained. The extract was collected and the final volume was made up to 100 ml. An aliquot (0.5–1.0 ml) of the above extract was made to uniform volume of 2.5 ml with distilled water. It was then mixed thoroughly with 10 ml of freshly prepared anthrone reagent (100 mg of anthrone in 100 ml of chilled concentrated sulphuric acid) in a cold water bath. The tubes were then kept in a boiling water bath for 15 minutes and cooled in running tap water. Absorbance was measured at 620 nm in a spectrophotometer (Model : GS570155, EC India Ltd.). A blank and two freshly prepared glucose standards were also included with each set of samples. Starch content was calculated by multiplying the glucose values by 0.9 (Pucher *et al.*, 1948) and expressed in mg g^{-1} DW.

(f) Total non-structural carbohydrate

The total non-structural carbohydrate was computed by adding total soluble sugar and starch content (Allen *et al.*, 1988) and expressed in mg g^{-1} DW.

3.4.8 Carbon

Carbon content was estimated by wet digestion following the modified Walkley-Black method (Walkley and Black, 1934). The dried plant samples were oxidized with a mixture of potassium dichromate and concentrated sulphuric acid using heat of dilution of the acid. The unused potassium dichromate was estimated by back titration with ferrous ammonium sulphate.

Reagents

- i. **Standard potassium dichromate solution (1N)** : 49.04 g of AR grade potassium dichromate ($K_2Cr_2O_7$) (dried at $105^\circ C$ for 2 hrs) was dissolved in distilled water and diluted to 1000 ml in a volumetric flask.
- ii. **Ferrous ammonium sulphate solution (0.5 N)** : 196.1 g of AR grade ferrous ammonium sulphate [$FeSO_4(NH_4)_2SO_4 \cdot 6H_2O$] was dissolved in about 800 ml of distilled water. A 20 ml of concentrated sulphuric acid (H_2SO_4) was added to it and then allowed to cool. The solution was diluted to 1000 ml in a volumetric flask.
- iii. **Diphenylamine indicator** : 0.5 g of diphenylamine [$(C_6H_5)_2NH$] was dissolved in a mixture of 20 ml distilled water and 100 ml concentrated H_2SO_4 (specific gravity 1.84 and concentration >96%) and was stored in amber coloured bottle.
- iv. **Orthophosphoric acid (85% v/v)** : Orthophosphoric acid (H_3PO_3) reagent was prepared by diluting it in distilled water.

Carbon content in plant parts was estimated using powdered plant material. Fifty milligram of plant sample was placed in a dry 500 ml conical

flask. Ten milliliter of $K_2Cr_2O_7$ solution was added to it. Flask was gently swirled and 20 ml of concentrated sulphuric acid was rapidly added to it followed by immediate swirling so that the sample and the reagent were mixed. The flask was swirled several times and allowed to stand for 30 min. This was followed by addition of 200 ml of distilled water and 10 ml of orthophosphoric acid. After adding 1 ml of diphenylamine indicator solution, the content was titrated with ferrous ammonium sulphate solution till the colour flashes from bluish violet to green. A blank (without sample) titration was also carried out. The carbon content was calculated using following formula and expressed in percentage.

$$C\% = \frac{(X-Y) \times (\text{Normality of ferrous ammonium sulphate solution}) \times (0.003)}{A} \times 100$$

Where, A= weight of the sample, X= volume (ml) of ferrous ammonium sulphate solution required for blank titration, Y=volume (ml) of ferrous ammonium sulphate needed for the sample. The carbon percentage was obtained by multiplying this C % with a constant, 1.3, as only 77 per cent recovery was presumed from oxidation of sample in this procedure (Rao, 1993).

3.4.9 Nitrogen

Nitrogen content in plant parts was measured by Kjeltac Auto 1028 Analyzer. The dried plant material was digested with concentrated H_2SO_4 in the presence of catalyst to convert the nitrogen to ammonium sulphate. Ammonia was liberated and collected in boric acid solution as ammonium borate by steam distillation of the salt in the presence of a strong alkali which is estimated against a standard acid titration

Digestion

The dried samples were ground to powdery form. Hundred milligram of sample was transferred to different digestion tubes. To this tube, 10 ml of concentrated sulfuric acid was added. One Kjeltab (containing 3.5 g K_2SO_4 + 12.48 mg $CuSO_4 \cdot 5H_2O$) was added to the digestion tube. An assembly of 20 digestion tubes were put in digestion block and covered with fume hood. The digestion temperature was raised to $400^{\circ}C$ till the samples turned turquoise (about 1 hr). The digestion tubes were removed and allowed to cool for 5-10 minutes. About 50 ml of distilled water was added and mixed well.

Preparation of reagents (Tecator, 1985)

- i. **40% NaOH** : 40 g of sodium hydroxide (NaOH) was dissolved in 100 ml of water.
- ii. **Receiving solution** : Hundred gram of H_3BO_3 was dissolved in 10 litres of distilled water. To this, 100 ml bromocresol green solution (100 mg in 100 ml methanol) and 70 ml methyl red solution (100 mg in 100 ml methanol) was added. Finally 5 ml of 40% NaOH was added and the pH adjusted to 4.5.
- iii. **Standard acid (0.1 M HCl)** : HCl was standardized by titration against a solution of sodium carbonate (Na_2CO_3). 400 mg (W_1) of oven dried Na_2CO_3 was transferred to a conical flask. It was dissolved in 40 ml of distilled water and 10 drops of methyl red indicator solution (100 mg per 100 ml ethanol) was added. The solution was titrated to pink colour with HCl and the volume of HCl used (A_2) was noted. The solution was boiled for a few minutes and was cooled rapidly to room temperature under running tap

water. Titration was continued until the next pink colour change occurred. The ml of HCl used (A_2) was noted.

Calculation

$$\text{Molarity of HCl} = \frac{18.868 \times W_1}{(A_1 + A_2)}$$

Procedure

Calibration was done with ammonium iron (II) sulphate (mol. wt. 392.14), which contains 7.145 per cent, N. Distillation of 500 mg iron (II) sulphate and titration with standard HCl (0.1 M) was done and display value of (ml-blank) was noted. This value was compared with calculated (ml-blank) value for calibration.

$$\text{ml-blank (calculated)} = \frac{\% \text{ N} \times \text{g sample}}{\text{Molarity of HCl} \times 1.401}$$

Where, %N = 7.145 for ammonium iron (II) sulphate, g sample = 0.5 g,
Molarity of HCl = 0.1 M

The digested extract was made up 100 ml with distilled water. The tube was then fitted to the splash heat for distillation. The instrument was operated as per Tecator (1985) manual. When the distillation and titration cycle is over, the result is displayed on the front panel.

Percent N is calculated as

$$\% \text{N} = \frac{(V_{\text{sample}} - V_{\text{blank}}) \times M \times 1.401}{\text{g sample}}$$

Where, V_{sample} = the volume (ml) standard HCl for titration of the sample

V_{blank} = the volume (ml) standard HCl for titration of the sample

M = molarity of solution,

g sample = dry weight of sample

3.4.10 Leaf soluble protein

Leaf soluble protein was estimated by the method of Lowry *et al.* (1951).

Reagents

- i. **Solution A** : 2% sodium carbonate in 0.1 N sodium hydroxide solution.
- ii. **Solution B** : Prepared just prior to its use by mixing equal volume of a) 1% copper sulphate solution and b) 2% sodium potassium tartarate (Rochelle salt).
- iii. **Alkaline cupric tartarate solution (Lowry's reagent)** : Prepared just prior to use by mixing solution A and solution B in 50 : 1 ratio.
- iv. **Folin-ciocalteu reagent (1N)**

Fresh leaf material was cut into small pieces (10 mm). The representative sample (0.5 g) was extracted with 5 ml of 0.1 M phosphate buffer pH 7.5 using pestle and mortar at 4°C and centrifuged for 15 minutes in 10,000 g at 4°C. The supernatant was decanted and equal amount of 15 per cent of fresh trichloro acetic acid (TCA) was added. This solution was kept overnight at room temperature and centrifuged at 3,000 g for 10 minutes. Supernatant was removed by aspiration and pellets were dissolved in 0.1N NaOH and used for protein analysis.

The reaction mixture for protein estimation comprised of 0.5 ml extract, 0.5 ml water, 5 ml of Lowry's reagent and 0.5 ml of 1.0 N Folin

reagent. This assay mixture was mixed well by vortexing and kept in dark for 30 minutes before measurements were made. The absorbance was read at 660 nm Vs. prepared blank. The protein content in the samples was calculated and results were expressed as mg protein g⁻¹ FW by calibration through standard BSA protein.

3.4.11 Enzymes

Sampling for enzymes

Uppermost fully expanded leaves were detached from five different plants from each treatment at different stages of growth before 12.00 noon when solar PPFD-500 $\mu\text{mol m}^{-2}\text{s}^{-1}$. The biochemical analysis was carried using three replications for each observations. Samples were quickly immersed in ice bucket for enzymatic study and 4°C temperature was maintained throughout the estimation. Following enzymes were assayed and the activity was measured at vegetative, heading and ripening stages.

3.4.11.1 Superoxide dismutase (SOD; EC 1.15.1.1)

The superoxide dismutase (SOD; EC1.15.1.1) activity was determined spectrophotometrically by measuring the inhibition of blue diformazone formation in the presence of riboflavin/nitro-blue tetrazolium (NBT) and light (Beauchamp and Fridovich, 1971).

Reagent

- i. Methionine solution (200 mM)
- ii. Riboflavin solution (75 μM)
- iii. Nitro-blue tetrazolium solution (1.125 mM)
- iv. EDTA disodium solution (1.5 mM)

- v. Phosphate buffer (50 mM; pH 7.0)
- vi. Phosphate buffer (50 mM; pH 7.8)

Enzyme extraction

Leaf sample weighing 500 mg was homogenized in ice-cold 50 mM phosphate buffer (pH 7.0) containing 0.5 mM EDTA in a pre-chilled pestle and mortar. The homogenate was centrifuged at 4°C for 30 minutes at 30,000 g. The supernatant was transferred to another tube and used as enzyme extract.

Assay

The assay solution consisted of 0.2 ml methionine (200 mM), 0.2 ml NBT (2.25 mM), 0.2 ml EDTA (1.5 mM), 40 µl enzyme extract, 2.19 ml phosphate buffer at pH 7.8, and 0.2 ml Riboflavin (75 µM). Riboflavin was added as the last component. Tubes were shaken and placed 30 cm below a light source, consisting of two 15 W fluorescent tubes. The reaction was started by switching on the light and was allowed to run for 10 min. Light was switched off after 10 min to stop the reaction. The tubes were covered with black cloth immediately after switching off the light. A non-irradiated reaction mixture containing enzyme extract, which did not develop colour, was used as control. Blanks were lacking enzyme in reaction mixture and developed maximum colour. The absorbance of the reaction mixture was read at 560 nm. The volume of the enzyme extract producing 50 per cent inhibition of the reaction was read from the resultant graph. Activity is expressed as unit min⁻¹ mg⁻¹ protein. One unit of SOD activity was defined as the amount of enzyme that inhibited the reaction by 50% (Beauchamp and Fridovich, 1971).

3.4.11.2 Ascorbate peroxidase (APX, EC 1.11.1.11)

Ascorbate peroxidase activity was measured by a modified spectrophotometric procedure based on the rate of decrease in absorption of ascorbate at 290 nm during ascorbate oxidation (Dalton *et al.*, 1986).

Reagent

- i. 50 mM $\text{KH}_2\text{PO}_4/\text{K}_2\text{HPO}_4$ (pH 7.0)
- ii. 0.5 mM EDTA
- iii. 250 μM ascorbate
- iv. 1.5 mM H_2O_2

Enzyme extraction

Leaf sample weighing 500 mg was homogenized in ice-cold 50 mM phosphates buffer (pH 7.0) containing 0.5 mM EDTA in a pre-chilled pestle and mortar. The homogenate was centrifuged at 30,000 g in 4°C for 30 minutes. The supernatant was transferred to another tube and used as enzyme extract.

Assay

The assay was performed in a 1 ml cuvette containing 250 μM ascorbate, 50 mM $\text{KH}_2\text{PO}_4/\text{K}_2\text{HPO}_4$ (pH 7.0) and 0.50 EDTA, 1.5 mM H_2O_2 and 100 μL enzyme extract. The rate of decrease in absorption of ascorbate at 290 nm during ascorbate oxidation recorded spectrophotometrically and enzyme activity was expressed as $\mu\text{mol min}^{-1} \text{g}^{-1}$.

3.4.11.3 Glutathione reductase (GR, EC 1.6.4.2)

Glutathione reductase activity was measured by a spectrophotometric

procedure based on the rate of increase in absorbance at 412 nm in presence of substrate, oxidized glutathione (GSSG) following the method of Smith *et al.* (1988).

Reagent

- i. 0.1 M potassium phosphate buffer (pH 7.5)
- ii. 0.2 M potassium phosphate buffer (pH 7.5)
- iii. 0.5 mM EDTA]
- iv. 1 mM EDTA
- v. 3M DTNB
- vi. 2 mM NADPH
- vii. 20 mM GSSG (oxidized glutathione)

Enzyme extraction

Leaf sample weighing 500 mg was macerated in 10 ml of 0.1 M potassium phosphate buffer (pH 7.5) containing 0.05 mM EDTA and filtered through cheese cloth. The filtrate was centrifuged for 15 minutes at 15, 000 g. Supernatant was collected and used as enzyme extract.

Assay

The assay mixture comprised of 0.5 ml of 3 M DNTB (5,5-dithiobis-2-nitrobenzoic acid) prepared in phosphate buffer (pH 7.5), 1.0 ml of 0.2 M potassium phosphate buffer pH 7.5 containing 1 mM EDTA), 0.2 ml of 2 mM NADPH and 0.2 ml of enzyme extract and final volume was made to 2.9 ml with distilled water. The increase in absorbance at 412 nm was measured immediately after adding GSSG over a period of 10 minutes

with an interval of 1 minute. Glutathione reductase activity was expressed as $\Delta OD_{412} \text{ nm min}^{-1} \text{ mg}^{-1} \text{ protein}$.

3.4.11.4 Sucrose phosphate synthase (SPS)

SPS activity was measured by the method of Huber and Huber (1992). Leaf extracts were prepared by grinding the liquid N_2 frozen tissue in a pre-cooled mortar. The tissue-to-buffer ratio was 1:7, and the buffer contained 50 mM Hepes, 4 mM $MgCl_2$, 1 mM EDTA, 1% PVP-40 (polyvinyl pyrrolidone), 0.01% triton X-100, 1 mM PMSF (phenylmethyl sulfonyl fluoride), 1 mM Na_2MoO_4 , 10 μM leupetin and 5 mM DTT (dithiothreitol) at pH 7.5. The extract was centrifuged at 12000 g for 90s at 4°C. the supernatant was rapidly desalted on a Sephadex G-25 column equilibrated with extraction buffer at 4°C, and assayed immediately.

The assay conditions were optimized for the rice cultivar used in this study (Hussain, 1992). Incubate 100 μl of desalted enzyme extract with 12 mM UDP-Glc, 4 mM Fru-6-P, 20 mM Glc-6-P, 50 mM Hepes-NaOH, 4 mM $MgCl_2$, 1 mM EDTA, 1 mM $NaMoO_4$, 5 mM DTT at pH 7.5 in a final volume of 200 μl . The incubation temperature was 30°C and the reaction was terminated after 15 min with 150 μl of 1.2 N NaOH. Unreacted Fru-6-P was degraded by placing the tubes in boiling water for 10 min. After cooling, 0.25 mL of 0.1% (v/v) resorcinol in 95% (v/v) ethanol and 0.75 mL of 9 N HCl were added, and the tubes were incubated at 80°C for 8 min. Tubes were cooled, and the absorbance at 520 nm was determined as a measure of sucrose and sucrose-P production. The enzyme activity was expressed as $\mu\text{mole of sucrose synthesized mg}^{-1} \text{ protein min}^{-1}$.

3.4.11.5 Nitrate reductase activity (NR) (*in vivo* assay)

NR activity in the leaves at different stages was estimated by the method of Evans and Nason (1953).

Reagents

- i. **Potassium nitrate solution, 0.2 M** : 2.02 g of potassium nitrate (mol wt. 101) free from nitrite was dissolved in 100 ml distilled water.
- ii. **Phosphate buffer, 0.2 pH 7.5** : 4.35 g KH_2PO_4 (mol wt. 136) and 29.23 g K_2HPO_4 (mol wt. 174) was dissolved in 500 ml water and made up the volume to one litre. Prepared (a) KH_2PO_4 , 0.2 M: 27.2 g KH_2PO_4 in 1 litre water; (b) K_2HPO_4 , 0.2 M: 34.8 g K_2HPO_4 was dissolved in one litre water. Mix (a) and (b) in the ratio of 16:84, respectively. Adjust the pH to 7.5.
- iii. **n-Propanol**
- iv. **Sulphanilamide solution (Reagent A)** : 1% w/v in 1N HCl.
- v. **N(1-naphthyl) ethylene diamine dihydrochloride (Reagent B)**: 0.02% w/v in distilled water.

Leaves are sliced to 8-10 mm in diameter. After thorough mixing, representative sample weighing 200-500 mg was placed in culture tube of 30 ml capacity containing ice-cold incubation medium consisting of 3 ml each of phosphate buffer (0.2 M, pH 7.5) and potassium nitrate solution (0.2 M). Add 0.2 ml of n-propanol to each tube to facilitate the penetration of substrate into the plant tissues. Remove the tubes from ice bath and evacuate (infiltrate) them with the help of vacuum pump for about 1-2 min, until all the cut materials sink below the surface of incubation medium.

After infiltration, tubes are incubated in metabolic water-bath maintained at 30°C for 30 min in dark. Terminate the reaction by keeping the tubes in boiling water for 2 min. It will help in leaching out of nitrite formed in the plant tissue into the incubation medium. Cool the tubes at room temperature. Nitrite formed by the catalytic action of the enzyme NR, is then estimated colorimetrically by Snell and Snell's (1949) method. To estimate nitrate content, take 0.2 ml of suitable aliquot from the tube 1 ml of sulphanilamide solution. After shaking the tube, 1 ml of NEDD solution is added and mixed well. A pink colour was formed immediately. The pink colour was allowed to develop for 20 minutes, after which volume was made upto 6 ml with distilled water. The absorbance of pink colour is read at 540 nm using spectro-photometer. By using the standard curve, the nitrate content in the sample is calculated.

The *in vivo* activity of NR is expressed as $\mu\text{moles NO}_3^-$ reduced (or NO_2^- formed) g^{-1} fr. wt. of tissue hr^{-1} .

3.4.12 Yield and yield components

Plants were destructively sampled at the time of harvest. Panicles per plant were separated for each replication. Number of panicles per plant was determined by counting the total number of panicles per plant for each replication and the mean values were recorded. Panicle length for each replication was measured using a meter scale and the mean values were recorded and expressed in terms of cm plant^{-1} .

At the time of harvest, plant sampling was done for 1m^2 area in the fields of OTC and FACE. In the plant growth chambers, 30 plants were sampled from each chamber at the time of harvest. Grain yield, number of grains per panicle and 1000-grain mass were determined after oven

drying (70°C for 48 hrs.) and threshing each panicle. In Phytotron, the grain yield per plant was determined. Harvest index (HI) was then calculated as the ratio of grain yield per plant to the shoot biomass per plant (Baker *et al.*, 1990).

3.4.13 Grain quality

The effect of elevated CO₂ and the interactive effect of temperature and high CO₂ on the chemical composition of rice grain was studied. Following nutrient constituents were analysed.

1. **Reducing sugars** in the grain was determined by the method of Nelson (1944).
2. **Non-reducing sugars** in the grain was measured using the method of McCready *et al.* (1950).
3. McCready's *et al.* (1950) method was used for estimating the **total sugar** content in the grain.
4. **Starch content** was estimated by Anthrone method (McCready *et al.*, 1950).
5. **Amylose** : The amylose content in the grain was determined by the method of McCready *et al.* (1950).

Reagents

1. 1N NaOH
2. 0.1% phenolphthalein indicator
3. Distilled ethanol
4. Iodine reagent : Dissolved 1g of iodine and 10 g of KI in distilled water and made up to 500 ml in a volumetric flask. It was covered

with black cloth.

6. **Standard amylose** : 100 mg amylose in 10 ml of 1N NaOH and made up to 100 ml with water (1 mg/ml)

Procedure

One ml of distilled ethanol was added to 100 mg of powdered sample and mixed it thoroughly. Ten ml of 1N NaOH was added to this mixture and was left over night. The volume was made up to 100 ml. About 20 ml of distilled water and 3 drops of phenolphthalein indicator was added to 2.5 ml of the extract and mixed well. HCl (0.1 N) was added drop by drop until the pink colour disappeared. Then 1 ml of iodine reagent was added and the volume was made upto 50 ml. The absorbance was read at 590 nm. The amount of amylose (range 0.2-1.0 mg) was calculated against a blank for which 1 ml of iodine reagent was diluted to 50 ml with distilled water.

7. **Total non-structural carbohydrate content** in the grain was calculated by adding total soluble sugar and total starch content (Allen *et al.*, 1988).
8. **Nitrogen content** in the grain was estimated by the method of Tecator (1985).
9. **The protein content** was calculated by multiplying the nitrogen content of the grain by 5.95 (Takecheu, 1966).
10. **Total potassium:** Potassium content of the grains was determined by tri-acid digestion using a flame photometer (Jackson, 1962).

Reagents

1. **1000 ppm K solution:** About 1.907 g AR grade potassium chloride

was dissolved in 200 ml of distilled water and the volume was made up to one litre with distilled water.

2. **100 ppm K solution:** 100 ml of 1000 ppm K solution was taken in a volumetric flask and the volume was made up to 100 ml with distilled water.
3. **25 and 50 ppm K solutions:** 25 and 50 ml of 100 ppm K solution was taken in 100 ml flasks and the volume was made up to 100 ml with distilled water.

Procedure

A standard curve with 0, 25, 50, 100 ppm K solution was prepared by adjusting the flame photometer with 100 ppm solution. Fifty ml of tri-acid digest made for total P analysis (aliquot should be taken after warming up the digest) in a porcelain dish and it was evaporated to dryness on water bath. The sides of the dish was washed with water and again evaporated to dryness. The residue left out was dissolved in water and transferred to 100 ml volumetric flask and the volume was made up. The solution was positioned to the capillary of the flame photometer and the readings were noted as ppm of K. For samples low in K, tri-acid digest made for P analysis can be directly analysed.

$$\text{Per cent in plant material} = \text{ppm K in plant material} \times 10^{-4}$$

11. Calcium

Calcium content was measured by the method of Piper (1950).

A. Dry ashing

About 0.1 to 1 g of powdered grain material was taken in a silica

crucible and enough dilute alcoholic sulphuric acid solution was added drop by drop (1% v/v conc., H_2SO_4 solution in 95% ethanol) to moist the sample. The sample was ignited with the pipette (used for adding alcoholic sulphuric acid solution) torch to remove excess alcohol. After the flame subsidised, the crucible was transferred to a muffle furnace and ignited at 525°C for 45 minutes or longer till a grey-white ash free of carbon was obtained.

B. Extraction of Ca

About 5 ml of 2N HCl was added to the crucible and allowed to stand for 15 minutes and then the contents were transferred to a 100 ml volumetric flask and the volume was made up to 100 ml. The solution was then filtered.

Reagents

1. **0.01N standard Ca solution:** 0.5 g of calcium carbonate was weighed and dried at 150°C into 1 litre volumetric flask. About 200 ml of 1M HCl was added slowly and with shaking and made up the solution to 1 litre.
2. **0.01N EDTA solution:** About 0.7306 g EDTA was dissolved in about 200 ml distilled water and made up the volume to 1 litre.
3. **2% NaCN or KCN solution:** 20 g NaCN or KCN was dissolved in 1 litre of distilled water.
4. **Murexide indicator:** 0.2g Murexide (Ammonium purpurate) and 40 g potassium sulphate was mixed well.
5. **2N sodium hydroxide solution:** Dissolved 80 g Na OH in 200 ml water and made up to one litre.

Procedure

About 25 ml of the extract was transferred to a porcelain dish. Five drops of NaCl solution was added and mixed well with a policeman tipped glass rod and added 10 ml of 2N NaOH solution. After that a pinch of Murexide indicator was added and titrated with EDTA solution. When all Ca present was chelated by EDTA, the colour changed to purple.

Since the colour change took place slowly and the detection of end point was rather difficult, it was always better to keep a standard purple colour obtained by titrating standard Ca solution with EDTA solution of known strength. A blank was prepared and used for the experiment.

$$\% \text{ Ca in the plant sample} = \frac{\text{ml EDTA for sample - blank) } \times \text{Normality of EDTA} \times 20 \times 400}{\text{Sample weight in mg}}$$

3.4.14 Statistical analysis

Statistical analysis of data was done following the method of analysis variance (ANOVA) given by Panse and Sukhatme (1967). The critical difference (CD) values were calculated at 5 per cent probability level.

4. RESULTS

Studies on the response of two basmati rice varieties, Pusa RH-10 (PRH-10) (hybrid) and Pusa Sugandh-2 (PS-2) to elevated CO₂ were carried out using Open Top Chamber (OTC) and Free Air Carbon dioxide Enrichment (FACE) facilities at Indian Agricultural Research Institute, New Delhi during the rice crop seasons of 2002 and 2003. The interactive effect of elevated carbon dioxide (CO₂) and temperature was studied in the controlled plant growth chambers at the National Phytotron Facility, Indian Agricultural Research Institute, New Delhi. The growth, productivity, physiological and biochemical processes were studied at vegetative, heading and ripening stages in all the three experiments.

4.1 OPEN TOP CHAMBER (OTC) STUDIES

4.1.1 Plant growth

4.1.1.1 Plant height

Elevated CO₂ brought about significant increase in the height of the plant (Table 1). The increase ranged from 12% (heading) to 19% (ripening) in PRH-10 and from 16% (vegetative) to 19% (heading) in PS-2. The variety x CO₂ interaction was significant at the vegetative and heading stages. PS-2 had greater plant height than PRH-10 irrespective of the treatments.

4.1.1.2 Number of tillers

CO₂ enrichment brought about significant increase in the production of

Table 1. Effect of elevated CO₂ on the plant height (cm) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	56.36	60.94	80.92	85.92	89.62	99.01
Elevated CO ₂	64.12	70.93	90.67	102.74	106.72	115.72
CD at 5%						
Variety (V)		1.442		2.434		3.211
CO ₂		1.442		2.434		3.211
V x CO ₂		2.039		3.442		NS

Table 2. Effect of elevated CO₂ on the number of tillers of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	8.00	8.50	9.00	9.00	9.50	9.00
Elevated CO ₂	10.00	10.50	12.00	12.50	13.00	12.50
CD at 5%						
Variety (V)		NS		NS		NS
CO ₂		0.62		0.41		0.67
V x CO ₂		NS		NS		NS

tillers (Table 2). The increase was 25% (vegetative), 33% (heading) and 37% (ripening) in PRH-10 and in PS-2, it was 23%, 38% and 38%, respectively. The variety x CO₂ interaction was not significant. There was no significant difference between the varieties on the production of tillers.

4.1.1.3 Number of leaves

Elevated CO₂ significantly increased the number of leaves per plant in both the varieties (Table 3). The CO₂ induced increase in the production of leaves ranged from 25% (ripening) to 56% (vegetative) in PRH-10 whereas this enhancement was varied from 25% (ripening) to 48% (vegetative) in PS-2. The variety x CO₂ interaction was significant at vegetative and ripening stages. The leaf production was maximum at the vegetative stage. The number of leaves were more in PS-2 compared to PRH-10.

4.1.1.4 Leaf area

Elevated CO₂ significantly increased the leaf area in both the varieties (Table 4). This increase ranged from 13% (vegetative) to 29% (heading) in PRH-10 and from 18% (vegetative) to 36% (heading) in PS-2. The interaction of variety x CO₂ was significant at all the three stages. PS-2 variety had greater leaf area than PRH-10.

4.1.1.5 Root length

Elevated CO₂ treatment significantly increased the length of root in both the varieties (Table 5). The increase was more in PRH-10 (i.e. 32% at vegetative to 52% at heading) than PS-2 (i.e. 29% at ripening to 48% at vegetative). The variety x CO₂ interaction was significant throughout the growth period. The root length was greater in PS-2 compared to PRH-10 irrespective of treatments.

Table 3. Effect of elevated CO₂ on the number of leaves of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	24.92	32.69	40.38	50.00	53.00	61.00
Elevated CO ₂	38.83	48.32	57.32	63.80	66.38	76.00
CD at 5%						
Variety (V)	1.588		1.674		2.007	
CO ₂	1.588		1.674		2.007	
V x CO ₂	2.246		2.368		NS	

Table 4. Effect of elevated CO₂ on the leaf area (cm²) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	632.64	702.79	874.84	926.77	1074.81	1107.38
Elevated CO ₂	713.72	824.70	1129.82	1268.38	1326.82	1392.92
CD at 5%						
Variety (V)	20.05		44.90		52.14	
CO ₂	20.05		44.90		52.14	
V x CO ₂	28.36		63.51		73.74	

Table 5. Effect of elevated CO₂ on the root length (cm) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	4.35	4.92	8.24	10.82	11.36	12.57
Elevated CO ₂	5.73	7.29	12.56	15.32	15.38	16.24
CD at 5%						
Variety (V)		0.160		0.510		0.577
CO ₂		0.160		0.510		0.577
V x CO ₂		0.226		NS		NS

Table 6. Effect of elevated CO₂ on the leaf area index of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	1.58	1.76	2.19	2.32	2.69	2.77
Elevated CO ₂	1.78	2.06	2.82	3.17	3.32	3.48
CD at 5%						
Variety (V)		0.0714		0.0925		0.1038
CO ₂		0.0714		0.0925		0.1038
V x CO ₂		0.1010		0.1308		NS

4.1.2 Growth analysis

4.1.2.1 Leaf area index (LAI)

Higher CO₂ brought about significant increase in the leaf area index (Table 6). This increase ranged from 13% (vegetative) to 29% (heading) in PRH-10 and from 17% (vegetative) to 36% (heading) in PS-2. The interaction of variety and CO₂ was significant throughout the growth period. The maximum leaf area index was observed at the heading stage. PS-2 had higher leaf area index than that of PRH-10.

4.1.2.2 Specific leaf area (SLA)

A significant reduction in specific leaf area was observed at elevated CO₂ condition (Table 7). This reduction varied from 8% (vegetative) to 18% (ripening) in PRH-10 and from 12% (vegetative) to 13% (ripening) in PS-2. The interaction variety x CO₂ was found significant. Specific leaf area was maximum at the heading stage for PRH-10 and at vegetative stage for PS-2. The SLA was greater in PRH-10 at the heading and ripening stage compared to PS-2.

4.1.2.3 Specific leaf weight (SLW)

A significant increase in specific leaf weight was observed under high levels of CO₂ (Table 8). The increase ranged from 10% (vegetative) to 22% (heading and ripening) in PRH-10 and in case of PS-2, it was 4% (heading) to 15% (ripening). The interaction of variety and CO₂ on SLW was significant at the heading stage. Maximum specific leaf weight was observed in the ripening stage. The SLW was greater in PRH-10 than that of PS-2 at the vegetative stage.

Table 7. Effect of elevated CO₂ on the specific leaf area (cm² g⁻¹) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	112.57	147.34	127.71	97.86	94.61	82.39
Elevated CO ₂	103.29	129.67	105.39	94.23	77.50	71.54
CD at 5%	5.9469		3.7986		3.5107	
Variety (V)	5.9469		3.7986		3.5107	
CO ₂	8.4102		5.3720		4.9649	
V x CO ₂						

Table 8. Effect of elevated CO₂ on the specific leaf weight (1 x 10⁻³ g cm⁻²) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	8.883	6.787	7.830	10.218	10.569	12.137
Elevated CO ₂	9.682	7.712	9.488	10.612	12.903	13.978
CD at 5%						
Variety (V)	0.3174		0.3677		0.4935	
CO ₂	0.3174		0.3677		0.4935	
V x CO ₂	NS		0.5200		NS	

4.1.2.4 Net assimilation rate (NAR)

Elevated CO₂ brought about significant increase in the net assimilation rate (Table 9). The CO₂ induced increase in NAR was 32% (vegetative-heading) in PRH-10, whereas it was 23% (vegetative-heading) in PS-2. The interactive effect of variety and CO₂ on NAR was significant at the heading-ripening stage. The net assimilation rate was maximum at the vegetative-heading stages. The NAR of PRH-10 was greater than that of PS-2 at vegetative-heading stage.

4.1.2.5 Crop growth rate (CGR)

Higher CO₂ brought about significant increase in the CGR (Table 10). This increment ranged from (heading-ripening) to 60% (vegetative-heading) in PRH-10 and in PS-2, it ranged from 9% (heading-ripening) to 10% (vegetative-heading). The interaction effect of variety and CO₂ was significant throughout the growth period. Maximum CGR was observed at the heading-ripening stage. The varietal differences for this character showed greater CGR in PRH-10 compared to PS-2.

4.1.3 Phenology

4.1.3.1 Days to maximum tillering

Elevated CO₂ brought about significantly early tillering irrespective of the varieties (Table 11). The PRH-10 variety at elevated CO₂ concentration reached maximum tillering 3 days earlier to that of ambient condition, whereas it was one day earlier in case of PS-2. The variety x CO₂ interaction was significant at all growth stages. PRH-10 reached maximum tillering stage earlier than that of PS-2.

Table 9. Effect of elevated CO₂ on the net assimilation rate ($1 \times 10^{-3} \text{ g cm}^{-2} \text{ day}^{-1}$) of the rice varieties in OTC

Treatments	Vegetative-Heading stage		Heading-ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	0.290	0.342	0.348	0.330
Elevated CO ₂	0.382	0.421	0.218	0.274
CD at 5%				
Variety (V)		0.0133		0.0106
CO ₂		0.0133		0.0106
V x CO ₂		NS		0.0150

Table 10. Effect of elevated CO₂ on the crop growth rate ($\text{g m}^{-2} \text{ day}^{-1}$) of the rice varieties in OTC

Treatments	Vegetative-Heading stage		Heading-ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	4.99	6.37	7.78	7.72
Elevated CO ₂	7.97	6.99	8.98	8.38
CD at 5%				
Variety (V)		0.264		0.211
CO ₂		0.246		0.211
V x CO ₂		0.373		0.298

4.1.3.2 Days to flower initiation

Higher CO₂ brought about early flowering in both the varieties (Table 11). Flower initiation in PRH-10 and PS-2 was 2 days earlier under elevated CO₂ compared to ambient CO₂. The variety x CO₂ was significant throughout the growth period. PRH-10 flowered earlier compared to PS-2.

4.1.4 Dry matter production

4.1.4.1 Leaf dry mass

CO₂ enrichment brought about significant increase in the leaf dry mass (Table 12). This increase in leaf dry mass was more in PRH-10 compared to PS-2. The increase ranged from 30% (vegetative) to 57% (heading) in PRH-10 and in case of PS-2, it ranged from 33% (vegetative) to 44% (ripening). The interactive effect of variety and CO₂ was significant only at the vegetative stage. The leaf dry mass was more in PS-2 compared to PRH-10.

4.1.4.2 Stem dry mass

A significant increase in the shoot dry mass was recorded under elevated CO₂ (Table 13). The increase varied from 37% (ripening) to 79% (vegetative) in PRH-10 whereas in PS-2, it varied from 58% (heading) to 84% (vegetative). The interaction effect of variety and CO₂ was significant at all growth stages. Shoot dry mass was greater in PS-2 compared to PRH-10.

4.1.4.3 Root dry mass

Higher CO₂ brought about significant increase in the root dry mass (Table 14). This CO₂ induced enhancement varied from 40% (ripening) to 67% (vegetative) in PRH-10 and from 26% (ripening) to 70% (heading) in PS-2. The variety x CO₂ interaction was significant at all growth stages. PS-2 has greater root biomass compared to PRH-10.

Table 11. Effect of elevated CO₂ on the phenology of the rice varieties in OTC

Treatments	Days to maximum tillering (days)		Flower initiation (days)	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	52.66	56.33	80.33	87.33
Elevated CO ₂	49.33	55.33	78.33	85.66
CD at 5%				
Variety (V)		1.778		2.115
CO ₂		1.778		2.115
V x CO ₂		2.514		NS

Table 12. Effect of elevated CO₂ on the leaf dry mass (g) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	5.62	4.77	6.85	9.47	11.36	13.44
Elevated CO ₂	6.91	6.36	10.72	13.46	17.12	19.47
CD at 5%						
Variety (V)		0.166		0.288		0.485
CO ₂		0.166		0.288		0.485
V x CO ₂		0.235		NS		NS

Table 13. Effect of elevated CO₂ on the stem dry mass (g) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	4.93	5.61	9.76	10.78	14.73	14.72
Elevated CO ₂	8.82	10.34	15.45	18.92	20.23	23.77
CD at 5%						
Variety (V)		0.187		0.438		0.614
CO ₂		0.187		0.438		0.614
V x CO ₂		0.264		0.619		0.868

Table 14. Effect of elevated CO₂ on the root dry mass (g) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	3.51	4.27	7.33	7.32	11.30	12.82
Elevated CO ₂	5.85	7.02	11.32	12.45	15.79	16.12
CD at 5%						
Variety (V)		0.166		0.288		0.442
CO ₂		0.166		0.288		0.442
V x CO ₂		0.235		0.409		0.625

4.1.4.4 Panicle dry mass

Elevated CO₂ brought about significant increase in the dry mass of panicle in both the varieties of rice (Table 15). This increase ranged from 21% (ripening) to 31% (heading) in PRH-10 and from 18% (ripening) to 28% (heading) in PS-2. The interaction effect of CO₂ and variety was significant throughout the growth period. The dry mass of panicle was greater for PRH-10 compared to PS-2.

4.1.4.5 Total plant dry mass

Elevated CO₂ induced significant increase in the whole plant dry mass in both the varieties of rice (Table 16). The increase ranged from 8% (vegetative) to 13% (ripening) in PRH-10 and it was from 9% (vegetative) to 17% (ripening) in PS-2. The interaction effect of variety and CO₂ was significant for all growth stages. PS-2 had greater whole plant dry mass than PRH-10 irrespective of treatment.

4.1.5 Photosynthesis

Elevated CO₂ increased the photosynthetic rate significantly in both the varieties of rice (Table 17). The enhancement ranged from 28% (heading) to 39% (vegetative) in PRH-10 and from 26% (ripening) to 33% (reproductive) in PS-2. The variety x CO₂ interaction was significant at the vegetative stage. Photosynthetic rate was maximum at the vegetative stage irrespective of treatments and varieties. The photosynthetic rate in general was more in PRH-10 compared to PS-2.

