AN ABSTRACT OF THE THESIS OF

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Title: The Effects of Enhanced Atmospheric CO_2 and N Fertilization on Growth and Development of Rice (*Oryza sativa* L.)

Abstract approved: Redacted for Privacy
Dale N Moss

The current global rise in atmospheric carbon dioxide concentration [CO_2] has stimulated interest in the response of agricultural crops to CO_2. Response of field crops at elevated CO_2 depends on the amount of mineral nutrients available. Nitrogen is deficient in rice (*Oryza sativa* L .) soils in Asia. Studies were therefore conducted to determine the effect of increased [CO_2] and N nutrition on growth and development of rice. Rice cultivar IR72 and KDML 105 seedlings were exposed to different levels of [CO_2] and N nutrition inside sunlit chambers located in a glass house. Both single leaf CO_2 assimilation and total biomass increased with increased CO_2 up to a concentration of 545 μmol mol^{-1}. The magnitude of the response depended on the N status of the plant. Increased [CO_2] increased seedling vigor, diluted leaf N, and increased partitioning of biomass to non leafy parts. Field studies in open top chambers compared the response of transplanted "IR72" rice to ambient and high [CO_2], (700 μmol mol^{-1}) as affected by the rate of N fertilizer application (0, 50, and 100 kg ha^{-1} in the 1993 wet season, and 0, 90, and 200 kg ha^{-1} in the 1994 dry season). Increased atmospheric [CO_2] had no direct effect on phenology of rice. Leaf phyllochron interval (degree-days leaf^{-1}), thermal time to panicle initiation (PI), and flowering were not affected by [CO_2]. Phyllochron value increased after PI. Both, single leaf and whole canopy assimilation increased with increased [CO_2]. An increase in leaf mesophyll resistance at high CO_2 suggested that an acclimation of leaves to high CO_2 occurred. As CO_2 increased, fertilizer N recovery increased, but leaf N decreased, due to partitioning of less total N to leaves and increased specific leaf weight. Consequently, single leaf respiration decreased. Canopy respiration, however, did not increase in proportion to the growth enhancement at high CO_2 due to decreased partitioning of total plant N to leaves. Tillering increased because of more assimilates, but neither leaf area index (LAI) nor radiation interception was affected directly by increased [CO_2]. Radiation interception was curvilinearly and LAI was linearly related to total above ground N, suggesting that the plant N requirement for light interception remained constant as [CO_2] increased. Increased tillering at high [CO_2] did not result in a proportionate increase in panicles, due to decreased plant N concentration and greater competition for light, which induced tiller abortion. Radiation use efficiency (RUE) increased from 1.3 g Mj^{-1} at ambient to 1.7 g Mj^{-1} at high [CO_2]. Radiation use efficiency at high [CO_2] was more sensitive to decreased leaf N than that at ambient [CO_2]. Thus, increased N fertilization is essential to sustain higher leaf assimilation at high [CO_2] with cultivar IR72. However, if a new cultivar with less unproductive tillers and greater ability to partition N to the leaf is developed, with increased fertilizer N recovery at high [CO_2], the N fertilizer requirement for tropical lowland rice could remain constant or even decrease with future increases in atmospheric [CO_2].

The Effects of Enhanced Atmospheric CO_2 and N Fertilization on Growth and Development of Rice (*Oryza sativa* L.)

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed November 22, 1994

Commencement June 1995

APPROVED:

Redacted for Privacy

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Date thesis is presented November 22, 1994

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ACKNOWLEDGEMENT

I wish to express my sincere gratitude to my major professor Dr. Dale N. Moss for his unwavering support, encouragement, and guidance throughout the study and his constructive criticisms in preparing the thesis manuscripts.

I am also grateful to Dr. Keith Ingram and Dr. David Olszyk for their contribution as committee members and for support and guidance rendered to me during the study and in preparation of the thesis manuscripts. I am also very grateful to Dr. Lewis Ziska for his invaluable advise and guidance during the field research at IRRI. I am thankful to the members of my graduate committee, Dr. John Potter, Dr. Gary Jolliff, and Dr. W.D. Loomis for their advice, time and interest throughout my graduate study.

I wish to thank, Dr. D. Senadhira, Dr. Martin Kropff and Dr. K.G. Cassman for their support during my stay at IRRI. Many thanks are due to my colleagues at IRRI, Mrs. Pacita Manalo, Mrs. Ofelia Namuco, Mr Rico Pamplona and all EPA-APPA staff for their invaluable support during the field research at IRRI.

I collectively express my gratitude to Suraj, Weranjala, Sydney and all the Sri Lankan community for their kindness and hospitality during my stay in Corvallis. I am also thankful to Dr. H. Somapala and Dr. M Sikurajapathy for your guidance through my carrier as a researcher.

I am very much grateful to my father Tikiri Banda and my mother Tikiri Menike for laying the foundations, continued blessings and their endless support. Finally my deepest and heartfelt appreciation to my loving wife Sugeewa and our sons, Pramuditha and Vidharshena for their love, patience and understanding throughout my study period.

The support given by the department of Agriculture, Sri Lanka, U.S. Environmental protection agency, and the International Rice Research Institute are greatly appreciated.

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CHAPTER 1

GENERAL INTRODUCTION

Global atmospheric carbon dioxide (CO_2) concentration is increasing. Since the beginning of the industrial revolution, global CO_2 emission from fossil fuel combustion has been increasing. The current rate of emission from the fossil fuel is about 6.0 ± 0.5 Gt of carbon (C) per year and the estimates of release as a result of land use changes are in the range of 1.6 ± 0.5 Gt of C per year (IPCC, 1992). Mauna Loa observatory records show a 12% increase in mean annual concentration of CO_2 in 32 years, from 316 $\mu mol\ mol^{-1}$ in 1959 to 354 $\mu mol\ mol^{-1}$ in 1990 (Keeling and Whorf, 1992). Along with the increase in CO_2, other greenhouse gases, such as methane, nitrous oxide, and chlorofluorocarbons (CFC's), are increasing (Thomas et al., 1992). The atmospheric residence times for these gases range from several decades to centuries (Crane, 1992), thus ruling out any sudden decreases of their atmospheric concentrations.

CO_2 is relatively transparent to visible sunlight, but absorbs longer wave length infrared radiation emitted by the earth's surface (Gates, 1965), leading to a global warming. General circulation models (GCM's) predict a $2.5 - 4.5^0$ C increase in global mean surface air temperature with the doubling of CO_2 concentration predicted for sometime in the next century (Crane, 1992). Elevated CO_2 concentration has a significant interaction with increased temperature on plant growth and resource acquisition and allocation. The strength and direction of these effects depends on the plant species (Coleman et al., 1992).

The primary direct effect of increase CO_2 concentration on plants that have the C_3 pathway of photosynthesis is to increase net CO_2 assimilation (Akita and Tanaka, 1973).

Elevated CO_2 concentration influences net CO_2 assimilation by providing more substrate and suppressing photorespiration. Cure and Acock (1986) observed that C_4 crops respond less to increased CO_2 than do C_3 crops, presumably because C_4 plants already have a CO_2 concentrating mechanism.

Cure and Acock (1986) summarized the response of 10 major crop species in the world and observed an average 52% increase in CO_2 assimilation on the first exposure to enriched CO_2 concentration (about 700 μmol mol^{-1}), but only 29% higher after plants had been subjected to long periods of higher CO_2 concentration. Saga et al.(1989) showed that leaf CO_2 assimilation in plants grown under elevated CO_2 may be lower than for plants grown at ambient CO_2 when measured at common high CO_2 concentration. Therefore, development of photosynthetic organs under high CO_2 concentration may result in acclimation, which could partly offset the increase in assimilation at high CO_2 concentration. In contrast to the increase in CO_2 assimilation, evidence for both increase and decrease CO_2 respiration with enriched CO_2 have been reported (Amthor, 1991; Wullschleger et al.,1994). Most of these observations were made on single leaves.

Increased CO_2 concentrations do not affect rate of development for many crops (Havelka et al., 1984; Mohapatra, 1990; and Rogers et al., 1986), however, an increase in days to flowering in soybean (*Glycine max* L. Merr.) by Baker et al. (1989) and wheat (*Triticum aestivum* L.) by Schonfeld et al. (1989) was observed, indicating indirect effects of CO_2 concentration on crop phenology.