4.1.6 Chlorophyll

4.1.6.1 Chlorophyll 'a'

There was significant reduction in the amount of chlorophyll 'a' in the

Table 15. Effect of elevated CO₂ on the panicle dry mass (g) of the rice varieties in OTC

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	3.07	3.01	5.23	5.12
Elevated CO ₂	4.02	3.86	6.33	6.09
CD at 5%				
Variety (V)		0.126		0.138
CO ₂		0.126		0.138
V x CO ₂		0.178		0.196

Table 16. Effect of elevated CO₂ on total plant dry mass (g) in the rice varieties under OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	14.06	21.58	27.01	41.51	42.62	59.47
Elevated CO ₂	14.65	23.72	30.58	48.69	46.10	65.65
CD at 5%						
Variety (V)	0.874		1.717			2.120
CO ₂	0.874		1.717			2.120
V x CO ₂	1.236		2.428			2.998

Table 17. Effect of elevated CO₂ on photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	16.82	15.72	25.36	24.47	22.81	21.34
Elevated CO ₂	23.44	20.88	32.34	31.38	29.42	26.91
CD at 5%						
Variety (V)	0.516		0.747		0.947	
CO ₂	0.516		0.747		0.947	
V x CO ₂	0.730		NS		NS	

Table 18. Effect of elevated CO₂ on the chlorophyll 'a' (mg g⁻¹ FW) content of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	0.660	0.640	0.750	0.750	0.600	0.580
Elevated CO ₂	0.610	0.580	0.650	0.640	0.570	0.530
CD at 5%						
Variety (V)	0.017		0.019		0.010	
CO ₂	0.017		0.019		0.010	
V x CO ₂	0.024		0.027		0.014	

leaves at elevated level of CO₂ (Table 18). The reduction in chlorophyll 'a' content of the leaves at the vegetative, heading and ripening stage were 8%, 13% and 5% in PRH-10 and 9%, 15% and 9% in PS-2, respectively. The interactive effect of variety and CO₂ was significant in all the three stages. The amount of chlorophyll 'a' was maximum at the heading stage. The chlorophyll 'a' content was more in PRH-10 compared to PS-2.

4.1.6.2 Chlorophyll 'b'

CO₂ enrichment resulted in a significant decrease in the chlorophyll 'b' content in the leaves (Table 19). The reduction in PRH-10 ranged from 7% (heading) (ripening) to 8% (vegetative) and in PS-2, it was from 7% (vegetative) to 9% (heading). The variety x CO₂ interaction was significant at all the growth stages. Higher amount of chlorophyll 'b' was observed at the heading stage. The chlorophyll 'b' content of leaves was more in PRH-10 compared to PS-2.

4.1.6.3 Total chlorophyll

Elevated CO₂ brought about significant reduction in the total chlorophyll content of the leaves (Table 20). This reduction ranged from 7% (vegetative) to 11% (heading) in PRH-10 and from 8% (vegetative) to 12% (heading) in PS-2. However, variety x CO₂ interaction was not significant. The amount of total chlorophyll was maximum at the heading stage. PRH-10 had greater amount of total chlorophyll than PS-2 irrespective of treatments.

4.1.7 Stomatal conductance

Elevated CO₂ significantly reduced the stomatal conductance in both the varieties of rice (Table 21). The reduction in case of PRH-10 ranged from 23% (heading) to 28% (vegetative), whereas in PS-2, it was from 26%

Table 19. Effect of elevated CO₂ on the chlorophyll 'b' (mg g⁻¹ FW) content of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	0.490	0.480	0.510	0.530	0.440	0.440
Elevated CO ₂	0.450	0.450	0.470	0.480	0.430	0.420
CD at 5%						
Variety (V)	0.011		0.018		0.012	
CO ₂	0.011		0.018		0.012	
V x CO ₂	0.015		0.025		0.017	

Table 20. Effect of elevated CO₂ on the total chlorophyll (mg g⁻¹ FW) content of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	1.15	1.12	1.26	1.28	1.04	1.02
Elevated CO ₂	1.06	1.03	1.12	1.13	1.00	0.95
CD at 5%						
Variety (V)	NS		NS		NS	
CO ₂	0.04		0.04		0.04	
V x CO ₂	NS		NS		NS	

Table 21. Effect of elevated CO₂ on stomatal conductance (mol m⁻² s⁻¹) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	0.883	0.816	1.48	1.43	1.143	1.154
Elevated CO ₂	0.629	0.606	1.13	1.02	0.780	0.732
CD at 5%						
Variety (V)	0.017		0.032		0.029	
CO ₂	0.017		0.032		0.029	
V x CO ₂	0.024		0.046		0.041	

Table 22. Effect of elevated CO₂ on respiration (μmol m⁻² s⁻¹) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	6.14	5.89	8.93	8.46	6.77	6.24
Elevated CO ₂	4.93	5.57	5.62	5.12	5.53	5.24
CD at 5%						
Variety (V)	0.199		0.114		0.102	
CO ₂	0.199		0.114		0.102	
V x CO ₂	0.281		NS		0.145	

(vegetative) to 37% (ripening). The variety x CO₂ interaction was significant at the heading stage. The stomatal conductance was more at the heading stage. Among the varieties, PRH-10 had more stomatal conductance compared to PS-2.

4.1.8 Respiration

The respiration rate was decreased significantly under elevated CO₂ condition (Table 22). The reduction varied from 18% (ripening) to 37% (heading) in PRH-10 and in case of PS-2, it varied from 16% (ripening) to 39% (heading). The interaction of variety of CO₂ was significant except at the heading stage. The respiration rate was maximum at the heading stage. PRH-10 had significantly greater rate of respiration than PS-2.

4.1.9 Carbohydrate content in leaves

4.1.9.1 Reducing sugars

There was significant increase in the reducing sugar content in the leaves at elevated CO₂ in both the varieties (Table 23). The increase in reducing sugar ranged from 48% (heading) to 71% (vegetative) in PRH-10 variety and it varied from 55% (heading) to 62% (vegetative and ripening stages) in the variety PS-2. The interactive effect of variety and CO₂ was significant at all growth stages. Maximum amount of reducing sugars in leaves was observed at the heading stage. The reducing sugar content was more in PRH-10 compared to PS-2.

4.1.9.2 Non-reducing sugars

Elevated CO₂ treatment resulted in the significant enhancement of non-reducing sugar content of leaves in both the varieties (Table 24). This increase ranged from 41% (heading) to 100% (vegetative) in PRH-10 and

Table 23. Effect of elevated CO₂ on the reducing sugar content (mg g⁻¹ DW) in the leaves of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	28.49	26.94	40.25	35.92	33.47	30.39
Elevated CO ₂	48.95	43.71	59.44	55.84	55.92	49.25
CD at 5%						
Variety (V)	1.246		0.901		1.419	
CO ₂	1.246		0.901		1.419	
V x CO ₂	1.762		NS		2.008	

Table 24. Effect of elevated CO₂ on the non-reducing sugars (mg g⁻¹ DW) content in the leaves of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	29.23	27.21	43.15	36.44	34.94	33.26
Elevated CO ₂	49.47	45.91	61.26	57.51	57.80	51.32
CD at 5%						
Variety (V)	1.397		1.706		1.535	
CO ₂	1.397		1.706		1.535	
V x CO ₂	NS		2.412		2.171	

from 54% (ripening) to 68% (vegetative) in PS-2. The interaction of variety and CO₂ was significant at the ripening and heading stages. The maximum non-reducing sugar content was observed at the heading stage. PRH-10 had greater amount of non-reducing sugar than PS-2.

4.1.9.3 Total sugars

Elevated CO₂ caused significant increase in total sugar content in both the varieties (Table 25). This increase varied from 45% (heading) to 71% (vegetative) in PRH-10 and 45% (heading) to 67% (ripening) in PS-2. The variety x CO₂ interaction was significant at all the stages. The total sugar content was maximum at the heading stage. Total sugar content was more in PRH-10 than that of PS-2 irrespective of treatments.

4.1.9.4 Starch

Increase in CO₂ level markedly enhanced the starch content in the leaves (Table 26). In PRH-10, the increase at the vegetative, heading and ripening stages were 101%, 66% and 71% and in PS-2, it was 99%, 60% and 66%, respectively. The interaction of variety and CO₂ effect was significant at all stages of growth. The maximum amount of starch content was observed in the heading stage. Starch content was more in PRH-10 compared to PS-2.

4.1.9.5 Total non-structural carbohydrates (TNC)

Elevated CO₂ brought about significant increase in the total non-structural carbohydrate content of leaves in both the varieties (Table 27). At the vegetative, heading and ripening stages, the increase was 80%, 52% and 68%, in PRH-10 and 76%, 58% and 53%, in PS-2 respectively. The variety x CO₂ interaction was significant at the vegetative and ripening stages. The

Table 25. Effect of elevated CO₂ on the total sugar (mg g⁻¹ DW) in the leaves of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	57.67	53.92	83.34	72.35	68.36	63.63
Elevated CO ₂	98.38	89.57	120.65	113.24	113.82	93.47
CD at 5%						
Variety (V)	2.411		1.984		8.729	
CO ₂	2.411		1.984		8.729	
V x CO ₂	3.409		2.806		12.345	

Table 26. Effect of elevated CO₂ on the starch content (mg g⁻¹ DW) in the leaves of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	26.47	23.68	41.94	40.34	33.21	30.97
Elevated CO ₂	53.22	47.35	69.49	64.38	56.92	51.36
CD at 5%						
Variety (V)	1.370		1.899		1.722	
CO ₂	1.370		1.899		1.722	
V x CO ₂	1.937		2.686		2.435	

Table 27. Effect of elevated CO₂ on the total non-structural carbohydrates (mg g⁻¹ DW) content in the leaves of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	84.12	77.63	125.26	112.69	101.53	94.54
Elevated CO ₂	151.59	136.89	190.01	177.63	170.73	144.78
CD at 5%						
Variety (V)	3.523		3.871		9.764	
CO ₂	3.523		3.871		9.764	
V x CO ₂	4.983		NS		13.808	

Table 28. Effect of elevated CO₂ on the reducing sugar (mg g⁻¹ DW) content in the stem of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	15.71	14.72	20.41	19.63	19.47	18.52
Elevated CO ₂	27.31	22.36	37.38	29.40	33.63	28.14
CD at 5%						
Variety (V)	0.591		0.909		0.704	
CO ₂	0.591		0.909		0.704	
V x CO ₂	0.837		1.285		0.995	

TNC content was maximum at heading stage for both the varieties. Among the varieties, TNC content was higher in PRH-10.

4.1.10 Carbohydrate content in stem

4.1.10.1 Reducing sugars

A significantly higher level of reducing sugar was observed in the shoots of rice varieties under elevated CO₂ condition (Table 28). The increase varied from 72% (ripening) to 83% (heading) in PRH-10 and in case of PS-2, the enhancement ranged from 49% (heading) to 52% (vegetative). The interaction of variety x CO₂ on reducing sugar content was significant at all the growth stages. The reducing sugar content in the stem was maximum at the ripening stage. Greater amount of reducing sugars was observed in PRH-10 compared to PS-2.

4.1.10.2 Non-reducing sugars

CO₂ enrichment resulted in a significant increase in the non-reducing sugar content of the stem (Table 29). The increase ranged from 47% (vegetative) to 50% (ripening) in PRH-10 and from 47% (heading) to 53% (ripening) in PS-2. The variety x CO₂ interaction was not significant. The non-reducing sugar content of stem was maximum at the heading stage. Among the varieties PRH-10 had higher amount of non-reducing sugars in the stem.

4.1.10.3 Total sugars

The total sugar content in the stem increased significantly at elevated CO₂ condition (Table 30). CO₂ induced enhancement varied from 55% (vegetative) to 58% (heading) in PRH-10, and from 47% (heading) to 54% (ripening) in PS-2. The variety x CO₂ interaction effect was significant throughout the growth period. The total sugar content was more at heading

Table 29. Effect of elevated CO₂ on the non-reducing sugar (mg g⁻¹ DW) content in the stem of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	38.45	35.91	47.70	45.84	44.22	40.11
Elevated CO ₂	56.57	54.73	70.49	67.45	66.52	61.71
CD at 5%						
Variety (V)		1.953		1.845		1.423
CO ₂		1.953		1.845		1.423
V x CO ₂		NS		NS		NS

Table 30. Effect of elevated CO₂ on the total sugar content (mg g⁻¹ DW) in the stem of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	54.11	50.35	68.09	65.46	63.68	58.51
Elevated CO ₂	84.10	77.01	107.85	96.79	100.11	90.26
CD at 5%						
Variety (V)		1.912		2.634		1.734
CO ₂		1.912		2.634		1.734
V x CO ₂		2.704		3.726		2.452

stage in both the varieties irrespective of treatments and varieties PRH-10 had more total sugar content than PS-2.

4.1.10.4 Starch content

High levels of CO₂ brought about significant increase in the starch content of the stem (Table 31). The increase ranged from 46% (heading) to 74% (vegetative) in PRH-10 and from 45% (heading) to 76% (vegetative) in PS-2. The variety x CO₂ interaction effect was significant. The starch content in the stem was maximum at the heading stage. The starch content was greater for PRH-10 compared to PS-2.

4.1.10.5 Total non-structural carbohydrates (TNC)

CO₂ enrichment brought about a significant increase in the total non-structural carbohydrates content of the stem in both the varieties (Table 32). The increase was 64%, 53% and 57%, in PRH-10 and 63%, 47% and 54% in PS-2, at the vegetative, heading and ripening stages respectively. The interaction of variety and CO₂ was significant all stages of plant growth. TNC content was maximum at the heading stage for both the varieties. It was higher greater for PRH-10 compared to PS-2.

4.1.11 Carbohydrate content in panicle

4.1.11.1 Reducing sugars

CO₂ enrichment brought about significant increase in the amount of reducing sugars in the panicle (Table 33). The enhancement ranged from 32% (heading) to 42% (ripening) in PRH-10 and from 24% (heading) to 42% (ripening) in PS-2. The interaction of variety and CO₂ was significant. Reducing sugar was maximum at the ripening stage irrespective of treatment and varieties. Reducing sugar was more in PRH-10.

Table 31. Effect of elevated CO₂ on the starch (mg g⁻¹ DW) content in the stem of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	36.77	33.60	53.89	50.26	42.67	40.34
Elevated CO ₂	64.13	59.45	78.73	73.15	66.43	62.65
CD at 5%						
Variety (V)	1.953		2.042		1.552	
CO ₂	1.953		2.042		1.552	
V x CO ₂	2.762		2.887		2.195	

Table 32. Effect of elevated CO₂ on the total non-structural carbohydrate (mg g⁻¹ DW) content in the stem of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	90.53	83.94	122.01	115.70	106.35	99.22
Elevated CO ₂	148.22	136.45	186.58	169.90	166.53	152.90
CD at 5%						
Variety (V)	3.760		4.814		3.018	
CO ₂	3.760		4.814		3.018	
V x CO ₂	5.317		6.808		4.268	

Table 33. Effect of elevated CO₂ on the reducing sugar (mg g⁻¹ DW) content in the panicle of the rice varieties in OTC

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	51.37	50.36	67.85	64.30
Elevated CO ₂	67.90	62.50	96.23	91.57
CD at 5%				
Variety (V)	1.373			2.538
CO ₂	1.373			2.538
V x CO ₂	1.941			3.589

Table 34. Effect of elevated CO₂ on the non-reducing sugar (mg g⁻¹ DW) content in the panicle of the rice varieties in OTC

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	65.70	61.31	80.32	78.15
Elevated CO ₂	78.35	74.23	117.42	101.32
CD at 5%				
Variety (V)	2.834			3.450
CO ₂	2.834			3.450
V x CO ₂	4.008			4.879

4.1.11.2 Non-reducing sugars

CO₂ enrichment brought about significant increase in the non-reducing sugar content of the panicle of rice varieties (Table 34). The enhancement ranged from 19% (heading) to 46% (ripening) in PRH-10 and from 21% (heading) to 29% (ripening) in PS-2. The interactive effect of variety and CO₂ was found significant at heading and ripening stages of growth. Non-reducing sugar content in the panicle was maximum at the ripening stage. PRH-10 had greater amount of non-reducing sugars in the panicle than that of PS-2 irrespective of treatments.

4.1.11.3 Total sugars

Elevated CO₂ brought about significant increase in the total sugar content in the panicle (Table 35). The increase varied from 25% (heading) to 44% (ripening) in PRH-10 and from 22% (heading) to 35% (ripening) in PS-2. The variety x CO₂ interaction was significant at the ripening stage. Total sugar content was high at the ripening stage. It was more in variety PRH-10 compared to PS-2.

4.1.11.4 Starch

Starch content in the panicle was significantly increased at high levels of CO₂ (Table 36). This enhancement ranged from 33% (heading) to 41% (ripening) in PRH-10 and 30% (heading) to 42% (ripening) in PS-2. The interactive effect was significant throughout the growth period. Greater amount of starch production in the panicle was at the heading stage. Variety, PRH-10 had greater starch content than PS-2 irrespective of treatments.

4.1.11.5 Total non-structural carbohydrate (TNC)

CO₂ enrichment brought about a significant increase in the total non-

Table 35. Effect of elevated CO₂ on the total sugar (mg g⁻¹ DW) content in the panicle of the rice varieties in OTC

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	117.07	111.97	148.17	142.45
Elevated CO ₂	146.25	136.73	213.65	192.89
CD at 5%				
Variety (V)		6.98		8.40
CO ₂		6.98		8.40
V x CO ₂		NS		11.89

Table 36. Effect of elevated CO₂ on the starch content (mg g⁻¹ DW) in the panicle of the rice varieties on OTC

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	130.45	121.90	163.90	152.56
Elevated CO ₂	173.41	158.33	231.88	217.71
CD at 5%				
Variety (V)		4.877		5.653
CO ₂		4.877		5.653
V x CO ₂		6.897		7.995

structural carbohydrate content of the panicle (Table 37). The increase ranged from 29% (heading) to 43% (ripening) in PRH-10 and from 26% (heading) to 39% (ripening) in PS-2. The interaction, variety x CO₂ was not significant. The TNC content in the panicle was high at the ripening stage compared to heading stage. It was greater in PRH-10 compared to PS-2.

4.1.12 Sucrose phosphate synthase (SPS)

CO₂ enrichment brought about a significant increase in the activity of sucrose phosphate synthase enzyme in the leaves of rice varieties (Table 38). The increase ranged from 14% (heading) to 21% (ripening) in PRH-10 and from 8% (vegetative) to 18% (heading) in PS-2. The interaction of variety and CO₂ was significant throughout the growth period. SPS activity was maximum at the heading stage irrespective of treatment and varieties. The SPS activity was more in PRH-10 compared to PS-2.

4.1.13 Antioxidant enzymes

4.1.13.1 Superoxide dismutase (SOD)

The higher CO₂ level significantly reduced the superoxide dismutase activity in the leaves of rice varieties (Table 39). The decrease in the SOD activity was 34% (vegetative), 37% (heading) and 18% (ripening) in PRH-10 and 24%, 35% and 21% in PS-2 at vegetative, heading and ripening stages, respectively. The interaction effect of variety and CO₂ was significant at vegetative and heading stages. Superoxide dismutase activity was maximum at the ripening stage. It was higher in PRH-10 than that of PS-2.

4.1.13.2 Ascorbate peroxidase (APX)

Elevated CO₂ brought about a significant reduction in the activity of ascorbate peroxidase (Table 40). The reduction was maximum at ripening

Table 37. Effect of elevated CO₂ on the total non-structural carbohydrate (mg g⁻¹ DW) in the panicle of the rice varieties in OTC

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	247.52	233.87	312.07	295.01
Elevated CO ₂	319.66	295.06	445.53	410.60
CD at 5%				
Variety (V)				15.93
CO ₂	13.15			15.93
V x CO ₂	13.15			NS
	NS			

Table 38. Effect of elevated CO₂ on the activity of sucrose phosphate synthase (μmol mg⁻¹ protein min⁻¹) in the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	23.92	23.46	27.45	25.12	23.56	22.88
Elevated CO ₂	27.59	25.12	31.23	29.76	28.46	25.66
CD at 5%						
Variety (V)		0.790		1.221		1.065
CO ₂		0.790		1.221		1.065
V x CO ₂		1.117		1.727		1.506

Table 39. Effect of elevated CO₂ on superoxide dismutase activity (units min⁻¹ mg⁻¹ protein) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	13.46	12.38	21.23	19.38	25.43	23.38
Elevated CO ₂	8.92	9.38	13.38	12.66	20.82	18.47
CD at 5%						
Variety (V)		NS		0.525		0.607
CO ₂		0.486		0.525		0.607
V x CO ₂		0.688		0.742		NS

Table 40. Effect of elevated CO₂ on the ascorbate peroxidase activity (μmol of ascorbate oxidised min⁻¹ FW) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	115.56	111.38	130.47	124.32	162.58	157.38
Elevated CO ₂	56.78	54.58	80.43	77.38	70.38	67.92
CD at 5%						
Variety (V)		3.759		3.193		5.068
CO ₂		3.759		3.193		5.068
V x CO ₂		NS		NS		NS

stage (57%) followed by vegetative (51%) and heading stages (38%) in both the varieties of rice. The interaction effect was not significant. APX activity was maximum at the heading stage irrespective of varieties and treatment. PRH-10 had higher APX activity than PS-2.

4.1.13.3 Glutathione reductase (GR)

CO₂ enrichment significantly decreased the activity of glutathione reductase in the leaves of rice varieties (Table 41). The reduction in GR activity ranged from 50% (vegetative) to 56% (ripening) in PRH-10 and in case of PS-2 it varied from 37% (vegetative) 66% (ripening). The variety x CO₂ interaction was significant at all the growth stages of the crop. GR activity was maximum at the heading stage. PRH-10 showed greater GR activity compared to PS-2.

4.1.14 Carbon (C)

Leaves

CO₂ enrichment significantly increased the carbon content in the leaves of rice varieties (Table 42). The increase ranged from 8% (vegetative) to 15% (ripening) in PRH-10 and from 7% (vegetative) to 23% (heading) in PS-2. The interaction of variety and CO₂ was significant at heading stage. Carbon content in the leaves was maximum at the vegetative stage irrespective of treatment and varieties. The carbon content was more for PRH-10 compared to PS-2.

Stem

Carbon content in the stem was significantly increased at higher concentration of CO₂ (Table 43). The increase in the carbon content ranged from 14% (heading) to 19% (ripening) in PRH-10 and from 13% (ripening) to

Table 41. Effect of elevated CO₂ on the glutathione reductase activity (Δ OD min⁻¹ mg⁻¹ protein) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	0.14	0.08	0.26	0.23	0.23	0.21
Elevated CO ₂	0.07	0.05	0.13	0.09	0.10	0.07
CD at 5%						
Variety (V)		0.0019		0.0072		0.0045
CO ₂		0.0019		0.0072		0.0045
V x CO ₂		0.0026		0.0101		0.0063

Table 42. Effect of elevated CO₂ on the carbon content (% DM) in the leaves of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	41.35	40.72	34.27	29.24	36.54	34.68
Elevated CO ₂	44.68	43.65	38.70	36.11	42.17	39.17
CD at 5%						
Variety (V)		1.134		0.925		1.001
CO ₂		1.134		0.925		1.001
V x CO ₂		NS		1.308		NS

Table 43. Effect of elevated CO₂ on the carbon content (% DM) in the stem of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	42.88	41.01	34.68	32.91	35.12	35.12
Elevated CO ₂	44.17	41.76	39.45	37.59	41.81	39.78
CD at 5%						
Variety (V)		NS		NS		0.732
CO ₂		NS		NS		0.732
V x CO ₂		NS		NS		1.035

Table 44. Effect of elevated CO₂ on the carbon content (% DM) in the roots of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	43.02	40.20	33.01	29.17	37.46	34.21
Elevated CO ₂	43.37	41.68	37.18	35.82	40.22	38.31
CD at 5%						
Variety (V)		1.072		0.921		1.101
CO ₂		1.072		0.921		1.101
V x CO ₂		1.516		1.302		1.558

14% (heading) in PS-2. The interaction of CO₂ x variety was significant only at the ripening stage. The maximum amount of carbon was found at the vegetative stage. PRH-10 had more carbon content compared to PS-2.

Root

CO₂ enrichment brought about significant increase in the carbon content of root (Table 44). The increase varied from 7% (ripening) to 13% (heading) in PRH-10 and from 12% (ripening) to 23% (heading) in PS-2. The variety x CO₂ interaction was significant. The carbon content was maximum at the vegetative stage for both varieties. Variety, PRH-10 had greater carbon content than that of PS-2.

4.1.15 Nitrogen (N)

Leaves

The nitrogen content of the leaves was significantly reduced under elevated CO₂ conditions (Table 45). This reduction ranged from 9% (vegetative) to 14% (heading) in PRH-10 and from 9% (ripening) to 14% (vegetative and heading) in PS-2. The interaction of variety and CO₂ was significant at vegetative and ripening stage. Nitrogen content in the leaves was maximum at the vegetative stage. The nitrogen content was more in PRH-10 compared to PS-2.

Stem

The nitrogen content in the stem markedly reduced at higher levels of CO₂ (Table 46). The decrease ranged from 10% (heading) to 14% (vegetative) in PRH-10 and in case of PS-2, it ranged from 12% (vegetative) to 18% (heading). The variety x CO₂ interaction was significant at the

Table 45. Effect of elevated CO₂ on the nitrogen (% DM) in the leaves of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	4.62	4.42	2.75	2.71	4.17	3.82
Elevated CO ₂	4.19	3.81	2.35	2.34	3.62	3.48
CD at 5%						
Variety (V)	0.078		0.049		0.102	
CO ₂	0.078		0.049		0.102	
V x CO ₂	0.110		NS		0.145	

Table 46. Effect of elevated CO₂ on the nitrogen content (% DM) in the stem of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	4.48	3.79	3.62	3.07	3.86	3.55
Elevated CO ₂	3.87	3.32	3.27	2.52	3.41	3.06
CD at 5%						
Variety (V)	0.068		0.099		0.079	
CO ₂	0.068		0.099		0.079	
V x CO ₂	0.096		0.140		NS	

vegetative and heading stages. Nitrogen was maximum at the vegetative stage. Among the varieties, PRH-10 had greater nitrogen than that of PS-2.

Roots

CO₂ enrichment brought about significant decrease in the nitrogen content of roots in both the varieties (Table 47). The reduction ranged from 14% (heading) to 16% (vegetative) in PRH-10 and in case of PS-2, it ranged from 7% (vegetative) to 16% (heading). The interactive effect of variety and CO₂ was significant at the vegetative stage. Nitrogen content of roots was maximum at the vegetative stage. Higher nitrogen content was recorded in PRH-10.

4.1.16 Carbon : nitrogen ratio

Leaves

A significant increase in the carbon : nitrogen ratio was observed at elevated CO₂ (Table 48). The increase in C/N ratio ranged from 19% (vegetative) to 32% (heading) in PRH-10 and from 24% (vegetative and ripening) to 43% (heading) in PS-2. The interaction of variety and CO₂ was significant at the heading stage. The ratio of carbon to nitrogen content was maximum at the heading stage. PS-2 had significantly greater C/N ratio than that of PRH-10 irrespective of treatments.

Stem

CO₂ enrichment brought about significant increase in the ratio of carbon to nitrogen content in the stem (Table 49). The increase ranged from 19% (vegetative) to 35% (ripening) in PRH-10 and from 16% (vegetative) to 37% (reproductive) in PS-2. The variety x CO₂ interaction was significant at

Table 47. Effect of elevated CO₂ on the nitrogen content (% DM) in the roots of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	3.85	2.89	2.65	2.40	2.86	2.76
Elevated CO ₂	3.21	2.68	2.26	2.02	2.41	2.35
CD at 5%						
Variety (V)	0.056		0.069		0.045	
CO ₂	0.056		0.069		0.045	
V x CO ₂	0.080		NS		NS	

Table 48. Effect of elevated CO₂ on the ratio of carbon to nitrogen content in the leaves of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	8.95	9.22	12.46	10.78	8.76	9.07
Elevated CO ₂	10.67	11.46	12.47	15.44	11.08	11.25
CD at 5%						
Variety (V)	0.373		0.350		0.350	
CO ₂	0.373		0.350		0.350	
V x CO ₂	NS		0.495		NS	

Table 49. Effect of elevated CO₂ on the ratio of carbon to nitrogen content in the stem of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	9.57	10.83	9.58	10.22	9.10	9.89
Elevated CO ₂	11.42	12.58	12.06	14.92	12.27	13.02
CD at 5%						
Variety (V)		0.307		0.316		0.704
CO ₂		0.307		0.316		0.704
V x CO ₂		NS		0.447		NS

Table 50. Effect of elevated CO₂ on the ratio of carbon to nitrogen in the roots of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	11.17	13.51	12.46	12.15	13.10	12.39
Elevated CO ₂	13.91	15.55	16.45	17.73	16.39	16.32
CD at 5%						
Variety (V)		0.480		0.374		0.297
CO ₂		0.480		0.374		0.297
V x CO ₂		0.679		0.529		0.420

the heading stage. The C/N ratio was maximum at the heading stage. PS-2 had greater C/N ratio compared to PRH-10.

Root

Elevated CO₂ brought about significant increase in the ratio of root carbon to nitrogen content (Table 50). The increase ranged from 25% (ripening) to 32% (heading) in PRH-10 and incase of PS-2, it was from 15% (vegetative) to 45% (heading). The variety x CO₂ interaction was significant at all growth stages. The C/N ratio was higher at heading stage. The C/N ratio was significantly greater for PS-2 compared to PRH-10 irrespective of treatments.

4.1.17 Total soluble protein

Total soluble protein content in the leaves in both the varieties significantly reduced under elevated CO₂ condition (Table 51). The decrease ranged from 10% (heading) to 20% (vegetative) in PRH-10 and from 15% (vegetative) to 25% (ripening) in PS-2. The interaction of variety and CO₂ was significant at all the three stages. Leaf soluble protein was maximum at the heading stage. PRH-10 had greater amount of leaf soluble protein compared to PS-2.

4.1.18 Nitrate reductase activity (NR)

Higher CO₂ brought about significant increase in the nitrate reductase activity in both the varieties (Table 52). The increase in NR activity ranged from 1.0 fold (vegetative) to 2.0 fold (ripening) in both the varieties. The interaction of variety and CO₂ was significant at all the three stages. The NR activity was maximum at the heading stage. The NR activity was high in PRH-10 irrespective of treatments.

Table 51. Effect of elevated CO₂ on the leaf soluble protein content (mg g⁻¹ FW) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	5.01	4.93	7.56	7.48	7.02	6.57
Elevated CO ₂	4.03	4.21	6.81	6.43	5.13	4.93
CD at 5%						
Variety (V)		0.141		0.159		0.257
CO ₂		0.141		0.159		0.257
V x CO ₂		0.200		0.224		0.364

Table 52. Effect of elevated CO₂ on the nitrate reductase activity (μmol of NO₂ g⁻¹ hr⁻¹) of the rice varieties in OTC

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	0.910	0.880	1.320	1.280	0.980	0.830
Elevated CO ₂	1.930	1.820	3.240	2.380	2.890	2.510
CD at 5%						
Variety (V)		0.059		0.063		0.080
CO ₂		0.059		0.063		0.080
V x CO ₂		0.083		0.088		0.113

4.1.19 Yield and yield components

4.1.19.1 Grain yield per square meter

Elevated CO₂ brought about a significant increase in the grain yield per square meter (Table 53). The increase was 21% in PRH-10 and 18% in PS-2. The interaction of variety and CO₂ was significant. The grain yield was higher in PRH-10 (683.42 g m⁻²) compared to PS-2 (570.36 g m⁻²).

4.1.19.2 Number of panicles per plant

There was significant increase in number of panicles per plant at high levels of CO₂ in both the varieties (Table 53). The CO₂ induced increase in PRH-10 was 53% whereas in PS-2, it was 50%. The interaction of variety and CO₂ was not significant. The number of panicles per plant was more in PRH-10 compared to PS-2 irrespective of treatments.

4.1.19.3 Length of panicle

CO₂ enrichment brought about a significant increase in the length of the panicle (Table 53). The increase was 12% in PRH-10 and 11% in PS-2. The interactive effect of variety and CO₂ was not significant. Panicle length was greater for PRH-10 compared to PS-2.

4.1.19.4 Grain number per panicle

CO₂ enrichment significantly increased the grain number per panicle in both the varieties (Table 54). The increase in the grain number per panicle was 64% in PRH-10 and it was 55% in PS-2. The variety x CO₂ interaction was not significant. Number of grains per panicle was more for PRH-10 compared to PS-2.

4.1.19.5 1000-grain mass

Elevated CO₂ brought about a significant increase in the grain mass

Table 53. Effect of elevated CO₂ on the yield and yield components of the rice varieties in OTC

Treatments	Grain yield m ² (g m ⁻²)		Length of panicle (cm)		No. of panicles/plant	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	567.38	479.38	24.12	24.34	7.50	7.00
Elevated CO ₂	683.42	570.36	27.11	27.12	11.50	10.50
CD at 5%						
Variety (V)	19.88			1.008		NS
CO ₂	19.88			1.008		1.18
V x CO ₂	28.12			NS		NS

Table 54. Effect of elevated CO₂ on the yield components of the rice varieties in OTC

Treatments	Grain number per pancile		1000-grain mass (g)		Harvest index	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	135.00	130.12	20.36	20.14	0.35	0.34
Elevated CO ₂	221.80	201.38	27.45	25.82	0.44	0.42
CD at 5%						
Variety (V)	NS			0.706		0.012
CO ₂	16.83			0.706		0.012
V x CO ₂	NS			0.999		NS

(Table 54). The increase was 35% in PRH-10 and in case of PS-2, it was 25%. The variety x CO₂ interaction was significant. The 1000-grain mass was greater for PRH-10 (27.45 g) as compared to PS-2 (25.82 g).

4.1.19.6 Harvest index (HI)

There was a significant increase in the harvest index in both the varieties at elevated levels of CO₂ (Table 54). The increase in harvest index was 26% in PRH-10 and 24% in PS-2. The variety x CO₂ interaction was not significant. The HI increase was more in PRH-10 (0.44) than that of PS-2 (0.42).

4.1.20 Grain quality

4.1.20.1 Reducing sugar

CO₂ enrichment brought about a significant increase in the reducing sugar content of grain (Table 55a). The increase was 55% in PRH-10 and 52% in PS-2. The interactive effect of variety and CO₂ was significant. Reducing sugar content was greater in PRH-10 than that of PS-2.

4.1.20.2 Non-reducing sugar

Elevated CO₂ significantly increased the non-reducing sugar content of grain (Table 55a). The increase was 30% in PRH-10 and 27% in PS-2. The interaction of variety and CO₂ was not significant. There was no significant difference between the varieties on the non-reducing sugar content in grain.

4.1.20.3 Total sugars

Elevated CO₂ treatment resulted in the enhancement of the total sugar content in the grains (Table 55a). The increase was 42% in PRH-10 and 38% in PS-2. The interactive effect of variety and CO₂ was not significant. Among the varieties PRH-10 had higher total sugar content compared to PS-2.

Table 55a. Effect of elevated CO₂ on the grain quality parameters of the rice varieties in OTC

Treatments	Reducing sugar (mg g ⁻¹ DW)		Non-reducing sugar (mg g ⁻¹ DW)		Total sugar (mg g ⁻¹ DW)		Starch (mg g ⁻¹ DW)	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	84.11	79.62	101.27	103.06	185.37	182.68	201.40	195.32
Elevated CO ₂	130.02	121.26	132.39	130.58	262.41	251.84	279.42	271.46
CD at 5%								
Variety (V)	3.234		NS		8.55		6.85	
CO ₂	3.234		2.947		8.55		6.85	
V x CO ₂	4.574		NS		NS		NS	

Table 55b. Effect of elevated CO₂ on the grain quality parameters of the rice varieties in OTC

Treatments	Amylose (%)		TNC (mg g ⁻¹ DW)		Nitrogen (%)		Protein (%)	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	24.12	26.12	386.79	378.21	1.61	1.60	9.57	9.52
Elevated CO ₂	25.06	27.30	541.83	522.86	1.58	1.53	9.40	8.86
CD at 5%								
Variety (V)	0.704		11.604		NS		0.231	
CO ₂	0.704		11.604		NS		0.231	
V x CO ₂	NS		NS		0.076		0.326	

4.1.20.4 Starch

High levels of CO₂ brought about a significant increase in the starch content of the grain which was 39% in both the varieties (Table 55a). The interaction effect was not significant. The starch content of grain was higher in PRH-10.

4.1.20.5 Amylose

There was a significant increase in the amylose content of the grain (Table 55b). The increase was 4% in PRH-10 and 5% in PS-2. The variety x CO₂ interaction was not significant. The amylose content of the grain was more in PS-2 (27.3%) than PRH-10 (25.06%) at elevated CO₂.

4.1.20.6 Total non-structural carbohydrates (TNC)

The total non-structural carbohydrates content in the grain significantly increased under high levels of CO₂ (Table 55b). The increase was 40% in PRH-10 and 38% in PS-2. The interaction of variety and CO₂ was not significant. The amount of TNC content in grain was more in PRH-10 compared to PS-2.

4.1.20.7 Nitrogen (N)

The nitrogen content in grain decreased at elevated CO₂ concentration (Table 55b). The decrease was 2% in PRH-10 and 4% in PS-2. The interactive effect of variety and CO₂ was significant. There was no significant difference between the varieties on the nitrogen content of grain.

4.1.20.8 Protein

CO₂ enrichment brought about significant decrease in the protein content of grain (Table 55b). The reduction was 2% in PRH-10 and 7% in PS-

2. The variety x CO₂ interaction was significant. The protein content was more in PRH-10 (9.40%) compared to PS-2 (8.86%).

4.1.20.9 Calcium (Ca)

The calcium content of grains significantly increased under elevated CO₂ in both the varieties (Table 55c). The CO₂ induced increase was more in PRH-10 (19%) compared to PS-2 (12%). The interaction of variety and CO₂ was significant. The calcium content was greater in PRH-10 (0.087%) compared to PS-2 (0.083%).

4.1.20.10 Potassium (K)

CO₂ enrichment brought about significant enhancement in the potassium content of the grain (Table 55c). The increase was 28% in PRH-10 and 22% in case of PS-2. The interaction of variety and CO₂ on potassium content was significant. The potassium content was greater in PRH-10 (0.230%) than PS-2 (0.220%).

4.2 FREE AIR CARBON DIOXIDE ENRICHMENT (FACE) STUDIES

4.2.1 Plant growth

4.2.1.1 Plant height

CO₂ enrichment brought about a significant increase in the height of the plant (Table 56). The increase in PRH-10 was 21% at vegetative stage and 22% at heading and ripening stage and in PS-2, it was 15% at vegetative stage, 16% at heading stage and 19% at ripening stage. The interaction of variety and CO₂ on plant height was not significant. The plant height was greater in PS-2 compared to PRH-10.