Productivity of crops under field conditions depends on the interaction of many environmental factors such as temperature, radiation, moisture, humidity, wind, and edaphic factors such as nutrient availability. These will interact with the increase in CO_2 concentration. Lawlor and Mitchell (1991) showed that the additional growth induced by an increased CO_2 supply was distributed evenly between plant organs implying that the distribution mechanisms are not differentially affected by increased CO_2 concentration. These general observations hold true for many crops. However, the magnitude of response to increased CO_2 concentration vary with the crop species and the environment.

Rice (*Oryza sativa* L.) is the only major cereal grain used almost exclusively for human consumption. Globally, rice ranks second to wheat in area harvested with 147 million ha in 1991 (IRRI, 1993). Eighty five percent of the total rice production is consumed directly by humans compared with 60% for wheat and 25% for maize (*Zea mays* L.).

Rice is highly adaptable to diverse environments. It is grown from 50^0 N in Aihwei, China to 35^0 S in New South Wales, Australia. The crop is produced at sea level and to a height of 2600 m on the slope of Nepal's Himalayas. It is grown in the world wettest areas in Myanmar's Arakan coast with 5100 mm of average rainfall during growing season and in the driest deserts with less than 100 mm rainfall at Al Hasa Oasis in Saudi Arabia (IRRI, 1993). These extremes clearly shows its diversity of genotypes and the adaptability to different environments.

Although rice flourishes in the humid subtropics and in temperate climates, the bulk of rice production is centered in wet, tropical climates, mainly in South and SouthEast Asia. Of the 25 rice producing nations, 17 are located within South, SouthEast and East Asian regions. The eight other countries outside this region jointly produce less than 6% of the world rice (IRRI, 1993). World rice requirements are predicted to increase at a compound rate of 1.7% per year between now and year 2025. This means that by year 2025 the world needs an additional 13 million tons of rough rice each year. Much of that increase must come from additional production in Asia (IRRI, 1993). An increased atmospheric CO_2 concentration could be of great advantage in achieving that task. However, improvements of agronomic and cultural management of the crop to suit the new environment is vital in realizing the maximum benefit. Thus, understanding rice plant response to increased CO_2 concentration under tropical environments is of primary importance.

Rice does not appear to respond to increase in atmospheric CO_2 concentrations above 500 μmol mol^{-1} (Baker et al., 1990a). Contradictory evidence exists on photosynthetic acclimation of rice leaves to increased CO_2 (Baker et al., 1990a; Ziska and Teramura, 1992). Crop canopy dark respiration in rice may increase with increasing CO_2 concentration (Baker et al., 1992), while single leaf dark respiration may decrease with increased CO_2 concentration (Ziska and Teramura, 1992). These observations show that there is an uncertainty in the response of rice to increased CO_2 concentration. This may be partly a result of the experimental environment in which measurements were made.

Enrichment with CO_2 has been shown to increase phenological development of rice when compared between subambient and superambient CO_2 concentrations (Baker et al., 1992). However they did not observe differences in phenology between ambient and super ambient CO_2 environments. Manalo et al. 1994 observed an increase in phenological development with increased CO_2 only at lower temperatures. Increased atmospheric CO_2 increases growth such as, tillering, root growth, plant height, biomass accumulation, and harvest index of rice (Baker et al., 1990b; Imai and Murata, 1976; Imai et al., 1985; Manalo et al., 1994; Seneweera et al., 1994; Ziska and Teramura, 1992). Leaf area has been shown to either similar or decrease with increased CO_2 concentration (Baker et al., 1990b; Ziska and Teramura, 1992). Leaf transpiration (Baker et al., 1990a; Imai and Murata, 1976) decreases with increased CO_2 concentration. Most of these CO_2 studies were done under controlled environments with unlimited nutrient supply.

The increase in rice production from 1965 to date has been attributed to the use of high-yielding, photoperiod insensitive, early-maturing cultivars and to better crop nutrition, primarily increased fertilizer N. Today about 20% of all N produced in the world is applied to the rice fields of Asia (IRRI, 1993).

Even though plant growth responds to increased atmospheric CO_2 at lower nutrient concentrations, a limit to accumulation of nutrients is set by the soil nutrient availability. In natural conditions soil minerals may be exhausted by stimulated plant growth at high CO_2 and impose a constraint on further growth. Agronomic N use efficiency in rice soils is decreasing as a result of decrease in uptake while physiological N use efficiency remain same at ambient CO_2 (IRRI, 1993). Increased atmospheric CO_2 may alter these relationships by increasing N uptake as a result of increased root density. However no work had been reported on uptake efficiencies and distribution of rice plant N under elevated CO_2.

Two rice models namely ORYZA 1 (Kropff et al., 1993) and CERES-RICE (Singh and Padilla) are being developed to simulate rice plant growth and development. ORYZA 1 calculates daily canopy CO_2 assimilation by integrating instantaneous rates of leaf CO_2 assimilation to simulate dry matter production. CERES-RICE uses a simpler, constant relationship between cumulative light interception and dry matter production. For many crops, this relationship is linear (Charles-Edward, 1986 for guar [*Cyamopois tetragonoloba*]; Shible and Weber, 1965 for soybean [*Glycine max* L.]; Williams et al., 1965 for maize [*Zea mays* L.]; Milthorpe and Morby, 1979 for potato [*Solanum tubarosum*]; Gallagher and Biscoe, 1977 for Wheat [*Triticum aestivum* L.]). This relationship of biomass production to intercepted radiation under increased CO_2 could be altered by increasing the slope of the relationship, (i.e., increasing the radiation use efficiency or by altering the amount of radiation intercepted. CERES-RICE uses a nonlinear relationship between light intercepted and canopy biomass production, with theoretical modifications, to predict the effect of increased CO_2 concentration on rice. The algorithms of neither ORYZA 1 nor CERES-RICE have been validated with field data for tropical rice environments.

Therefore studies were undertaken to compare the effect of CO_2 enrichment of rice crop at different N nutrition under field conditions in a tropical environment to answer the following questions.

a. What will be the nature of rice response to an ever increasing atmospheric CO_2 concentration ?

b. How does the CO_2 *influx* and *efflux*, at both single leaf and canopy levels, respond to elevated atmospheric CO_2 concentration ?

c. How does increased atmospheric CO_2 concentration affect phenological development and growth ?

d. Will light interception and radiation use efficiency change with increased atmospheric CO_2 ?

This thesis has been written in the format of scientific journal articles. Chapter 1 is the general introduction. Chapter 2 to 5 are manuscripts for scientific journal articles.

Chapter 2 is from preliminary work done in controlled environment chambers in the U.S. Environmental Protection Agency, research laboratory in Corvallis, Oregon to evaluate the response of rice seedlings to different concentrations of CO_2 and N nutrition. The objective of this research was to determine how individual rice plant responds to superambient atmospheric CO_2 concentrations. This work was done to help to determine the treatments to be used in field experiments, to be done in tropical rice fields at the International Rice Research Institute in the Philippines.

Chapter 3 focuses on assimilation and respiration of rice at elevated atmospheric CO_2 in a tropical field environment. This is important in terms of productivity, as well as for the estimation of a global carbon budget. Implications of plant N content on assimilation and respiration are discussed in this chapter.

Chapter 4 deals with phenological development and growth of rice at elevated atmospheric CO_2 in a tropical field environment. Distribution of biomass within the plant, plant N uptake and distribution, tissue N concentrations, and soil N recovery by rice are discussed in this chapter.

Chapter 5 gives the effect of CO_2 concentration on radiation interception and radiation use efficiency (RUE). Relationships between interception and RUE at different N fertilizer levels and in different atmospheric CO_2 environments are given in chapter 5.

Chapter 6 is a short summary and conclusion which evaluates the more general meaning of these experiments.

Literature cited in these studies is given in a concluding literature section.

CHAPTER 2

THE EFFECTS OF INCREASED ATMOSPHERIC CO_2 AND N NUTRITION ON LEAF CO_2 ASSIMILATION AND GROWTH OF RICE (*Oryza sativa* L.) SEEDLINGS

Introduction

Global atmospheric carbon dioxide (CO_2) concentration at the Mauna Loa observatory increased from 316 μmol mol^{-1} in 1959 to 354 μmol mol^{-1} in 1990 (Keeling and Whorf, 1992). It is projected to reach 700 μmol mol^{-1} during the mid 21st century (Conway et al., 1988). The primary direct effect of increased CO_2 on C_3 plants is increased net photosynthesis. Productivity of a large number of C_3 plants may increase an average of 33% (Cure & Acock, 1986; Kimball, 1983). Rice (*Oryza sativa* L.) is a C_3 plant and its biomass productivity has been shown to respond positively to increased atmospheric CO_2 (Baker et al., 1990a; Imai et al., 1985).

One plant characteristic that enables modern rice cultivars to produce higher yields is their responsiveness to fertilizer N. In rice excess vegetative growth tends to dilute leaf N concentration which, in turn, reduces light saturated C assimilation (Dingkuhn et al., 1992). Therefore, an increase in biomass due to increased CO_2 concentration could similarly decrease leaf N concentration. The objectives of this study were (I) to understand the effect of CO_2 and different levels of N fertilizer on growth and on dry matter partitioning of two rice cultivars during seedling growth, and (II) to determine the effect of leaf N concentration on leaf C assimilation at different CO_2 concentrations.

Materials and Methods

An experiment was conducted during the summer of 1992 at the U.S. Environmental Protection Agency's environmental research laboratory in Corvallis, OR, USA. Experiments began on 11 June and repeated on 01 August 1992. Seeds of rice cultivars IR72 and KDML105 were soaked in tap water for 36 h and allowed to germinate on moist filter paper for 2 days. The germinating seeds were planted in 6.4 cm diameter, 25 cm tall, bottom sealed plastic tubes filled with silt loam soil. Thirty-six tubes were placed in each of eight small exposure chambers (1 m^3 cube with wood frames covered with clear Teflon film) located inside a glass house. Water level was maintained at field capacity for three days to give good seedling establishment. Thereafter, plants were grown under a flooded condition in North Carolina State University phytotron nutrient solution, excluding N. Seedlings were thinned to one per tube at 4 days after sowing (DAS). Beginning the second day after sowing, CO_2 was injected into the exposure chamber using mass flow controllers (Model 825, Edwards High Vacuum International, Wilmington, MA). Chamber CO_2 concentrations were monitored with infra-red gas analyzers (Model 6251, Lambda Inst. Co., Lincoln, NE), linked to a sequential sampling system (Model SAMS 6-12, Scanivalve Corp., San Diego, CA), and a HP3052A data acquisition System, equipped with a HP9816 computer, which maintained average CO_2 concentrations of 373 (ambient), 545, 723, and 895 μmol mol^{-1} in individual exposure chambers. Each CO_2 treatment was replicated in two chambers.

Three levels of fertilizer N were applied at the rate of 12.25 mg (N_{12}), 24.5 mg (N_{24}), and 36.5 mg (N_{36}) of N per plant at 5 DAS in the form of NH_4NO_3. Nitrogen treatments were replicated thrice within a chamber. A preliminary study showed considerable chlorosis in rice plants by 20 DAS if no N was added because of poor soil N (less than 0.05% N). Therefore, no zero N treatment was used in this study.

Three tubes were sampled from each treatment at 08.00 - 09.00 hr on 14, 21, and 28 DAS and leaf number, tiller number, leaf area were measured for each tube sampled. Leaf dry weight, sheath and culm dry weight, and root dry weight for each tube were measured after drying for 72 h at 70° C. Average leaf N content for IR72 was analyzed from destructive samples at 21 and 28 DAS. Green leaf blades were dried at 70^0 C for 72 h, ground and sieved and leaf C and N concentration were determined using an elemental analyzer, Carlo Erba CHNS-O (model EA1108).

At 25 DAS, leaf CO_2 assimilation at the growth CO_2 concentration was measured using a Li-Cor 6200 gas exchange system, using the most fully developed leaf of the main culm. The leaf was allowed to acclimate for about a 60 s inside the 250 ml leaf cuvette, at each CO_2 concentration, before taking CO_2 exchange measurements. Li-Cor 6200 was calibrated with a known CO_2 gas but no blank tests without leaf were made. Relationships between leaf CO_2 assimilation and leaf N was derived using a non linear logistic equation derived by Sinclair and Horie (1989).

Average relative humidity inside the exposure chambers was uncontrolled and varied with air temperature between 40 - 50% during the first 10 days and increased to 65 - 75% after 15 DAS. Average daily maximum temperature in the chamber was about 33^0 C. However, midday maximum temperatures reached 38^0 C on 17 and 22 DAS in the first experiment, and on 6, 11, and 16 DAS in the second experiment. Average photosynthetically active radiation at noon, measured using a Li-cor quantum sensor inside the chamber, was approximately 900 μmol PAR m^{-2} sec^{-1}. Statistical analyses were done using CO_2 as the main factor, and variety and N as subfactors in an split plot design. Analysis of variance (ANOVA) was performed using STATGRAPHICS statistical graphics system. Mean comparisons were made using Duncan's Multiple range test at $P<0.05$.

Results and Discussion

There were no statistically significant differences between the two experiments. Therefore, we combined data from both experiments for analysis. None of the variables had significant treatment effects at 14 DAS. Therefore, those results are not included.

There was no interaction between cultivars and growth CO_2 concentration for any variable tested in this study. We did not observe differences in partitioning of assimilates between cultivars, presumably due to short period of exposure to elevated CO_2. Therefore, no interaction effects between cultivar and CO_2 concentration does not necessarily mean that there will be no cultivar differences in response to elevated CO_2.

Growth responses

Tiller number increased with increased atmospheric CO_2 concentration, with the highest increase occurring between 373 and 545 μmol mol^{-1} (Table 2.1). There was no significant increase in tiller number with increased CO_2 concentration above 545 μmol mol^{-1}. Development of an initiated tiller from the leaf axil of each unelongated node into an autotrophic tiller depends on availability of assimilates. Increased CO_2 assimilation at elevated CO_2 would have supported more initiated tillers to develop into autotrophic tillers. However, there was no further increase in CO_2 assimilation at CO_2 concentration above 545 μmol mol^{-1}. Therefore, lack of additional assimilates stopped further increases in tillering with increasing CO_2 above 545 μmol mol^{-1} (Fig.2.4). Increased tillering also depended on N availability (Table 2.1). There was no significant increase in tiller number with increased CO_2 concentration at N_{12}, but at N_{24} and N_{36} tiller number increased by 39% and 46% when CO_2 concentration was increased from 373 to 545 μmol mol^{-1}. Yoshida (1981) showed that

Table 2.1. Leaf number and tiller number per rice plant grown at different CO_2 concentrations and different rates of fertilizer N at 21 and 28 days after sowing.

CO_2 concentration µmol mol^{-1}	Leaf number per plant				Tiller number per plant			
	21 DAS			28 DAS	21 DAS			28 DAS
	N_{12}	N_{24}	N_{36}	Mean	N_{12}	N_{24}	N_{36}	Mean
373	13.7 b	15.6 a	14.6 a	18.7 a	2.7 a	3.4 a	3.5 a	4.2 a
545	14.6 b	18.8 b	19.9 b	20.7 b	3.0 ab	4.7 b	5.1 b	5.1 b
723	14.6 b	19.6 b	19.7 b	19.9 b	3.3 ab	4.9 b	4.9 b	4.9 b
895	15.3 b	18.9 b	20.4 b	20.2 b	3.5 b	4.8 b	5.4 b	5.0 b
Mean	14.5 a	18.3 b	18.6 b	19.9	3.1 a	4.5 b	4.8 b	4.8

In a column, (means at different CO_2 levels) and row (main N effect across CO_2) followed by a common letter are not significantly different at $p<0.05$ by DMRT.

tillering in rice increased linearly with the increase in plant N up to a content of 5%. Increased tiller number with increased CO_2 concentration confirms results of studies by Baker et al. (1990b) and Imai et al. (1985). Increase in early tillering could have a significant effect on number of panicles per plant, and this could be the reason for greater panicle number in rice at elevated CO_2 as reported by many researchers. IR72 had a significantly more tillers than the KDML 105. However, there was no interaction between CO_2 concentration and cultivar.

Increased tillering at elevated CO_2 increased leaf number per plant when N was available. For example, at 21 DAS leaf number per plant grown at 545 μmol mol^{-1} compared to 373 μmol mol^{-1} was 20% greater at N_{24} and 35% at N_{36} (Table 2.1). At 28 DAS, there was no significant interaction between CO_2 and N on leaf number. Differences in leaf number per plant above 545 μmol mol^{-1} CO_2 were not significant (Table 2.1). Although, leaf number per plant increased with increased tillering at high CO_2, there were fewer leaves per tiller at higher CO_2 concentrations presumably due to fewer leaves with newly develop tillers (Table 2.2). For example, there were 8.9 and 8.8% fewer leaves per tiller at 21 DAS and 28 DAS in 373 compared to 545 μmol mol^{-1} CO_2 (Table 2.2). Dilution of leaf N at the higher CO_2 would also have enhanced leaf senescence. Lack of interaction between CO_2 and fertilizer nitrogen for leaf number per tiller suggests that N has relatively the same effect on leaf and tiller number and any decrease in plant N content is compensated by decreased tillering and increased leaf senescence. There were no differences between cultivars in response to atmospheric CO_2 for leaf number per plant and leaf number per tiller (data not shown).