4.2.1.2 Number of tillers

Elevated CO₂ brought about a significant increase in the production of

Table 55c. Effect of elevated CO₂ on the grain quality parameters of the rice varieties in OTC

Treatments	Calcium (%)		Potassium (%)	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂				
Elevated CO ₂	0.073	0.074	0.180	0.180
CD at 5%	0.087	0.083	0.230	0.220
Variety (V)		0.002		0.004
CO ₂		0.002		0.004
V x CO ₂		0.008		0.007

Table 56. Effect of elevated CO₂ on plant height (cm) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	53.14	62.37	82.34	91.74	91.38	99.82
Elevated CO ₂	64.22	71.92	100.13	106.43	111.42	118.82
CD at 5%						
Variety (V)	2.104		3.987		2.514	
CO ₂	2.104		3.987		2.514	
V x CO ₂	NS		NS		NS	

Table 57. Effect of elevated CO₂ on the number of tillers of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	10.00	11.00	10.66	11.33	11.00	11.67
Elevated CO ₂	13.00	13.33	14.66	14.66	15.00	15.00
CD at 5%						
Variety (V)	0.41		NS		NS	
CO ₂	0.41		0.91		0.41	
V x CO ₂	NS		NS		NS	

tillers (Table 57). The CO₂ induced enhancement was high in PRH-10 varying from 30% (vegetative) to 38% (heading) whereas in PS-2, the enhancement ranged from 21% (vegetative) to 30% (heading). The variety x CO₂ interaction was not significant. The number of tillers for both the varieties was almost same at all the stages.

4.2.1.3 Number of leaves

Production of leaves was significantly increased due to CO₂ enrichment in both the rice varieties (Table 58). The enhancement in PRH-10 was 52% at vegetative, 20% at heading and 19% at ripening stages whereas in PS-2, it was 31%, 46% and 32%, respectively. The interaction of variety and CO₂ on the production of leaves was significant at all the three stages of crop growth. The leaf production was more in PS-2 compared to PRH-10.

4.2.1.4 Leaf area

Significant increase in the leaf area expansion under elevated CO₂ condition was observed in both the rice varieties (Table 59). The increase ranged from 30% (vegetative) to 45% (heading) in PRH-10, whereas in PS-2 it ranged from 30% (vegetative) to 38% (heading). The interaction effect was significant throughout the growth period. The leaf area was more in case of PS-2 compared to PRH-10.

4.2.1.5 Root length

Elevated CO₂ significantly increased the length of root in both the varieties (Table 60). The increase ranged from 27% (heading) to 43% (vegetative) in PRH-10 and from 25% (vegetative) to 44% (ripening) in PS-2. The variety x CO₂ interaction was significant except at the heading stage.

Table 58. Effect of elevated CO₂ on the number of leaves of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	31.33	40.66	51.33	53.66	59.33	66.33
Elevated CO ₂	47.66	53.33	61.66	78.33	70.33	87.66
CD at 5%						
Variety (V)		1.628		1.743		2.223
CO ₂		1.628		1.743		2.223
V x CO ₂		2.302		2.465		3.144

Table 59. Effect of elevated CO₂ on the leaf area (cm²) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	668.32	725.31	950.73	1021.43	985.73	1151.83
Elevated CO ₂	851.34	943.82	1381.34	1417.80	1378.92	1456.82
CD at 5%						
Variety (V)		21.46		39.00		30.09
CO ₂		21.46		39.00		30.09
V x CO ₂		30.36		55.10		42.55

Table 60. Effect of elevated CO₂ on the root length (cm) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	4.53	5.37	9.74	13.72	15.54	14.74
Elevated CO ₂	6.47	7.71	13.78	17.12	19.76	18.46
CD at 5%						
Variety (V)		0.185		0.630		0.541
CO ₂		0.185		0.630		0.541
V x CO ₂		0.261		NS		0.766

Table 61. Effect of elevated CO₂ on the leaf area index of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	1.67	1.81	2.38	2.55	2.46	2.88
Elevated CO ₂	2.13	2.36	3.45	3.54	3.45	3.64
CD at 5%						
Variety (V)		0.765		0.1093		0.1193
CO ₂		0.765		0.1093		0.1193
V x CO ₂		NS		NS		0.1688

Root length was greater for PS-2 at the vegetative and heading stage compared to PS-2.

4.2.2 Growth analysis

4.2.2.1 Leaf area index (LAI)

High levels of CO₂ brought about significant increase in the leaf area index (Table 61). The increase ranged from 28% (vegetative) to 45% (heading) in PRH-10 and from 26% (ripening) to 39% (heading) in PS-2. The interaction of variety and CO₂ was significant. PS-2 had greater leaf area index compared to PRH-10.

4.2.2.2 Specific leaf area (SLA)

CO₂ enrichment brought about a significant decrease in SLA in both the varieties (Table 62). The reduction ranged from 6% (heading) to 9% (ripening) in PRH-10 and from 6% (vegetative) to 12% (ripening) in PS-2. The interaction of variety and CO₂ on SLA was significant at the vegetative and heading stages of growth. The SLA was maximum at the vegetative stage. PRH-10 had significantly greater SLA than PS-2.

4.2.2.3 Specific leaf weight (SLW)

CO₂ enrichment significantly increased the specific leaf weight in both the varieties (Table 63). The increase ranged from 6% (heading) to 29% (vegetative) in PRH-10 and 6% (vegetative) to 13% (ripening) in PS-2. The interactive effect was significant except at the ripening stage. Specific leaf weight was maximum at the ripening stage. PS-2 had greater SLW than PRH-10.

4.2.2.4 Net assimilation rate (NAR)

Elevated CO₂ brought about significant increase in the NAR in both the

Table 62. Effect of elevated CO₂ on specific leaf area (cm² g⁻¹) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	141.59	141.39	116.94	91.77	78.05	78.25
Elevated CO ₂	106.02	132.56	109.98	99.08	70.78	68.65
% increase/decrease	25.12	6.24	5.95	7.96	9.31	12.26
CD at 5%						
Variety (V)	5.5238		3.8693			NS
CO ₂	5.5238		NS			2.3978
V x CO ₂	7.819		5.4721			NS

Table 63. Effect of elevated CO₂ on specific leaf weight (1 x 10⁻³ g cm⁻²) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	7.062	7.073	8.551	10.896	12.813	12.780
Elevated CO ₂	9.432	7.544	9.093	10.093	14.128	14.566
CD at 5%						
Variety (V)	0.2464		0.2923			NS
CO ₂	0.2464		NS			0.3640
V x CO ₂	0.3485		0.4134			NS

rice varieties (Table 64). This increase was 5% in both PRH-10 and PS-2. The interactive effect of variety and CO₂ on NAR was significant at all the stages of growth. The varieties showed no significant difference on the NAR.

4.2.2.5 Crop growth rate (CGR)

CO₂ enrichment brought about significant increase in the CGR of both the varieties (Table 65). The enhancement ranged 14% (heading-ripening) to 30% (vegetative-heading) in PRH-10 and from 15% (heading-ripening) to 42% (vegetative-heading) in PS-2. The interaction of variety x CO₂ was significant at the vegetative-heading stage. PS-2 had greater CGR compared to PRH-10.

4.2.3 Phenology

4.2.3.1 Days to maximum tillering

Elevated CO₂ brought about early tillering in both the varieties (Table 66). PRH-10 reached the maximum tillering stage 3 days earlier to ambient condition, whereas in PS-2, it was 2 days earlier. The variety and CO₂ interaction was not significant. PRH-10 reached the maximum tillering stage early to PS-2.

4.2.3.2 Days to flower initiation

Elevated CO₂ brought about early flowering in both the varieties (Table 66). Flower initiation was 3 days earlier in PRH-10 and 2 days early in PS-2. The variety x CO₂ interaction was not significant. Flowering was earlier in PRH-10 compared to PS-2.

4.2.4 Dry matter production

4.2.4.1 Leaf dry mass

At elevated CO₂ condition, a significant increase in the leaf dry mass was observed in both the varieties (Table 67). The increase varied from 54%

Table 64. Effect of elevated CO₂ on net assimilation rate (1x10⁻³ g cm⁻² day⁻¹) of the rice varieties in FACE

Treatments	Vegetative -Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	0.345	0.410	0.396	0.306
Elevated CO ₂	0.363	0.433	0.316	0.267
CD at 5%				
Variety (V)				0.0123
CO ₂		NS		0.0123
V x CO ₂		0.019		0.0175
		0.026		

Table 65. Effect of elevated CO₂ on crop growth rate (g m⁻² day⁻¹) of the rice varieties in FACE

Treatments	Vegetative -Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	6.69	8.17	8.83	7.65
Elevated CO ₂	8.69	11.62	10.05	8.82
CD at 5%				
Variety (V)				0.3197
CO ₂		0.336		0.3197
V x CO ₂		0.356		NS
		0.503		

Table 66. Effect of elevated CO₂ on the phenology of rice varieties in FACE

Treatments	Days to maximum tillering (days)		Flower initiation (days)	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	51.33	55.66	79.66	85.33
Elevated CO ₂	48.33	53.33	76.33	83.33
CD at 5%				
Variety (V)		1.967		3.824
CO ₂		1.967		3.824
V x CO ₂		NS		NS

Table 67. Effect of elevated CO₂ on the leaf dry mass (g) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	4.72	5.13	8.13	11.13	12.63	14.72
Elevated CO ₂	8.03	7.12	12.56	14.31	19.48	21.22
CD at 5%						
Variety (V)		0.248		0.177		0.427
CO ₂		0.248		0.177		0.427
V x CO ₂		0.351		0.251		0.604

(ripening) to 70% (vegetative) in PRH-10 whereas in PS-2, it ranged from 29% (heading) to 44% (ripening). The variety x CO₂ was significant at all the growth stages. Leaf dry mass was higher for PS-2 compared to PRH-10.

4.2.4.2 Stem dry mass

A significant increase in the shoot dry mass was observed at elevated CO₂ condition (Table 68). The increase was more in PRH-10 and it ranged from 33% (ripening) to 89% (vegetative) and in case of PS-2, it ranged from 60% (ripening) to 69% (vegetative). The interaction of variety x CO₂ was significant at all the stages of plant growth. Shoot dry mass was greater for PS-2 compared in PRH-10.

4.2.4.3 Root dry mass

CO₂ enrichment brought about significant increase in the root dry mass (Table 69). The increase ranged from 35% (ripening) to 66% (vegetative) in PRH-10 from 25% (ripening) to 83% (vegetative) in PS-2. The variety x CO₂ interaction was significant at all stages of growth. PS-2 had greater root biomass compared to PRH-10.

4.2.4.4 Panicle dry mass

The dry mass of panicle in both the varieties was significantly increased under elevated CO₂ condition (Table 70). The increase varied from 15% (heading) to 18% (ripening) in PRH-10 and from 11% (heading) to 13% (ripening) in PS-2. The interaction of variety x CO₂ was significant. Panicle dry mass was greater than that of PRH-10 than that of PS-2.

4.2.4.5 Total plant dry mass

Elevated CO₂ significantly increased the dry mass of whole plant in both the varieties (Table 71). The increase ranged from 17% (vegetative) to

Table 68. Effect of elevated CO₂ on the stem dry mass (g) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	6.02	6.82	11.38	13.60	17.83	17.13
Elevated CO ₂	11.38	11.50	17.52	22.82	23.74	27.43
CD at 5%						
Variety (V)		0.258		0.407		0.588
CO ₂		0.258		0.407		0.588
V x CO ₂		0.366		0.576		0.831

Table 69. Effect of elevated CO₂ on the root dry mass (g) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	4.13	4.42	8.22	8.93	13.18	14.68
Elevated CO ₂	6.80	8.13	13.04	14.26	17.83	18.34
CD at 5%						
Variety (V)		0.185		0.273		0.313
CO ₂		0.185		0.273		0.313
V x CO ₂		0.262		0.387		0.443

Table 70. Effect of elevated CO₂ on panicle dry mass (g) of the rice varieties in FACE

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	3.87	3.13	5.62	5.56
Elevated CO ₂	4.82	4.42	6.98	6.52
CD at 5%				
Variety (V)		0.103		0.122
CO ₂		0.103		0.122
V x CO ₂		0.145		0.173

Table 71. Effect of elevated CO₂ on total plant dry mass (g) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	14.87	26.21	31.60	47.94	48.26	68.03
Elevated CO ₂	16.37	26.75	36.79	55.81	52.09	73.51
CD at 5%						
Variety (V)		0.977		2.206		2.343
CO ₂		0.977		2.206		2.343
V x CO ₂		NS		NS		NS

20% (ripening) in PRH-10 and from 12% (vegetative) to 16% (ripening) in PS-2. The interaction effect of variety and CO₂ was significant. The whole plant dry mass was greater for PS-2 compared to PRH-10.

4.2.5 Photosynthesis

CO₂ enrichment under FACE condition brought about a significant increase in the photosynthetic rate in both the varieties at all the stages of growth (Table 72). The increase in photosynthetic rate ranged from 35% (vegetative) to 42% (heading) in PRH-10 and in case of PS-2, it ranged from 30% (ripening) to 36% (heading). The interaction effect of variety and CO₂ was significant. Higher photosynthetic rates were recorded at the heading stage. Photosynthetic rate was higher for PRH-10 compared to PS-2.

4.2.6 Chlorophyll

4.2.6.1 Chlorophyll 'a'

Elevated CO₂ brought about significant reduction in the chlorophyll 'a' content of leaves (Table 73). The reduction in the chlorophyll content ranged from 5% (vegetative) to 11% (heading) in PRH-10 and from 5% (vegetative) to 11% (heading) in PS-2. The interaction effect of variety and CO₂ was not significant. The amount of chlorophyll 'a' was more at the heading stage. However, it was greater in PRH-10 compared to PS-2.

4.2.6.2 Chlorophyll 'b'

Similarly chlorophyll 'b' content was also decreased under elevated CO₂ condition in both the varieties (Table 74). The reduction ranged between 3% to 10% in both the varieties. The interaction of variety and CO₂ was significant at the heading stage. The amount of chlorophyll 'b' was maximum at heading stage. PRH-10 had higher content of chlorophyll 'b' than PS-2.

Table 72. Effect of elevated CO₂ on photosynthesis ($\mu\text{mol m}^{-2}\text{s}^{-1}$) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	19.49	18.79	26.75	25.26	24.27	23.14
Elevated CO ₂	26.37	25.79	37.84	34.26	33.48	30.24
CD at 5%						
Variety (V)		0.713		0.812		0.730
CO ₂		0.713		0.812		0.730
V x CO ₂		NS		1.149		1.033

Table 73. Effect of elevated CO₂ on the chlorophyll 'a' content (mg g⁻¹ FW) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	0.672	0.660	0.761	0.751	0.601	0.610
Elevated CO ₂	0.638	0.630	0.680	0.651	0.582	0.542
CD at 5%						
Variety (V)		0.020		0.018		NS
CO ₂		0.020		0.018		0.080
V x CO ₂		NS		NS		NS

Table 74. Effect of elevated CO₂ on the chlorophyll 'b' content (mg g⁻¹ FW) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	0.511	0.491	0.502	0.512	0.462	0.453
Elevated CO ₂	0.463	0.472	0.482	0.490	0.445	0.431
CD at 5%						
Variety (V)	NS		0.527		0.007	
CO ₂	0.018		0.527		0.007	
V x CO ₂	NS		0.745		NS	

Table 75. Effect of elevated CO₂ on the total chlorophyll content (mg g⁻¹ FW) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	1.167	1.134	1.257	1.263	1.070	1.060
Elevated CO ₂	1.093	1.090	1.160	1.145	1.020	0.970
CD at 5%						
Variety (V)	NS		NS		NS	
CO ₂	0.032		0.019		0.057	
V x CO ₂	NS		NS		NS	

4.2.6.3 Total chlorophyll

The total chlorophyll content was significantly reduced under elevated levels of CO₂ (Table 75). The reduction ranged from 5% (ripening) to 8% (heading) and in PRH-10 and from 5% (ripening) to 9% (heading) in PS-2. The interaction effect of variety x CO₂ was not significant. The total chlorophyll content was maximum at the heading stage. The amount of total chlorophyll was more in variety PRH-10 than that of PS-2 irrespective of treatment.

4.2.7 Stomatal conductance

Elevated CO₂ significantly reduced the stomatal conductance in both the rice varieties (Table 76). The reduction ranged from 27% (heading) to 30% (vegetative) in PRH-10 and from 31% (ripening) to 39% (heading) in PS-2. The interaction of variety x CO₂ was significant. The stomatal conductance was maximum at the heading stage. It was higher in PRH-10 compared to PS-2.

4.2.8 Respiration

A significant reduction in the respiration rate was recorded at the elevated levels of CO₂ in both the varieties (Table 77). The reduction in respiration rate ranged from 12% (ripening) to 39% (heading) in PRH-10 and from 18% (vegetative) to 35% (heading) in PS-2. The interaction of variety x CO₂ was significant in all the three growth stages. The respiration rate was maximum at the vegetative stage. Rate of respiration was higher in PRH-10 compared to PS-2.

4.2.9 Carbohydrate content in the leaves

4.2.9.1 Reducing sugars

CO₂ enrichment brought about significant increase in the reducing

Table 76. Effect of elevated CO₂ on stomatal conductance ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	0.800	0.760	1.29	1.37	1.090	1.050
Elevated CO ₂	0.560	0.500	0.94	0.83	0.780	0.720
CD at 5%						
Variety (V)	0.021		0.038		0.029	
CO ₂	0.021		0.038		0.029	
V x CO ₂	NS		0.053		NS	

Table 77. Effect of elevated CO₂ on respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	5.68	4.53	8.14	7.46	7.25	6.55
Elevated CO ₂	4.26	3.72	4.99	4.88	6.36	5.14
CD at 5%						
Variety (V)	0.096		0.136		0.107	
CO ₂	0.096		0.136		0.107	
V x CO ₂	0.136		0.193		0.152	

sugar content of the leaves in both the varieties (Table 78). The increase varied from 43% (heading) to 66% (vegetative) in PRH-10 and in case of PS-2, it ranged from 51% (ripening) to 73% (heading). The interaction of variety and CO₂ was significant at all the growth stages. Amount of reducing sugars was maximum at the heading stage. It was more in PRH-10 compared to PS-2 irrespective of treatment.

4.2.9.2 Non-reducing sugars

A significant increase in the non-reducing sugar content of leaves was observed under elevated CO₂ conditions (Table 79). The CO₂ induced increase ranged from 56% (heading) to 63% (ripening) in PRH-10 and from 63% (heading) to 68% (vegetative) in PS-2. The interaction effect of variety and CO₂ was significant at the vegetative stage. The amount of non-reducing sugar was maximum at the heading stage. The non-reducing content was higher in PRH-10 than that of PS-2 irrespective of the treatments.

4.2.9.3 Total sugars

Elevated CO₂ significantly increased the total sugar content of leaves in both the rice varieties (Table 80). The increase ranged from 50% (heading) to 58% (vegetative and ripening) in PRH-10 and from 61% (vegetative) to 73% (ripening) in PS-2. The variety x CO₂ interaction was significant at all the three growth stages. The total sugar content in the leaves was maximum at the heading stage. It was higher in PRH-10 than that of PS-2.

4.2.9.4 Starch

Elevated CO₂ brought about significant increase in the starch content of the leaves in both the varieties (Table 81). The increase varied from 61% (heading) to 115% (vegetative) in PRH-10 and in case of PS-2, it varied from

Table 78. Effect of elevated CO₂ on the reducing sugar content (mg g⁻¹ DW) in the leaves of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	15.48	13.64	23.68	17.82	19.76	13.79
Elevated CO ₂	25.68	21.71	33.91	30.84	29.82	25.84
CD at 5%						
Variety (V)	0.497		0.687		0.578	
CO ₂	0.497		0.687		0.578	
V x CO ₂	0.702		0.972		0.818	

Table 79. Effect of elevated CO₂ on the non-reducing sugar content (mg g⁻¹ DW) in the leaves of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	32.83	29.39	42.27	37.80	36.78	34.39
Elevated CO ₂	51.81	47.84	65.87	61.75	59.92	57.82
CD at 5%						
Variety (V)	1.501		1.526		1.096	
CO ₂	1.051		1.526		1.096	
V x CO ₂	1.487		NS		NS	

Table 80. Effect of elevated CO₂ on the total sugar content (mg g⁻¹ DW) in the leaves of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	48.25	43.01	66.58	55.60	56.73	48.15
Elevated CO ₂	76.45	69.18	99.57	92.20	89.72	83.30
CD at 5%						
Variety (V)		1.803		2.435		1.348
CO ₂		1.803		2.435		1.348
V x CO ₂		NS		3.444		1.906

Table 81. Effect of elevated CO₂ on the starch content (mg g⁻¹ DW) in the leaves of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	26.39	24.32	43.65	41.39	36.72	31.97
Elevated CO ₂	56.79	50.28	70.42	65.68	60.43	55.79
CD at 5%						
Variety (V)		0.901		1.45		1.30
CO ₂		0.901		1.45		1.30
V x CO ₂		1.275		2.04		NS

59% (heading) to 107% (vegetative). The interaction effect of variety and CO₂ was significant except at the ripening stage. Maximum amount of starch in leaves was recorded at the heading stage. It was higher in PRH-10 compared to PS-2.

4.2.9.5 Total non-structural carbohydrate (TNC)

CO₂ enrichment brought about a significant increase in total non-structural carbohydrate content of leaves (Table 82). The increase ranged from 54% (heading) to 79% (vegetative) in PRH-10 and from 62% (heading) to 77% (vegetative) in PS-2. The interactive effect of variety and CO₂ was significant. The total non-structural carbohydrate content was maximum at the ripening stage. It was more in PRH-10 at all the growth stages compared to PS-2.

4.2.10 Carbohydrate content in the stem

4.2.10.1 Reducing sugars

CO₂ enrichment significantly increased the reducing sugar content of the stem (Table 83). The increase ranged from 55% (heading) to 85% (vegetative) in PRH-10 and from 56% (heading and ripening) to 81% (vegetative) in PS-2. The interaction of variety and CO₂ was significant throughout the growth. The maximum amount was observed at the heading stage for both the varieties. The total sugar content was higher in PRH-10 irrespective of treatments.

4.2.10.2 Non-reducing sugars

Elevated CO₂ brought about significant increase in the non-reducing sugar content of the stem (Table 84). The increase ranged from 40% (vegetative) to 45% (heading) in PRH-10 and from 45% (heading) to 50%

Table 82. Effect of elevated CO₂ on the total non-structural carbohydrate content (mg g⁻¹ DW) in the leaves of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	74.63	67.32	110.22	96.98	93.45	80.14
Elevated CO ₂	133.88	119.46	169.98	157.20	150.14	139.11
CD at 5%						
Variety (V)		2.41		3.47		2.42
CO ₂		2.41		3.47		2.42
V x CO ₂		3.42		NS		NS

Table 83 Effect of elevated CO₂ on the reducing sugar content (mg g⁻¹ DW) in the stem of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	17.49	15.37	26.35	23.68	22.63	20.39
Elevated CO ₂	32.39	27.82	40.76	36.84	37.46	31.73
CD at 5%						
Variety (V)		0.952		0.531		0.728
CO ₂		0.952		0.530		0.728
V x CO ₂		1.346		0.751		

Table 84. Effect of elevated CO₂ on the total non-reducing sugar content (mg g⁻¹ DW) in the stem of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	42.46	39.49	52.34	48.64	48.67	44.39
Elevated CO ₂	59.39	58.74	75.79	70.78	68.72	66.82
CD at 5%						
Variety (V)		1.355		1.604		1.804
CO ₂		1.355		1.604		1.804
V x CO ₂		1.916		2.269		2.552

Table 85. Effect of elevated CO₂ on the total sugar content (mg g⁻¹ DW) in the stem of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	59.90	54.83	78.65	72.12	71.31	64.75
Elevated CO ₂	91.74	86.55	116.51	107.23	106.17	115.26
CD at 5%						
Variety (V)		2.481		1.769		NS
CO ₂		2.481		1.769		2.537
V x CO ₂		NS		2.502		NS

(ripening) in PS-2. The interactive effect of variety and CO₂ was significant at the three growth stages. The non-reducing sugar content was maximum at heading stage. The amount of non-reducing sugar was higher in PRH-10 at all the stages of growth.

4.2.10.3 Total sugars

Total sugars content in the stem was significantly increased at elevated CO₂ (Table 85). The increase ranged as 58% (vegetative), 49% (heading) and 48% (ripening) in PS-2, and 53% (vegetative), 48% (heading), 49% (ripening) in PRH-10. The interaction effect of variety and CO₂ was significant at the heading stage. The total sugar content was maximum at the heading stage. The amount of total sugar was more in PRH-10 compared to PS-2.

4.2.10.4 Starch

CO₂ enrichment brought about significant increase in the starch content of the stem (Table 86). The increase in PRH-10 ranged from 50% (heading) to 83% (vegetative) and in case of PS-2, it ranged from 41% (heading) to 76% (vegetative). The interaction of variety and CO₂ was significant. Maximum starch content was recorded at the ripening stage. It was more in PRH-10 compared to PS-2.

4.2.10.5 Total non-structural carbohydrate (TNC)

A significant increase in the total non-structural carbohydrate of the stem was observed under elevated CO₂ condition in both the varieties (Table 87). The increase varied from 45% (ripening) to 64% (vegetative) in PRH-10 and in case of PS-2, it ranged from 45% (heading) to 64% (vegetative). The interaction of variety and CO₂ on TNC was significant except at the ripening stage. The maximum production of total non-structural carbohydrate was

Table 86. Effect of elevated CO₂ on the starch content (mg g⁻¹ DW) in the stem of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	36.73	35.46	55.68	53.68	44.63	44.67
Elevated CO ₂	67.26	62.42	83.24	75.45	71.38	65.29
CD at 5%						
Variety (V)	1.44		1.97			1.80
CO ₂	1.44		1.97			1.80
V x CO ₂	2.04		2.78			2.55

Table 87. Effect of elevated CO₂ on the total non-structural carbohydrate content (mg g⁻¹ DW) in the stem of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	96.60	90.36	134.32	125.78	122.43	109.41
Elevated CO ₂	158.97	148.96	199.75	182.66	177.55	177.20
CD at 5%						
Variety (V)	2.56		2.37			NS
CO ₂	2.56		2.37			21.30
V x CO ₂	3.61		3.35			

found at the heading stage. PRH-10 had greater total non-structural carbohydrate than PS-2.

4.2.11 Carbohydrate content in panicle

4.2.11.1 Reducing sugars

Elevated CO₂ significantly increased the reducing sugar content in the panicle of both the varieties (Table 88). The increase was 30% and 38% in PRH-10 and 24% and 34%, in PS-2 at heading and ripening respectively. The variety and CO₂ interaction was significant at heading and ripening stages. The reducing sugar was maximum at the ripening stage irrespective of treatments and varieties. It was more in PRH-10 compared to PS-2.

4.2.11.2 Non-reducing sugars

Non-reducing sugar content of the panicle was significantly higher under elevated CO₂ condition (Table 89). The CO₂ induced increase ranged from 17% (heading) to 39% (ripening) in PRH-10 and from 15% (heading) to 36% (ripening) in PS-2. The variety x CO₂ interaction was not significant. The non-reducing sugar was maximum at the ripening stage. It was more in PRH-10 compared to PS-2 irrespective of treatments.

4.2.11.3 Total sugars

CO₂ enrichment brought about a significant increase in the total sugar content in the panicle (Table 90). The increase ranged from 22% (heading) to 38% (ripening) in PRH-10 and from 19% (heading) to 36% (ripening) in PS-2. The interaction variety x CO₂ was significant at all the stages of growth. Maximum amount of total sugar was found at ripening stage. The total sugar in the panicle was more in PRH-10 compared to PS-2.

Table 88. Effect of elevated CO₂ on reducing sugar content (mg g⁻¹ DW) in the panicle of the rice varieties in FACE

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	59.41	57.45	80.20	78.31
Elevated CO ₂	75.39	71.52	110.41	105.37
CD at 5%				
Variety (V)		1.36		2.46
CO ₂		1.36		2.46
V x CO ₂		1.92		3.49

Table 89. Effect of elevated CO₂ on the non-reducing sugar content (mg g⁻¹ DW) in the panicle of the rice varieties in FACE

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	74.72	71.40	90.91	88.99
Elevated CO ₂	87.50	82.41	126.26	121.40
CD at 5%				
Variety (V)		2.12		2.79
CO ₂		2.12		2.79
V x CO ₂		NS		NS

Table 90. Effect of elevated CO₂ on the total sugar content (mg g⁻¹DW) in the panicle of the rice varieties in FACE

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	134.06	128.80	171.31	167.20
Elevated CO ₂	162.90	153.81	236.75	226.71
CD at 5%				
Variety (V)		3.59		5.28
CO ₂		3.59		5.28
V x CO ₂		NS		NS

Table 91. Effect of elevated CO₂ on the starch content (mg g⁻¹ DW) in the panicle of the rice varieties in FACE

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	151.40	142.50	180.67	175.31
Elevated CO ₂	198.45	182.71	249.40	231.90
CD at 5%				
Variety (V)		5.016		5.413
CO ₂		5.016		5.413
V x CO ₂		7.094		7.655

4.2.11.4 Starch

Starch content in the panicle was significantly increased at elevated CO₂ condition (Table 91). It ranged from 31% (heading) to 38% (ripening) in PRH-10 and from 28% (heading) to 32% (ripening) in PS-2. The interaction of variety and CO₂ was significant throughout the growth period. Maximum starch content was observed at the ripening stage. The starch content was more in PRH-10 compared to PS-2.

4.2.11.5 Total non-structural carbohydrate (TNC)

The total non-structural carbohydrate content in the panicle showed a significant increase at higher CO₂ condition (Table 92). The increase ranged from 27% (heading) to 36% (ripening) in PRH-10 and in PS-2, it varied from 24% (heading) to 33% (ripening). The interactive effect of variety and CO₂ was significant at the ripening stage. Maximum amount of total non-structural carbohydrate was recorded at ripening stage irrespective of treatments. The TNC content was more in PRH-10.

4.2.12 Sucrose phosphate synthase (SPS)

CO₂ enrichment brought about a significant increase in the activity of sucrose phosphate synthase (Table 93). The increase ranged from 20% (vegetative) to 26% (heading) in PRH-10 and in case of PS-2, it was from 15% (ripening) to 28% (heading). The interaction effect of variety and CO₂ was significant at the heading stage. SPS activity was maximum at the heading stage. PRH-10 showed greater activity of SPS at all growth stages compared to PS-2.

Table 92. Effect of elevated CO₂ on the total non-structural carbohydrates (mg g⁻¹DW) in the panicle of the rice varieties in FACE

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	283.38	271.24	358.42	342.41
Elevated CO ₂	361.17	336.37	486.07	458.30
CD at 5%				
Variety (V)		8.13		14.69
CO ₂		8.13		14.69
V x CO ₂		11.49		NS

Table 93. Effect of elevated CO₂ on sucrose phosphate synthase activity (μmol mg⁻¹ protein min⁻¹) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	24.23	23.56	27.47	26.11	23.46	23.14
Elevated CO ₂	29.17	28.72	34.62	33.62	29.12	26.66
CD at 5%						
Variety (V)		0.832		0.831		1.082
CO ₂		0.832		0.831		1.082
V x CO ₂		1.177		1.175		1.533

4.2.13 Antioxidant enzymes

4.2.13.1 Superoxide dismutase (SOD)

The activity of superoxide dismutase significantly decreased at high concentrations of CO₂ (Table 94). The reduction ranged from 38% (heading) to 43% (vegetative) in PRH-10 and from 42% (ripening) to 45% (vegetative) in PS-2. The interactive effect of variety and CO₂ on SOD was significant at the heading stage. The activity of SOD was maximum at the ripening stage. PRH-10 showed higher activity of SOD.

4.2.13.2 Ascorbate peroxidase (APX)

Elevated CO₂ significantly reduced the ascorbate peroxidase activity in both the rice varieties (Table 95). The reduction ranged from 56% (ripening) to 61% (vegetative) in PRH-10 and from 58% (ripening) to 61% (vegetative) in PS-2. The interaction between variety and CO₂ was significant at vegetative and heading stages. Higher activity of APX was observed at the ripening stage. PRH-10 showed higher activity of APX at all growth stages compared to PS-2.

4.2.13.3 Glutathione reductase (GR)

Elevated CO₂ significantly decreased the activity of glutathione reductase (Table 96). The reduction in GR activity ranged from 50% (vegetative) to 63% (heading) in PRH-10 and from 57% (vegetative) to 67% (heading) in PS-2. The variety and CO₂ interaction was significant at all growth stages. The activity of GR was maximum at the ripening stage. Higher activity of GR was observed in the variety PRH-10.

Table 94. Effect of elevated CO₂ on the superoxide dismutase activity (units min⁻¹ mg⁻¹ protein) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	11.17	11.13	15.10	15.42	18.77	17.43
Elevated CO ₂	6.39	6.12	9.37	8.85	11.46	10.16
CD at 5%						
Variety (V)		NS		NS		0.435
CO ₂		0.357		0.336		0.435
V x CO ₂		NS		0.475		NS

Table 95. Effect of elevated CO₂ on the ascorbate peroxidase activity (μmol ascorbate oxidised min⁻¹ mg⁻¹ FW) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	92.32	86.91	113.69	97.22	117.79	112.32
Elevated CO ₂	36.46	33.49	45.82	40.43	51.88	46.81
CD at 5%						
Variety (V)		2.06		1.71		3.56
CO ₂		2.06		1.71		3.56
V x CO ₂		2.92		2.43		

Table 96. Effect of elevated CO₂ on the glutathione reductase activity (Δ OD min⁻¹ mg⁻¹ protein) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	0.12	0.07	0.21	0.18	0.24	0.21
Elevated CO ₂	0.06	0.03	0.08	0.07	0.09	0.07
CD at 5%						
Variety (V)	0.0014		0.0044		0.0037	
CO ₂	0.0014		0.0044		0.0037	
V x CO ₂	0.0020		0.0063		0.0053	

Table 97. Effect of elevated CO₂ on the carbon content (% DM) in the leaves of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	42.41	39.48	37.25	31.48	40.34	36.82
Elevated CO ₂	45.14	43.76	40.57	38.21	44.72	42.72
CD at 5%						
Variety (V)	1.067		0.926		0.892	
CO ₂	1.067		0.926		0.892	
V x CO ₂	1.510		1.310		1.262	

4.2.14 Carbon (C)

Leaves

Elevated CO₂ brought about significant increase in the carbon content of the leaves (Table 97). The increase ranged from 9% (heading) to 11% (ripening) in PRH-10 and from 11% (vegetative) to 22% (heading) in PS-2. The interaction of variety and CO₂ concentration was significant at all the growth stages. The carbon content was maximum at the vegetative stage. It was greater in PRH-10 compared to PS-2 irrespective of treatments.

Stem

Elevated CO₂ significantly increased the carbon content of the stem (Table 98). The maximum increase was 12% (heading) in both the varieties. The interaction CO₂ x variety was significant at the ripening stage. The carbon content was maximum at the vegetative stage. Among the varieties, PRH-10 had greater carbon content compared to PS-2.

Root

A significant increase in carbon content of the root was observed at high concentrations of CO₂ (Table 99). The CO₂ induced enhancement ranged from 8% (ripening) to 27% (heading) in PRH-10 and from 12% (ripening) to 24% (heading) in PS-2. The interactive effect of variety x CO₂ was not significant. Higher amount of carbon in the roots was observed at the vegetative stage irrespective of treatments. PRH-10 had higher carbon content compared to PS-2.

4.2.15 Nitrogen (N)

Leaves

CO₂ enrichment brought about a significant decrease in the nitrogen

Table 98. Effect of elevated CO₂ on the carbon content (% DM) in the stem of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	44.60	42.72	38.41	33.94	41.70	36.80
Elevated CO ₂	45.69	43.98	42.82	38.14	43.80	41.40
CD at 5%						
Variety (V)		0.763		1.001		0.772
CO ₂		0.763		1.001		0.772
V x CO ₂		NS		NS		1.092

Table 99. Effect of elevated CO₂ on the carbon content (% DM) in the roots of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	43.73	42.78	31.72	30.19	39.42	36.52
Elevated CO ₂	44.82	43.79	40.23	37.53	42.75	40.72
CD at 5%						
Variety (V)		1.321		1.430		0.916
CO ₂		1.321		1.430		0.916
V x CO ₂		NS		NS		NS

content of the leaves (Table 100). The reduction in PRH-10 was 7%, 9% and 10% and in case of PS-2, it was 13%, 13% and 10% at vegetative, heading and ripening stages, respectively. The interactive effect of variety and CO₂ was significant. The nitrogen content was maximum at the vegetative stage. PRH-10 had greater amount of nitrogen compared to PS-2.

Stem

High CO₂ brought about significant reduction in the nitrogen content of the stem (Table 101). The reduction ranged from 12% (vegetative and heading) to 13% (ripening) in PRH-10 and from 13% (ripening) to 18% (heading) in PS-2. The interaction between CO₂ and variety was significant throughout the growth period. The nitrogen content was maximum at the vegetative stage. Greater nitrogen content was recorded in PRH-10 compared to PS-2.

Root

A significant decrease in the nitrogen content of root was observed at high concentration of CO₂ (Table 102). The reduction ranged from 12% (heading) to 21% (vegetative) in PRH-10 and from 13% (ripening) to 32% (vegetative) in PS-2. The interaction of CO₂ and variety was significant at all the three stages. The nitrogen content was maximum at the vegetative stage. PRH-10 had greater amount of nitrogen compared to PS-2.