Rice leaf area did not increase with increased CO_2 concentration contrary to observations in many upland crops. Morison and Gifford (1984) found an increase in leaf area with increased atmospheric CO_2 in 14 crop species, including wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), and maize (*Zea mays*). Similar results were found by Ackerly et al. (1992), with Amaranths (*Amaranths retroflexus*) and Jones et al. (1984) with soybean (*Glycine max* L.merr.). Imai et al. (1985) reported an increase in leaf area with increased CO_2 in rice during the vegetative phase, but that difference had disappeared by the ripening phase. Findings by Baker et al. (1990b) and Morison and Gifford (1984) are consistent with our data that rice leaf area does not respond to elevated CO_2 (Table 2.2). Nevertheless, that does not necessarily mean that there is no change in interception of radiation. Increase in total leaf number and decrease in leaf size may create a better distribution of leaves under elevated CO_2 for capturing radiation.

There was no difference in total plant dry weight among CO_2 concentrations above 545 μmol mol^{-1} at either 21 DAS (Table 2.2) or 28 DAS (Fig. 2.1), which supports findings by Baker et al. (1990b). This suggests that rice seedlings do not respond to elevated CO_2 concentration above 545 μmol mol^{-1}. The response to increased CO_2 concentration from ambient to 545 μmol mol^{-1} also depended on level of fertilizer N. When N was limiting at 28 DAS in N_{12}, there was no significant increase in total dry weight, but there was an increase at N_{24} by 20% and N_{36} by 42%, with increased CO_2 concentration from 373 to 545 μmol mol^{-1} (Fig 2.1). This suggest that the response of rice plant to increased CO_2 concentration depends on the level of N supply.

The response of different plant organs to elevated CO_2 concentration also depended on N status of the rice plant. Interaction of CO_2 concentration and fertilizer N for any variable was not statistically significant at 21 DAS. Total leaf blade dry weight at 21 DAS increased with increased CO_2 concentration from 373 to 545 μmol mol^{-1}, but there were no differences in leaf blade dry weight among CO_2 treatments above 545 μmol mol^{-1} (Table 2.2). At 28 DAS, leaf blade dry weight did not increase with increased CO_2 concentration from 373 to

Table 2.2. Total dry weight, root:shoot ratio, leaf number per tiller, leaf area, leaf blade dry weight, sheath dry weight, root dry weight, and leaf blade N concentration of rice seedlings grown at different CO_2 concentrations and different rates of fertilizer N at 21 and 28 days after sowing (DAS).

Growth characteristics	DAS	Growth CO_2 concentration (μmol mol^{-1})				Fertilizer Nitrogen		
		373	545	723	895	N_{12}	N_{24}	N_{36}
Total dry weight (g plant^{-1})	21	0.54 a	0.81 b	0.79 b	0.81 b	0.66 a	0.79 b	0.75 b
Root : Shoot	21	0.20 a	0.27 a	0.29 a	0.28 a	0.37 a	0.25 b	0.19 c
(g / g)	28	0.40 a	0.50 b	0.46 b	0.51 b	0.59 a	0.48 b	0.39 c
leaf number/ tiller	21	4.8 a	4.4 b	4.3 b	4.2 b	4.8 a	4.4 b	4.2 b
	28	4.7 a	4.3 b	4.2 b	4.2 b	4.7 a	4.1 b	3.9 b
Leaf area (m^{-2} plant^{-1})	28	0.016 a	0.017 a	0.015 a	0.015 a	0.009 a	0.016 b	0.021 c
Leaf blade weight (g plant^{-1})	21	0.26 a	0.34 b	0.32 b	0.33 b	0.25 a	0.34 b	0.35 b
Sheath and culm weight (g plant^{-1})	21	0.19 a	0.29 b	0.29 b	0.30 b	0.23 a	0.29 b	0.28 b
Root weight (g/plant)	21	0.09 a	0.18 b	0.18 b	0.18 b	0.18 a	0.16 b	0.12 b
Leaf N (g/100g)	21	4.24 a	3.77 b	3.61 b	3.63 b	2.84 a	3.89 b	4.71 c

In a row, means followed by a common letter are not statistically significant at $P<0.05$ by DMRT.

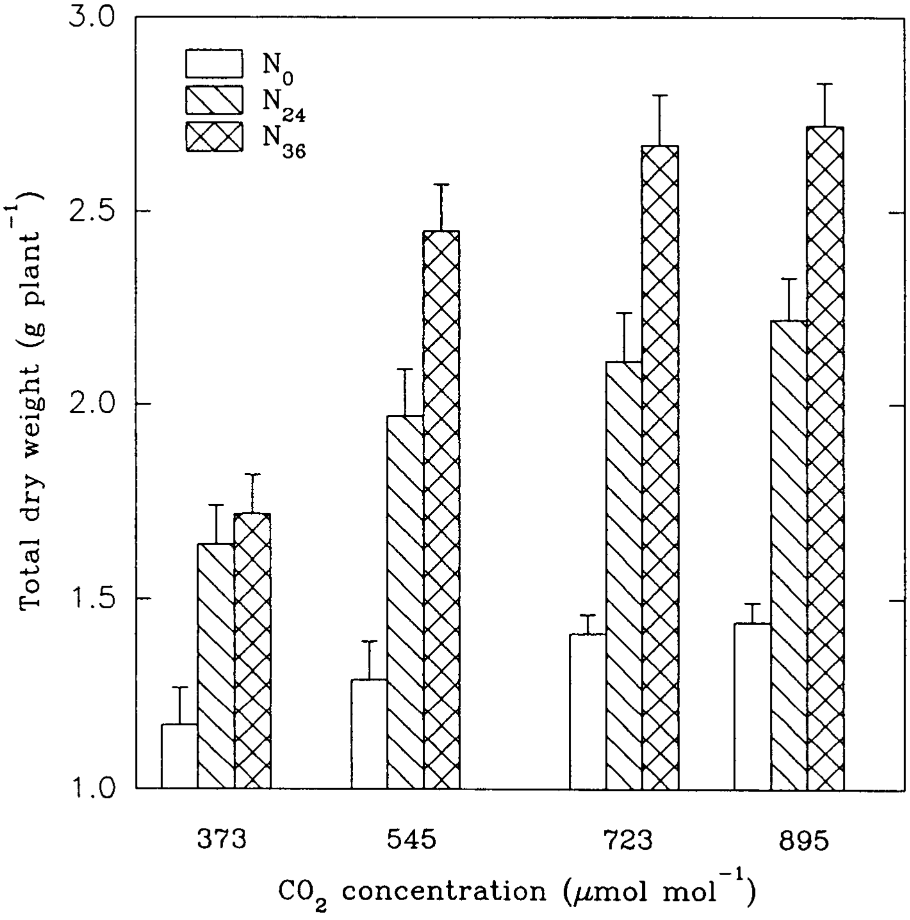

Figure 2.1. Total above ground dry weight of rice seedlings grown at ambient and elevated CO_2 concentrations with different rates of fertilizer N at 28 DAS.

545 μmol mol^{-1} at N_{12} and N_{24} , but at N_{36} the leaf dry weight was significantly higher at high CO_2 (Table 2.3).

Although we did not observe any statistically significant change in the specific leaf blade dry weight, an increase in leaf blade dry weight with increased CO_2 concentration in the higher N treatment, with no change in leaf area, suggests a marginal change in specific leaf weight. However, change in leaf blade dry weight with increased CO_2 concentration was small compared to changes in leaf sheath plus culm and root dry weights. In fact, increase in total above-ground biomass with increased CO_2 concentration was largely due to increased leaf sheath plus culm weight. Increased tillering with increased CO_2 concentration created an additional sink for photosynthate. Leaf sheath plus culm dry weight at 21 DAS was about 52% greater at 545 compared to 373 μmol mol^{-1} CO_2 concentration (Table 2.2). There was no further change in sheath dry weight with further increases in CO_2 concentration. At 28 DAS in N_{12}, increase in CO_2 concentration did not increase sheath weight, but at N_{24} and N_{36}, sheath weight was 17% and 43% greater when CO_2 concentration increased from 373 to 545 μmol mol^{-1} (Table 2.3).