4.2.16 Carbon : nitrogen ratio

Leaves

The ratio of carbon to nitrogen content in the leaves significantly increased at elevated CO₂ (Table 103). The increase in C/N ratio ranged from 16% (vegetative) to 23% (ripening) in PRH-10 and from 28% (vegetative) to

Table 100. Effect of elevated CO₂ on the nitrogen content (% DM) in the leaves of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	4.72	4.47	2.72	2.81	4.24	3.85
Elevated CO ₂	4.38	3.88	2.47	2.44	3.81	3.47
CD at 5%						
Variety (V)	0.139		0.051		0.022	
CO ₂	0.139		0.051		0.022	
V x CO ₂	0.197		0.07		0.031	

Table 101. Effect of elevated CO₂ on the nitrogen content (% DM) in the stem of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	4.47	3.90	3.77	3.11	4.07	3.51
Elevated CO ₂	3.92	3.87	3.31	2.57	3.53	3.07
CD at 5%						
Variety (V)	0.092		0.056		0.098	
CO ₂	0.092		0.056		0.098	
V x CO ₂	0.131		0.079		0.138	

Table 102. Effect of elevated CO₂ on the nitrogen content (% DM) in the roots of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	3.90	3.13	2.70	2.52	3.02	2.71
Elevated CO ₂	3.10	2.12	2.39	2.15	2.63	2.57
CD at 5%						
Variety (V)		0.088		0.055		0.118
CO ₂		0.088		0.055		0.118
V x CO ₂		0.125		0.079		0.167

Table 103. Effect of elevated CO₂ on the ratio of carbon to nitrogen in the leaves of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	8.99	8.83	13.69	11.20	9.51	9.55
Elevated CO ₂	10.38	11.28	16.43	15.67	11.74	12.42
CD at 5%						
Variety (V)		0.376		0.509		0.272
CO ₂		0.376		0.509		0.272
V x CO ₂		0.532		0.720		0.385

40% (heading) in PS-2. The variety and CO₂ interaction was significant at all growth stages. The carbon : nitrogen ratio was maximum at the heading stage. PRH-10 had greater C/N ratio compared to PS-2 at the vegetative and heading stages.

Stem

Elevated CO₂ significantly increased the C/N ratio in the stem (Table 104). This increase ranged from 11% (vegetative) to 27% (heading) in PRH-10 and from 28% (ripening) to 35% (heading) in PS-2. The interaction of variety and CO₂ was significant at all the three stages of crop growth. The C/N ratio was maximum at the heading stage. PS-2 had greater C/N ratio compared to PRH-10.

Root

CO₂ enrichment brought about a significant increase in the ratio of carbon to nitrogen content in the root (Table 105). The increase ranged from 25% (ripening) to 43% (heading) in PRH-10 and from 12% (ripening) to 51% (vegetative) in PS-2. The variety and CO₂ interaction was significant at the vegetative and ripening stages. The C/N ratio was maximum at the heading stage. Among the varieties, PS-2 had greater C/N ratio compared to PRH-10.

4.2.17 Total soluble protein

Higher levels of CO₂ brought about a significant reduction in the total leaf soluble protein (Table 106). The reduction in PS-2, ranged from 23% (heading) to 37% (vegetative) whereas it ranged from 24% (heading) to 34% (vegetative) in PRH-10. The interactive effect of variety and CO₂ was significant at the heading and ripening stages. The leaf soluble protein content

Table 104. Effect of elevated CO₂ on the ratio of carbon to nitrogen in the stem of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	9.98	10.98	10.19	10.93	10.25	10.46
Elevated CO ₂	11.04	11.47	12.91	14.84	12.41	13.47
CD at 5%						
Variety (V)		0.366		0.456		0.445
CO ₂		0.366		0.456		0.445
V x CO ₂		NS		0.645		0.629

Table 105. Effect of elevated CO₂ on the ratio of carbon to nitrogen in the roots of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	11.21	13.66	11.75	11.98	13.05	13.47
Elevated CO ₂	14.45	20.66	16.83	17.46	16.25	15.04
CD at 5%						
Variety (V)		0.411		0.392		NS
CO ₂		0.411		0.392		0.405
V x CO ₂		0.581		NS		0.572

Table 106. Effect of elevated CO₂ on the leaf soluble protein (mg g⁻¹ FW) content of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	5.63	5.36	8.31	7.80	7.61	7.12
Elevated CO ₂	3.70	3.40	6.31	6.02	5.22	4.69
CD at 5%						
Variety (V)		0.145		0.230		0.236
CO ₂		0.145		0.230		0.236
V x CO ₂		NS		0.325		0.334

Table 107. Effect of elevated CO₂ on the nitrate reductase activity (μmol NO₂ g⁻¹ hr⁻¹) of the rice varieties in FACE

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	1.13	0.97	1.59	1.54	1.33	1.07
Elevated CO ₂	2.43	2.48	3.74	2.68	3.79	2.57
CD at 5%						
Variety (V)		0.063		0.082		0.065
CO ₂		0.063		0.082		0.065
V x CO ₂		0.090		0.117		0.092

was maximum at the heading stage irrespective of treatments. PRH-10 had greater leaf soluble protein content than PS-2.

4.2.18 Nitrate reductase activity (NR)

CO₂ enrichment significantly increased the activity of nitrate reductase (Table 107). The increase was from 1.1 fold (vegetative) to 1.8 fold (heading) in PRH-10 and in case of PS-2, it ranged from 1.0 fold (heading) to 1.5 fold (vegetative). The interactive effect of CO₂ and varieties was found significant in all the three growth stages. The activity of NR was maximum at heading stage. PRH-10 showed greater activity of NR compared to PS-2.

4.2.19 Yield and yield components

4.2.19.1 Grain yield per square metre

Grain yield per square metre significantly increased under elevated CO₂ (Table 108). The increase was 24% in PRH-10 and 20% in PS-2. The interaction effect of variety and CO₂ on grain yield was significant. Grain yield was greater in PRH-10 compared to PS-2 irrespective of treatment.

4.2.19.2 Number of panicle per plant

There was a significant increase in the number of panicle per plant under elevated CO₂ conditions (Table 108). The increase 50% in PRH-10 and from 36% in PS-2. The variety and CO₂ interaction was significant. The number of panicles were more in PRH-10 compared to PS-2.

4.2.19.3 Length of panicle

At elevated levels of CO₂, a significant increase in the panicle length was observed (Table 108). The increase was 23% in PRH-10 and 20% in PS-2. The interaction effect of variety and CO₂ was significant. Panicle length was more in PRH-10.

Table 108. Effect of elevated CO₂ on the yield and yield components of the rice varieties in FACE

Treatments	Grain yield/m ² (g/m ²)		Length of panicle		No. of panicles/plant	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	613.46	550.38	23.40	23.10	9.33	10.33
Elevated CO ₂	757.38	661.38	28.70	27.80	14.00	14.00
CD at 5%						
Variety (V)	28.68		0.392		NS	
CO ₂	28.68		0.392		0.62	
V x CO ₂	NS		0.554		NS	

Table 109. Effect of elevated CO₂ on the yield components of the rice varieties in FACE

Treatments	Grain No./panicle		Harvest index		1000-grain mass (g)	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	147.30	142.12	0.381	0.370	21.12	19.91
Elevated CO ₂	240.34	220.31	0.460	0.451	27.68	27.41
CD at 5%						
Variety (V)	6.98		0.011		0.379	
CO ₂	6.98		0.011		0.379	
V x CO ₂	9.88		NS		0.536	

4.2.19.4 Grain number per panicle

CO₂ enrichment brought about significant increase in the grain number per panicle in both the varieties (Table 109). The increase was 63% in PRH-10 and 55% in PS-2. The interaction of variety and CO₂ was significant. More number of grains per panicle was observed in PRH-10.

4.2.19.5 1000-grain mass

Elevated CO₂ significantly increased the grain mass of both the varieties (Table 109). The increase was 31% for PRH-10 and 37% for PS-2. The interaction effect of variety and CO₂ was significant. The 1000-grain mass was higher in PRH-10 compared to PS-2.

4.2.19.6 Harvest index

CO₂ enrichment brought about significant increase in the harvest index of both the varieties (Table 109). The increase was 21% in PRH-10 and 22% in PS-2. The variety and CO₂ interaction was not significant. The harvest index was more in PRH-10 as compared to PS-2.

4.2.20 Grain quality

4.2.20.1 Reducing sugar

Reducing sugar content in grains significantly increased under elevated CO₂ condition (Table 110a). The CO₂ induced enhancement was 55% in PRH-10 and 58% in PS-2. The interaction effect of variety and CO₂ was significant. PRH-10 has greater amount of reducing sugars compared to PS-2.

4.2.20.2 Non-reducing sugar

Elevated CO₂ significantly increased the non-reducing sugars in grain (Table 110a). The enhancement was 10% in PRH-10 and 18% in PS-2. The

interaction effect was significant. PRH-10 had greater amount of non-reducing sugars than PS-2.

4.2.20.3 Total sugar

The total sugar content of the grain significantly increased at elevated levels of CO₂ (Table 110a). The increase was 30% in PRH-10 and 35% in PS-2. The variety and CO₂ interaction was not significant. The amount of total sugars in the grain was more in PRH-10 (274 mg g⁻¹ DW) compared to PS-2 (270 mg g⁻¹ DW).

4.2.20.4 Starch

CO₂ enrichment brought about a significant increase in the starch content of grain (Table 110a). The increase was 28% in PRH-10 and 25% in PS-2. The interaction effect of variety and CO₂ was not significant. Starch content was more in the grains of PRH-10 (294.67 mg g⁻¹ DW) than that of PS-2 (280.91 mg g⁻¹ DW).

4.2.20.5 Amylose

The amylose content in the grain significantly increased at elevated CO₂ concentration (Table 110b). The increase was 3% in PRH-10 and 8% in PS-2. The interaction between CO₂ and variety was significant. The amylose content was 25.41% in PRH-10, whereas it was 27.73% in PS-2.

4.2.20.6 Total non-structural carbohydrate (TNC)

CO₂ enrichment brought about a significant increase in the total non-structural carbohydrate content of grain (Table 110b). The increase was 29% in PRH-10 and 30% in PS-2. The interactive effect of variety and CO₂ was not significant. TNC content was greater in PRH-10 compared to PS-2.

Table 110a. Effect of elevated CO₂ on the grain quality parameters of the rice varieties in FACE

Treatments	Reducing sugars (mg g ⁻¹ DW)		Non-reducing sugars (mg g ⁻¹ DW)		Total sugars (mg g ⁻¹ DW)		Starch (mg g ⁻¹ DW)	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	88.33	82.71	122.34	118.32	210.43	200.32	230.22	224.37
Elevated CO ₂	137.12	131.36	134.14	139.63	274.14	270.40	294.67	280.91
CD at 5%								
Variety (V)		2.856		NS		NS		6.98
CO ₂		2.856		4.875		28.79		6.98
V x CO ₂		4.039		6.894		NS		NS

Table 110b. Effect of elevated CO₂ on the grain quality parameters of the rice varieties in FACE

Treatments	Amylose (%)		TNC (mg g ⁻¹ DW)		Nitrogen (%)		Protein (%)	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂	24.81	25.70	441.36	424.69	1.62	1.59	9.63	9.46
Elevated CO ₂	25.41	27.73	568.81	551.01	1.59	1.54	9.46	9.16
CD at 5%								
Variety (V)		0.813		18.96		0.039		0.236
CO ₂		0.813		18.96		0.039		0.236
V x CO ₂		1.149		NS		NS		NS

4.2.20.7 Nitrogen (N)

The nitrogen content in grains significantly decreased under elevated CO₂ (Table 110b). The reduction was 2% in PRH-10 and 3% in PS-2. The interaction effect was not significant. Nitrogen content was greater in PRH-10 compared to PS-2.

4.2.20.8 Protein

Elevated CO₂ brought about significant decrease in the protein content of the grain (Table 110b). The reduction at elevated CO₂ was 2% for PRH-10 and 3% for PS-2. The variety and CO₂ interaction was not significant. Protein content was more for PRH-10 (9.46%) compared to PS-2 (9.16%).

4.2.20.9 Calcium (Ca)

The calcium content of grain significantly increased under the elevated CO₂ in both the varieties (Table 110c). The reduction was 15% in PRH-10 and 14% in PS-2. The variety and CO₂ interaction was not significant. The calcium content was more in PRH-10 compared to PS-2.

4.2.20.10 Potassium (K)

CO₂ enrichment brought about a significant increase in the potassium content of the grain (Table 110c). The increase was 39% in PRH-10 and 41% in PS-2. The interaction between variety and CO₂ was not significant. The K content was more in PRH-10 compared to PS-2.

4.3 PHYTOTRON STUDIES

Studies on the response of rice varieties to the interaction of elevated CO₂ and temperature was done in controlled plant growth chamber at the National Phytotron Facility, Indian Agricultural Research institute, New Delhi.

Table 110c. Effect of elevated CO₂ on the grain quality parameters of the rice varieties in FACE

Treatments	Calcium (%)		Potassium (%)	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂				
Elevated CO ₂	0.081	0.079	0.180	0.170
	0.093	0.090	0.250	0.240
CD at 5%				
Variety (V)		0.002		0.005
CO ₂		0.002		0.005
V x CO ₂		NS		NS

4.3.1 Plant growth

4.3.1.1 Plant height

Elevated CO₂ brought about significant increase in the height of plants in both the varieties throughout the growth period (Table 111). The increase ranged from 41% (heading) to 57% (ripening) in PRH-10 and in case of PS-2, it varied from 20% (ripening) to 39% (heading) irrespective of the treatments. The increase in temperature significantly decreased the plant height throughout the growth period. The reduction in PRH-10 at the heading stage was 20% under ambient condition and 18% under elevated CO₂. In case of PS-2, the reduction in plant height at the heading stage was 14% and 16% at the elevated and ambient conditions, respectively. The interaction effect of CO₂ and temperature was significant at the heading stage for both the varieties. The plant height was significantly greater in PS-2 compared to the hybrid PRH-10.

4.3.1.2 Number of tillers

Elevated CO₂ brought about significant increase in the production of tillers in both the varieties (Table 112). The increase in the number of tillers was more in PRH-10 (20% in vegetative, 16% in heading and ripening stages) and in case of PS-2, it ranged from 16% (vegetative) to 25% (ripening). The higher temperature brought about a significant reduction in the tiller production. The reduction was 23% in PRH-10 and 25% in PS-2 under ambient condition. At elevated CO₂, the reduction was 20% in PRH-10 and 22% in PS-2. The CO₂ and temperature interaction was not significant. More number of tillers were produced in PRH-10 compared to PS-2 at the vegetative stage.

Table 111. Interactive effect of elevated CO₂ and temperature on plant height (cm) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	64.56	71.63	96.56	101.76	104.10	114.20
Elevated CO ₂ + ambient temp.	64.40	70.83	100.50	105.00	110.40	116.33
Ambient CO ₂ + elevated temp.	56.36	60.70	76.56	84.23	89.43	95.07
Elevated CO ₂ + elevated temp.	53.26	61.43	81.16	90.90	95.32	99.63
CD at 5%						
Variety (V)	1.133		1.459		0.675	
CO ₂	NS		1.459		0.675	
V x CO ₂	NS		NS		NS	
T	1.133		1.459		0.675	
V x T	NS		NS		NS	
CO ₂ x T	NS		2.064		NS	
V x CO ₂ x T	NS		2.918		1.351	

Table 112. Interactive effect of elevated CO₂ and temperature on the number of tillers per plant in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	10.00	10.33	12.33	12.33	13.00	12.33
Elevated CO ₂ + ambient temp.	12.00	12.33	14.67	14.67	15.00	15.00
Ambient CO ₂ + elevated temp.	7.67	8.00	9.00	9.00	9.33	9.00
Elevated CO ₂ + elevated temp.	9.67	10.33	11.33	11.33	11.67	11.67
CD at 5%						
Variety (V)	0.21			NS		NS
CO ₂	0.21			0.33		0.39
V x CO ₂	NS			NS		NS
T	0.21			0.33		0.39
V x T	NS			NS		NS
CO ₂ x T	NS			NS		NS
C x CO ₂ x T	NS			NS		NS

4.3.1.3 Number of leaves

A significant increase in the number of leaves per plant was observed in both the varieties at the elevated CO₂ condition (Table 113). The increase ranged from 10% (vegetative) to 17% (ripening) in PRH-10, whereas in PS-2, it ranged from 15% (vegetative) to 21% (ripening). Elevated temperature rise brought about a significant reduction in the leaf number at both ambient and elevated CO₂ condition. At ambient CO₂, the reduction in PRH-10 variety ranged from 20% (ripening) to 28% (heading) and, it ranged from 20% (ripening) to 35% (heading) incase of PS-2. The reduction under elevated CO₂ ranged from 7% (ripening) to 19% (heading) in PRH-10 and it ranged from 18% (vegetative) to 33% (heading) in case of PS-2. The CO₂ and temperature interaction effect was significant at the heading and ripening stages in both the varieties. Among the varieties, PS-2 had significantly more number of leaves compared to PRH-10 irrespective of treatments.

4.3.1.4 Leaf area

The increase in CO₂ concentration significantly increased the leaf area (Table 114). The increase in PRH-10 varied from 22% (ripening) to 28% (vegetative) and in case of PS-2, it was from 21% (heading) to 27% (vegetative). Elevated temperature significantly reduced the leaf area in both the varieties under ambient and elevated CO₂ conditions. The reduction under ambient and elevated CO₂ ranged from 24% (vegetative) to 26% (heading) and from 21% (vegetative) to 22% (heading), respectively in PRH-10 and in case of PS-2, it ranged from 24% (ripening) to 30% (vegetative) and from 21% (heading) to 22% (vegetative), respectively. The temperature and CO₂

Table 113. Interactive effect of elevated CO₂ and temperature on number of leaves per plant in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	41.33	45.33	54.66	65.33	64.33	71.33
Elevated CO ₂ + ambient temp.	45.33	52.33	61.33	78.33	69.33	86.33
Ambient CO ₂ + elevated temp.	25.66	31.66	39.33	42.66	51.66	57.66
Elevated CO ₂ + elevated temp.	29.66	39.33	49.33	52.33	57.33	70.33
CD at 5%						
Vareity (V)						
CO ₂	0.603		0.586			0.679
V x CO ₂	0.603		0.586			0.679
T	0.853		0.829			0.961
V x T	0.603		0.586			0.679
CO ₂ x T	NS		0.829			0.961
V x CO ₂ x T	NS		0.829			0.961
	1.207		1.172			1.359

Table 114. Interactive effect of elevated CO₂ and temperature on leaf area (cm²) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	694.36	734.33	1073.26	1150.46	1056.50	1076.43
Elevated CO ₂ + ambient temp.	889.86	935.80	1363.63	1390.56	1293.96	1345.50
Ambient CO ₂ + elevated temp.	528.40	613.00	792.53	845.36	748.56	812.50
Elevated CO ₂ + elevated temp.	687.90	728.16	1053.43	1094.50	978.76	1048.56
CD at 5%						
Variety (V)	23.09		8.59			6.35
CO ₂	23.09		8.59			6.35
V x CO ₂	NS		12.15			8.98
T	23.09		8.59			6.35
V x T	NS		NS			8.98
CO ₂ x T	32.65		12.15			8.98
V x CO ₂ x T	NS		17.18			12.70

interaction effect was significant throughout the growth period in both the varieties. The leaf area was greater in PS-2 compared to PRH-10.

4.3.1.5 Root length

Elevated CO₂ significantly increased the length of roots in both the varieties (Table 115). The increase ranged from 14% (ripening) to 25% (heading) in PRH-10 and from 13% (ripening) to 17% (heading) in PS-2. The increase in temperature brought about significant reduction in root length in both the varieties. The reduction in PRH-10 ranged from 28% (ripening) to 33% (vegetative) and from 23% (heading) to 25% (ripening) under ambient and elevated CO₂, respectively. In case of PS-2, it ranged from 27% (ripening) to 33% (vegetative) under ambient CO₂ and it ranged from 23% (ripening) to 28% (heading) under elevated CO₂. The interaction effect of CO₂ and temperature was significant at the heading stage. PS-2 had greater root length compared to PRH-10.

4.3.2 Growth analysis

4.3.2.1 Leaf area index (LAI)

Elevated CO₂ significantly increased the leaf area index in both the varieties (Table 116). The increase in PRH-10 ranged from 21% (ripening) to 29% (vegetative) and in PS-2, from 24% (ripening) to 28% (heading). Increase in temperature caused significant reduction in LAI. The reduction under ambient condition ranged from 16% (heading) to 23% (vegetative) in PRH-10 and from 17% (vegetative) to 21% (ripening) in PS-2. The reduction under elevated condition ranged from 15% (ripening) to 20% (heading) in PRH-10 and from 17% (heading) to 20% (vegetative) in PS-2. The interactive

Table 115. Interactive effect of elevated CO₂ and temperature on root length (cm) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	5.40	6.26	11.00	12.13	14.16	15.01
Elevated CO ₂ + ambient temp.	6.36	7.33	13.53	14.50	16.53	17.26
Ambient CO ₂ + elevated temp.	3.63	4.06	7.66	8.36	10.46	11.03
Elevated CO ₂ + elevated temp.	4.36	5.33	10.60	10.03	12.23	13.56
CD at 5%						
Variety (V)		0.159		0.299		0.604
CO ₂		0.159		0.299		0.604
V x CO ₂		NS		NS		NS
T		0.159		0.299		0.604
V x T		0.225		NS		NS
CO ₂ x T		NS		0.423		NS
V x CO ₂ x T		NS		NS		NS

Table 116. Interactive effect of elevated CO₂ and temperature on leaf area index in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	1.74	1.84	2.68	2.88	2.89	2.94
Elevated CO ₂ + ambient temp.	2.22	2.34	3.41	3.48	3.48	3.61
Ambient CO ₂ + elevated temp.	1.32	1.53	2.23	2.36	2.84	2.38
Elevated CO ₂ + elevated temp.	1.67	1.82	2.38	2.51	2.45	2.87
CD at 5%						
Variety (V)	0.0595		0.0961		0.0737	
CO ₂	0.0595		0.0961		0.0737	
V x CO ₂	NS		NS		0.1042	
T	0.0595		0.0961		0.0737	
V x T	NS		NS		0.1042	
CO ₂ x T	0.0842		0.1359		0.1042	
V x CO ₂ x T	NS		NS		0.1774	

effect of CO₂ and temperature was significant. Leaf area index was greater for PS-2 compared to PRH-10.

4.3.2.2 Specific leaf area (SLA)

A significant reduction in specific leaf area was observed under elevated CO₂ (Table 117). The decrease was 26% in PRH-10 and 13% in PS-2. Elevated temperature significantly reduced the specific leaf area. The reduction under ambient and elevated CO₂ in PRH-10 ranged from 11% (heading) to 46% (ripening) and from 2% (heading) to 8% (vegetative) respectively. In case of PS-2, it ranged from 14% (vegetative) to 16% (heading) and from 5% (heading) to 12% (vegetative) respectively. The interaction of elevated CO₂ and temperature for the character was significant. The SLA was greater for PRH-10 at the heading and ripening stages.

4.3.2.4 Specific leaf weight (SLW)

Elevated CO₂ concentration brought about a significant increase in SLW (Table 118). The increase ranged from 5% (heading) to 36% (vegetative) in PRH-10 and from 12% (vegetative) to 15% (ripening) in PS-2. Elevated temperature caused a significant reduction in SLW. The reduction under ambient condition ranged from 10% (heading) to 32% (ripening) in PRH-10 and from 5% (ripening) to 18% (vegetative) in PS-2. The reduction under elevated condition varied from 3% (heading) to 9% (vegetative) in PRH-10 and from 4% (heading) to 14% (vegetative) in PS-2. The CO₂ x temperature interaction was significant at heading and ripening stages.

4.3.2.4 Net assimilation rate (NAR)

CO₂ enrichment brought about significant increase in the net assimilation rate. The increase was 20% in PRH-10 and 5% in PS-2 at the

Table 117. Interactive effect of elevated CO₂ and temperature on specific leaf area (cm² g⁻¹) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	103.17	118.44	114.66	92.04	74.81	92.05
Elevated CO ₂ + ambient temp.	112.64	135.62	117.55	96.57	75.35	69.83
Ambient CO ₂ + elevated temp.	128.88	129.05	137.31	112.14	112.60	76.47
Elevated CO ₂ + elevated temp.	153.19	151.70	123.78	96.59	76.89	80.54
CD at 5%						
Variety (V)	3.9117					2.8641
CO ₂	3.9117		3.3696			2.8641
V x CO ₂	NS		NS			4.0505
T	3.9117		3.3696			2.8641
V x T	5.5320		NS			4.0505
CO ₂ x T	5.5320		4.7654			4.0505
V x CO ₂ x T	NS		NS			5.7282

Table 118. Interactive effect of elevated CO₂ and temperature on specific leaf weight (1 x 10⁻³ g cm⁻²) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	9.692	8.443	8.721	10.865	13.368	16.117
Elevated CO ₂ + ambient temp.	8.878	7.373	8.507	10.356	12.272	14.320
Ambient CO ₂ + elevated temp.	7.759	7.749	7.283	8.917	8.881	13.077
Elevated CO ₂ + elevated temp.	6.528	6.592	8.079	10.353	13.006	12.416
CD at 5%						
Variety (V)		0.2283		0.3025		0.2703
CO ₂		0.2283		0.3025		0.2703
V x CO ₂		NS		NS		0.3823
T		0.2283		0.3025		0.2703
V x T		0.3229		NS		NS
CO ₂ x T		NS		0.4278		0.3823
V x CO ₂ x T		NS		0.6050		0.5407

heading-ripening stage (Table 119). Elevated temperature significantly reduced the net assimilation rate. The reduction under the ambient condition was 18-53% in PRH-10 and 22-37% in PS-2, whereas under the elevated CO₂ condition, it was 3-9% in PRH-10 and 10-16% in PS-2. The interaction of CO₂ and temperature on NAR was significant at vegetative-heading stages.

4.3.2.6 Crop growth rate (CGR)

High levels of CO₂ brought about significant increase in the crop growth rate (Table 120). The increase was 17-27% in PRH-10 and 6-10% of PS-2. Elevated temperature significantly reduced the crop growth rate. The reduction under ambient condition was 5-15% in PRH-10 and 32% in PS-2, whereas under elevated CO₂, it was 11-14 in PRH-10 and 6-10% in PS-2. The CO₂ and temperature interaction was significant at the heading-ripening stage.

4.3.3 Phenology

4.3.3.1 Days to maximum tillering

Elevated CO₂ brought about early tillering in both the varieties (Table 121). At elevated CO₂, tillering was 3 days earlier in PRH-10 and 2 days earlier in PS-2 compared to the ambient CO₂ conditions. Increase in temperature brought about tillering one day earlier in both the varieties under ambient and elevated CO₂ condition. The interaction of elevated CO₂ and temperature was not significant.

4.3.3.2 Days to flower initiation

CO₂ enrichment brought early flowering in both the varieties (Table 121). The flower initiation was 2 days earlier in both the varieties at elevated CO₂ compared to the ambient condition. The rise in temperature initiated flowering one day earlier in PRH-10 and PS-2 under elevated and ambient

Table 119. Interactive effect of elevated CO₂ and temperature on net assimilation rate (1 x 10⁻³ g cm⁻² day⁻¹) in the rice varieties

Treatments	Vegetative-heading stage		Heading-ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	0.321	0.390	0.326	0.271
Elevated CO ₂ + ambient temp.	0.349	0.454	0.404	0.298
Ambient CO ₂ + elevated temp.	0.152	0.306	0.323	0.390
Elevated CO ₂ + elevated temp.	0.330	0.392	0.397	0.285
CD at 5%				
Variety (V)		0.0118		0.0097
CO ₂		0.0118		0.0097
V x CO ₂		0.0167		0.0137
T		0.0118		0.0097
V x T		0.0167		NS
CO ₂ x T		0.0167		NS
V x CO ₂ x T		0.0237		0.0194

Table 120. Interactive effect of elevated CO₂ and temperature on the crop growth rate (g m⁻² day⁻¹) in the rice varieties

Treatments	Vegetative -heading stage		Heading -ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	6.98	9.69	7.81	7.99
Elevated CO ₂ + ambient temp.	8.21	10.32	9.96	8.84
Ambient CO ₂ + elevated temp.	6.44	5.41	7.56	8.51
Elevated CO ₂ + elevated temp.	6.15	7.74	8.84	7.05
CD at 5%				
Variety (V)		0.1808		0.2560
CO ₂		0.1808		0.2560
V x CO ₂		0.2558		0.3621
T		0.1808		0.2560
V x T		0.2558		NS
CO ₂ x T		NS		0.3621
V x CO ₂ x T		0.3617		0.5120

Table 121. Interactive effect of elevated CO₂ and temperature on the phenology of the rice varieties

Treatments	Days to maximum tillering (days)		Flower initiation (days)	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	52.66	56.66	80.33	87.33
Elevated CO ₂ + ambient temp.	49.33	54.66	78.66	85.33
Ambient CO ₂ + elevated temp.	53.34	58.33	81.66	88.66
Elevated CO ₂ + elevated temp.	48.33	55.66	77.33	86.33
CD at 5%				
Variety (V)		1.056		2.381
CO ₂		NS		NS
V x CO ₂		1.493		NS
T		1.056		2.381
V x T		1.493		NS
CO ₂ x T		NS		NS
V x CO ₂ x T		NS		NS

condition. The interaction of elevated CO₂ and temperature was not significant.

4.3.4 Dry matter production

4.3.4.1 Leaf dry mass

CO₂ enrichment brought about a significant increase in leaf dry mass (Table 122). The increase ranged from 16% (heading) to 20% (ripening) in PRH-10 and in case of PS-2, it was from 11% (vegetative) to 15% (heading). Elevated temperature resulted in a significant reduction in leaf dry mass. The reduction under ambient and elevated conditions varied from 34% (heading) to 47% (vegetative) and from 31% (ripening) to 33% (heading), respectively in PRH-10 and it ranged from 31% (ripening) to 34% (vegetative) and from 27% (heading) to 31% (ripening), respectively in PS-2. The CO₂ x temperature interaction was significant at the vegetative and heading stages. PS-2 had significantly greater leaf dry mass compared to PRH-10 at the heading and ripening stages.

4.3.4.2 Stem dry mass

Elevated CO₂ conditions brought about significant increase in the stem dry mass (Table 123). The increase in PRH-10 ranged from 12% (ripening) to 14% (vegetative) and in PS-2, it was from 22% (heading) to 27% (ripening). Elevated temperature brought about significant reduction in the stem dry mass. The reduction in PRH-10 ranged from 30% (ripening) to 41% (heading) under ambient condition and from 24% (ripening) to 38% (vegetative) under elevated CO₂. The reduction in PS-2 at ambient and elevated conditions ranged from 33% (ripening) to 48% (heading) and from 35% (ripening) to 39% (heading), respectively. The CO₂ and temperature interaction was significant

Table 122. Interactive effect of elevated CO₂ and temperature on leaf dry mass (g) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	6.73	6.20	9.96	12.50	15.46	18.06
Elevated CO ₂ + ambient temp.	7.90	6.90	11.60	14.40	18.50	20.70
Ambient CO ₂ + elevated temp.	3.52	4.05	6.50	8.43	10.20	12.43
Elevated CO ₂ + elevated temp.	4.36	4.80	7.70	10.40	12.73	14.26
CD at 5%						
Variety (V)	NS			0.212		0.483
CO ₂	0.232			0.212		0.483
V x CO ₂	NS			NS		0.683
T	0.232			0.212		0.483
V x T	0.328			0.299		NS
CO ₂ x T	0.328			0.299		NS
V x CO ₂ x T	NS			0.424		NS

Table 123. interactive effect of elevated CO₂ and temperature on stem dry mass (g) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	8.47	8.11	14.37	16.70	18.31	20.63
Elevated CO ₂ + ambient temp.	9.65	10.38	16.08	20.42	20.58	26.37
Ambient CO ₂ + elevated temp.	4.70	4.60	8.39	8.60	12.74	13.67
Elevated CO ₂ + elevated temp.	5.98	6.14	10.03	12.35	15.53	16.95
CD at 5%						
Variety (V)	0.351					0.733
CO ₂	0.351		0.322			0.733
V x CO ₂	0.496		0.455			NS
T	0.351		0.322			0.733
V x T	0.496		0.455			1.037
CO ₂ x T	0.496		NS			1.037
V x CO ₂ x T	0.702		NS			NS

except at the heading stage. PS-2 had greater shoot dry mass compared to PRH-10 irrespective of treatments.

4.3.4.3 Root dry mass

Elevated CO₂ brought about significant increase in the root dry mass (Table 124). The enhancement in root dry mass under elevated CO₂ conditions in PRH-10 at the vegetative, heading and ripening stages were 8%, 15% and 18%, respectively and it was 17%, 15% and 12%, respectively in case of PS-2. There was a significant reduction in the root dry mass for both the varieties under the increased temperature conditions. The reduction under ambient and elevated CO₂ ranged from 29% (ripening) to 43% (heading) and from 25% (ripening) to 38% (heading), respectively in PRH-10 and in PS-2, it ranged from 42% (vegetative) to 52% (heading) and from 21% (ripening) to 42% (vegetative), respectively in PS-2. The interaction of CO₂ and temperature was significant at the heading stage. Root dry mass was significantly more in PS-2 compared to PRH-10.

4.3.4.4 Panicle dry mass

Elevated CO₂ conditions brought about a significant increase in dry mass of panicle (Table 125). The increase was 7% in PRH-10 and 3% in PS-2. Elevated temperature brought about significant reduction in the panicle dry mass. The reduction under ambient CO₂ varied from 16% (heading) to 25% (ripening) in PRH-10 and from 14% (ripening) to 25% (heading) in PS-2. Under elevated CO₂, it was from 14% (ripening) to 23% (heading) in PRH-10 and from 13% (ripening) to 20% (heading) in PS-2. The interaction effect of elevated CO₂ and temperature was not significant. Among the varieties, PRH-10 had significantly more panicle dry mass compared to PS-2.

Table 124. Interactive effect of elevated CO₂ and temperature on root dry mass (g) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	5.74	6.46	10.75	11.97	14.11	15.35
Elevated CO ₂ + ambient temp.	6.23	7.61	12.46	13.80	16.67	17.18
Ambient CO ₂ + elevated temp.	3.09	3.74	6.11	5.72	9.98	11.48
Elevated CO ₂ + elevated temp.	3.55	4.34	7.66	8.80	12.39	13.46
CD at 5%						
Variety (V)						
CO ₂	0.160		0.169			0.362
V x CO ₂	0.160		0.169			0.362
T	0.227		0.240			NS
V x T	0.160		0.169			0.362
CO ₂ x T	NS		0.240			NS
V x CO ₂ x T	NS		0.240			NS
	NS		0.339			NS

Table 125 . Interactive effect of elevated CO₂ and temperature on panicle dry mass (g) in the rice varieties

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	3.92	3.62	6.13	5.89
Elevated CO ₂ + ambient temp.	4.13	3.90	6.44	6.11
Ambient CO ₂ + elevated temp.	2.91	2.70	5.11	5.04
Elevated CO ₂ + elevated temp.	3.12	3.09	5.53	5.37
CD at 5%				
Variety (V)				
CO ₂		0.082		0.126
V x CO ₂		0.082		0.126
T		NS		NS
V x T		0.082		0.126
CO ₂ x T		NS		0.178
V x CO ₂ x T		NS		NS
				NS

4.3.4.5 Total plant dry mass

CO₂ enrichment brought about significant increase in the whole plant dry mass (Fig. 19). The increase in PRH-10 ranged from 13% (vegetative) to 15% (ripening) and from 15% (ripening) to 29% (vegetative) in PS-2. Increase in temperature brought about significant reduction in the total dry mass. The reduction ranged from 27% (ripening) to 38% (heading) in PRH-10 and from 30% (ripening) to 43% (heading) in PS-2, at the ambient condition. At elevated CO₂, the reduction ranged from 26% (ripening) to 35% (heading) in PRH-10 and from 29% (ripening) to 31% (heading) in PS-2. The CO₂ x temperature interaction was significant except at the heading stage. Among the varieties, the total dry matter production was more for PS-2 irrespective of treatments.

4.3.5 Photosynthesis

CO₂ enrichment brought about significant increase in photosynthetic rate throughout the growth period (Table 126). CO₂ induced enhancement ranged from 20% (vegetative) to 31% (ripening) in PRH-10 and from 22% (heading) to 24% (ripening) in PS-2. Elevated temperature significantly decreased the rate of photosynthesis in both the varieties. The reduction at the ambient and elevated CO₂ conditions in PRH-10 varied from 26% (ripening) to 36% (heading) and from 23% (ripening) to 25% (heading), respectively. The reduction in PS-2 varied from 24% (ripening) to 37% (vegetative) under ambient condition and from 26% (heading) to 27% (vegetative) at elevated CO₂. The interaction effect was significant at the heading and ripening stages of growth. PRH-10 had significantly higher photosynthetic rate compared to PS-2.

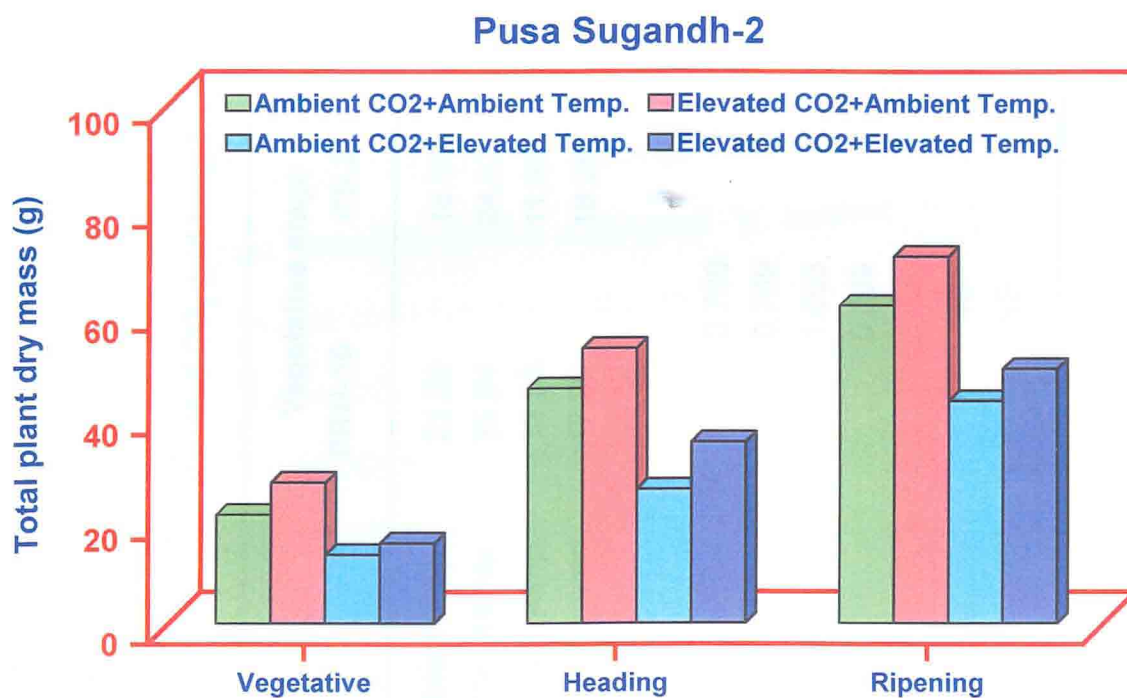
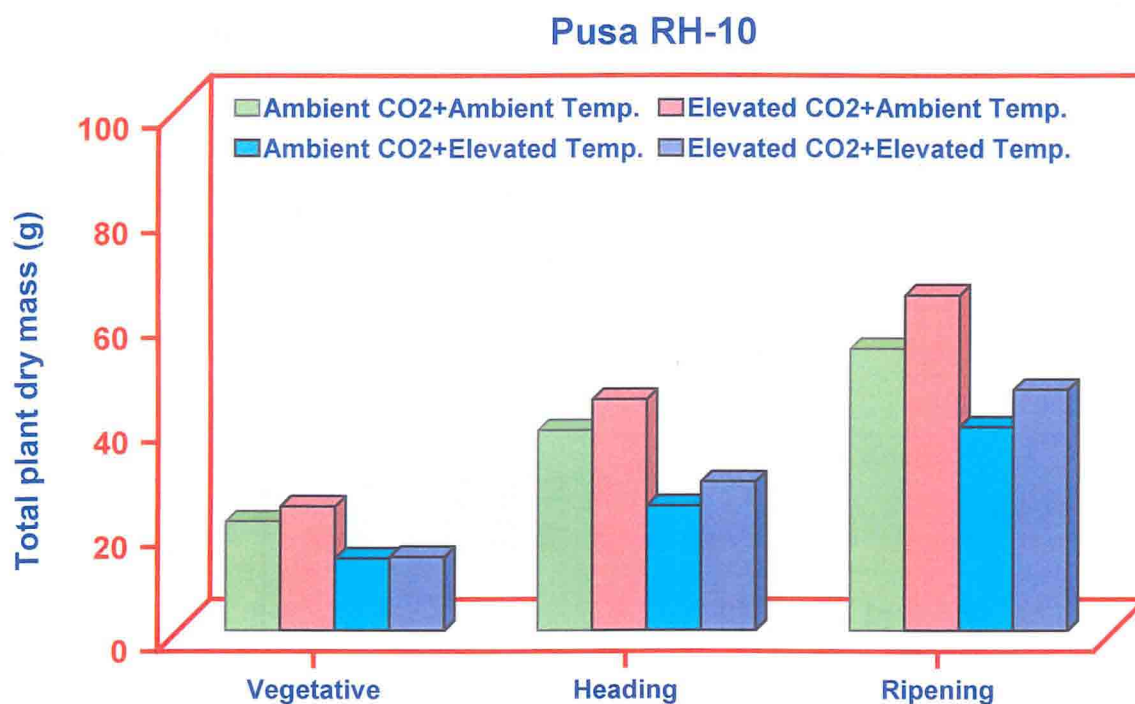


Fig. 19. Interactive effect of elevated CO₂ and temperature on total plant dry mass (g) in the rice varieties

Table 126. Interactive effect of elevated CO₂ and temperature on photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	21.52	18.95	29.57	27.24	27.72	23.35
Elevated CO ₂ + ambient temp.	25.94	24.87	36.35	33.60	32.49	29.06
Ambient CO ₂ + elevated temp.	12.73	11.80	18.78	17.13	15.85	17.74
Elevated CO ₂ + elevated temp.	17.59	18.28	26.90	24.79	23.94	22.74
CD at 5%						
Variety (V)	0.709					0.817
CO ₂	0.709		0.527		0.527	0.817
V x CO ₂	1.003		NS		NS	NS
T	0.709		0.527		0.527	0.817
V x T	1.003		NS		NS	NS
CO ₂ x T	NS		0.745		1.155	
V x CO ₂ x T	NS		NS		NS	

4.3.6 Chlorophyll

4.3.6.1 Chlorophyll 'a'

Higher CO₂ significantly reduced the chlorophyll 'a' content of the leaves (Table 127). CO₂ induced reduction ranged from 8-12% in both the varieties. Increase in temperature significantly reduced the chlorophyll 'a' content in the leaves. The reduction under ambient condition was 7-10% and under the elevated CO₂ condition, it was 4-6% in both the varieties. The interaction effect of CO₂ and temperature was significant at the vegetative stage. Chlorophyll 'a' content was significantly more in PRH-10 compared to PS-2.

4.3.6.2 Chlorophyll 'b'

The chlorophyll 'b' content in the leaves decreased significantly at the elevated CO₂ concentration (Table 128). The reduction under elevated CO₂ ranged from 8% (vegetative) to 9% (heading) in PRH-10 and in PS-2, it ranged from 8% (vegetative) to 12% (heading). Elevated temperature brought about significant reduction in the chlorophyll 'b' content of leaves. The temperature induced reduction under the ambient condition was 6-7% and under the elevated CO₂ condition, it was 4% for both the varieties. The interaction effect of CO₂ and temperature was not significant. The chlorophyll 'b' content was higher in PRH-10.

4.3.6.3 Total chlorophyll

The total chlorophyll content in the leaves was significantly decreased under elevated CO₂ (Table 129). This reduction ranged from 5% (ripening) to 9% (heading) in PRH-10 and from 7% (ripening) to 10% (heading) in PS-2. Increase in temperature brought about a significant reduction in the total

Table 127. Interactive effect of elevated CO₂ and temperature on chlorophyll 'a' (mg g⁻¹ FW) content in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	0.687	0.663	0.767	0.740	0.620	0.593
Elevated CO ₂ + ambient temp.	0.630	0.607	0.670	0.653	0.567	0.533
Ambient CO ₂ + elevated temp.	0.627	0.573	0.637	0.610	0.540	0.512
Elevated CO ₂ + elevated temp.	0.650	0.600	0.717	0.699	0.570	0.540
CD at 5%						
Variety (V)		0.008		0.009		0.009
CO ₂		0.008		0.009		0.009
V x CO ₂		NS		NS		NS
T		0.008		0.009		0.009
V x T		NS		NS		NS
CO ₂ x T		0.012		NS		NS
V x CO ₂ x T		NS		NS		NS

Table 128. Interactive effect of elevated CO₂ and temperature on chlorophyll 'b' (mg g⁻¹ FW) content in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	0.500	0.497	0.530	0.540	0.450	0.437
Elevated CO ₂ + ambient temp.	0.463	0.457	0.483	0.477	0.433	0.423
Ambient CO ₂ + elevated temp.	0.430	0.430	0.460	0.450	0.413	0.403
Elevated CO ₂ + elevated temp.	0.470	0.467	0.498	0.507	0.420	0.401
CD at 5%						
Variety (V)	NS		NS			0.007
CO ₂	0.008		0.007			0.007
V x CO ₂	NS		NS			NS
T	0.008		0.007			0.007
V x T	NS		NS			NS
CO ₂ x T	NS		NS			NS
V x CO ₂ x T	NS		NS			NS

Table 129. Interactive effect of elevated CO₂ and temperature on total chlorophyll (mg g⁻¹ FW) content in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	1.187	1.197	1.297	1.280	1.060	1.030
Elevated CO ₂ + ambient temp.	1.093	1.080	1.183	1.158	0.980	0.957
Ambient CO ₂ + elevated temp.	1.033	1.003	1.097	1.073	0.950	0.901
Elevated CO ₂ + elevated temp.	1.120	1.070	1.190	1.181	0.961	0.932
CD at 5%						
Variety (V)		NS		0.013		0.017
CO ₂		0.024		0.013		0.017
V x CO ₂		NS		NS		NS
T		0.024		0.013		0.017
V x T		NS		NS		NS
CO ₂ x T		NS		NS		NS
V x CO ₂ x T		NS		NS		NS

chlorophyll content of the leaves. The reduction under ambient condition was 8-10% and under elevated CO₂, it was 5-7% in both the varieties. The interaction of CO₂ and temperature effect was not significant throughout the growth period. Total chlorophyll content in the leaves was significantly higher for PRH-10 than PS-2 at the heading and ripening stages.

4.3.7 Stomatal conductance

The stomatal conductance was reduced significantly by elevated CO₂ (Table 130). CO₂ induced reduction ranged from 10% (vegetative) to 27% (ripening) in PRH-10 and from 18% (vegetative) to 36% (ripening) in PS-2. Increase in temperature significantly reduced the stomatal conductance. The reduction under ambient and elevated CO₂ ranged from 18% (vegetative) to 22% (heading) and from 12% (ripening) to 18% (heading), respectively in PRH-10 whereas in PS-2, it was from 19% (vegetative) to 38% (ripening) and from 12% (ripening) to 19% (heading), respectively. The interactive effect of CO₂ and temperature was significant at the vegetative and ripening stages for both the varieties. Among the varieties, PRH-10 had greater stomatal conductance than PS-2.

4.3.8 Respiration

The elevated CO₂ significantly decreased the rate of respiration per unit leaf area in both the rice varieties (Table 131). The decrease ranged from 15% (heading) to 22% (ripening) in PRH-10 variety and from 10% (ripening) to 11% (heading) in PS-2. Higher temperature brought about significant increase in the rate of respiration. The temperature induced increase ranged from 11% (ripening) to 27% (vegetative) in PRH-10 and from 26% (vegetative) to 55% (heading) in PS-2 under ambient condition. On the other hand, under

Table 130. Interactive effect of elevated CO₂ and temperature on stomatal conductance (mol m⁻² s⁻¹) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	0.82	0.79	1.42	1.32	1.13	1.18
Elevated CO ₂ + ambient temp.	0.73	0.64	1.08	0.86	0.82	0.75
Ambient CO ₂ + elevated temp.	0.67	0.65	1.10	0.84	0.91	0.73
Elevated CO ₂ + elevated temp.	0.63	0.52	0.88	0.76	0.72	0.66
CD at 5%						
Variety (V)						
CO ₂	0.025		0.063			NS
V x CO ₂	0.025		0.063			0.037
T	NS		NS			NS
V x T	0.025		0.063			0.037
CO ₂ x T	NS		NS			NS
V x CO ₂ x T	0.036		NS			0.052
	NS		NS			0.074

Table 131. Interactive effect of elevated CO₂ and temperature on respiration rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	5.63	4.91	6.53	5.85	7.70	6.63
Elevated CO ₂ + ambient temp.	4.43	3.84	5.50	5.19	6.02	5.98
Ambient CO ₂ + elevated temp.	7.13	6.20	10.38	9.10	8.57	8.61
Elevated CO ₂ + elevated temp.	5.38	4.78	8.51	7.54	7.00	6.71
CD at 5%						
Variety (V)	0.388		0.271		0.432	
CO ₂	0.388		0.271		0.432	
V x CO ₂	NS		NS		NS	
T	0.388		0.271		0.432	
V x T	NS		0.383		NS	
CO ₂ x T	NS		0.383		NS	
V x CO ₂ x T	NS		NS		NS	

elevated CO₂ condition the increase ranged from 16% (ripening) to 21% (vegetative) in PRH-10 and from 24% (vegetative) to 45% (heading) in PS-2. The CO₂ and temperature interaction was significant at the heading stage. Respiration rate was higher for PRH-10 compared to PS-2.

4.3.9 Carbohydrate content in leaves

4.3.9.1 Reducing sugars

CO₂ enrichment brought about a significant increase in the reducing sugars (Table 132). The increase ranged from 18% (vegetative) to 26% (heading) in PRH-10 and from 18% (vegetative) to 25% (heading) in PS-2. Increased temperature brought about significant decrease in the reducing sugar content throughout the growth period. The reduction varied from 34% (ripening) to 36% (heading) in PRH-10 and from 35% (heading) to 42% (heading) in PS-2 under ambient condition. The reduction under elevated CO₂ condition varied from 28% (ripening) to 30% (heading) in PRH-10 and from 30% (ripening) to 32% (heading) in PS-2. The interactive effect of CO₂ and temperature was significant at the vegetative and ripening stages. Higher amount of reducing sugars in the leaves was found in PRH-10 irrespectively of treatments.

4.3.9.2 Non-reducing sugars

CO₂ enrichment brought about significant increase in the non-reducing sugar content in leaves (Table 133). The increase ranged from 11% (heading) to 16% (ripening) in PRH-10 and from 9% (heading) to 11% (vegetative) in PS-2. Higher temperature significantly reduced the non-reducing sugars content in both the varieties. The reduction under ambient and elevated CO₂ conditions varied from 37% (heading) to 40% (ripening) and from 26%

Table 132. Interactive effect of elevated CO₂ and temperature on reducing sugar content (mg g⁻¹ DW) in the leaves of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	19.96	17.41	25.93	23.71	23.57	20.45
Elevated CO ₂ + ambient temp.	23.60	20.44	31.52	30.05	25.68	23.57
Ambient CO ₂ + elevated temp.	9.82	7.26	16.46	13.80	15.47	13.18
Elevated CO ₂ + elevated temp.	15.53	13.76	21.52	18.15	18.29	16.47
CD at 5%						
Variety (V)	0.371					0.491
CO ₂	0.371		0.729			0.491
V x CO ₂	0.525		NS			NS
T	0.371		0.729			0.491
V x T	NS		NS			NS
CO ₂ x T	0.525		1.031			NS
V x CO ₂ x T	NS		NS			NS

Table 133. Interactive effect of elevated CO₂ and temperature on non-reducing sugar content (mg g⁻¹ DW) in the leaves of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	46.30	41.72	57.14	54.94	50.34	46.69
Elevated CO ₂ + ambient temp.	50.19	46.37	63.15	59.73	58.19	54.86
Ambient CO ₂ + elevated temp.	26.19	24.43	35.67	30.87	30.22	27.44
Elevated CO ₂ + elevated temp.	30.77	27.07	46.32	37.67	35.96	39.38
CD at 5%						
Variety (V)	0.620		3.352			NS
CO ₂	0.620		3.352			3.336
V x CO ₂	NS		NS			NS
T	0.620		3.352			3.336
V x T	0.877		NS			NS
CO ₂ x T	NS		NS			NS
V x CO ₂ x T	1.240		NS			NS

(heading) to 38% (ripening), respectively in PRH-10. It ranged from 41% (vegetative) to 44% (heading) and from 28% (ripening) to 36% (heading) in PS-2 under ambient and elevated CO₂ conditions, respectively. The CO₂ and temperature interaction was not significant. The non-reducing sugar content was greater for PRH-10 compared to PS-2.

4.3.9.3 Total sugars

Elevated CO₂ significantly increased the total sugar content in the leaves (Table 134). The enhancement ranged from 11% (vegetative) to 14% (heading) in PRH-10 and from 10% (vegetative) to 13% (heading) in PS-2. Increased temperature brought about significant reduction in the total sugar content. The reduction varied from 33% (heading) to 38% (ripening) in PRH-10 and from 39% (ripening) to 47% (heading) in PS-2 under ambient CO₂ conditions. The reduction under elevated CO₂ ranged from 29% (heading) to 34% (ripening) in PRH-10 and from 29% (ripening) to 38% (heading) in PS-2. The interaction of CO₂ and temperature was not significant. Total sugar content was higher for PRH-10 compared to PS-2.

4.3.9.4 Starch

CO₂ enrichment significantly increased the starch content in the leaves (Table 135). The increase ranged from 10% (heading) to 12% (vegetative) in PRH-10 and from 6% (heading) to 8% (ripening) in PS-2. Elevated temperature brought about significant reduction in starch content of the leaves. Under ambient condition, the reduction ranged from 38% (heading) to 45% (vegetative) in PRH-10 and from 39% (heading) to 49% (ripening) in PS-2. Under elevated CO₂, the reduction ranged from 35% (heading) to 40% (ripening) in PRH-10 and from 35% (heading) to 44% (vegetative) in PS-2.

Table 134. Interactive effect of elevated CO₂ and temperature on total sugar content (mg g⁻¹ DW) in the leaves of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	66.26	60.58	83.07	78.65	73.91	67.14
Elevated CO ₂ + ambient temp.	73.79	66.81	94.67	89.78	83.87	78.43
Ambient CO ₂ + elevated temp.	38.01	32.10	55.13	47.47	45.69	40.62
Elevated CO ₂ + elevated temp.	44.30	37.83	67.84	55.82	54.25	55.85
CD at 5%						
Variety (V)		1.25		1.21		0.96
CO ₂		1.25		1.21		0.96
V x CO ₂		NS		NS		1.36
T		1.25		1.21		0.96
V x T		NS		1.71		1.36
CO ₂ x T		NS		NS		NS
V x CO ₂ x T		NS		NS		1.92

Table 135. Interactive effect of elevated CO₂ and temperature on the starch content (mg g⁻¹ DW) in the leaves of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	45.37	34.32	65.01	62.04	56.30	49.52
Elevated CO ₂ + ambient temp.	50.57	44.51	71.52	66.01	58.92	53.82
Ambient CO ₂ + elevated temp.	24.93	20.49	40.05	38.11	29.94	24.84
Elevated CO ₂ + elevated temp.	27.30	24.73	45.16	42.63	35.30	34.06
CD at 5%						
Variety (V)	0.516		0.587		0.749	
CO ₂	0.516		0.587		0.749	
V x CO ₂	NS		0.830		NS	
T	0.516		0.587		0.749	
V x T	0.731		0.830		NS	
CO ₂ x T	0.731		NS		1.123	
V x CO ₂ x T	NS		NS		1.589	

The CO₂ and temperature interactive effect was significant except at the heading stage. Among the varieties, PRH-10 had greater starch content in the leaves compared to PS-2.

4.3.9.5 Total non-structural carbohydrate (TNC)

Elevated CO₂ significantly increased the total non-structural carbohydrate content in leaves (Table 136). The increase at elevated CO₂ ranged from 10% (vegetative) to 12% (heading) in PRH-10 and from 10% (ripening) to 11% (vegetative) in PS-2. The higher temperature treatment brought about reduction in the TNC content and the reduction was more in PS-2 than PRH-10. Under ambient and elevated CO₂ condition, the reduction varied from 36% (heading) to 42% (ripening) and from 31% (heading) to 32% (ripening), respectively in PRH-10. The reduction in PS-2, ranged from 39% (heading) to 45% (ripening) and from 31% (heading) to 32% (ripening) under ambient and elevated CO₂ condition, respectively. The interaction effect was significant except at the heading stage. Among the varieties, PRH-10 had greater TNC content than that of PS-2.

4.3.10 Carbohydrate content in the stem

4.3.10.1 Reducing sugars

Elevated CO₂ significantly increased the reducing sugar content in the stem (Table 137). The CO₂ induced increase ranged from 15% (vegetative) to 26% (heading) in PRH-10 and it was 24% in PS-2. Temperature rise brought about significant reduction in the reducing sugar content in both the varieties. The reduction in PRH-10 varied from 41% (ripening) to 47% (vegetative) and from 28% (heading) to 40% (ripening) under ambient and elevated CO₂ concentration, respectively. The reduction varied from 37% (ripening) to 45%

Table 136. Interactive effect of elevated CO₂ and temperature on total non-structural carbohydrate content (mg g⁻¹ DW) in the leaves of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	116.63	105.91	148.08	140.69	130.21	119.66
Elevated CO ₂ + ambient temp.	129.36	118.32	166.19	155.79	142.79	132.25
Ambient CO ₂ + elevated temp.	63.94	50.18	95.18	85.58	75.63	65.46
Elevated CO ₂ + elevated temp.	71.60	62.56	114.01	98.45	89.55	89.91
CD at 5%						
Variety (V)	1.74		2.27		2.04	
CO ₂	1.74		2.278		2.04	
V x CO ₂	NS		NS		2.89	
T	1.74		2.27		2.04	
V x T	NS		NS		2.89	
CO ₂ x T	2.46		NS		2.89	
V x CO ₂ x T	NS		NS		4.09	

Table 137. Interactive effect of elevated CO₂ and temperature on the reducing sugar content (mg g⁻¹ DW) in the stem of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	26.32	22.03	37.21	25.92	28.01	24.32
Elevated CO ₂ + ambient temp.	30.23	22.79	37.80	34.58	35.28	30.29
Ambient CO ₂ + elevated temp.	13.92	12.06	18.69	16.02	16.31	15.32
Elevated CO ₂ + elevated temp.	17.88	15.34	26.91	24.00	21.30	21.01
CD at 5%						
Variety (V)	0.982		3.730		0.829	
CO ₂	0.982		3.730		0.829	
V x CO ₂	1.390		NS		NS	
T	0.982		3.730		0.829	
V x T	1.390		NS		1.173	
CO ₂ x T	NS		NS		1.173	
V x CO ₂ x T	NS		NS		NS	

(vegetative) and from 30% (ripening) to 33% (vegetative) in PS-2 under ambient and elevated CO₂ condition, respectively. The interactive effect of CO₂ and temperature was significant at the ripening stage. The reducing sugar content was significantly more in PRH-10 compared to PS-2.

4.3.10.2 Non-reducing sugars

Higher CO₂ brought about significant increase in the non-reducing sugar content of stem (Table 138). This increase ranged from 6% (vegetative) to 9% (ripening) in PRH-10 and from 9% (vegetative) to 11% (ripening) in PS-2. Elevated temperature resulted in significant reduction of non-reducing sugar content. The temperature induced reduction ranged from 31% (vegetative) to 35% (ripening) in PRH-10 and from 35% (ripening) to 36% (vegetative) in PS-2 under ambient condition. Under elevated CO₂, the reduction ranged from 28% (vegetative) to 32% (heading) in PRH-10 and from 34% (vegetative) to 35% (ripening) in PS-2. The interactive effect was significant for both the varieties of all the growth stages. PRH-10 had significantly higher non-reducing sugar content compared to PS-2.

4.3.10.3 Total sugars

CO₂ enrichment brought about significant increase in the total sugar content in the stem (Table 139). The increase ranged from 9% (vegetative) to 11% (ripening) in PRH-10 and from 7% (vegetative) to 10% (heading) in PS-2. Increase in temperature brought about reduction in the total sugar content in both the varieties. The reduction under ambient and elevated CO₂ ranged from 37% (ripening) to 39% (heading) and from 30% (heading) to 32% (vegetative), respectively in PRH-10 and it ranged from 34% (heading) to 36% (vegetative) and from 34% (vegetative) to 35% (ripening) in PS-2,

Table 138. Interactive effect of elevated CO₂ and temperature on the non-reducing sugar content (mg g⁻¹ DW) in the stem of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	55.73	51.53	67.43	59.43	65.64	57.10
Elevated CO ₂ + ambient temp.	59.09	56.34	73.30	66.30	68.73	65.64
Ambient CO ₂ + elevated temp.	38.11	33.06	45.10	40.80	42.39	37.30
Elevated CO ₂ + elevated temp.	42.10	36.99	49.76	47.34	46.07	42.83
CD at 5%						
Variety (V)	0.611		1.373			0.770
CO ₂	0.611		1.373			0.770
V x CO ₂	0.935		1.942			1.090
T	0.661		1.373			0.770
V x T	0.935		1.942			1.090
CO ₂ x T	0.935		1.942			1.090
V x CO ₂ x T	NS		NS			NS

Table 139. Interactive effect of elevated CO₂ and temperature on the total sugar content (mg g⁻¹ DW) in the stem of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	82.05	73.56	104.64	90.68	93.65	81.42
Elevated CO ₂ + ambient temp.	89.32	79.13	111.10	100.88	104.01	95.93
Ambient CO ₂ + elevated temp.	52.03	47.12	63.79	59.82	58.70	55.00
Elevated CO ₂ + elevated temp.	59.98	52.33	76.67	71.34	67.37	63.84
CD at 5%						
Variety (V)		1.25		2.18		1.72
CO ₂		1.25		2.18		1.72
V x CO ₂		NS		NS		NS
T		1.25		2.18		1.72
V x T		1.77		3.09		2.44
CO ₂ x T		NS		NS		2.44
V x CO ₂ x T		NS		NS		3.45

respectively. The interaction effect of CO₂ and temperature was significant at the ripening stage. The total sugar content was significantly more in PRH-10 compared to PS-2.

4.3.10.4 Starch

The increase in starch content in the stem under elevated CO₂ was significant (Table 140). This increase ranged from 7% (heading) to 9% (vegetative) in PRH-10 and from 4% (ripening) to 6% (heading) in PS-2. Temperature rise brought about a significant reduction in the starch content. The reduction under ambient and elevated CO₂ ranged from 35% (heading) to 38% (ripening) and from 32% (heading) to 34% (ripening), respectively in PRH-10 and in case of PS-2, it ranged from 35% (heading) to 45% (vegetative) and from 32% (heading) to 43% (vegetative), respectively. The interactive effect of CO₂ and temperature was significant except at the heading stage. PRH-10 had higher amount of starch in the stem compared to PS-2.

4.3.10.5 Total non-structural carbohydrate (TNC)

Higher CO₂ resulted in significant increase of the total non-structural carbohydrate content in the stem (Table 141). The CO₂ induced increase ranged from 9% (vegetative) to 10% (heading) in PRH-10 and from 8% (heading) to 9% (vegetative) in PS-2. Elevated temperature significantly reduced the total non-structural carbohydrate content in the stem. The reduction varied from 36% (heading) to 38% (vegetative) and from 31% (heading) to 34% (ripening) under ambient and elevated CO₂ conditions, respectively in PRH-10. The reduction was varied from 35% (ripening) to 40% (vegetative) and from 33% (ripening) to 37% (vegetative) in PS-2 under

Table 140. Interactive effect of elevated CO₂ and temperature on the starch content (mg g⁻¹ DW) in the stem of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	60.80	55.37	76.37	71.83	64.36	61.13
Elevated CO ₂ + ambient temp.	66.38	61.00	81.56	75.83	68.87	64.03
Ambient CO ₂ + elevated temp.	33.28	30.12	49.36	46.70	39.67	34.73
Elevated CO ₂ + elevated temp.	37.33	34.77	55.09	52.46	45.30	43.00
CD at 5%						
Variety (V)	NS		0.649		0.605	
CO ₂	0.495		0.649		0.605	
V x CO ₂	0.700		NS		NS	
T	NS		0.649		0.605	
V x T	0.700		0.917		NS	
CO ₂ x T	0.700		NS		0.856	
V x CO ₂ x T	NS		NS		1.211	

Table 141. Interactive effect of elevated CO₂ and temperature on total non-structural carbohydrates (mg g⁻¹ DW) in the stem of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	142.85	128.93	181.01	162.51	158.01	142.55
Elevated CO ₂ + ambient temp.	155.70	140.13	192.66	176.71	172.88	159.96
Ambient CO ₂ + elevated temp.	88.31	77.69	114.15	107.52	98.37	92.73
Elevated CO ₂ + elevated temp.	97.31	87.10	131.76	123.80	112.67	106.84
CD at 5%						
Variety (V)	3.29			2.73		3.10
CO ₂	3.29			2.73		3.10
V x CO ₂	NS			3.86		NS
T	3.29			2.73		3.10
V x T	NS			NS		4.39
CO ₂ x T	NS			3.86		NS
V x CO ₂ x T	NS			5.46		NS

ambient and elevated CO₂ conditions, respectively. The interaction effect of CO₂ and temperature was significant at the heading stage. PRH-10 had higher amount of TNC.

4.3.11 Carbohydrate content in the panicle

4.3.11.1 Reducing sugars

CO₂ enrichment brought about significant increase in the reducing sugar content of the panicle (Table 142). The enhancement ranged from 11% (ripening) to 12% (heading) in PRH-10 and from 13% (heading) to 14% (ripening) in PS-2. Higher temperature brought about significant reduction of the reducing sugar content in both the varieties. The reduction under ambient and elevated CO₂ conditions ranged from 23% (heading) to 28% (ripening) and from 20% (heading) to 26% (ripening) respectively in PRH-10 and in case of PS-2, it ranged from 20% (heading) to 28% (ripening) and from 8% (ripening) to 20% (heading), respectively. The interaction of elevated CO₂ and temperature was significant. Among the varieties PRH-10 had higher amount of reducing sugars in the panicle.

4.3.11.2 Non-reducing sugars

Elevated CO₂ significantly increased the non-reducing sugars in the panicle (Table 143). The increase ranged from 6% (ripening) to 8% (heading) in PRH-10 and from 9% (heading) to 12% (ripening) in PS-2. Increase in temperature caused a reduction in the non-reducing sugar content in both the varieties. The reduction under ambient and elevated CO₂ conditions varied from 17% (heading) to 32% (ripening) and from 13% (heading) to 27% (ripening), respectively in PRH-10 and in PS-2, it ranged from 17% (heading) to 17% (ripening) and from 14% (heading) to 25% (ripening), respectively.

Table 142. Interactive effect of elevated CO₂ and temperature on the reducing sugar content (mg g⁻¹ DW) in the panicle of the rice varieties

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	64.25	60.15	91.69	86.42
Elevated CO ₂ + ambient temp.	71.35	68.19	102.47	98.72
Ambient CO ₂ + elevated temp.	49.31	48.40	64.35	61.84
Elevated CO ₂ + elevated temp.	56.42	54.36	74.70	91.40
CD at 5%				
Variety (V)	0.639			0.732
CO ₂	0.639			0.732
V x CO ₂	NS			NS
T	0.639			0.732
V x T	0.923			0.947
CO ₂ x T	1.242			1.528
V x CO ₂ x T	1.567			2.168

Table 143. Interactive effect of elevated CO₂ and temperature on the non-reducing sugar content (mg g⁻¹ DW) in the panicle of the rice varieties

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	76.37	70.64	113.45	97.41
Elevated CO ₂ + ambient temp.	82.81	77.25	120.40	110.34
Ambient CO ₂ + elevated temp.	63.25	59.30	76.70	71.50
Elevated CO ₂ + elevated temp.	71.47	66.47	85.49	83.24
CD at 5%				
Variety (V)		2.41		2.23
CO ₂		2.41		2.23
V x CO ₂		NS		NS
T		2.41		2.23
V x T		NS		3.16
CO ₂ x T		NS		NS
V x CO ₂ x T		NS		NS

The interaction between CO₂ and temperature was not significant. PRH-10 had significantly greater non-reducing sugar content compared to PS-2 irrespective of treatments.

4.3.11.3 Total sugars

CO₂ enrichment significantly increased the total sugar content in the panicle in both the varieties (Table 144). The CO₂ induced increase varied from 9% (heading) to 10% (ripening) in PRH-10 and from 11% (heading) to 13% (ripening) in PS-2. Increase in temperature brought about a significant reduction in the total sugar content in the panicle. The reduction under ambient condition in PRH-10 ranged from 19% (heading) to 29% (ripening). Similarly the reduction in PS-2 ranged from 18% (heading) 28% (ripening). Temperature induced reduction ranged from 17% (heading) to 27% (ripening) in PRH-10 and 18% (heading) to 27% (ripening) in PS-2 under elevated CO₂. The interaction of CO₂ and temperature was not significant. Total sugar content was significantly higher in PRH-10 compared to PS-2.

4.3.11.4 Starch

Elevated CO₂ significantly increased the starch content in the panicle (Table 145). This enhancement ranged from 8% (ripening) to 14% (heading) in PRH-10 and from 4% (ripening) to 8% (heading) in PS-2. The increased temperature brought about a significant reduction in the starch content of both the varieties. The reduction under ambient and elevated CO₂ condition varied from 23% (heading) to 29% (ripening) and from 20% (heading) to 27% (ripening) in PRH-10, respectively. It ranged from 21% (heading) to 33% (ripening) and from 15% (heading) to 27% (ripening) in PS-2 under ambient and elevated CO₂ conditions, respectively. The interaction between CO₂ and

Table 144. Interactive effect of elevated CO₂ and temperature on the total sugar content (mg g⁻¹ DW) in the panicle of the rice varieties

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	139.71	130.77	205.21	183.82
Elevated CO ₂ + ambient temp.	154.13	145.59	222.91	209.04
Ambient CO ₂ + elevated temp.	112.54	107.71	142.20	133.41
Elevated CO ₂ + elevated temp.	127.90	120.76	160.20	154.65
CD at 5%				
Variety (V)		2.43		5.63
CO ₂		2.43		5.63
V x CO ₂		NS		NS
T		2.43		5.63
V x T		NS		NS
CO ₂ x T		NS		NS
V x CO ₂ x T		NS		NS

Table 145. Interactive effect of elevated CO₂ and temperature on the starch content (mg g⁻¹ DW) in the panicle of the rice varieties

Treatments	Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	160.46	151.83	221.74	212.63
Elevated CO ₂ + ambient temp.	183.47	164.38	239.34	222.51
Ambient CO ₂ + elevated temp.	123.46	119.40	155.32	142.38
Elevated CO ₂ + elevated temp.	145.49	139.48	171.70	164.44
CD at 5%				
Variety (V)		4.04		6.42
CO ₂		4.04		6.42
V x CO ₂		NS		NS
T		4.04		6.42
V x T		5.72		NS
CO ₂ x T		NS		NS
V x CO ₂ x T		NS		NS

temperature was not significant. The starch content in PRH-10 was significantly greater than that of PS-2.

4.3.11.5 Total non-structural carbohydrate (TNC)

CO₂ enrichment brought about a significant increase in the total non-structural carbohydrate content in the panicle (Fig. 20). The increase ranged from 8% (ripening) 12% (heading) in PRH-10 and from 8% (heading) to 9% (ripening) in PS-2. The temperature increase caused a significant reduction in the TNC content in both the varieties. The reduction ranged from 21% (heading) to 30% (ripening) and from 19% (heading) to 28% (ripening) in PRH-10 under ambient and elevated CO₂ conditions, respectively. The reduction in PS-2 ranged from 20% (heading) to 35% (ripening) and from 16% (heading) to 30% (ripening) under ambient and elevated CO₂ conditions, respectively. The interaction effect was significant except at the vegetative stage. PRH-10 had significantly greater amount of TNC content than that of PS-2, irrespective of treatments.

4.3.12 Sucrose phosphate synthase (SPS)

The elevated CO₂ significantly increased the sucrose phosphate synthase activity (Fig. 21). The increase ranged from 5% (heading) to 18% (vegetative) in PRH-10 and in case of PS-2, it ranged from 4% (vegetative) to 12% (ripening). The rise in temperature brought about significant decline in the activity of SPS in both the varieties. The decline in the SPS activity under ambient and elevated CO₂ conditions ranged from 14% (ripening) to 18% (vegetative) and from 12% (heading) to 14% (vegetative), respectively in PRH-10 and in case of PS-2, it ranged from 17% (vegetative) to 20% (heading) and from 13% (ripening) to 14% (heading), respectively. The CO₂

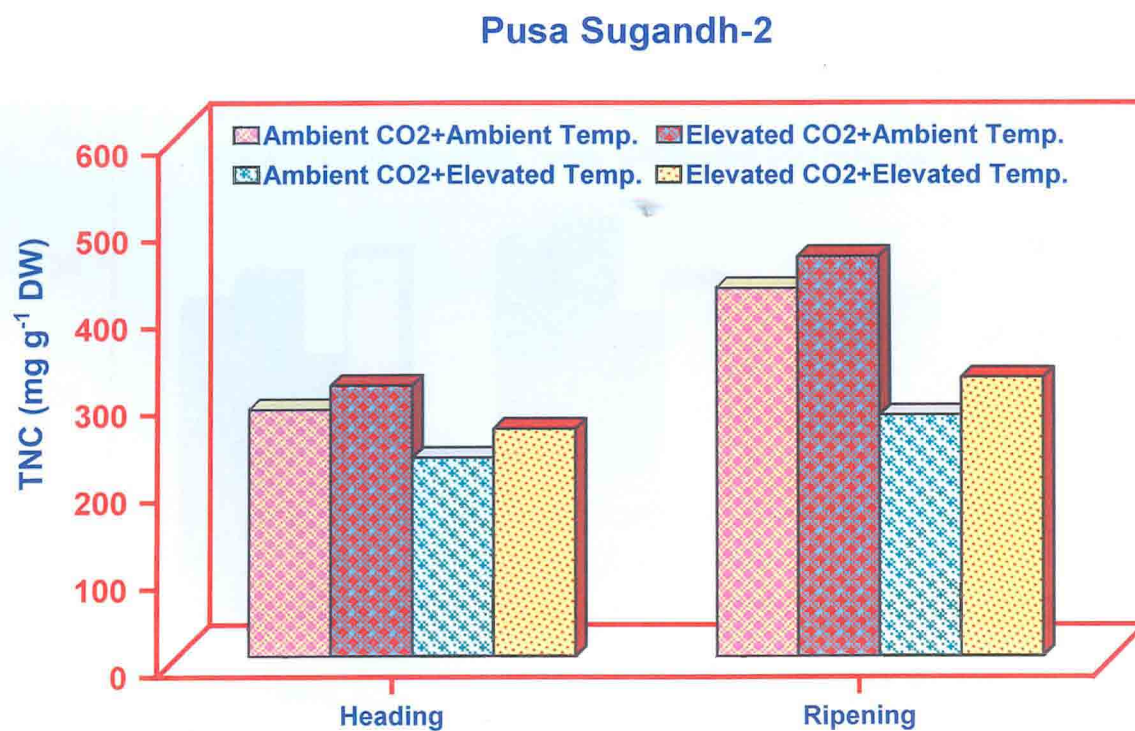
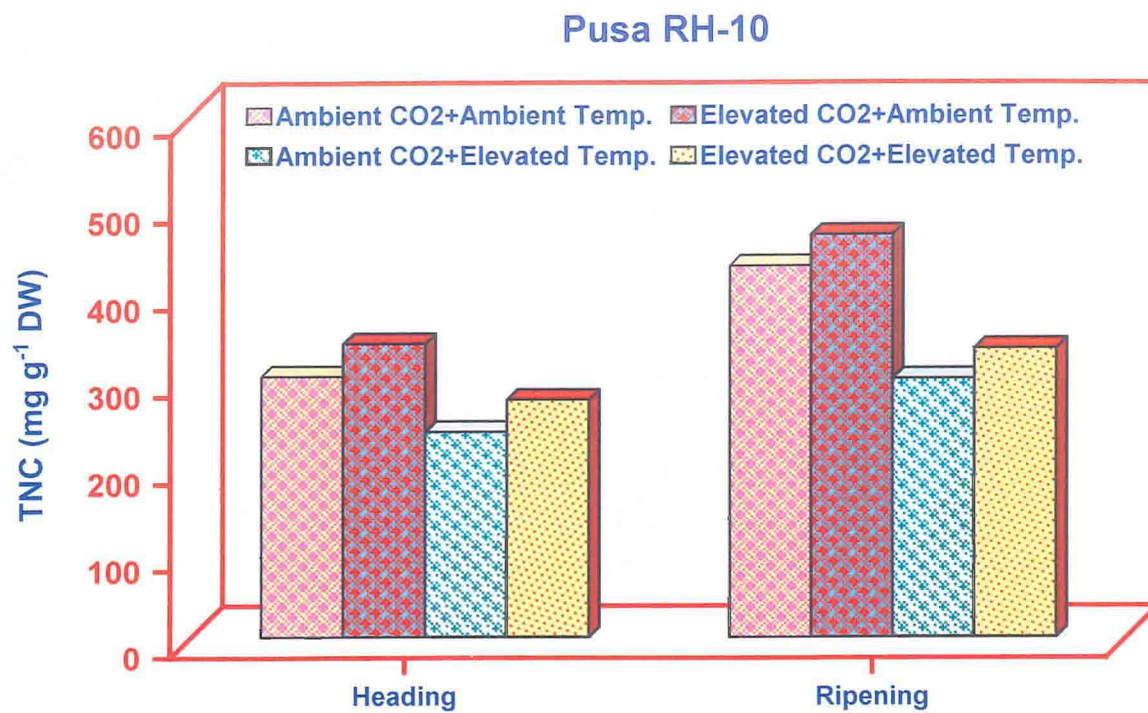


Fig. 20. Interactive effect of elevated CO₂ and temperature on the total non-structural carbohydrate content (mg g⁻¹ DW) in the panicle of the rice varieties

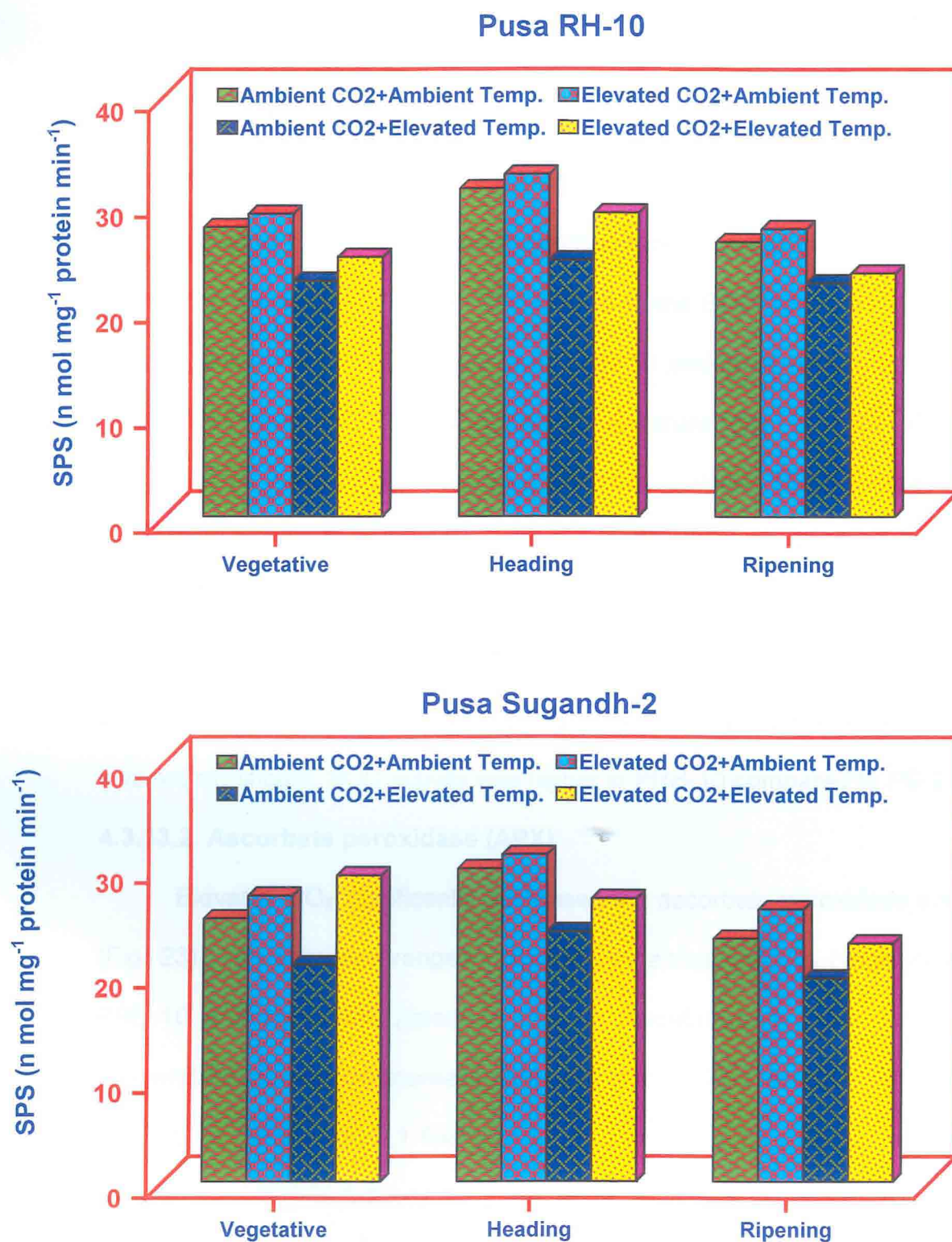


Fig. 21. Interactive effect of elevated CO₂ and temperature on the activity of sucrose phosphate synthase ($\mu\text{mol mg}^{-1}\text{ protein min}^{-1}$) in the rice varieties

and temperature interaction was significant at heading stage. PRH-10 had significantly higher SPS activity than PS-2 irrespective of treatments.