The effect of CO_2 on root weight was more pronounced than for any other growth variables. There was an increase in root:shoot ratio at 28 DAS with increased CO_2 concentration, and a decrease with increased fertilizer N in both harvests (Table 2.2). This was consistent with previous observations that there is a greater increase in root weight, than other plant parts, and an increase in root:shoot ratio as CO_2 concentrations increase (Baker et al., 1990b; Christan and John, 1992; Curtis et al., 1990; Imai et al., 1985 and Olszyk et al., 1993). Baker et al. (1990b) found that roots grew faster and penetrated deeper into the soil at higher CO_2 concentrations.

Table 2.3. Leaf blade, sheath and culm, and root dry weight (g plant^{-1}) grown at different CO_2 concentrations and different rates of fertilizer N at 28 days after sowing.

CO_2 concentration	Leaf blade			Sheath and culm			Root		
μmol mol^{-1}	N_{12}	N_{24}	N_{36}	N_{12}	N_{24}	N_{36}	N_{12}	N_{24}	N_{36}
373	0.33 a	0.54 a	0.65 a	0.43 a	0.62 a	0.67 a	0.41 a	0.48 a	0.40 a
545	0.34 a	0.57 a	0.75 b	0.46 a	0.73 ab	0.96 b	0.49 b	0.67 b	0.74 b
745	0.34 a	0.56 a	0.75 b	0.53 a	0.85 d	1.19 c	0.54 b	0.70 cb	0.73 b
895	0.34 a	0.56 a	0.75 b	0.54 a	0.90 d	1.13 c	0.56 b	0.76 c	0.84 c
mean	0.33 a	0.56 b	0.73 c	0.49 a	0.78 b	0.99 c	0.49 a	0.65 b	0.68 c

In a column, and row (main effect of N across CO_2), means followed by a common letter are not significantly different at $p<0.05$ by DMRT.

Higher N treatments decreased partitioning of assimilates to roots at 21 DAS (Table 2.2). Unlike other parameters, increased root weight with increased CO_2 concentration was significant even at lower fertilizer N at 28 DAS (Table 2.3). At N_{12}, an increased CO_2 concentration from 373 to 545 µmol mol^{-1} increased root weight by 20%. In N_{24} and N_{36}, root weight increased by 39% and 83% as CO_2 concentration was increased from 373 to 545 µmol mol^{-1} (Table 2.3). This difference was partly because, unlike sheath and culm, root dry weight at 373 µmol mol^{-1} did not increase with increased N, but did increase at high CO_2. Greater allocation of assimilates towards roots at high CO_2 with increased N could be due to the higher assimilate supply, accompanied with dilution of N.

Greater increase in sheath and culm dry weight than root dry weight when both CO_2 concentration and N were increased showed that the sheath stores more assimilates than roots when N is not limiting, presumably because of more tillers at higher N (Table 2.3). At low N, rice partitions more biomass to roots under elevated CO_2 (Table 2.3).

These findings suggest that it is the reduction of plant N concentration under higher CO_2 concentration that favored partitioning towards roots, compared to other plant organs. Increased root weight at elevated CO_2 concentration could have a significant influence on fertilizer N recovery. Rice is predominantly grown in flooded conditions, which causes leaching losses from the rhizosphere. Greater root density could reduce leaching losses through increased absorption. Increased assimilate supply to roots at high CO_2 could also increase rate of absorption of N. Therefore, fertilizer N recovery by rice plants could increase if atmospheric CO_2 increases in the future.

Leaf N

Leaf N was analyzed only for the cultivar IR72. Leaf N concentration decreased with increasing CO_2 concentration at both 21 DAS (Table 2.2) and at 28 DAS (Fig 2.2). There was a sharp drop in leaf N concentration when growth CO_2 concentration was increased from 373 to 545 µmol mol^{-1}; no further significant decrease occurred as CO_2 increased above 545 µmol mol^{-1} in both sampling dates. At N_{24} and N_{36} leaf N was 18% and 21% lower in 373 than 545 µmol mol^{-1} CO_2 (Fig. 2.2). That decrease in leaf N could be due to dilution at elevated CO_2 because with increased CO_2 concentration biomass accumulation increased. Greater biomass accumulation in leaf sheaths and roots would have decreased partitioning of N to the leaf as CO_2 increased. However, average decrease in leaf N from 21 DAS to 28 DAS was greater than that due to increased CO_2. For example, average leaf N at N_{36} across growth CO_2 concentrations decreased from 4.71% at 21 DAS to 2.60% at 28 DAS. Leaf C:N ratio at 21 and 28 DAS increased as the CO_2 concentration increased from 373 to 545 µmol mol^{-1} (Fig. 2.3). leaf C:N ratio decreased with increased fertilizer N.

Single leaf CO_2 assimilation

Leaf CO_2 assimilation in plants grown at different CO_2 concentration is confounded as a result of differences in leaf N content. A decrease in leaf N with increasing CO_2 concentration could reduce single leaf CO_2 assimilation as it is curvilinearly related to leaf N (Fig. 2.4). There was little response of single leaf CO_2 assimilation to leaf N concentrations greater than 3 g 100g^{-1} in either ambient or elevated CO_2. This relationship is consistent with the findings of Sinclair and Horie (1989) that light-saturated leaf CO_2 assimilation has a nonlinear relationship with the leaf N concentrations. Yoshida and Coronel (1976) however found a linear relationship. Plants grown under higher CO_2 concentration had a higher N use efficiency in terms of assimilation than ambient (Fig. 2.4) but did not significantly differ among the super ambient CO_2 concentrations. There was no significant difference in leaf CO_2 assimilation among superambient CO_2 concentrations above 545 μmol mol^{-1}, at any given leaf N, but all superambient CO_2 concentration grown plants had higher rates of CO_2 assimilation for a given leaf N content than did ambient-grown plants (Fig. 2.4). This is consistent with the biomass response observed in this experiment. Saturation of rice plant with CO_2 concentration above 550 μmol mol^{-1} is consistent with the findings by Baker et al. (1990a). This suggests that the rice cultivar IR72 may saturate with atmospheric CO_2 concentration before it reaches the projected atmospheric CO_2 of 700 μmol mol^{-1} somewhere in the next century. The saturation of rice leaves with a CO_2 concentration of about 545 μmol mol^{-1} at higher level of leaf N suggests that leaf N might not be the limiting factor for further increase in CO_2 assimilation at CO_2 concentration above 545 μmol mol^{-1}.

These results suggests that, when interpreting leaf CO_2 assimilation in rice for plants grown under different concentrations of atmospheric CO_2, the effects of dilution of leaf N should be considered. Such effects cannot be ignored even on rice seedlings as young as 21 DAS.

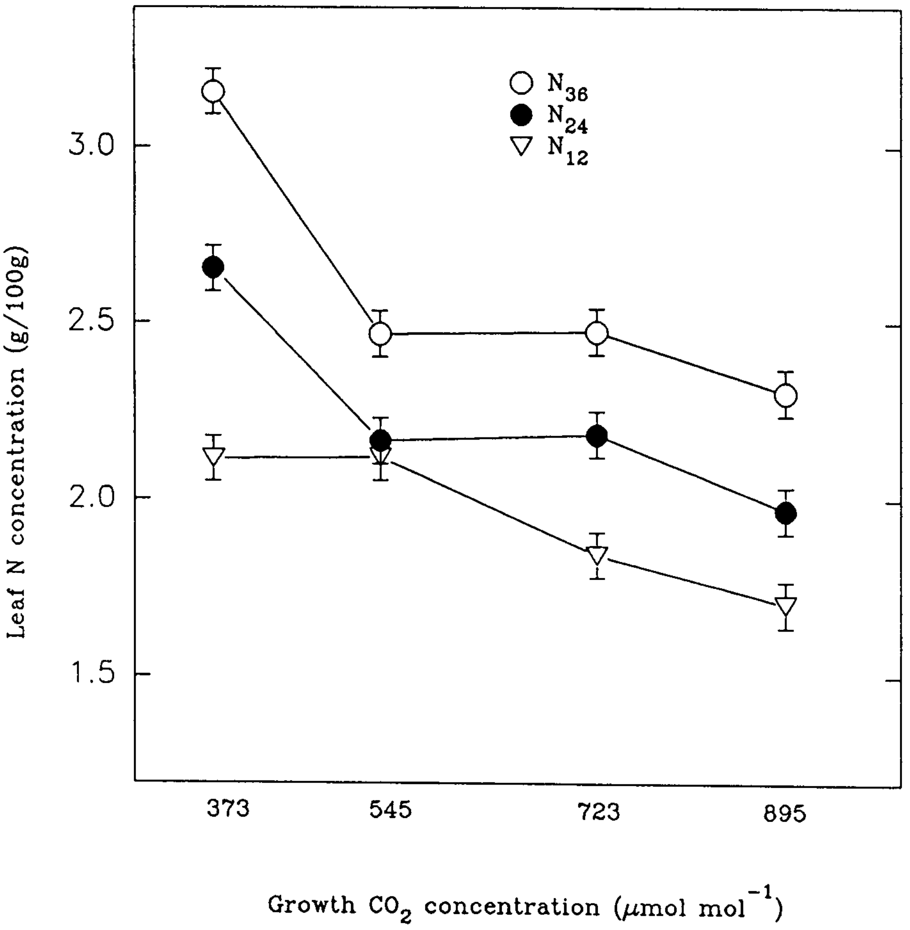

Figure 2.2. Leaf N concentration of IR72 rice at 28 DAS as a function of CO_2 concentration inside the exposure chambers for seedlings grown at three N fertility rates. Error bars represent standard error of mean.

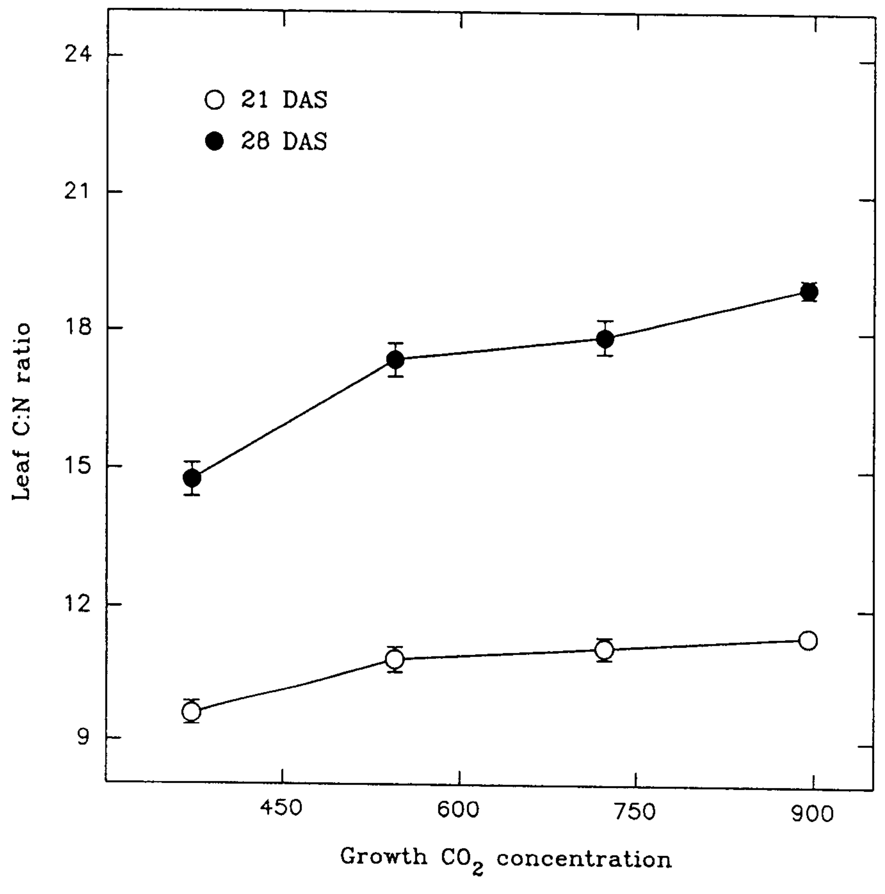

Figure 2.3. Carbon : Nitrogen ratio of IR72 rice leaves at 21 DAS and 28 DAS as a function of CO_2 concentration inside the exposure chambers. Error bars represent standard error of mean.

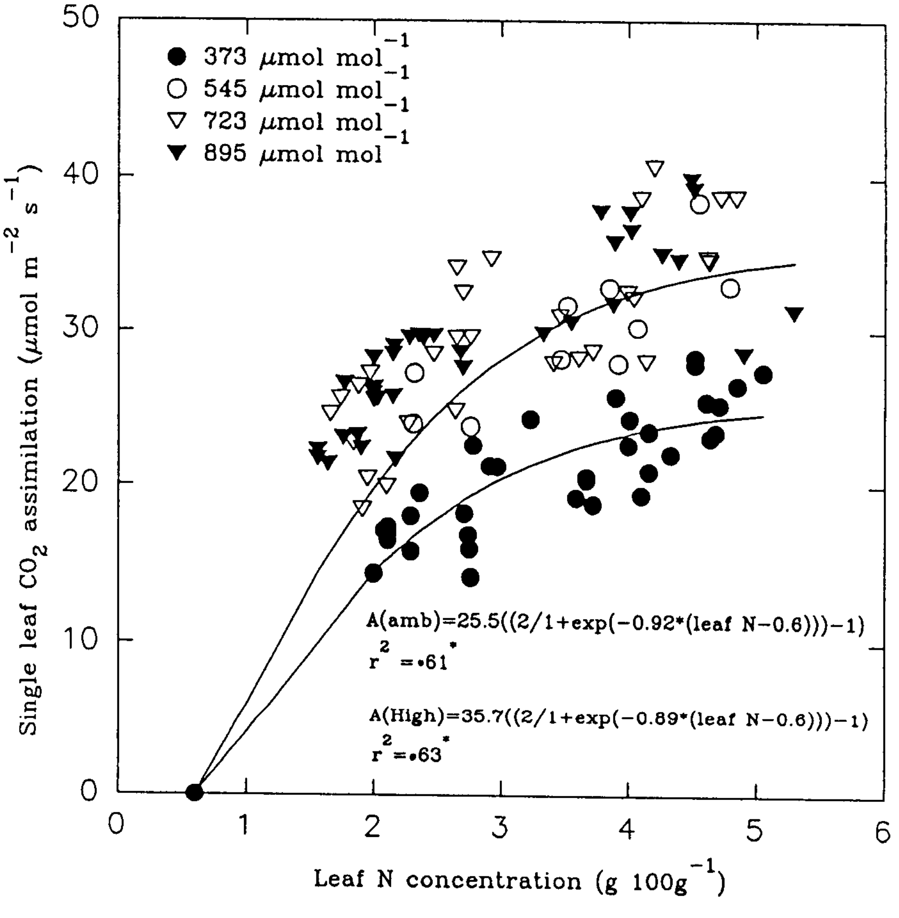

Figure 2.4. Single leaf CO_2 assimilation as a function of leaf N concentration in rice seedlings grown and measured at ambient and elevated atmospheric CO_2 concentrations. Leaf N at zero assimilation was from Dingkuhn et al.(1992). Light intensity at the time of measurement was about 1250 μmol PAR m^{-2} s^{-1}. The curves were fitted for assimilation at ambient and for all high CO_2 levels using a nonlinear logistic equation given by Sinclair and Horie (1989).

Summary and Conclusions

Response of rice seedlings to increased atmospheric CO_2 were limited to concentrations less than 545 μmol mol^{-1}. This suggests that seedlings of rice cultivars tested in this study would be saturated with CO_2 well before the doubling of atmospheric CO_2 concentration predicted for some time in the next century. Leaf CO_2 assimilation increased with increased CO_2 concentration from 373 to 545 μmol mol^{-1} and was dependent on level of leaf N. Increasing CO_2 concentration above 545 μmol mol^{-1} did not significantly increase CO_2 assimilation emphasizing that rice leaves would be saturated with CO_2 at concentrations below 545 μmol mol^{-1}. Increase in total seedling dry weight at high CO_2 suggests that seedling vigor, which is considered as a superior agronomic trait, increases with increased atmospheric CO_2. However, dilution of leaf N could reduce potential increase in CO_2 assimilation, thereby reduce seedling vigor at high CO_2. There was a 20% decrease in leaf N with increased CO_2 concentration between 373 and 545 μmol mol^{-1} but no further decrease among higher CO_2 concentrations. Leaf C:N ratio decreased with increased CO_2 concentration, which could reduce leaf dark respiration. There was no difference between cultivar IR72 and KDML 105 in response to different CO_2 concentrations during the seedling stage.