4.3.13 Antioxidant enzymes

4.3.13.1 Superoxide dismutase (SOD)

Elevated CO₂ brought about significant decrease in the activity of the superoxide dismutase (Fig. 22). The decline in the SOD activity ranged from 36% (ripening) to 48% (vegetative) in PRH-10 and from 44% (ripening) to 49% (vegetative) in PS-2. Elevated temperature rise brought about a significant increase in the superoxide dismutase activity. The increase under ambient CO₂ was less than or equal to 1.0 fold in both the varieties. The increase under elevated CO₂ conditions was more which ranged from 1.6 fold (ripening) to 2.0 fold (heading) in PRH 10 and in case of PS-2, it ranged from 2.0 fold (vegetative) at 2.2 fold (heading). The CO₂ x temperature interaction was not significant. SOD activity was higher in PRH-10 compared to PS-2

4.3.13.2 Ascorbate peroxidase (APX)

Elevated CO₂ significantly decreased the ascorbate peroxidase activity (Fig. 23). The decrease ranged from 56% (ripening) to 61% (vegetative) in PRH-10 and from 59% (ripening) to 63% (vegetative) in PS-2. Increased temperature significantly increased the APX activity. This increase varied from 1.0 fold (vegetative) to 2.1 fold (heading) under ambient condition and from 4.7 fold (ripening) to 5.2 fold (heading) at elevated CO₂ level in PRH-10. The temperature induced increase ranged from 1.0 fold (vegetative) to 1.3 fold (heading) at ambient condition and from 4.7 fold (vegetative) to 5.6 fold (heading) at elevated CO₂ conditions in PS-2. The CO₂ and temperature

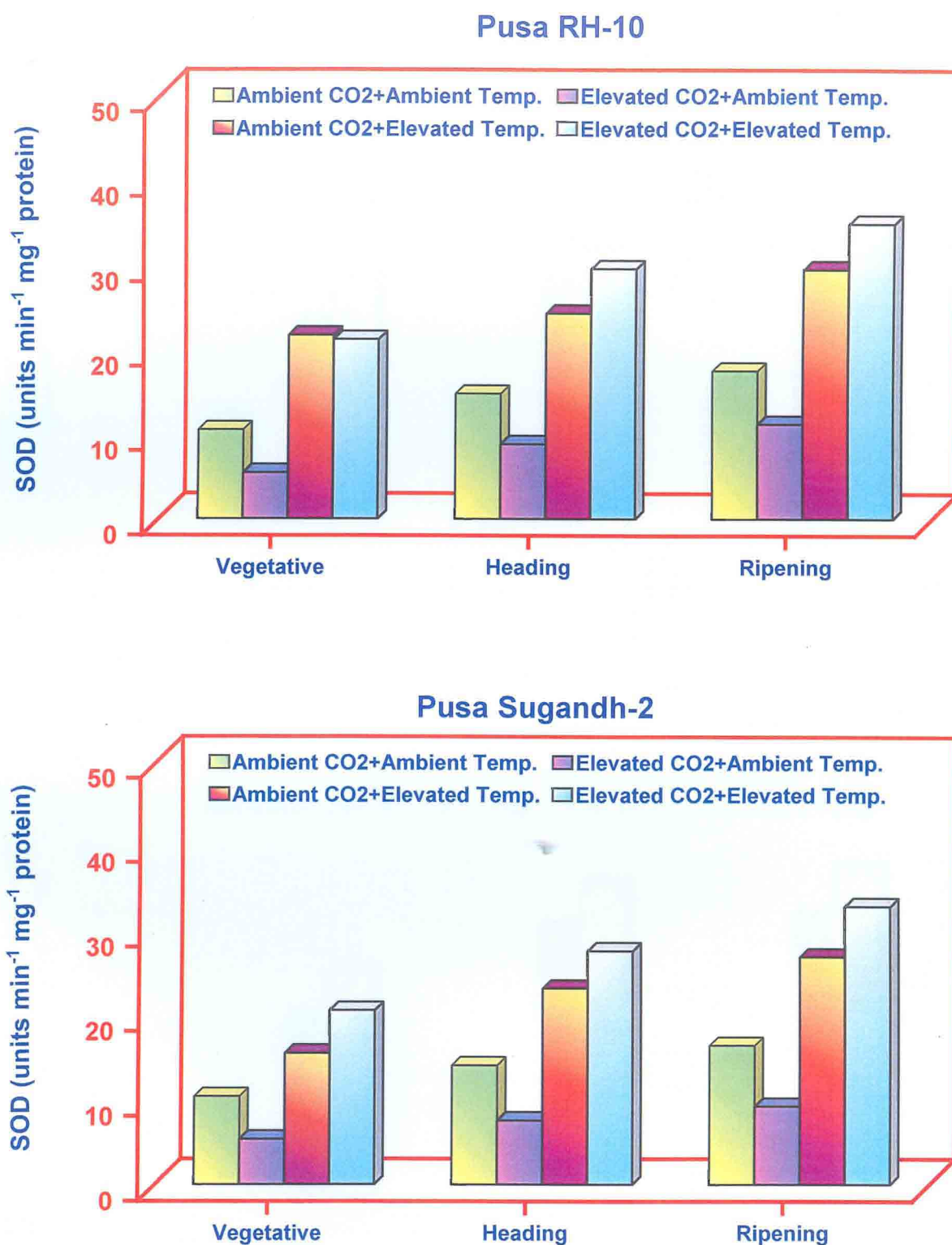


Fig. 22. Interactive effect of elevated CO₂ and temperature on the activity of superoxide dismutase (units min⁻¹ mg⁻¹ protein) in the rice varieties

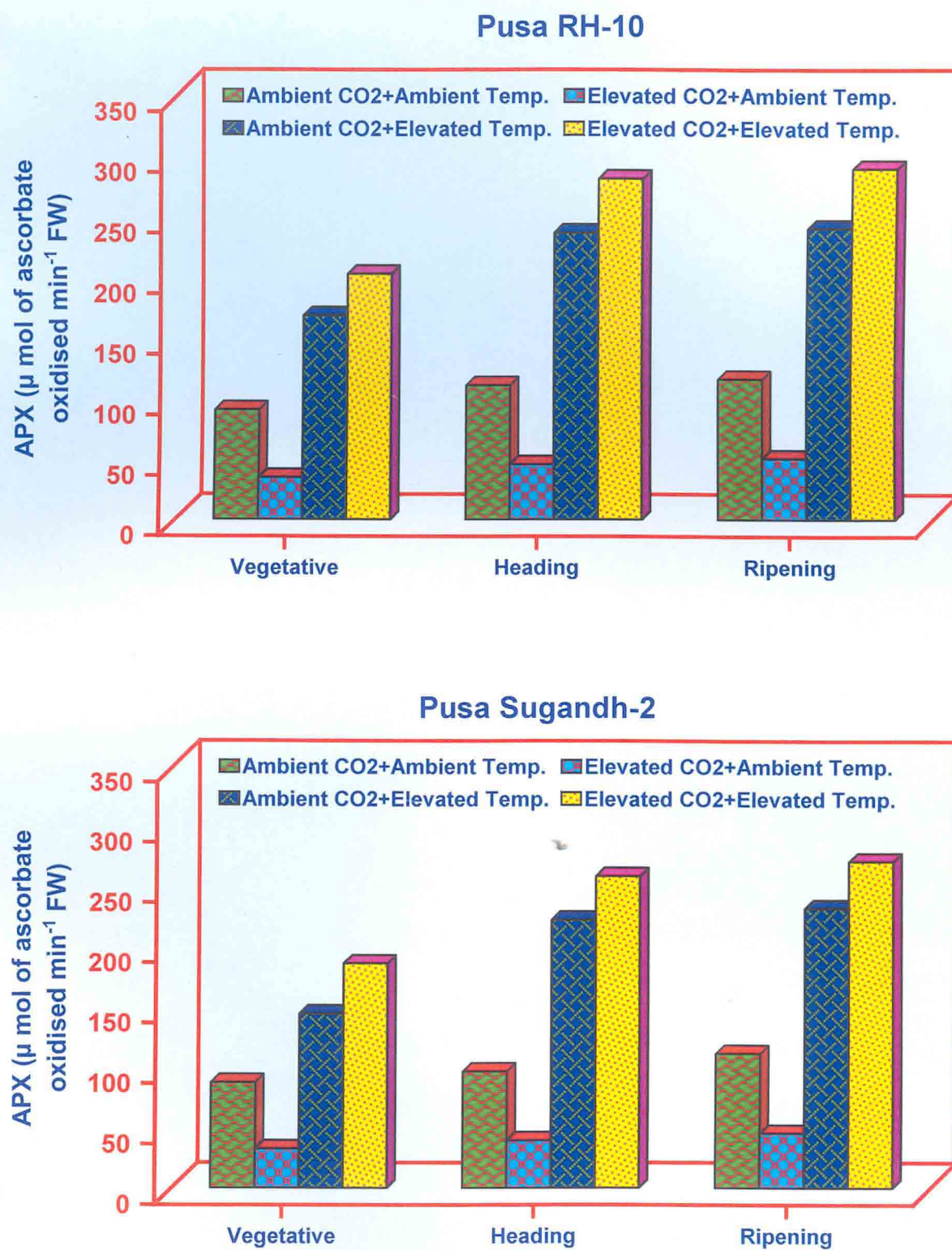


Fig. 23. Interactive effect of elevated CO₂ and temperature on the activity of ascorbate peroxidase (μ mol of ascorbate oxidised min⁻¹ FW) in the rice varieties

interaction effect was significant. APX activity was higher in PRH-10 compared to PS-2.

4.3.13.3 Glutathione reductase (GR)

There was significant decrease in the glutathione reductase enzyme activity under enhanced levels of CO₂ (Fig. 24). The decrease ranged from 54-55% in PRH-10 and from 60-66% in PS-2. Increase in temperature significantly increased the GR activity. The temperature induced increase was 1.1 fold in PRH-10 and 1.5 fold in PS-2 under ambient condition. Under elevated condition, the increase ranged from 2.0 fold (ripening) to 5.0 fold (vegetative) in PRH-10 and from 4.4 fold (heading) to 7.3 fold (vegetative) in PS-2 under elevated CO₂ condition. The CO₂ x temperature interaction was not significant. GR activity was higher in PRH-10 compared to PS-2.

4.1.14 Carbon (C)

Leaves

The carbon content of the leaves increased significantly at the elevated CO₂ (Table 146). This increase ranged from 3% (heading) to 4% (vegetative) in PRH-10 and from 3% (ripening) to 5% (heading) in PS-2. Higher temperature treatment resulted in a significant decrease of the carbon content in leaves. The reduction ranged from 12% (ripening) to 16% (heading) and from 7% (ripening) to 8% (heading) in PRH-10 under ambient and elevated CO₂ condition, respectively. Temperature induced reduction ranged from 15% (ripening) to 19% (heading) and from 11% (ripening) to 17% (heading) under ambient and elevated CO₂ conditions, respectively in PS-2 variety. The interaction of CO₂ and temperature was significant except at the vegetative

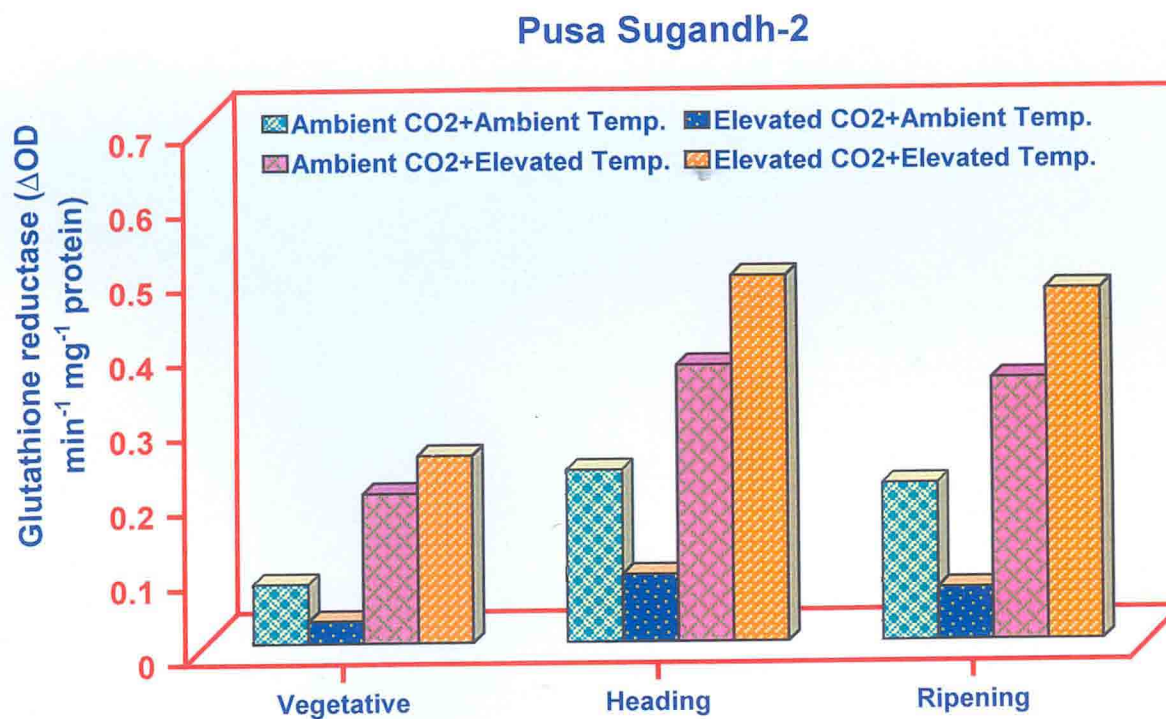
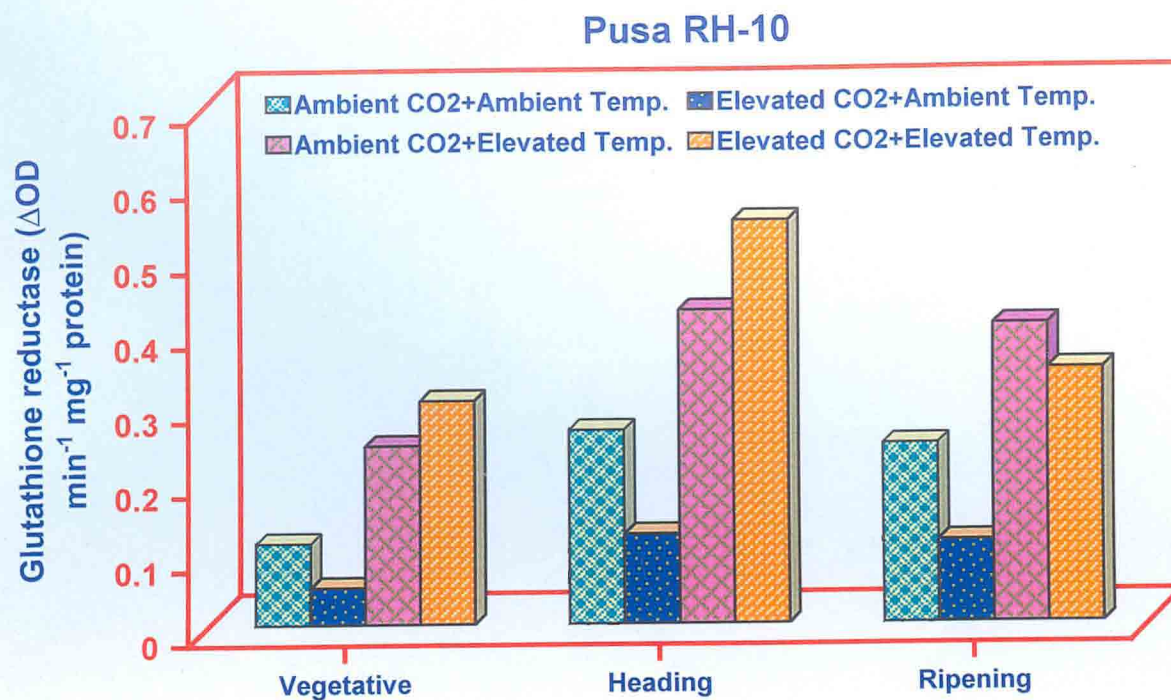


Fig. 24. Interactive effect of elevated CO₂ and temperature on the activity of glutathione reductase ($\Delta OD \text{ min}^{-1} \text{ mg}^{-1}$) in the rice varieties

Table 146. Interactive effect of elevated CO₂ and temperature on the carbon content (% DM) in the leaves of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	43.76	43.60	38.66	35.36	42.36	40.23
Elevated CO ₂ + ambient temp.	45.53	43.90	39.96	37.16	42.70	41.50
Ambient CO ₂ + elevated temp.	41.10	40.50	32.46	28.83	36.90	33.80
Elevated CO ₂ + elevated temp.	41.63	40.10	36.46	30.70	39.46	36.53
CD at 5%						
Variety (V)		0.522		0.390		0.889
CO ₂		0.522		0.390		0.889
V x CO ₂		0.739		0.552		NS
T		0.522		0.390		0.889
V x T		NS		0.552		NS
CO ₂ x T		NS		0.552		1.257
V x CO ₂ x T		NS		0.781		NS

stage. The carbon content in the leaves was significantly greater for PRH-10 than PS-2.

Stem

CO₂ enrichment significantly increased the carbon content of stem in both the varieties (Table 147). The increase ranged from 3% (heading) to 10% (vegetative) in PRH-10 and from 2% (heading) to 11% (vegetative) in PS-2. A significant reduction in the carbon content of stem was observed under elevated temperature. The reduction under ambient condition ranged from 12% (ripening) to 16% (heading) in PRH-10 and from 19% (heading) to 21% (ripening) in PS-2. At elevated CO₂, the reduction was 6-10% in PRH-10 and 11-13% in PS-2. The CO₂ and temperature interaction was significant at the heading and the ripening stages. PRH-10 had higher amount of carbon in the stem as compared to PS-2.

Root

Elevated CO₂ concentration significantly increased the carbon content in roots (Table 148). This increase ranged from 5% (vegetative) to 7% (heading) in PRH-10 and it was 3% in PS-2. Increase in temperature brought about a significant reduction in the carbon content of roots. The reduction was 11-20% in PRH-10 and 14-26% in PS-2 under ambient condition. Under the elevated CO₂ condition, it was 8-13% in PRH-10 and 10-17% in PS-2. The interactive effect of CO₂ and temperature was significant at the heading and ripening stages. The carbon content in the roots was greater for PRH-10 compared to PS-2.

Table 147. Interactive effect of elevated CO₂ and temperature on the carbon content (% DM) in the stem of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	41.12	38.26	39.30	37.46	41.40	39.46
Elevated CO ₂ + ambient temp.	45.32	42.53	40.33	38.03	42.63	40.06
Ambient CO ₂ + elevated temp.	35.46	32.31	32.76	30.46	36.73	31.03
Elevated CO ₂ + elevated temp.	43.90	41.80	35.96	33.06	40.03	35.66
CD at 5%						
Variety (V)	0.220		0.590		0.539	
CO ₂	0.220		0.590		0.539	
V x CO ₂	0.311		NS		0.762	
T	0.220		0.590		0.539	
V x T	NS		NS		0.762	
CO ₂ x T	NS		0.835		0.762	
V x CO ₂ x T	NS		NS		NS	

Table 148. Interactive effect of elevated CO₂ and temperature on the carbon content (% DM) of the roots in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	43.56	41.43	36.36	35.76	39.70	38.63
Elevated CO ₂ + ambient temp.	43.76	42.10	38.90	36.86	41.73	39.33
Ambient CO ₂ + elevated temp.	42.73	40.53	28.90	26.26	35.33	33.30
Elevated CO ₂ + elevated temp.	43.13	41.00	33.46	30.50	38.10	35.56
CD at 5%						
Variety (V)		0.218		0.717		0.441
CO ₂		0.218		0.717		0.441
V x CO ₂		NS		NS		0.624
T		0.218		0.717		0.441
V x T		NS		1.014		NS
CO ₂ x T		NS		1.014		0.624
V x CO ₂ x T		NS		NS		NS

4.3.15 Nitrogen (N)

Leaves

CO₂ enrichment significantly reduced the nitrogen content in the leaves (Table 149). The reduction at elevated CO₂ ranged from 9-13% in both the varieties. Elevated temperature significantly reduced the nitrogen content of leaves. The reduction under ambient and elevated CO₂ condition ranged from 6% (vegetative and ripening) to 12% (heading) and from 5% (ripening) to 10% (vegetative), respectively in PRH-10 and in case of PS-2, it ranged from 7% (heading and ripening) to 13% (vegetative) and from 4% (vegetative) to 11% (ripening), respectively. The CO₂ x temperature interaction was not significant. The nitrogen content was greater for PRH-10 compared to PS-2.

Stem

Higher CO₂ brought about significant decrease in the nitrogen content of stem (Table 150). The reduction at elevated CO₂ ranged from 10% (vegetative) to 12% (ripening) in PRH-10 and in case of PS-2, it ranged from 12% (vegetative) to 17% (heading) in PS-2. Elevated temperature brought about significant reduction in the nitrogen content of stem. This reduction ranged from 15% (heading) to 20% (ripening) in PRH-10 and from 5% (vegetative) to 11% (heading) in PS-2 under ambient CO₂ condition. The reduction ranged from 10% (heading) to 13% (vegetative) in PRH-10 and from 3% (heading) to 7% (vegetative) in PS-2 under elevated CO₂ condition. The CO₂ and temperature interaction effect was significant at the vegetative and ripening stages. PRH-10 had significantly higher amount of nitrogen in the stem compared to PS-2.

Table 149. Interactive effect of elevated CO₂ and temperature on the nitrogen content (% DM) of the leaves in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	4.87	4.50	3.11	2.89	4.23	3.90
Elevated CO ₂ + ambient temp.	4.45	3.95	2.48	2.52	3.71	3.56
Ambient CO ₂ + elevated temp.	4.59	3.91	2.71	2.69	3.97	3.64
Elevated CO ₂ + elevated temp.	4.00	3.80	2.29	2.32	3.51	3.17
CD at 5%						
Variety (V)		0.050		NS		0.100
CO ₂		0.050		0.035		0.100
V x CO ₂		0.071		NS		NS
T		0.050		0.035		0.100
V x T		NS		NS		NS
CO ₂ x T		NS		NS		NS
V x CO ₂ x T		NS		NS		NS

Table 150. Interactive effect of elevated CO₂ and temperature on the nitrogen content (% DM) in the stem of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	4.54	3.94	3.77	3.20	4.07	3.61
Elevated CO ₂ + ambient temp.	4.07	3.46	3.39	2.66	3.58	3.17
Ambient CO ₂ + elevated temp.	3.75	3.76	3.31	2.86	3.25	3.35
Elevated CO ₂ + elevated temp.	3.54	3.21	3.03	2.57	3.22	3.22
CD at 5%						
Variety (V)	0.044		0.043			0.142
CO ₂	0.044		0.043			0.142
V x CO ₂	0.063		NS			0.202
T	0.044		0.043			0.142
V x T	0.063		NS			NS
CO ₂ x T	0.063		NS			0.202
V x CO ₂ x T	0.089		0.087			NS

Roots

Elevated CO₂ concentration significantly decreased the nitrogen content in roots (Table 151). The reduction ranged from 12% (ripening) to 20% (heading) in PRH-10, whereas it ranged from 13% (heading) to 15% (vegetative) in PS-2. Temperature increase brought about significant reduction in the nitrogen content of roots. The reduction varied from 6% (vegetative) to 15% (heading) and from 5% (ripening) to 8% (heading) under ambient and elevated CO₂ conditions, respectively in PRH-10. The decrease ranged from 10% (vegetative) to 11% (ripening) and from 8% (vegetative) to 10% (ripening) in PS-2 under ambient and elevated CO₂ conditions, respectively. The interaction of elevated CO₂ and temperature was significant at the heading stage.

4.1.16 Carbon : nitrogen ratio

Leaves

Elevated CO₂ brought about significant increase in the ratio of carbon to nitrogen content in the leaves (Table 152). The increase at elevated CO₂ ranged from 3% (vegetative) to 10% (heading and ripening) in PRH-10 and from 4% (vegetative) to 8% (ripening) in PS-2. Elevated temperature resulted in a significant reduction in the ratio of carbon to nitrogen content. The reduction under ambient condition ranged from 11% (vegetative) to 27% (heading) in PRH-10 and from 11% (vegetative) to 23% (heading) in PS-2. The reduction in the C/N ratio of the leaves was 16-19% in PRH-10 and 17-26% in PS-2 at elevated CO₂. The CO₂ x temperature interaction was significant at the heading and ripening stages. PRH-10 had greater C/N ratio compared to PS-2 at the heading and ripening stages.

Table 151. Interactive effect of elevated CO₂ and temperature on the nitrogen content (% DM) of roots in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	3.98	3.14	2.93	2.46	3.02	2.81
Elevated CO ₂ + ambient temp.	3.44	2.66	2.34	2.14	2.65	2.41
Ambient CO ₂ + elevated temp.	3.74	2.84	2.47	2.20	2.62	2.51
Elevated CO ₂ + elevated temp.	3.17	2.46	2.14	2.11	2.51	2.18
CD at 5%						
Variety (V)	0.070					0.091
CO ₂	0.070		0.060			0.091
V x CO ₂	NS		0.086			NS
T	0.070		0.060			0.091
V x T	0.100		0.086			NS
CO ₂ x T	NS		0.086			NS
V x CO ₂ x T	NS		NS			NS

Table 152. Interactive effect of elevated CO₂ and temperature on the C:N ratio in the leaves of the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	9.94	10.47	15.08	13.23	10.72	11.05
Elevated CO ₂ + ambient temp.	10.23	11.11	16.11	14.74	11.50	11.65
Ambient CO ₂ + elevated temp.	8.95	9.37	11.97	10.71	9.29	9.28
Elevated CO ₂ + elevated temp.	8.54	8.91	12.97	10.84	9.32	13.58
CD at 5%						
Variety (V)		0.225		0.403		0.350
CO ₂		0.225		NS		0.350
V x CO ₂		NS		NS		0.496
T		0.225		0.403		0.350
V x T		NS		NS		0.495
CO ₂ x T		NS		0.570		0.495
V x CO ₂ x T		NS		NS		0.701

Stem

Elevated CO₂ brought about significant increase in the ratio of carbon to nitrogen content in the stem (Table 153). The increase ranged from 10% (heading) to 11% (vegetative) in PRH-10 and from 7% (heading) to 9% (vegetative) in PS-2. Higher temperature brought about a significant reduction in the C/N ratio of stem. The reduction under ambient and elevated CO₂ was less in both the varieties. The interaction of CO₂ x temperature was significant at heading and ripening stages. The C/N ratio in the stem was significantly higher in PS-2 compared to PRH-10.

Root

CO₂ enrichment brought about a significant increase in the C/N ratio of the root (Table 154). The increase ranged from 7% (heading) to 18% (vegetative) in PRH-10 and from 7% (vegetative) to 13% (ripening) in PS-2. Higher temperature brought about a significant reduction in the C/N ratio of the roots. The C/N ratio was 7-13% under ambient CO₂ and 14-19% under elevated CO₂ at the elevated temperature conditions. The CO₂ x temperature interaction was not significant. The C/N ratio was significantly higher for PS-2 at the vegetative and ripening stages.

4.3.17 Total soluble protein

CO₂ enrichment brought about significant decrease in the soluble protein content of leaves (Table 155). The decrease ranged from 16% (heading) to 21% (ripening) in PRH-10 and from 13% (heading) to 20% (ripening) in PS-2. Elevated temperature caused significant reduction in total soluble protein content in both the varieties. Temperature induced reduction under ambient condition ranged from 14% (heading) to 17% (ripening) in

Table 153. Interactive effect of elevated CO₂ and temperature on the C:N ratio of stem in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	10.48	11.72	10.97	13.57	10.85	12.25
Elevated CO ₂ + ambient temp.	11.05	12.29	11.89	14.29	11.90	12.63
Ambient CO ₂ + elevated temp.	11.46	11.02	9.33	10.65	11.30	10.15
Elevated CO ₂ + elevated temp.	9.67	10.60	9.53	10.33	9.90	9.87
CD at 5%						
Variety (Cv.)		0.360		0.224		0.328
CO ₂		0.360		0.224		0.328
V x CO ₂		0.509		NS		0.464
T		0.360		0.224		0.328
V x TS		NS		0.317		0.464
CO ₂ x T		NS		0.317		0.464
V x CO ₂ x T		NS		0.449		NS

Table 154. Interactive effect of elevated CO₂ and temperature on the C:N ratio of the root in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	11.23	14.82	15.23	16.94	14.81	15.36
Elevated CO ₂ + ambient temp.	12.72	15.82	16.62	17.22	15.74	16.31
Ambient CO ₂ + elevated temp.	11.42	14.27	11.70	11.67	13.48	13.23
Elevated CO ₂ + elevated temp.	0.83	13.05	11.41	12.39	12.61	12.65
CD at 5%						
Variety (V)		0.476		NS		0.570
CO ₂		0.476		NS		0.570
V x CO ₂		NS		NS		NS
T		0.476		0.506		0.570
V x T		NS		NS		0.806
CO ₂ x T		NS		NS		NS
V x CO ₂ x T		NS		NS		NS

Table 155. Interactive effect of elevated CO₂ and temperature on the leaf soluble protein (mg g⁻¹ FW) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	5.53	5.23	8.23	7.66	7.50	6.93
Elevated CO ₂ + ambient temp.	4.40	4.23	6.93	6.63	5.90	5.53
Ambient CO ₂ + elevated temp.	4.63	4.43	7.06	6.70	6.16	5.60
Elevated CO ₂ + elevated temp.	3.73	3.46	6.16	5.90	5.03	4.53
CD at 5%						
Variety (V)	0.122		0.118			0.167
CO ₂	NS		0.118			0.167
V x CO ₂	NS		NS			NS
T	0.122		0.118			0.167
V x T	NS		NS			NS
CO ₂ x T	0.173		0.168			0.236
V x CO ₂ x T	NS		NS			NS

PRH-10 and from 13% (heading) to 19% (ripening) in PS-2. At elevated CO₂, the decrease in leaf soluble protein content ranged from 13% (heading) to 18% (vegetative) in PRH-10 and from 12% (heading) to 22% (vegetative and ripening) in PS-2. The CO₂ and temperature interaction was significant at all the growth stages. Leaf soluble protein content was significantly higher for PRH-10 compared to PS-2.

4.3.18 Nitrate reductase activity (NR)

The nitrate reductase activity of the leaves increased significantly under high levels of CO₂ (Table 156). The increase was 1.0 to 1.3 fold for PRH-10 and 1.0 fold for PS-2. Temperature rise significantly reduced the activity of NR in the leaves. The reduction under ambient conditions was from 10% (vegetative) to 22% (heading) in PRH-10 and in case of PS-2, the reduction ranged from 18% (vegetative) to 27% (heading). At the elevated CO₂, the reduction ranged from 10% (vegetative) to 15% (heading) in PRH-10 and from 9% (vegetative) to 19% (ripening) in PS-2. The interaction effect was significant only at the ripening stage.

4.3.19 YIELD AND YIELD PARAMETERS

4.3.19.1 Grain yield per plant

CO₂ enrichment brought about a significant increase in the grain yield (Fig. 25). The increase was 26% for PRH-10 and 19% for PS-2. Higher temperature resulted in a significant decrease in the grain yield. The reduction under ambient CO₂ was 30% in PRH-10 and 38% in PS-2, however, it was 24% for PRH-10 and 36% for PS-2 under elevated CO₂ condition. The interaction of elevated CO₂ and temperature was significant. Grain yield per plant was higher for the variety PRH-10.

Table 156. Interactive effect of elevated CO₂ and temperature on the activity of nitrate reductase (μmol NO₂ g⁻¹ hr⁻¹) in the rice varieties

Treatments	Vegetative stage		Heading stage		Ripening stage	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	1.67	2.12	3.13	2.23	2.75	2.14
Elevated CO ₂ + ambient temp.	1.85	2.34	3.70	2.59	3.27	2.65
Ambient CO ₂ + elevated temp.	0.86	0.74	1.21	1.04	0.94	0.77
Elevated CO ₂ + elevated temp.	0.96	0.91	1.56	1.43	1.05	0.85
CD at 5%						
Variety (V)		NS		0.077		0.073
CO ₂		0.333		0.077		0.073
V x CO ₂		NS		0.110		NS
T		0.333		0.077		0.073
V x T		NS		0.110		0.103
CO ₂ x T		NS		NS		0.103
V x CO ₂ x T		NS		NS		NS

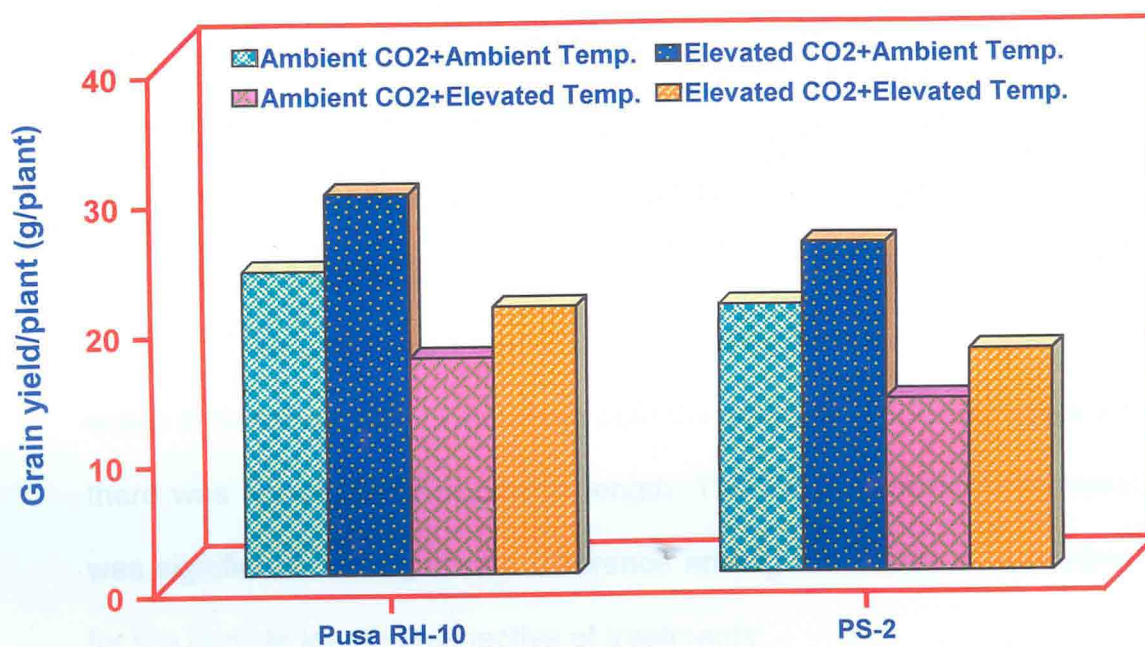


Fig. 25. Interactive effect of elevated CO₂ and temperature on the yield in the rice varieties

4.3.19.2 Number of panicle per plant

Higher CO₂ brought about significant increase in the production of panicles per plant (Table 157a). The increase was 41% in PRH-10 and 31% in PS-2. Elevated temperature significantly reduced the panicle production. The reduction was 14% in both the varieties under ambient condition, whereas under elevated CO₂ condition, it was 12% in PRH-10 and 13% in PS-2. The CO₂ x temperature interaction was significant. PRH-10 had significantly more number of panicles than PS-2.

4.3.19.3 Length of panicle

CO₂ enrichment significantly increased the length of panicle. The increase was 17% for both the varieties (Table 157a). A significant reduction in the panicle length was found under elevated temperature. The reduction under ambient condition was 4% in both the varieties, but under elevated CO₂ there was no reduction in panicle length. The CO₂ x temperature interaction was significant. No significant difference among the varieties were observed for the panicle length irrespective of treatments.

4.3.19.4 Grain number per panicle

CO₂ enrichment brought about a significant increase in the grain number per panicle (Table 157a). The increase was 17% in PRH-10 and 13% in PS-2. Temperature rise significantly decreased grain number per panicle. Under ambient condition, the reduction 40% in PRH-10 and 48% in PS-2 under elevated CO₂ conditions, it was 23% in PRH-10 and 34% in PS-2. The interaction of CO₂ and temperature was significant. More number of grains were observed in PRH-10 compared to PS-2.

Table 157a. Interactive effect of elevated CO₂ and temperature on the yield components in the rice varieties

Treatments	Length of panicle		Number of panicles/plant		Grain No./panicle	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	24.26	24.16	12.00	11.00	200.66	182.33
Elevated CO ₂ + ambient temp.	27.20	27.16	13.66	12.66	234.66	215.66
Ambient CO ₂ + elevated temp.	23.26	23.26	8.33	8.33	99.66	97.12
Elevated CO ₂ + elevated temp.	27.46	27.03	9.66	9.66	145.33	141.01
CD at 5%						
Variety (V)		NS		0.252		1.032
CO ₂		0.215		0.252		1.032
V x CO ₂		NS		0.256		NS
T		0.215		0.252		1.032
V x T		NS		0.256		1.459
CO ₂ x T		0.305		0.256		1.459
V x CO ₂ x T		0.431		NS		NS

4.3.19.5 1000-grain mass

Elevated CO₂ brought about significant increase in the grain mass (Table 157b). The increase was 8% in PRH-10 and 4% in PS-2. Temperature increase brought about a significant decrease in the grain mass. The reduction under ambient condition for PRH-10 was 30% whereas the reduction under elevated CO₂ conditions was 21%. The reduction was 32% under ambient and 26% under elevated CO₂ condition in PS-2. The interaction of CO₂ and temperature on grain mass was not significant. The grain mass was more in PRH-10 compared to PS-2.

4.3.19.6 Harvest index (HI)

CO₂ enrichment significantly increased the harvest index in both the varieties (Table 157b). The increase at elevated CO₂ was 10% for PRH-10 and 9% for PS-2. Temperature rise brought about significant reduction in the harvest index. The reduction was 19% for PRH-10 and 21% for PS-2 under ambient condition and 13% for PRH-10 and 16% for PS-2 under elevated CO₂ condition. The CO₂ x temperature interaction was not significant. The harvest index was greater for PRH-10 compared to PS-2.

4.3.20 Grain quality

4.3.20.1 Reducing sugar

Reducing sugar content in grains significantly increased at elevated CO₂ (Table 158a). The increase was 25% in PRH-10 and 22% in PS-2. The increased temperature brought about significant reduction in the reducing sugar content. The reduction under ambient condition was 26% for PRH-10 and 25% for PS-2, whereas under elevated condition, reduction was 22% for PRH-10 and 19% for PS-2. The CO₂ x temperature interaction was significant.

Table 157 b. Interactive effect of elevated CO₂ and temperature on the yield components in the rice varieties

Treatments	1000-grain mass (g)		Harvest index	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	26.83	24.99	0.42	0.41
Elevated CO ₂ + ambient temp.	28.10	26.99	0.46	0.45
Ambient CO ₂ + elevated temp.	18.38	16.90	0.34	0.32
Elevated CO ₂ + elevated temp.	23.61	19.29	0.40	0.38
CD at 5%				
Variety (V)		0.252		0.004
CO ₂		0.252		0.004
V x CO ₂		0.356		NS
T		0.252		0.004
V x T		0.356		NS
CO ₂ x T		NS		NS
V x CO ₂ x T		0.504		NS

Table 158a. Interactive effect of elevated CO₂ and temperature on grain quality parameters in the rice varieties

Treatments	Reducing sugar (mg g ⁻¹ DW)		Non-reducing sugar (mg g ⁻¹ DW)		Total sugar (mg g ⁻¹ DW)		Starch (mg g ⁻¹ DW)	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	101.26	96.68	149.08	136.11	250.34	245.37	258.31	256.93
Elevated CO ₂ + ambient temp.	126.47	116.54	153.66	145.87	270.13	262.31	289.41	277.66
Ambient CO ₂ + elevated temp.	74.32	71.38	105.14	95.38	179.46	171.70	194.29	175.23
Elevated CO ₂ + elevated temp.	98.63	95.41	110.51	102.89	208.14	197.30	226.33	198.36
CD at 5%								
Variety (V)		2.725		4.524		5.72		4.42
CO ₂		2.725		4.524		5.72		4.42
V x CO ₂		3.853		6.397		NS		NS
T		2.725		4.524		5.72		4.42
V x T		NS		NS		NS		NS
CO ₂ x T		3.853		6.397		NS		6.26
V x CO ₂ x T		NS		NS		NS		NS

PRH-10 had greater amount of reducing sugars in the grain compared to PS-2.

4.3.20.2 Non-reducing sugar

CO₂ enrichment significantly increased the non-reducing sugar content in the grains (Table 158a). CO₂ induced enhancement was 4% in PRH-10 and 6% in PS-2. Increase in temperature brought about significant reduction in the non-reducing sugar content. The reduction was 29% for PRH-10 and 30% for PS-2 under ambient CO₂, whereas at elevated CO₂, it was 27% for PRH-10 and 17% for PS-2. The interaction of CO₂ x temperature was significant. The non-reducing sugar content was greater for PRH-10 compared to PS-2.

4.3.20.3 Total sugar

Elevated CO₂ concentration brought about a significant increase in the total sugar content of the grains (Table 158a). The increase was 8% for PRH-10 and 6% for PS-2. Increase in temperature brought about a significant decrease in the total sugar content in both the varieties. The reduction under ambient condition was 28% in PRH-10 and 30% in PS-2 whereas, under elevated CO₂ condition, it was 22% in PRH-10 and 25% in PS-2. The interactive effect of CO₂ and temperature was not significant. PRH-10 had greater total sugar content in the grain than that of PS-2, irrespective of treatments.

4.3.20.4 Starch

The starch content of grain significantly increased at elevated CO₂ condition (Table 158a). The enhancement was 12% in PRH-10 and 18% in case of PS-2. Elevated temperature brought about a significant reduction in the starch content of grain which was 25% in PRH-10 and 31% in PS-2 under

ambient condition. On the other hand, reduction under elevated CO₂ condition was 21% for PRH-10 and 29% for PS-2. The CO₂ x temperature interaction was not significant. Higher starch content was observed in PRH-10.

4.3.20.5 Amylose

Elevated CO₂ condition brought about significant increase in the amylose content (Table 158b). The increase was 4% in PRH-10 and 5% in PS-2. The higher temperature brought about significant reduction in the amylose content in both the varieties. The reduction was 4% for both the varieties under ambient and elevated CO₂ condition. The CO₂ x temperature interaction was not significant. The amylose content in PRH-10 was less than PS-2 irrespective of treatments.

4.3.20.6 Total non-structural carbohydrates (TNC)

High CO₂ levels brought about a significant increase in total non-structural carbohydrates content in grain (Table 158b). The increase was 7% in PRH-10 and 5% in PS-2 varieties. Elevated temperature brought about significant reduction in TNC content in both varieties. The reduction in TNC at ambient CO₂ was 29% for both the varieties whereas at elevated CO₂, it was 21% for PRH-10 and 23% for PS-2. The interaction of CO₂ x temperature on TNC content in grain was significant. TNC was significantly more in PRH-10 compared to PS-2.

4.3.20.7 Nitrogen (N)

Elevated CO₂ brought about decrease in the nitrogen content of grain which was 4% in both the varieties (Table 158b). The increase in temperature rise brought about a significant reduction in both the varieties. The reduction under elevated CO₂ condition was 3% for PRH-10 and 5% for PS-2 whereas, under ambient condition, it was 4% for both the varieties. The CO₂ x

Table 158b . Interactive effect of elevated CO₂ and temperature on grain quality parameters in the rice varieties

Treatments	Amylose (%)		TNC (mg g ⁻¹ DW)		Nitrogen (%)		Protein (%)	
	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	24.36	26.16	523.65	505.72	1.58	1.55	9.40	9.22
Elevated CO ₂ + ambient temp.	25.09	27.59	559.54	539.97	1.61	1.59	9.57	9.46
Ambient CO ₂ + elevated temp.	23.99	25.09	373.75	357.93	1.52	1.49	9.10	8.86
Elevated CO ₂ + elevated temp.	24.02	27.19	434.47	417.66	1.55	1.51	9.22	8.98
CD at 5%								
Variety (V)	0.32		4.524		0.029			NS
CO ₂	NS		4.524		0.029			0.277
V x CO ₂	NS		6.397		NS			NS
T	0.32		4.524		0.029			NS
V x T	NS		NS		NS			NS
CO ₂ x T	NS		6.397		NS			NS
V x CO ₂ x T	NS		NS		NS			NS

temperature interaction effect was not significant. Nitrogen content was greater in PRH-10 compared to PS-2.

4.3.20.8 Protein

CO₂ enrichment brought about a significant decrease in the protein content (Table 158b). The decrease was 2% in PRH-10 and 3% in PS-2. Elevated temperature brought about further reduction but it was not significant. The temperature induced reduction under ambient and elevated CO₂ conditions was 3% in PRH-10 and 4% in PS-2. The interaction effect of CO₂ x temperature was not significant. There was no significant difference between the varieties on protein content in the grains.

4.3.20.9 Calcium

There was a significant increase in the Ca content of grain under high levels of CO₂ (Table 158c). The increase was 8% for PRH-10 and 9% for PS-2. Increase in temperature caused a significant reduction in the Ca content for both the varieties. The reduction was 14% for PRH-10 and 13% for PS-2 under ambient condition and it was 13% in PRH-10 and 15% in PS-2 under elevated CO₂ condition. The interaction of CO₂ and temperature on Ca content was not significant. PRH-10 had greater calcium content in the grain compared to PS-2.

4.3.20.10 Potassium

CO₂ enrichment brought about a significant increase in the K content of the grains (Table 158c). The increase was 14% in PRH-10 and 15% in case of PS-2. Higher temperature caused significant reduction in the potassium content of grains of rice varieties. The reduction under ambient CO₂ was 22% in PRH-10 and 20% in PS-2 and under elevated CO₂, it was 19% in PRH-10 and 18% in PS-2. The CO₂ x temperature interaction was significant. PRH-10 had greater amount of potassium in the grain compared to PS-2.

Table 158c. Interactive effect of elevated CO₂ and temperature on the grain quality parameters in the rice varieties

Treatments	Calcium (%)		Potassium (%)	
	PRH-10	PS-2	PRH-10	PS-2
Ambient CO ₂ + ambient temp.	0.084	0.082	0.21	0.20
Elevated CO ₂ + ambient temp.	0.091	0.089	0.24	0.23
Ambient CO ₂ + elevated temp.	0.072	0.066	0.16	0.16
Elevated CO ₂ + elevated temp.	0.079	0.075	0.19	0.19
CD at 5%				
Variety (V)		0.001		0.003
CO ₂		0.001		0.003
V x CO ₂		NS		NS
T		0.001		0.003
V x T		NS		0.005
CO ₂ x T		NS		0.005
V x CO ₂ x T		NS		NS

5. DISCUSSION

The exponential rise in carbon dioxide is one of the most important global climate change which effectively influences the productivity of crop plants and food security for mankind. The rising concentration of atmospheric CO₂ is believed to be due to burning of fossil fuels such as coal, gas and oil, urbanization, deforestation and expansion of agriculture. Burning of fossil fuels introduced approximately 5.0 GT whereas deforestation adds about 2.3 GT of carbon dioxide per annum in the atmosphere (Tans *et al.*, 1995). The current concentration of CO₂ in the atmosphere is about 372 $\mu\text{mol mol}^{-1}$. It is exponentially increasing at the rate of 1.8 $\mu\text{mol mol}^{-1}$ per annum and this concentration is likely to be doubled by the end of 21st century (Houghton *et al.*, 1996).

The increase in CO₂ concentration is expected to cause global warming by absorbing long wave heat radiation from earth's surface and may also affect cloudiness and precipitation. According to global circulation models (GCMs), the temperature changes may not be uniform. It may increase by 4-5°C at polar region and about 1°C at equator. This change in temperature may affect the agricultural productivity and such an effect is called **climatic effect**. This increase in CO₂ affects the photosynthetic carbon assimilation, by reducing photorespiratory activity and altering stomatal aperture. This **biological effect** of CO₂ has significant impact on the growth and productivity

of crop plants. It was reported that C_3 plants (rice, wheat, oilseeds, pulses etc.) respond to elevated CO_2 since it reduces oxygenase activity of RuBP carboxylase/oxygenase enzyme. C_4 plants (maize, sorghum, sugarcane etc.) on the other hand show little or no photosynthetic response to elevated CO_2 because they are not competitively inhibited by O_2 and are CO_2 saturated. However, there is no consensus on the quantitative effect of increasing CO_2 and temperature in plant processes and growth due to differences in response at different stages of growth, species of crop and because of growth limiting factors. The selection of varieties which are likely to be productive under new environmental conditions such as increase in CO_2 and temperature is a major imperative of the present study in which basmati rice varieties were examined for their responses to the interaction of higher CO_2 concentration and elevated temperature, for their growth, development and productivity.

Rice has been identified as the crop of present investigation because it provides a substantial portion of the dietary requirement of nearly 2.4 billion population (Anonymous, 2002). In order to keep pace with a rapidly increasing population, global rice production levels seen in 1991, will need to increase by atleast 46% by the year 2025 (Horie *et al.*, 2000). Global warming resulting from increased atmospheric carbon dioxide concentration and other green house gases (Hansen *et al.*, 1984) further hampers our ability to predict rice production and raises serious questions concerning food security in the near future. Accurate prediction of the impacts of climate change on rice productivity on a region by region basis is essential, not only for the estimation of world food security, but also for the continued sustainability of rice farming societies, which in most countries consist of small hectarage subsistence

farmers (Horie *et al.*, 2000).

Hybrid rice is a practically feasible and readily adoptable option to increase the rice production, as has been amply demonstrated in People's Republic of China, the first largest country in the world for rice production (Ahmed *et al.*, 2003). Two varieties of rice viz. Pusa RH 10 (PRH-10) and Pusa Sugandh-2 (PS-2) were used in the present investigation. PRH-10 was the first aromatic, super fine grained hybrid that has been released in 2001, whereas Pusa Sugandh-2 is an aromatic, pure line variety also released in the year 2001 (Zaman *et al.*, 2004). These varieties were identified for cultivation when the level of CO₂ was 360 $\mu\text{mol mol}^{-1}$ with the average temperature of the current period. Their response to the future concentration of CO₂ and temperature was the main objective of the present study.

To meet the requirement and to fill the gap of productivity for future, it was considered important to simulate conditions of high CO₂ and temperature to study the responses of these rice varieties. Such study is the present investigation was based on the following objectives:

1. To study the response of the rice varieties to the elevated CO₂ and rise in temperature.
2. Physiological and biochemical characterization of the response of these varieties to the elevated CO₂ individually and its interaction with the higher temperature.

This will help to develop rice plant type for future climate change. It will also help in identifying the cultivation and management techniques for the responsive varieties under future changed climatic conditions.

In the current investigation, facility of open top chambers (OTC) and

free air carbon dioxide enrichment (FACE) were used for studying the crop responses to the elevated CO₂. The temperature and CO₂ interaction studies were done in the phytotron. Open top chamber was one of the most widely used techniques for studying the response of crops and crop ecosystems to the elevated CO₂. Climate in OTC tracks the dynamic changes in temperature, light, rainfall etc. experienced in unenclosed area without costly and complex environmental controls (Uprety *et al.*, 1998). Another facility used for CO₂ enrichment in the present study under natural field condition was the free air carbon dioxide enrichment technology. It was developed at Indian Agricultural Research Institute, New Delhi for the South Asian Region (Uprety *et al.*, 2000 and Maini *et al.*, 2002). This technology has many advantages over other open and closed chamber systems used by earlier scientist (Uprety, 1998). FACE could enrich a larger area of vegetation with CO₂, without confounding effects of growth chamber, for extended period of time and lower cost per unit area than any other techniques. Both OTC and FACE provides almost natural conditions for the generation of realistic biological data on crop response to the rising atmospheric CO₂ (Uprety *et al.*, 2000 and Kimball *et al.*, 2002). Although experiments conducted using FACE system utilize true field grown conditions, however, factorial combinations of CO₂ and air temperature treatment was difficult. Therefore, the required factorial experiments were conducted in controlled plant growth chamber systems at the National Phytotron Facility, Indian Agricultural Research Institute, New Delhi.

An extensive description of the experimental findings has been given in the results, but it will be worthwhile to recapitulate the salient features before

discussing them.

Present investigation revealed that plant growth in terms of plant height, leaf number, tiller number, leaf area and root length increased at elevated CO₂. This increase in plant growth was more for PS-2 compared to PRH-10. Increase in a 4⁰C temperature under phytotron condition brought about reduction in most of the growth parameters. Such a reduction was not observed under elevated CO₂ concentration.

CO₂ enrichment increased the whole plant biomass in both the varieties. A larger proportion of that has been contributed to roots particularly at initial stages. Although, similar trend was observed in both the varieties, the intensity of accumulation of biomass was lesser in PS-2 compared to PRH-10, which was evident from the higher panicle dry mass in PRH-10. Elevated temperature brought about reduction in the biomass production. The reduction was less under elevated CO₂ condition and this effect of CO₂ was more in PRH-10 compared to PS-2.

Growth parameters like crop growth rate, net assimilation rate, specific leaf weight and leaf area index increased at enhanced levels of CO₂. The specific leaf area was lowered at high CO₂. Increase in temperature brought about reduction in most of the parameters which was compensated to some extent by elevated CO₂.

Elevated CO₂ brought about enhancement in the rate of development which brought about early tillering and flowering in the rice varieties.

Although, the chlorophyll content and stomatal conductance were decreased under elevated CO₂, the rate of photosynthesis remained higher throughout the growth period. Elevated CO₂ increased the photosynthetic rate

by 31 per cent in PRH-10 and by 24 per cent in PS-2. These three parameters were maximum at the heading stage and greater in PRH-10 compared to PS-2. Increase in temperature brought about reduction in these parameters which were, however, lowered under elevated CO₂.

Additional carbohydrates under elevated CO₂ brought about an incorporation of maximum carbohydrates in most of the plant parts. Sucrose phosphate synthase activity was increased and the enhancement was 18 per cent in PRH-10 and 12 per cent in PS-2. Higher activity of SPS increased the accumulation of sugars. PRH-10 was more responsive to elevated CO₂ because its carbohydrate production was more compared to PS-2. Increased temperature reduced the carbohydrate accumulation and the activity of SPS. The temperature induced effect was nullified to some extent under enhanced CO₂.

The activity of antioxidant enzymes like superoxide dismutase, ascorbate peroxidase and glutathione reductase were reduced markedly at elevated CO₂. Their activity was enhanced at elevated temperature and this enhancement was more when the plants were grown under elevated CO₂. Higher activity of these enzymes were observed in PRH-10 compared to PS-2.

Elevated CO₂ increased the accumulation of carbon in different plant parts. Though the nitrate reductase activity increased, the nitrogen concentration and the soluble protein content in the plant parts were reduced. Increase in temperature reduced the NR activity and the accumulation of carbon and nitrogen in different plant parts. However, this reduction was less under elevated CO₂.

Grain yield per plant increased by 26 per cent in PRH-10 and 19 per cent in PS-2 under elevated CO₂. Under enhanced CO₂ condition, the sink strength (grain number) was increased, total enhanced the yield. Increase in the grain mass also attributed to the higher yield. Elevated temperature reduced the grain yield which was lessened by 7 per cent in PRH-10 and 2 per cent in PS-2 under elevated CO₂.

The ratio of grain yield to plant biomass (harvest index) increased at elevated CO₂ which implies that the translocation of photoassimilates towards grain was increased by CO₂ enrichment. Elevated temperature decreased the harvest index. However, such reduction was less under elevated CO₂.

Grain mass and its chemical constituents was changed under elevated CO₂. By adding more sugars and starch, the grain mass increased. The increase in the chemical constituents like calcium and potassium improved the grain quality. Protein content was decreased in the grain at high CO₂. Elevated temperature reduced the grain quantity and quality and this reduction was lessened by CO₂ enrichment.

The experimental findings of the present study are discussed below.

Present investigation revealed an increase in photosynthetic rate and decrease in chlorophyll content of the leaf at elevated CO₂. Elevated temperature reduced both photosynthetic rate and chlorophyll content. Temperature induced reduction was ameliorated by elevated CO₂.

The increase in photosynthesis due to elevation of CO₂ results from two properties of Rubisco (Long *et al.*, 2004). (a) The K_m of the enzyme for CO₂ is close to the current atmospheric concentration, and elevated CO₂ increases the velocity of carboxylation, (b) CO₂ competitively inhibits the

oxygenation reaction, which produces glycolate leading to photorespiration. This latter effect is particularly important because it increases the efficiency of net CO₂ uptake by decreasing photorespiratory CO₂ loss and diverting ATP and NADP, which are generated in the light reactions, away from the photorespiratory metabolism to photosynthetic assimilation. Thus, the efficiency of net photosynthesis increases, regardless of other factors which limit gross photosynthetic rate (Long, 1991 and Long and Drake, 1992). However, in the present study, the enzyme, Rubisco was not studied. According to Hymus *et al.* (2001), the stimulation of C₃ photosynthesis at elevated CO₂ was because, the stimulation of electron flow to the photosynthetic carbon reduction cycle was greater than the competitive suppression of electron flow to the photosynthetic carbon oxidation cycle.

Baker and Allen (1993) reported that doubling CO₂ from 330 to 660 $\mu\text{mol mol}^{-1}$ increased rice canopy photosynthesis by 36%. The response of rice plant to an elevated CO₂ concentration possibly depend on the inherent sink strength of plants (Upreti *et al.*, 1998 and Morinaga, 2002). Thus, PRH-10 with more number of panicles responded more to elevated CO₂ for photosynthesis than that of PS-2.

Although, Upreti *et al.* (2003) observed reduction in the larger and smaller subunit of Rubisco protein, the high molecular mass photosystem-2 protein remained greater, that resulted in the sustainability of growth and photosynthesis throughout the growth period in the present study.

A good correlation has been demonstrated between the photosynthetic increase and specific leaf weight under elevated CO₂ in the present study. Thomas and Harvey (1983) attributed it to the addition of one extra layer of

palisade cells in the leaf of soybean plants under elevated CO₂ condition. Such a possibility was also expected in rice in the present study.

Lin *et al.* (1997) and Nakagawa *et al.* (1997) found that higher temperature stimulated single leaf photosynthesis of rice subjected to long-term CO₂ treatments during the vegetative stages. In contrast, Baker and Allen (1993) observed that rice canopy photosynthesis was relatively unaffected by a wide range of air temperature. However, in the present study on rice varieties, a lower rate of photosynthesis at increased temperature was observed. This was probably due to the change in the kinetic parameters of Rubisco and decreased solubility of CO₂ compared to O₂ which increased the photorespiration. Thus, warmer temperature accelerates leaf maturation and senescence, decreasing the duration of active photosynthesis. The temperature induced reduction was ameliorated by CO₂ enrichment, since one of the major effects of elevated CO₂ on net photosynthesis is through the suppression of photorespiration. It could be expected that optimum temperature for photosynthesis shifts upwards as CO₂ increases (Horie *et al.*, 2000). This type of interaction of temperature and CO₂ at leaf level photosynthesis has been defined by Long (1991) for some C₃ species. This type of leaf level response was confirmed in rice by Nakagawa *et al.* (1997).

The chlorophyll content was reduced under elevated CO₂ in the leaves of rice varieties. Wilkins *et al.* (1994) found that the reduction in chlorophyll was associated with lowered Rubisco protein. Upreti *et al.* (2003) demonstrated that the reduction in the Rubisco proteins did not affect the stimulation of photosynthesis, because of the increase in the light harvesting complex-II (LHC-II) proteins of the mature leaves in rice cultivars, thereby

decreasing the requirement of photon fluxes for Rubisco. Van Oosten *et al.* (1994) has explained the chlorophyll reduction on the basis of inhibition of transcription of *cab* genes by accumulation of soluble sugars. According to Wall *et al.* (2001), the reduction in chlorophyll was probably due to the reduced allocation of nitrogen to the leaves. The larger accumulation of non-structural carbohydrates appeared to be related to the reduction in the concentration of chlorophyll pigment (dilution effect) and possibly there may not be a real loss of chlorophyll from cells. Maevskaya *et al.* (1990) noted that a state of homeostasis was maintained and protein and chlorophyll synthesis was not disturbed in *Brassica juncea* grown under elevated CO₂. The present study reveals that though the chlorophyll content was reduced at elevated CO₂ in the rice varieties, the process of photosynthesis was sustained throughout the growth period. This indicated that at elevated CO₂ there was no actual reduction of chlorophyll and it appears to be decreased due to the dilution effect caused by the extra carbohydrate produced by the rice varieties.

Elevated CO₂ decreased the stomatal conductance (gs) to 27% in the variety PRH-10 and to 36% in PS-2 in the present study. Morison and Gifford (1984) also observed that a doubling of CO₂ decreased stomatal conductance by 36% in rice. In wheat, the gs was decreased by 30-40% under elevated CO₂ conditions (Samarakoon *et al.*, 1995). This was due to the changes in the stomata aperture since stomatal density and stomatal index are unaffected within a single season (Estiarte *et al.*, 1994).

Light and CO₂ interact in regulating stomatal movements with higher CO₂ concentration modifying and overriding the light effect (Murray, 1995).

The extent of opening is greater as light intensity increases or as CO₂ concentration decreases (Willmer, 1983). So, effective is the CO₂ mechanism of stomatal that a stream of CO₂ free air will promote stomatal opening even in darkness. Conversely, a high external concentration of CO₂ restricts opening, even at high light intensity. Water deficit overrides both light and CO₂ concentration, triggering stomatal closure (Murray, 1995). Upreti *et al.* (1995) observed that *Brassica* species responded to elevated CO₂ significantly under moisture stressed conditions mitigating the adverse effects on the stomatal conductance. In the present investigation also, a further reduction in the stomatal conductance was observed in the leaves of the rice varieties at elevated temperature. This reduction was lessened to some extent under the elevated CO₂ conditions.

Zeiger (1990) explains the mechanism of stomatal opening on the basis of carboxylation. Guard cells are always the only epidermal cells to possess chloroplasts and these chloroplasts do not lack rubisco activity as previously thought of. CO₂ was involved in the mechanism of stomatal opening, being required for PEP carboxylation to oxaloacetate, which is converted to malate by the irradiance inducible enzyme NAD malate dehydrogenase (Zeiger *et al.*, 1987). CO₂ in some way may inhibit the plasmalemma H⁺ extrusion pumps, or some buffering effects involving CO₂/carbonate/bicarbonate interchange may be involved (Gotow *et al.*, 1985). Since, there is a close correlation between photosynthetic and stomatal responses to CO₂, the photosynthetic C reduction pathways in the subsidiary cells of the stomatal complex may have an intricate role (Jarvis and Mansfield, 1981), in which case, stomatal aperture would be expected to acclimate to

elevated CO₂ as a result of photosynthetic acclimation. It has been suggested that ABA might act as a correlative messenger between mesophyll photosynthesis and stomatal conductance (Radin *et al.*, 1988).

Upreti *et al.* (2003) reported that the reduction in stomatal conductance in rice cultivars was due to the partial opening or closing of stomata to balance the resource use (Field *et al.*, 1995) and to maintain the ratio of intercellular CO₂, [CO₂]_i to atmospheric CO₂, [CO₂]_a under enhanced CO₂ conditions. According to Mooney *et al.* (1991), the lower stomatal conductance had a minor effect on photosynthesis because the gas diffusion was more rapid than the photochemical uptake of CO₂. Thus, with elevated CO₂, the [CO₂]_i increases, providing an enhanced CO₂ gradient to chloroplasts and enhanced activity of Rubisco, leading to increased carbohydrate production.

The decline in dark respiration in rice at elevated CO₂ was observed in the present investigation. This result was in accordance with the findings of Amthor (1997) and Curtis and Wang (1998). Wullschleger and Norby (1992) demonstrated a decrease of 12-37 per cent in growth respiration and 45-54 per cent in maintenance respiration in leaves of white oak sapling grown at elevated CO₂. Although the maintenance respiration is a small fraction of total energy cost, its increase was significant in rapidly growing plant as the plant size increases.

Imai (1995) asserted that the suppressed dark respiration at high CO₂ might generally increase the net production of rice unless it was too low to adversely affect the energetic processes. Thus, there was a variation in maintenance respiration that may significantly alter the total carbon budget.

Amthor (1994) reported that with the exception of actively growing cells, respiration was regulated mainly by the rate at which respiratory products, ATP, NAD(P)H and the carbon skeleton was used to meet the metabolic demands of growth, maintenance, transport and ion uptake. The higher photosynthetic rates reduce the demand for respiratory energy by making ATP and NAD(P)H more available (Turpin and Wager, 1990). The availability of photochemical energy might be greater at elevated CO₂ because of the suppression of photorespiration and subsequent conservation of photochemical energy, which could be utilized for carbon assimilation.

The growth and maintenance respiration were not measured separately, in the present investigation. The inhibitory effect of elevated CO₂ on the rate of respiration could be related to the inhibition of two enzymes involved in the respiratory processes (succinate dehydrogenase and cytochrome C oxidase) which was demonstrated in isolated mitochondria from *Glycine max* (Gonzalez-Meler *et al.*, 1996). The CO₂ dependent suppression of respiratory enzymatic activities, however, did not explain the CO₂ inhibition of respiration on the tissue and whole plant level (Gonzalez-Meler and Siedow, 1999).

The CO₂ induced reduction of dark respiration may be attributed to the reduction in the nitrogen and protein content of the tissue (Amthor, 1995). Bunce (2001) demonstrated that elevated CO₂ inhibited respiration to a greater extent due to non-substrate availability. According to Hamilton *et al.* (2001), elevated CO₂ may influence leaf respiration directly by altering growth rate, accumulation of non-structural carbohydrates and other changes in the tissue composition. Baker *et al.* (1992) found that dark respiration of rice per

unit land area was linearly related to the amount of plant nitrogen per unit land area.

The CO₂ induced reduction of dark respiration may be explained on the basis of the following points: (a) the use of cyanide-insensitive respiration was lesser as observed in wheat (Gifford *et al.*, 1985), (b) the decrease in the nitrogen and protein content of the tissue (Wullschleger *et al.*, 1994), (c) the inhibition of some respiratory enzymes as observed in *Scirpus olneyi* and *Lindera benzoin* (Azcon-Bieto *et al.*, 1994), and (d) lesser respiratory requirement as most of the biomass was used for structural parts of plants. These confirmed the present findings where the additional establishment of structural and storage tissue was not been affected reduced respiration as their respiratory requirement was substantially reduced.

Respiration in wheat increased markedly under high temperature in the short-term exposure to elevated CO₂ (Mitchell *et al.*, 1991) and the sensitivity was much less in the long-term condition (Gifford, 1995). The reduction in the respiration in wheat at high temperature for long-term exposure to elevated CO₂ was attributed to the reduction in maintenance respiration (Ziska and Bunce, 1993). This suggest that division of respiration into growth and maintenance, with the latter being highly temperature dependent tends to explain the temperature dependency of respiration. Elevated temperature increased the rate of respiration in the rice varieties where the elevated CO₂ reduced this increase by 6% in PRH-10 and 2% in PS-2.

CO₂ enrichment in rice enhanced the carbohydrate accumulation in different parts of the plant. Increased carbohydrate production of elevated CO₂ was due to the stimulation of photosynthesis (Roger *et al.*, 2004).

Ainsworth *et al.* (2002) observed a 45% increase in total non-structural carbohydrates (TNC) content in soybean. Prasad *et al.* (2004) reported in *Phaseolus* bean, that elevated CO₂ upregulated activities of the carbohydrate metabolizing enzymes, sucrose phosphate synthase (SPS) and adenosine-5'-diphosphoglucose pyrophosphorylase (AGP), resulting in greater accumulation and export of carbohydrates associated with photosynthetic activities, despite decline in rubisco activity and Rubisco protein content. Gesch *et al.* (2002) reported that elevated CO₂ significantly increased the activity of sucrose phosphate synthase (a key enzyme in the production of sucrose) and ADP glucose phosphorylase (a key enzyme in starch synthesis in rice). The present study with rice varieties showed that they avoid the onset of photosynthetic acclimation by synthesizing and exporting sucrose from source leaves into the sink tissues to avoid any photosynthetic end product accumulation in source leaves. Rice plants took full advantage of the increasing atmospheric CO₂ concentration through this mechanism and stimulated their productivity and growth, without exhibiting lower growth efficiencies resulting from photosynthetic acclimation. Hussain *et al.* (1999) also reported an increase in the sucrose phosphate synthase (SPS) activity in rice by about 29 per cent at elevated CO₂. The SPS activity increased as air temperature increased from 25⁰C to 34⁰C and decreased from 35⁰C to 37⁰C. The increased SPS activity was due to the reallocation of nitrogen away from Rubisco and into SPS, thus leading to a greater sucrose synthesis and export of photosynthates from the leaves. These studies conclude that rice responds to increasing CO₂ concentrations by shifting the priority of allocation of

carbohydrates more towards export than carbohydrate storage, thus preventing the feed back-inhibition (Rowland-Bamford *et al.*, 1990).

The excess accumulation of carbohydrates in the leaves was accepted to be one of the most important determinants for the development of new sinks (Stitt, 1991, Sage, 1994) which contribute to productivity. Chen (2002) reported an increased accumulation of non-structural carbohydrates in all the parts of the apple trees that led to enhanced fruit production.

Higher CO₂ enhanced the activity of sucrose phosphate synthase to 18 per cent in PRH-10 and 12 per cent in PS-2 that led to the higher sugar production in both the rice varieties. Additional sugars produced at the initial stages increased the number of productive tillers as observed by Stitt (1991). This enhanced the production of panicles which resulted in more number of grains. The higher amount of sugars produced at the heading stage was exported to these sinks, increasing the number of filled grains and grain mass, that contributed to higher yield. PRH-10 was more responsive to elevated CO₂ which was evident from the higher SPS activity, enhanced sugar production and increased panicle dry mass compared to PS-2. Temperature induced reduction in SPS activity reduced the sugar production to a greater extent in PS-2 compared to PRH-10. However, this temperature induced reduction was less under elevated CO₂ and this positive effect of elevated CO₂ was more pronounced in PRH-10.

The observations made in the present study indicated an obvious change in the plant chemical composition with larger accumulation of carbon (C) and concurrent decline in nitrogen (N) content. The post-photosynthetic events of carbohydrate partitioning and photoassimilate transport was

activated, as shown by the greater carbon sequestration to roots and stem. Yet another fraction of photoassimilate must have been utilized for leaf mesophyll growth. This was apparent from the significantly greater structural specific leaf weight. The reduction in N content was greater in roots than in leaves or stem under elevated CO₂. According to Makino *et al.* (2000), the decrease in the N content of rice was not due to the dilution of N caused by relative increase in plant mass, but the result of a change in the N allocation at the morphogenetic level of the whole-plant. According to Conroy and Hocking (1993), an increased limitation of N assimilate partitioning was responsible for the N deficit in plants at elevated CO₂. The performance of higher CO₂ grown rice with respect to photosynthesis and growth was not inhibited by the nitrogen status. It seemed that greater structural leaf weight compensated for the nitrogen reduction to a considerable extent Vu *et al.* (1989) suggested that the nitrogen reduction may be partially compensated by extra layers of mesophyll cells which according to Soussana *et al.* (1996) was for preserving the total photosynthetic machinery per unit leaf area. The carbon and nitrogen content in the different plant parts reduced in the rice varieties under elevated temperature condition which was ameliorated by elevated CO₂. Elevated CO₂ also brought about significant increase in the C:N ratio of the rice varieties.

In the present study, the CO₂ enrichment in the rice varieties enhanced the nitrate reductase activity (NR) to a greater extent. Geiger *et al.* (1998) also found an increased activity of NR and increased NR activation in young tobacco plants. This led to a very effective stimulation of nitrate uptake, nitrate assimilation and amino acid synthesis which helped in allowing faster growth

rates at enhanced carbon dioxide. Enhanced carbon dioxide led to a small increase in NR activity in mustard (Maveskaya *et al.*, 1990) and *Vigna radiata* (Sharma and Sengupta, 1990). Contradictory to this, a 2-fold decrease of NR activity in wheat (Hocking and Meyer, 1991) was observed.

The enhancement in NR activity of the rice varieties might be due to the increased amount of sugars produced at elevated CO₂. The increased amount of sugars will stimulate the expression of *nia* and the post-translational activation of NR (Geiger *et al.*, 1998). Thus, the increased NR activity and decreased N concentration in the leaves implies that an additional nitrogen nutrition is required to sustain the positive effects of CO₂ enrichment (Upreti and Mahalakshmi, 2000).