Root and shoot biomass, root:shoot biomass ratio, leaf and tiller number increased with CO_2 and N, with the greatest increase occurring between 373 to 545 μmol mol^{-1}. Biomass allocation to roots increased with increased CO_2 and N whereas, at 373 μmol mol^{-1} it remained the same or decreased with increased N. Allocation to leaf sheaths and culms followed the same pattern in both 373 μmol mol^{-1} and higher CO_2 with increased N, but the fraction allocated was always higher with high CO_2. This suggests that with increase in atmospheric CO_2 concentration there would be changes in partitioning patterns, and the response would be limited up to 545μmol mol^{-1}.

CHAPTER 3

THE EFFECTS OF INCREASED ATMOSPHERIC CO_2 CONCENTRATION AND N NUTRITION ON CO_2 ASSIMILATION AND DARK RESPIRATION OF FIELD-GROWN RICE (*Oryza sativa* L.)

Introduction

Global atmospheric CO_2 concentration is increasing steadily, mainly as a result of burning of fossil fuel and changes in land use patterns. Plants will likely benefit from increased CO_2 concentration through increased assimilation of CO_2. A substantial portion of CO_2 emitted to the atmosphere, about 14%, is removed every year as CO_2 assimilation by plants (Houghton and Woodwell, 1989). However, considerable debate exists as to whether future increases in atmospheric CO_2 concentration also would alter respiration, which could partially offset or contribute to the greater increases in net CO_2 uptake by plants.

Rice (*Oryza sativa* L.) is the only major cereal grain used almost exclusively for human consumption. The area of rice under cultivation is 147 million ha, which, in terms of world crops, is only second to wheat (*Triticum aestivum* L.). There is a considerable literature on the response of rice to elevated CO_2. However, little research on the effect of elevated CO_2 concentration has been done under tropical field conditions, where most of the world rice is grown.

The primary direct effect of increased atmospheric CO_2 concentration on C_3 plants, such as rice, is usually an increased CO_2 assimilation (Akita and Tanaka, 1973). Apart from the increased availability of substrate for assimilation, increased intercellular CO_2 concentration reduces competitive inhibition of C fixation by oxygen, which thus decreases photorespiration. However, photosynthetic acclimation with long-term increase in CO_2

concentration has also been documented for many crop species. Cure and Acock (1986) summarized the responses of 10 most widely grown crops to elevated CO_2. They observed that, at the first exposure to about 700 μmol mol^{-1} CO_2, assimilation increased by 52% compared to ambient CO_2, but with long-term exposure to the elevated CO_2 concentration the difference in assimilation at increased CO_2 was only 29%. A lower leaf CO_2 assimilation rate for plants grown and measured at high compared to plants grown at ambient but measured at high CO_2 has been reported for rice (Baker et al., 1990a) and tomato (*Licopersicon esculentum*, Yelle et al., 1989). Lower nutrient availability, especially leaf N, sink limitation and end product inhibition have been suggested to cause photosynthetic acclimation to high CO_2.

A substantial amount of leaf N is in the form of soluble chloroplast and thylakoid membrane proteins. Rice partitions about 28-37% of its leaf N into ribulose bisphosphate carboxylase (rubisco). The rate of CO_2 assimilation depends on rubisco activity at lower intercellular CO_2 (C_i). As C_i increases, regeneration of ribulose bis phosphate (RuBP) and, in some cases, the availability of inorganic phosphate could limit assimilation (Farquhar and Caemmerer, 1982). An up-regulation of RuBP at the expense of rubisco at high compared to ambient CO_2 in soybean (*Glycine max* L.) was observed by Vu et al. (1983). Therefore, any decrease in leaf N could have an significant effect on CO_2 assimilation, especially at high CO_2 concentrations. Sink limitation and end product inhibition have also being suggested to cause photosynthetic acclimation (Azcon-Bieto, 1986; Neales and Incoll, 1978).

A positive photosynthetic acclimation to increased CO_2 was also reported for rice (Ziska and Teramura, 1992), soybean (Campbell et al., 1988) and in *Scirpus olneyi*, a brackish marsh plant (Arp and Drake, 1991). In most of these findings leaf N concentration was either similar between growing environments or was not reported.

Despite the vast research on single leaf CO_2 assimilation, little attempt had been made to understand the effect of increased atmospheric CO_2 concentration on canopy CO_2 assimilation in rice. A rice crop canopy leaf area is far less responsive to CO_2 enrichment than are other crop species. Therefore, there will not likely be a large increase in canopy assimilation at high compared to ambient CO_2. Baker et al., (1990 a) suggested that there was a decrease in conductance to CO_2 transfer on a canopy basis, and suggested that there could be a profound acclimation of photosynthesis biochemical level with long-term enrichment of CO_2.

Plant respiration could be altered by its CO_2 history (Amthor, 1991). Both increased and decreased rate of leaf respiration to increased atmospheric CO_2 concentration have been reported (Amthor, 1991; Wullschleger et al., 1994). Several factors could be involved in this process such as the substrate pool, phytomass composition, growth rate, leaf temperature, humidity and the CO_2 concentration. The effect of CO_2 concentration on dark respiration could be a direct result of CO_2 concentration at the time of measurement and an indirect result of the CO_2 history of the plant (Amthor 1991). Wullschleger et al. (1994) suggest that the direct inhibitory effect of CO_2 on dark respiration could be through fixation of CO_2 into organic acids, a reaction which could be similar to crassulacean acid metabolism (CAM), or through direct inhibition of respiratory enzymes similar to the suppression of respiration which occurs in stored fruits at high atmospheric CO_2 concentrations (Kerbel et al., 1988). Amthor (1991) suggests that direct inhibition of enzymes at 700 μmol mol^{-1} CO_2 concentration may occur in leaf tissues, but not in other organs such as roots. .

Long-term effects of CO_2 on respiration, which are termed indirect effects by Amthor (1991), are most likely to effect *growth* and/or *maintenance* respiration (Wullschleger et al., 1994). Amthor et al. (1992) reported a 25-30% decrease in dark respiration when CO_2

concentration was doubled. Ziska and Bunce (1994), from their studies of alfalfa (*Medicago sativa*) and orchard grass (*Dactylus glomerata*), suggested that both direct and indirect inhibition of respiration are possible with increased atmospheric CO_2. Reduction in single leaf respiration rates on a leaf area basis with long-term exposure to elevated CO_2 concentrations have been also reported for water hyacinth (*Eichhornia crassipes*, Spencer and Bowes, 1986), tomato (Bunce, 1990), wheat (Gifford et al., 1985), and sour oranges (*Citrus aurantium*, Idso and Kimball, 1992). Ziska and Teramura (1992) reported an apparent decrease in leaf dark respiration in rice with increased CO_2 However, Imai and Murata (1978) found no change in dark respiration rice plants exposed for 7-15 days to enriched CO_2 (about 1000 μmol mol^{-1}).

In contrast, increasing rates of single leaf respiration with increased CO_2 have also been reported in Soybean (*Glycine max;* Hrubec et al., 1985; Thomas and Griffin, 1994) and cotton (*Gossypium hirsutum* L.; Thomas et al., 1993). In most of those studies leaf N per unit area was not affected by growth CO_2 concentration.

Penning de Vries (1975) defined growth respiration as the cost of producing new biomass, whereas maintenance respiration was the cost of protein turnover, membrane repair, maintaining an ion gradient, phloem loading and translocation. The energy needed for the resynthesis of protein on a leaf area basis may be lower for plants grown at high compared to ambient CO_2 concentrations if less protein is in the leaf. This could result in a lower growth respiration.

Leaf respiration could also be limited by substrate. However, with increased atmospheric concentration the leaf substrate supply should be greater. Accumulation of nonstructural carbohydrates with increased CO_2 concentration have been found in rice (Rowland-Bamford et al., 1990) and soybean (Allen et al., 1988). Therefore, substrate limitation of growth respiration may be minimized at high CO_2. *Maintenance* respiration is independent of the level of substrate (Amthor, 1991). Thus, maintenance respiration should not be limited by the availability of substrate in a high CO_2 atmosphere. However, Thomas et al. (1993) in Cotton and Hrubec et al. (1985) and Thomas and Griffin (1994) in soybean have observed a positive correlation between respiration rate and carbohydrate content in high CO_2 atmospheres.