Growth in terms of plant height, tiller number, leaf area and root length in rice was significantly increased due to CO₂ enrichment (Plate 1, 2, 3 & 4). Beaker *et al.* (1992) found relatively minor effects of CO₂ on tiller production across the CO₂ range from 330 to 660 $\mu\text{mol mol}^{-1}$. In contrast, Kim *et al.* (1996) and Ziska *et al.* (1997) found a marked increase in the tiller production by a doubling CO₂. This discrepancy was likely related to the differences in plant densities among the studies. Kim *et al.* (1996) and Ziska *et al.* (1997) utilized plant populations of 50 and 75 plants m⁻², respectively, whereas Baker *et al.* (1992) used a density of 235 plants m⁻², which was extraordinarily high. A high degree of mutual shading among plants at this high density would have suppressed the development of tiller primordia due to a greater competition for light. Therefore, under planting densities usually practiced in Asian rice cultures, elevated CO₂ may substantially promote tiller production. According to Upreti *et al.* (2003). The increase in the tiller number in rice cultivars was

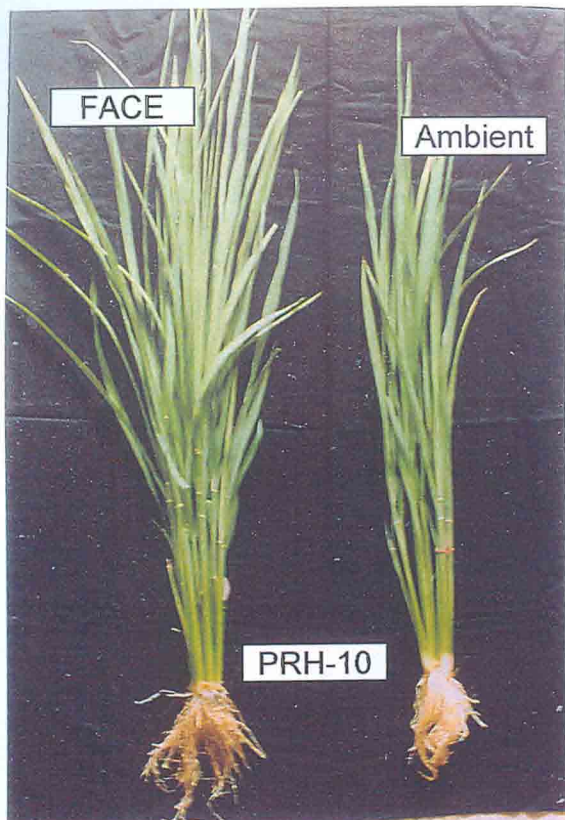


Plate 1. Effect of elevated CO₂ on plant growth of the rice varieties in FACE

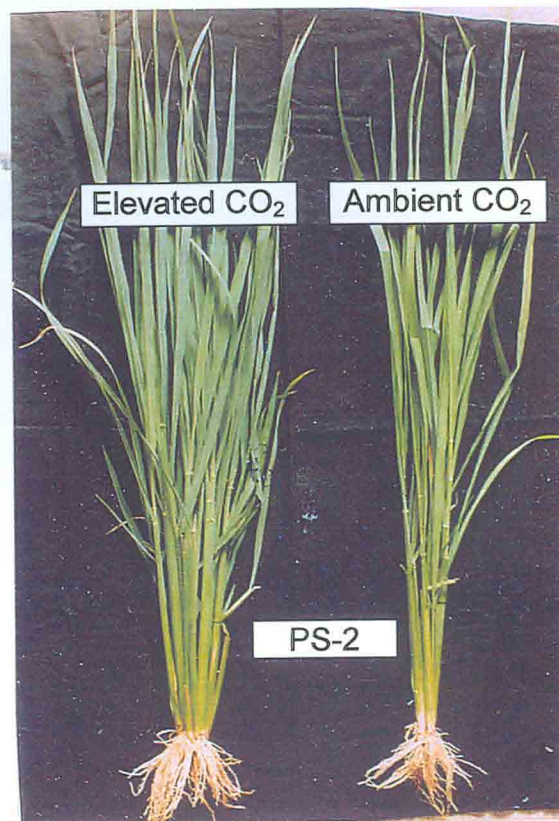
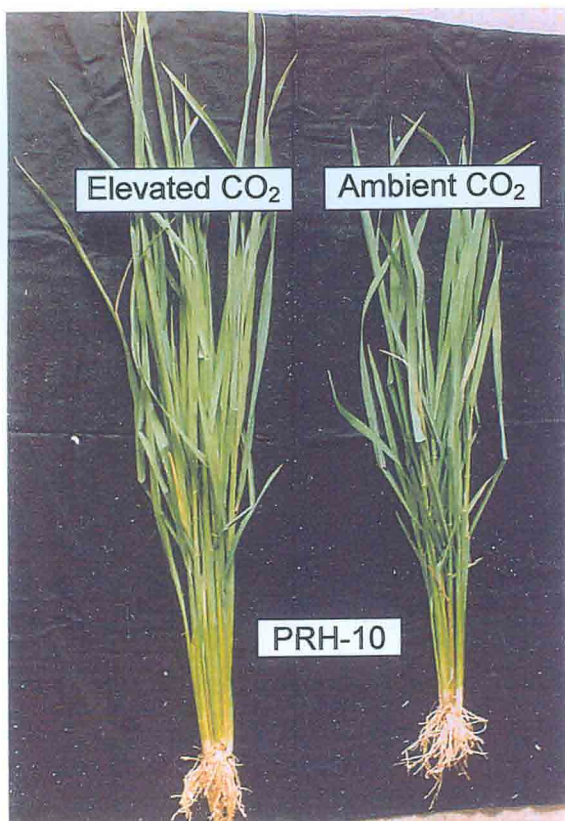


Plate 2. Effect of elevated CO₂ on plant growth of the rice varieties in OTC

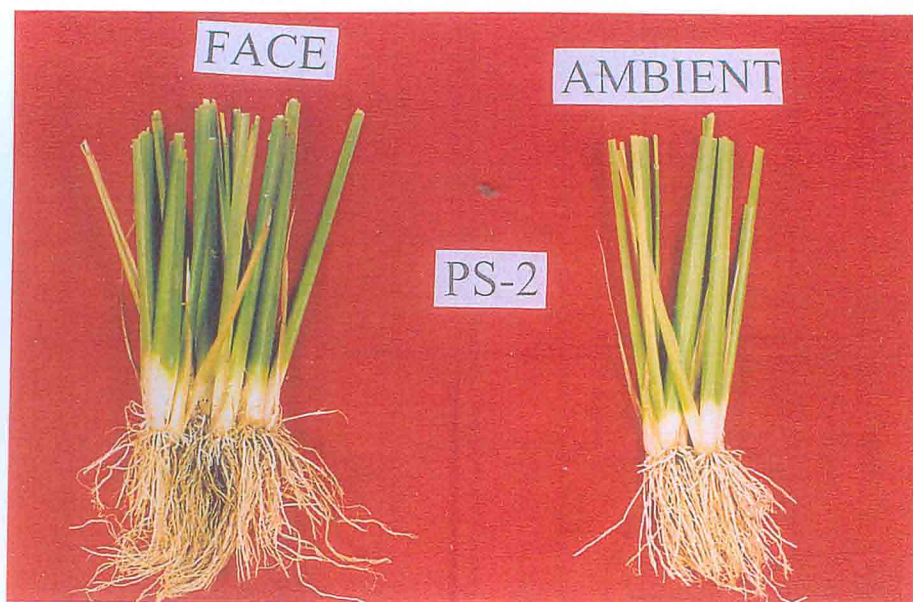
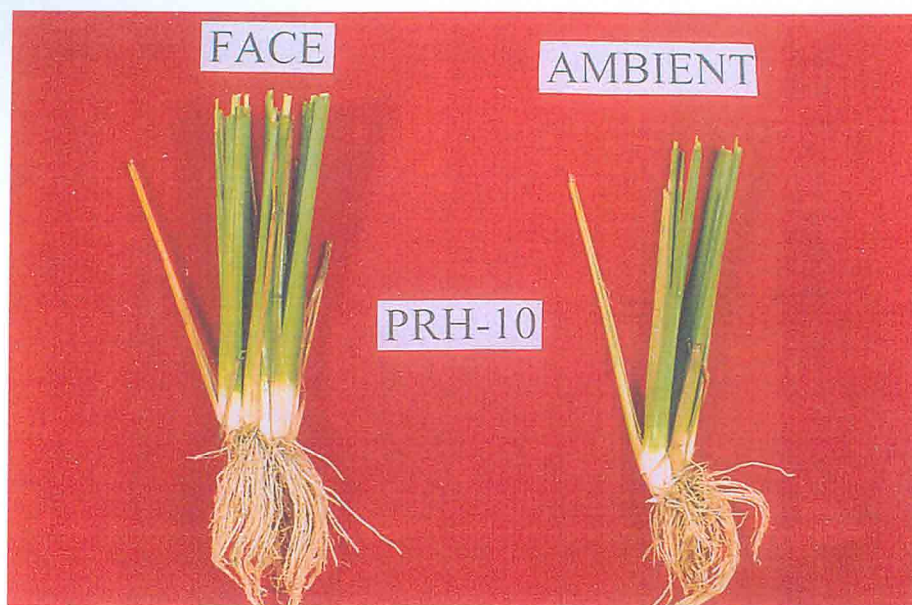


Plate 3. Effect of elevated CO₂ on root growth of the rice varieties in FACE

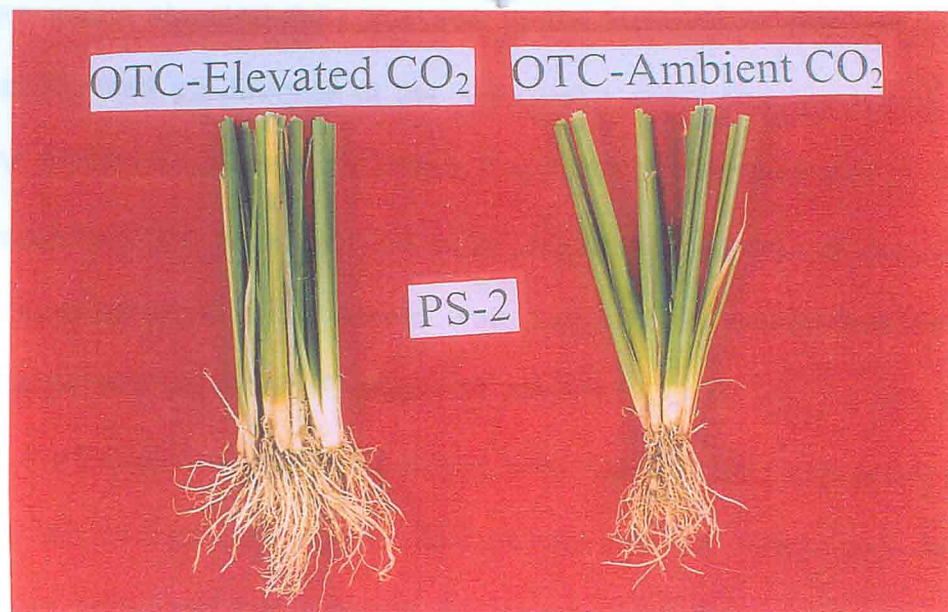
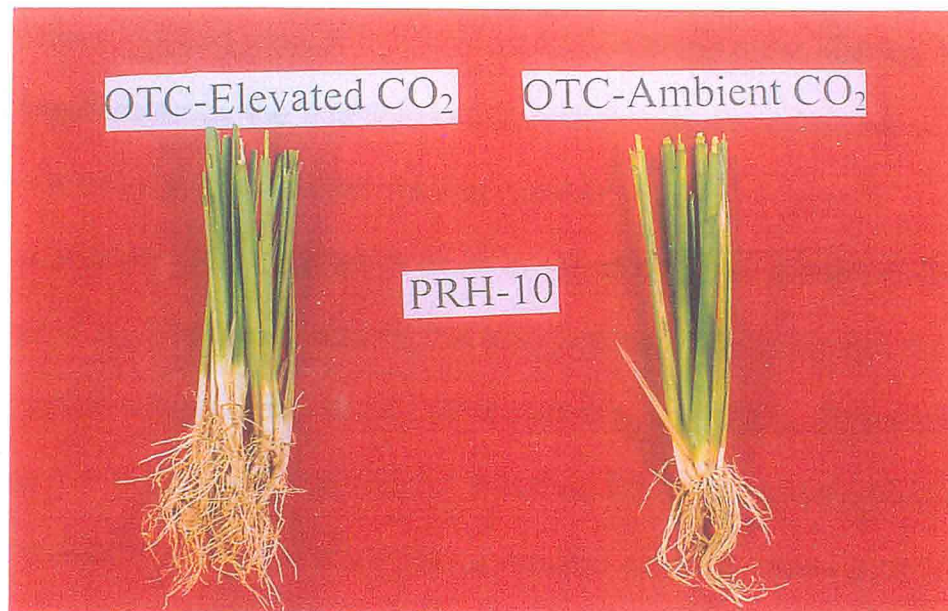


Plate 4. Effect of elevated CO₂ on root growth of the rice varieties in OTC

due to the production of additional sugars under the elevated CO₂ condition. Similar effect was studied in *Brassica* cultivars by Das (2003). The temperature induced reduction in tiller production in the present study appears to be ameliorated by the additional carbohydrates produced by elevated CO₂ in rice varieties, that increased the tiller number.

Elevated CO₂ resulted in only minor effects on individual leaf size (Beaker *et al.*, 1990) and also on the total leaf area of rice except during the initial growth stages (Imai *et al.*, 1985; Ziska *et al.*, 1997). This appears to indicate that N uptake of rice was not influenced by elevated CO₂ (Ziska *et al.*, 1996) except at the initial stage, since the leaf area increases proportionally with plant nitrogen uptake (Hasegawa and Horie, 1997). In contrast to this, the present study showed an increase in the leaf area at elevated CO₂ which was supported by Uprety *et al.* (2003) and Das (2003).

Ferris *et al.* (2001) reported an increase in the leaf area in *Populus* species under elevated CO₂ was due to the increase in the leaf cell wall extensibility and an increase in the Xyloglucan endotransglycosylase (XET) activity, a cell wall loosening enzyme. According to Yamakawa *et al.* (2004), the increase in leaf area was due to the increased N-uptake of rice, though the N concentration in the leaves was less. The increased leaf cell wall extensibility and higher XET activity at elevated CO₂, might be one of the reason for the expansion of leaf size in rice. However, in the present study, the leaf cell wall extensibility and XET activity was not determined. Another reason for increased leaf size can be explained on the basis of N-uptake. Though N-uptake was not determined in the present study, it can be substantiated by the increased nitrate reductase activity, which was markedly

higher at the vegetative and reproductive stages of rice growth, leading to increased leaf area at elevated CO₂.

Upreti *et al.* (2001) found an increase in the length of epidermal cells and the mesophyll cells (palisade parenchyma cells) at elevated CO₂ in the leaves of *Brassica* cultivars. However, there was no significant increase in the number of epidermal cells per unit leaf area. Thus, the cell enlargement was more sensitive to CO₂ than cell division, which explains the increase in leaf area of rice in the present study. According to them, the increase in the length of palisade cells and the concomitant increase in the number of chloroplast per leaf at elevated CO₂ allowed the loading of chloroplast with excessive oval starch grains to meet the adverse effect of drought in *Brassica* cultivars. This may probably be one of the reason by which elevated CO₂ compensated for the reduction in leaf area of rice caused by higher temperature.

The specific leaf weight (SLW) and net assimilation rate (NAR) increased whereas the specific leaf area (SLA) decreased on exposure of rice plants to high CO₂ condition. Baker *et al.* (1990) showed that at elevated CO₂ the SLW of rice increased during early growth, but it was less at the later stage. Das (2003) reported an increase in specific leaf weight and net assimilation rate in *Brassica* cultivars at high levels of CO₂. Yelle *et al.* (1990) suggested that the increase in NAR and SLW in CO₂ enriched tomato plants was due to the preferential accumulation of photoassimilates in the leaves as reserves rather than contributing to leaf expansion. Upreti *et al.* (2001) reported an increase in the leaf thickness in *Brassica* species at elevated CO₂ was due to the increased accumulation of more number of starch granules produced in the chloroplasts of larger mesophyll cells. This made the *Brassica*

species to combat moisture stress effect on leaf thickness. Present study showed a reduction in the leaf thickness of rice varieties at increased temperature conditions. However, the reduction was less under elevated CO₂. This might be due to the increased accumulation of the greater amount of starch produced at elevated CO₂, in the leaves. The reduction in the specific leaf area of rice varieties in the present study was because of the reallocation of biomass in the leaves to make them thicker, that would increase leaf mass more than leaf area (Kimball *et al.*, 2002).

Present experimental findings showed that the leaf area index (LAI) increased at elevated CO₂ concentrations in rice. According to Rogers *et al.* (1983) and Jones *et al.* (1985) the increase in LAI in soybean was due to the larger individual leaves and more number of leaves per plant. In the present findings also, the greater production of leaves and increased leaf area was possibly responsible for increased LAI. The higher temperature decreased the LAI due to the reduction in the leaf area and leaf number observed in the study. This reduction was lessened under enhanced levels of CO₂.

Growth at elevated concentrations of CO₂ may also affect the phenology or the rate of development of the plant (Kimball *et al.*, 2002). Nakagawa *et al.* (1993) reported in rice that elevated CO₂ brought early heading. In the present study, also, the phenological development was hastened by CO₂ enrichment. Rice plants came to early tillering and early flowering and this was reduced by one or two days under elevated CO₂ and temperature conditions. This CO₂ effect on rice development rate has been shown to be temperature dependent. For the *Japonica*-type rice cultivar, Akihikari, CO₂ enrichment reduced the number of days to heading by 6 per

cent and 11 per cent at air temperatures of 28⁰C and 30⁰C, respectively (Kim *et al.*, 1996). There are two potential explanations for this accelerated crop development rate with CO₂ enrichment (Horie *et al.*, 2000). First elevated CO₂ could increase plant temperature by increasing stomatal resistance, thus reducing transpirational cooling. Second, it has been shown that rice grown under elevated (CO₂) generally has higher carbon to nitrogen (C/N) ratio (Ziska *et al.*, 1996). A high C/N value has shown to be associated with accelerated plant development rates (Zeevaart, 1976). These developmental rates are slowed if the air temperature increases beyond the optimum for development.

The high carbon to nitrogen ratio observed in the present study appears to be associated with the early tillering and flowering in the two rice varieties as suggested by Zeevaart (1976).

In the present study, elevated carbon dioxide brought about greater increase in the accumulation of whole plant biomass. The variety PS-2 was less responsive to elevated CO₂ whereas PRH-10 was reasonably poor in growth and was able to express its full potential for growth at higher CO₂ concentration. Yamakawa *et al.* (2004) showed that the dry matter of rice increased at elevated CO₂. This increase in the dry matter after panicle initiation was greater in FACE grown rice than the ambient CO₂ rice. Horie and Sakurantani (1985) showed a good correlation between the biomass production and crop growth rate. According to them, the increased crop growth which was mainly due to the increased photosynthesis and decrease respiration enhanced the biomass production. The present study showed an

increase in the crop growth rate from vegetative to heading stage which might have increased the biomass in both the rice varieties.

Elevated CO₂ brought about lower leaf, shoot and root biomass and higher panicle dry mass in PRH-10 compared to PS-2. Elevated temperature brought about reduction in biomass in both the varieties. At elevated CO₂, the temperature induced reduction was lessened to greater extent in PRH-10 compared to PS-2. Thus, PRH-10 expressed its full potential to different treatments.

Increased biomass production of rice caused by elevated CO₂ has the potential to increase yield. Baker and Allen (1993) showed that doubling CO₂ from 330 to 660 $\mu\text{mol mol}^{-1}$ increased yield in rice by 44 per cent. Ziska *et al.* (1997) obtained an yield increase of 27 per cent with CO₂ enrichment for the cultivar IR-72 over that grown at ambient temperature. According to them, the enhancement in grain yield was due to the enhanced production of panicles per plant and increased grain mass.

Kim *et al.* (2003) reported that yield increases were related most strongly to greater spikelet number per unit ground area due to increases in both panicle number per square meter and spikelet number per panicle. Small increase in individual grain mass with elevated CO₂ had only a minor effect on the overall yield increases. In rice, the spikelet number per unit area is generally proportional to plant N content (Horie *et al.*, 1997) or to plant N concentration (Hasegawa *et al.*, (1994) at the spikelet initiation stage. The fact that elevated CO₂ increases the spikelet number despite a reduction in plant N concentration suggest that elevated CO₂ promoted spikelet production

efficiency per unit of plant N. Elevated CO₂ increases sink sizes by increasing the grain number and this generally leads to increased yield.

Elevated CO₂ increased the number of panicles per plant and grain number per panicle in the rice varieties. The increase in the grain number per panicle was 17 per cent in PRH-10 and 13 per cent in PS-2 resulting an increase in grain number per unit ground area. Grain number per unit ground area was dependent on the N-uptake at the panicle initiation stage (Kim *et al.*, 2001). Though the N-uptake was not determined in the present study, it can be substantiated on the basis of markedly increased activity of nitrate reductase at the heading stage of the rice growth. This increased grain number brought about an enhancement in the grain yield by 26 per cent in PRH-10 and 19 per cent in PS-2. Elevated CO₂ also significantly increased the grain mass by 8 per cent in PRH-10 (Plate 5a) and 4 per cent in PS-2 (Plate 5b), which also contributed to the higher grain yield in the rice varieties.

In terms of predicting the effects of potential future global warming on rice yield, studies that examine the effects and interactions of both temperature and CO₂ enrichment are far more relevant than the studies that examine only the effects of individual components. It has been well established that spikelet sterility in rice at mean daily temperature below 20°C can be caused by failure in pollen development at the microspore stage (Satake and Hayase, 1970) or injury sustained at flowering. Temperature above 35°C at flowering can also cause spikelet sterility (Satake and Yoshida, 1976). Baker *et al.* (1995) reported that grain yield in *Indica* type rice cultivars, IR-30, declined with increasing temperatures above 26°C to zero yield near 36°C for both ambient and elevated CO₂. Ziska *et al.* (1997) reported



Plate 5a. Interactive effect of elevated CO₂ and temperature on seed size of the variety, PRH-10



Plate 5b. Interactive effect of elevated CO₂ and temperature on seed size of the variety, PS-2

significant yield reductions for the *Indica* type rice cultivars, IR-72 caused by a 4°C rise in air temperature above ambient temperatures. Similar yield reductions at daily mean temperature above 26°C were reported for a *Japonica* type rice cultivars, Akihikari under both double and ambient CO₂ (Kim *et al.*, 1996a). Baker *et al.* (2004) reported that the southern US rice cultivars were more sensitive to high temperature stress during reproductive development than previously studied Asian *Indica* and *Japonica* cultivars. These US rice cultivars produced more number of panicles but failed to produce any seed yield at high temperature treatment.

In the present study, the temperature increase from 31°C to 35°C brought about reduction in the grain number and grain mass, which was comparatively less in PRH-10. This reduction was ameliorated under elevated CO₂ by about 16 per cent in case of grain number in both the varieties. In case of grain mass it was 3 per cent in PRH-10 and 2 per cent in PS-2 thus the variety PRH-10 had higher yield under elevated CO₂ and temperature conditions and proved to be more efficient than PS-2. These results thus point to the possibility of selecting or breeding rice cultivars with enhanced capability to take advantage of future global increase in CO₂.

Elevated CO₂ brought about a drastic reduction in the activity of antioxidant enzymes in the rice varieties used in the present investigation. Wullschlegel *et al.* (1994) explained this effect on the basis of reduced respiration and photorespiration in plants under elevated CO₂. Hydrogen peroxide (H₂O₂) and superoxide radical (O₂⁻) are the product of these two pathways and the necessity for their detoxification might be lessened in plants grown under elevated CO₂ concentration. It has been proposed that a shift

towards higher photosynthetic efficiency under elevated CO₂ might recycle the acceptor of photosynthesis, NADP⁺, more rapidly thus, suppressing O₂^{•-} (superoxide radical) in favour of NADPH production (Polle, 1996) Badiani *et al.* (1993) reported in soybean that the higher CO₂ enhanced the demand for photo-reducing power and this could reduce risk of oxy-radical formation. According to Pritchard *et al.* (2000), constitutive antioxidative enzymatic activities decreased under elevated CO₂ because of decrease in the production of cellular reactive oxygen species (ROS). It has been reported that higher concentration of CO₂ potentially reduced the oxygen activation and ROS formation (Halliwell and Gutteridge, 1989) with a consequent relaxation of the antioxidant defense system of the plant cell (Badiani *et al.*, 1993). ROS, if not detoxified by the antioxidant defense system, can initiate lipid (membrane) peroxidation, with the consequent biosynthesis of break down products, such as malondialdehyde (MDA) (Esterbauer, 1982).

Although there was marked variation in the activity of the antioxidant enzymes between these varieties, their respond to elevated CO₂ and temperature was markedly higher. Thus the upregulation and down-regulation of antioxidant system depend upon the extent of oxidative stress, CO₂ and genotypic interactions (Polle *et al.*, 1997). The decreased oxidative stress effect may be due to many reasons like

- a) an increase in CO₂ : O₂ ratio within the chloroplast which may decrease electron leakage from PS-I to O₂.
- b) an increased CO₂ : O₂ ratio that would decrease the oxygenase activity of rubisco reducing photorespiration and resultant cellular H₂O₂ production

c) by the stimulation of antioxidant activities.

Thus, the high CO₂ helped in the quick induction of antioxidant enzymes like superoxide dismutase (SOD), ascorbate peroxidase (APX) and glutathione reductase (GR) to scavenge the ROS produced by elevated temperature in the rice varieties. However, in the present study, the ROS was not determined. Increase in temperature markedly increased the activity of these antioxidant enzymes under elevated CO₂. The activity of these enzymes were greater in PRH-10 compared to PS-2. It was apparent that these rice varieties have their own systems of scavenging the reactive oxygen species (ROS) such as O₂⁻, H₂O₂ etc. Superoxide dismutase scavenge the O₂⁻ radicals to produce H₂O₂. The H₂O₂ was decomposed by catalase or ascorbate peroxidase, the latter enzyme oxidised ascorbate to monodehydro-ascorbate (MDHA), which was then reduced by NAD(P)H in reaction catalyzed by monodehydroascorbate reductase (MAR). Das (2003) reported a reduction of H₂O₂ and malondialdehyde (MDA) in *Brassica* under elevated CO₂ indicating the significant enhancement in the activity of antioxidant enzymes.

The enhanced production of carbohydrate reserve at elevated CO₂ also helped to combat the temperature induced effect (Schwanz *et al.*, 1996a). Thus the rice varieties developed strategy to combat the negative effect of elevated temperature by increasing the antioxidant enzyme activity, by the enhanced production of carbohydrate and by the reduction in the production of O₂⁻ radicals and H₂O₂ under elevated CO₂.

Carbon dioxide enrichment significantly improved the quality of rice grains. The reducing, non-reducing, total sugars and starch content

significantly increased in the grains of CO₂ enriched plants which ultimately increased the grain mass. Amylose content of the grain in PRH-10 variety increased to optimum levels, improving the grain quality. In PS-2, the amylose content was greatly increased to a level that will make the grains hard after cooking, thus decreasing the quality of the grain (Juliano, 1992). Elevated temperature decreased all these parameters which was ameliorated by the CO₂ enrichment. Similarly, the increased temperature conditions, also reduced the N, Ca and K content in the grain. The protein content of the grain was also decreased. This adverse effect was depressed by elevated CO₂.

Lieffering *et al.* (2004) found a decrease in the rice grain N concentration and observed no changes in the concentration of any other elements in the grain at elevated CO₂. Conroy *et al.* (1994) observed a reduction in N and protein content of wheat at high CO₂. This reduction might be due to the lower leaf N (Hocking and Mayer, 1991a) that could lead to changes in the wheat quality. Rice grain also showed similar reduction in N (Conroy *et al.*, 1994), which have little effect on rice grain quality because quality of rice was determined by factors such as amylose content which influence the cooking quality (Juliano, 1992). Ziska *et al.* (1997) showed no significant changes of Ca and K content in the grain at elevated CO₂. The present study showed a significant increase in Ca and K content at elevated CO₂. Conroy *et al.* (1994) showed an increase in Ca content in the rice grain at elevated CO₂. Thus, the rice grain quality was decreased in both the varieties in terms of N content of the grain, whereas the increased amylose content, a major determinant of cooking quality improved the grain quality in PRH-10 compared to PS-2.

Response studies of rice varieties using the open top chamber (OTC) and free air carbon dioxide enrichment (FACE) demonstrated a significant increase in growth and development, leaf area and tillering in both the rice varieties. The photosynthesis and carbohydrate accumulation along with activity of sucrose phosphate synthase enzyme was increased. Elevated CO₂ positively affected the nitrate reductase activity and C:N ratio. The antioxidant enzyme activity was decreased. Grain mass and grain quality in terms of greater accumulation of amylose, sugars and minerals like calcium and potassium were improved under elevated carbon dioxide conditions. However, these changes were adversely affected by the higher temperature under phytotron conditions. The elevated carbon dioxide under controlled conditions mitigated partially the adverse effect of temperature. Study also revealed the variation in the intensity of these effects. The effect was significantly more in the hybrid, Pusa RH-10 in terms of higher photosynthesis, greater sucrose phosphate activity, enhanced carbohydrate accumulation, increased panicle dry mass and higher grain yield and grain quality compared to the Pusa Sugandh-2 variety. This indicated Pusa RH-10 as the better responsive variety for future high carbon dioxide and temperature changes. The database collected in the present investigation outlining the highly responsive hybrid, Pusa RH-10 will help in developing plant type and in identifying the cultivation and nutrient management for future climatic changes.

Comparison of open top chamber, free air carbon dioxide enrichment and phytotron studies

Plants generally grow differently inside chambers, so we must be

concerned about whether or not the vast body of prior chamber-based research on the response of plants to elevated CO₂ is applicable to open field grown plants. So, a comparison study of the three technologies were made. Present investigation showed that the dry matter production was relatively more in both the varieties in FACE followed by Phytotron and OTC. The stomatal conductance was drastically reduced in FACE compared to other two chamber-based systems. According to Kimball *et al.* (2002), all the data for FACE and chamber-based systems, are consistent except for two parameters. The two parameters for which the FACE and chamber-based data appear to be inconsistent are stomatal conductance and root growth. FACE appears to reduce stomatal conductance about one and half times more than that observed in prior chamber experiments. Similarly, elevated CO₂ appears to stimulate root growth relatively more than shoot growth under FACE compared to chamber conditions.

In the present investigation, carbohydrate production in FACE has largely been increased compared to the chamber-based studies. Similar results were observed by Long *et al.* (2004), while comparing the FACE and the chamber-based studies. This was because, the FACE has no effect on the light reaching the vegetation. But plants in chamber studies generally receive less light than that of FACE and therefore, there is less probability that photosynthesis will exceed capacity to remove carbohydrates from leaves (Long *et al.*, 2004). Grain yield was also higher in FACE compared to the chamber-based systems which might be due to the increased production of carbohydrate. Present study also showed that the activity of antioxidant enzymes was less in FACE compared to phytotron and OTC which might be

due to the slight increase in temperature caused by the enclosed chambers. Van Oijen *et al.* (1999) reported that FACE eliminates the possibility of overestimation of CO₂ effect that can happen in open top chambers. McLeod and Long (1999) mentioned that FACE provides an appropriate scale for field trials of crops such as wheat so that appropriately sized buffers can be utilized to minimize the oasis effect. Thus, the more realistic FACE environment and the larger plot size will enable us to obtain more extensive multidisciplinary data sets, that are representative of open field, for the future high CO₂ world.

6. SUMMARY AND CONCLUSION

The anthropogenic rise in the atmospheric carbon dioxide concentration will significantly affect the agriculture both by rising the earth's temperature as well as by changing the biological processes in the plant system. Crops were selected for greater productivity under the current atmospheric carbon dioxide concentration and temperature, however, their responses to the future changed climatic conditions such as high carbon dioxide and temperature need to be studied. The expected doubling of carbon dioxide concentration in the near future (by the end of 21st century) needs to be simulated to study the response of crop plants. Technologies were developed to simulate the elevated carbon dioxide concentration and temperature to study the response of rice varieties to the elevated carbon dioxide and its interaction with higher temperature. Rice crop, selected for this study was due to its being the major food crop of the world particularly for south Asian region. It was also considered important to study these responses because of the development of high yielding hybrid rice to cater the need of farmers and rice consumers. Rice variety, Pusa Sugandh-2 and the hybrid, Pusa RH-10 were used in this study due to their higher productivity and wide range of cultivation in India, as an alternative to meet the requirement of future rice production.

Response studies of rice varieties using the open top chamber (OTC) and free air carbon dioxide enrichment (FACE) facilities demonstrated a

significant increase in growth, leaf area development and tillering in both the rice varieties. The photosynthesis and carbohydrate accumulation along with the activity of sucrose phosphate synthase enzyme was increased. Elevated CO₂ positively affected the nitrate reductase activity and the C:N ratio of the rice varieties. However, these changes were adversely affected by the higher temperature under phytotron conditions. Plants grown at elevated CO₂ demonstrated the protection mechanism against the oxidative stress, by markedly increasing the activity of the scavenging enzymes such as superoxide dismutase, ascorbate peroxidase and glutathione reductase. The elevated carbon dioxide, thus, mitigated partially the adverse effect of temperature. Study also revealed the variation in the intensity of these effects. The effect was significantly more in the hybrid, Pusa RH-10 compared to the pure line variety, Pusa Sugandh-2. The varietal difference in the response was reflected in the accumulation of biomass, grain yield and harvest index wherein, greater response was noted for sink development in terms of panicle dry mass in the hybrid, Pusa RH-10. A larger accumulation of the biomass was observed in roots compared to other component of plant. The distribution pattern of the dry matter in terms of the accumulation of photosynthates was greater in Pusa RH-10 compared to Pusa Sugandh-2. Grain mass and grain quality in terms of greater accumulation of amylose, sugars and minerals like calcium and potassium was more improved in Pusa RH-10 under elevated carbon dioxide. The differential response of rice varieties indicated the selection of Pusa RH-10 as the better responsive variety for future high carbon dioxide and temperature changes. The overall characterization of the responses of both the varieties to the interaction of high CO₂ and temperature

suggest a suitable cultivation and nutrient management system for the future changed climatic conditions. The data collected in the present investigation outlining the physiological and biochemical characterization of the response of highly responsive rice hybrid Pusa RH-10 to the elevated CO₂ and temperature will help in developing plant type and model for future climate changes.

Comparison of the responses of rice varieties to elevated carbon dioxide in open top chambers, free air carbon dioxide enrichment technology and phytotron were made in the present investigation. The responses were similar with all the technologies, however, the intensity were different for several parameters in FACE. The biomass production was relatively more in FACE for both the rice varieties whereas, the stomatal conductance was greatly reduced compared to the chamber-based system. Higher carbohydrate production and yield, and lower antioxidant enzyme activity in FACE was because, FACE has no confounding effect as that of the chamber based system. Thus, the more realistic FACE environment and the larger plot size will enable us to obtain more extensive multidisciplinary data sets, that are representative of open field, for the future high CO₂ world.

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Appendix I. Weekly metrological data during the crop period for 01.06.2002 to 31.11.2002

	Standard weeks	Rainfall (cm)	wind velocity	Sunshine	R.H (%)	Maximum temperature	Minimum temperature
June	23	0.28	6.5	7.5	45	40	28.8
	24	0.0	9.1	5.6	51	41.5	28.7
	25	0.26	8.6	7.5	53	40.3	28.8
	26	2.4	8.8	5.6	63	36.2	28.6
July	27	0.0	10.3	5.7	54	39.4	30.0
	28	0.0	12.2	6.4	49	40.5	21.5
	29	1.48	9.2	6.8	51	39.7	29.6
	30	0.0	11.6	3.9	51	38.2	29.9
August	31	0.15	6.3	2.3	67	36.7	28.4
	32	4.2	5.7	2.3	74	35.2	27.7
	33	4.9	3.4	2.9	76	32.3	26.9
	34	0.14	6.2	5.1	71	34.1	26.8
September	35	1.42	4.6	6.0	73	38.4	26.3
	36	1.5	2.9	4.0	82	30.8	23.8
	37	15.85	1.8	3.9	89	31.1	23.0
	38	0.25	3.2	8.2	71	32.5	23.5
October	39	0.0	3.4	8.5	59	33.7	21.7
	40	0.0	2.9	9.2	53	35.8	19.2
	41	0.2	3.4	7.8	64	32.2	20.8
	42	0.0	1.1	6.7	68	31.9	19.3
November	43	0.0	2.5	7.4	58	30.7	15.9
	44	0.0	1.2	5.9	60	31.3	16.3
	45	0.0	1.1	3.3	66	28.3	14.5
	46	0.0	2.7	6.4	62	26.8	13.2
	47	0.0	1.5	6.4	54	27.3	10.5

Appendix II. Weekly metrological data during the crop period for 01.06.2003 to 31.11.2003

	Standard weeks	Rainfall (cm)	Wind velocity	Sunshine	R.H (%)	Temperature maximum (°C)	Temperature minimum (°C)
June	23	0.2	7.1	3.4	41.0	43.1	31.0
	24	0.0	5.2	5.5	41.1	42.8	30.0
	25	2.08	3.2	2.8	73.1	35.1	26.6
	26	0.81	3.7	3.2	59.7	37.5	27.9
July	27	12.32	3.5	6.2	67.7	36.0	26.8
	28	24.3	2.4	3.2	86.7	31.0	24.8
	29	10.64	2.7	3.9	88.0	32.0	26.0
	30	8.20	4.2	7.5	76.4	33.8	26.6
August	31	5.76	2.2	1.3	79.3	29.6	25.8
	32	0.70	2.1	5.0	74.0	32.9	26.9
	33	9.48	1.6	3.3	68.0	31.2	25.5
	34	0.46	1.1	6.3	76.6	33.9	27.0
September	35	0.98	0.4	4.7	85.1	30.5	26.9
	36	3.02	1.0	3.1	71.3	31.3	25.0
	37	1.10	2.9	0.9	68.8	30.8	24.9
	38	0.0	1.3	5.7	57.6	33.7	25.0
	39	0.0	0.9	6.6	52.4	31.9	22.5
October	40	0.0	5.7	9.2	62.7	33.9	17.8
	41	0.0	6.6	7.0	52.7	33.6	17.6
	42	0.0	0.9	6.5	55.0	33.4	16.1
	43	0.0	2.0	5.0	64.0	32.3	15.1
November	44	0.0	5.0	6.1	58.6	31.2	13.6
	45	0.0	1.0	6.6	62.0	30.8	13.4
	46	0.0	9.0	3.5	54.0	31.3	12.3
	47	0.0	1.9	6.3	62.7	26.4	8.6

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