Respiration and growth rates are positively correlated in many plant species. When substrate, O_2 and enzymes are not limiting, respiration is regulated by the regeneration of ADP or utilization of ATP (Amthor, 1991). Increased CO_2 concentration increases the relative growth rates in rice, which requires more respiratory energy. For example, the respiration rate of *Plantago major* was greatest when relative growth rate was greatest, which occurred at an elevated atmospheric CO_2 concentration (Poorter et al., 1988). Thomas and Griffin (1994) for soybean and Thomas et al. (1993) for cotton also found that leaf dark respiration rates were strongly correlated with the relative growth rate in both ambient and high CO_2 enrichments. Hrubec et al. (1985) found an increase in respiration at elevated CO_2 concentrations in young, growing soybean leaves, but not in mature leaves where growth rates were lower.

The respiration rates at the crop canopy level could respond quite differently than individual leaves to higher CO_2 concentration. With the increase in atmospheric CO_2 concentration, the canopy will be larger and the canopy respiration should increase to meet the energy requirement of the larger canopy. However, little work has been done on the effect of CO_2 concentration on canopy dark respiration of rice.

Apart from these physiological and environmental factors, the effect of CO_2 concentration on dark respiration could be interpreted differently due to the way data are analyzed, since the increased atmospheric CO_2 concentration affects many of the growth processes. Therefore, in this study we attempted to analyzed respiration on the basis of both leaf area and dry mass at the leaf level and ground area and dry mass at and the canopy level.

The objectives of this study were; to determine the effect of long-term enrichment of the atmosphere with CO_2 on leaf and canopy level CO_2 assimilation and dark respiration of field-grown rice in a tropical environment; to determine its relationships with leaf and canopy N concentrations; and to investigate possible adaptive responses of rice to season-long CO_2 enrichment.

Materials and Methods

Rice was grown in the field from transplanting to maturity inside eighteen open top chambers at the International Rice Research Institute (IRRI), Los Banos, Philippines (latitude 14^0 N, longitude 121^0 E) in the dry season, 1994. The open top chambers were located in the wetland research site of the institute and were exposed to natural sunlight.

The octagonal chambers were 2 m in height and had a cross sectional area of 3.3 m^2 (Collins et al., 1994). A Mylar-covered frustrum, with a top opening of 120 cm diameter, was installed atop the 2 m high chambers to reduce effects of wind turbulence. The chamber framework was constructed with PVC pipes joined together with adjustable fittings to form an octagonal ring. Chambers were anchored to the experimental plot with PVC pipes extending 30 cm into the soil. Five of the chamber walls were covered with Mylar film. The north-facing wall consisted of a 6.4 mm thick acrylic panel.

Air was flushed continuously through the chamber at of approximately 3 exchanges per minute. Each chamber had high pressure exhaust fans connected to nine, 5 cm diameter exhaust manifolds, located just above the water surface. This allowed a proper mixing of air within the chamber. CO_2 was injected through a secondary air handling system connected to the acrylic panel. The CO_2 enriched air was injected into the chamber at a volumetric flow of 2.55 m^3 per minute. To maintain the desired CO_2 concentration at the top of the rice canopy, the inlet for CO_2 enriched air entering the chamber was raised periodically as the crop grew to keep it above the canopy.

The CO_2 supply for enriched chambers was stored in a central, refrigerated large container which had a capacity of 10 t of liquid CO_2. The CO_2 concentrations inside chambers were monitored with infrared gas analyzers, IRGA (Li-Cor, LI-6552). Air near the center of the chamber just above the canopy height was drawn through a 6.35 mm Tygon sampling tube by a continuously operated pump to a 3-way solenoid valve (Skinner Valve # V53LB2100), which was connected to the IRGA. This system was programmed to allow four chambers to be sequentially sampled per IRGA (Collins et al., 1994). Each chamber was monitored at 8 minute intervals and the results recorded by a datalogger. The CO_2 injection rate for the enriched chambers was controlled through proportional solenoid valves (Skinner valve # BT2EV0012), which were controlled using a CR10T programmable microprocessor (Campbell scientific) connected with a dedicated computer (Tatung 486). In addition to the control and recording of data for CO_2, data from solarimeters and shielded thermocouples were averaged and recorded at regular intervals using the CR10T datalogger, which was downloaded every day to the hard drive of the computer.

Temperatures inside the chamber were measured using three radiation-shielded copper-constantan thermocouples placed at different locations inside each chamber. Total radiation energy was measured every minute using tube solarimeters (Type TSL, Delta T Devices, Cambridge, UK), averaged over 5 minutes and the average recorded by a CR10T datalogger. Similarly, air temperatures were averaged over 10-minute intervals and recorded by the datalogger.

Plant culture

The experimental design was a randomized complete block design with three replications. Treatments consisted of two concentrations of CO_2, ambient and elevated (700 μmol mol^{-1}), and three rates of N nutrition, (no fertilizer N [N_0], 90 [N_{90}] and 200 [N_{200}] kg N ha^{-1}). A lowland-adapted, short duration, semi-dwarf, photoperiod-insensitive rice cultivar, IR72, was used for the study. Seeds were imbibed in tap water for 36 h and sown on seedling trays. The seedlings were raised for 14 days inside two open-top chambers in either enriched or ambient CO_2. Three seedlings per hill were transplanted at a hill spacing of 20 by 20 cm in an Andaqueptic Haplaquoll soil. Nine of the chambers were maintained at ambient CO_2 (about 350 µmol mol^{-1}) and nine at a enriched CO_2 concentration (about 700 µmol mol^{-1}). Soil inside the chambers was manually puddled to a depth of about 25 cm and levelled before transplanting. The immediate borders surrounding of the chambers were planted with seedlings of the same cultivar to minimize border effects. The field was kept flooded throughout the growing season.

Plant sampling for biomass was done 2-3 days after each set of measurements of canopy CO_2 assimilation and dark respiration. Four to six hills from each chamber were pulled by hand, placed into a plastic bag, and kept in an ice chest until analysis inside the laboratory. Sampled hills were immediately replanted by plants of similar size obtained from the plot outside the chamber. Plant samples were analyzed within the same day of the harvest for leaf area index (LAI), plant height, and dry weight. Analysis for micro Kjeldahl total N concentrations of leaf, sheath and culm, root and panicles were done later on tissues dried for 72 h at 70°C.

CO_2 Assimilation.

Leaf CO_2 assimilation measurements were made on cloudless days, between 10:30 and 12:30, using the most recently fully expanded leaf of biggest culm of the hill. Measurements were made on 3-5 leaves per chamber at a light intensity of above 1750 µmol (PAR) m^{-2} s^{-1} using a LI-COR 6200 gas exchange system. The air flow rate inside the 250 ml cuvette was about 100 mol s^{-1} which maintain the relative humidity at about 65%. Sampling duration was 15 seconds. When measuring assimilation at either ambient or high CO_2 concentrations using the same leaf, assimilation was first measured at the CO_2 concentration of the growing environment, then at the CO_2 concentration of the opposite treatment.

Canopy CO_2 assimilation was measured in a closed system using a 0.4 by 0.4 by 0.6 m chamber covered with transparent Mylar film which enclosed four hills (1.6 m^2). Measurements were made between 10:30 and 12:30 h. The assimilation chamber was connected to a Li-Cor 6200 gas exchange system by two 2 mm diameter 2 m long tygon tubes. Four 5 cm-diameter fans were positioned at opposing sides of the sample chamber to provide better mixing of air and to simulate wind. A smoke test confirmed that the air inside the chamber mixed well. The section of the sampling tube that was inside the chamber was perforated with tiny holes to allow sampling of air across the chamber. The opening of the inlet tube was placed next to a fan to ensure mixing of air returning from the analyzer. During measurements of CO_2 assimilation, a Li-Cor quantum sensor was placed outside on the assimilation chamber to measure the light intensity. Light interception by the chamber material was about 10%, but no correction was made to radiation data for the reduction in light reaching the leaves due to absorption or reflection from assimilation chamber walls. Before canopy measurements, several test runs over the flooded paddies without plants were done to estimate CO_2 flux from flood water. Canopy assimilation data were corrected accordingly. This procedure also helped to detect chamber leaks. A 0.4 by 0.4 by 1 m chamber was used for canopy assimilation measurements beginning when plants were about 0.5 cm tall.

For each measurement, an assimilation chamber was placed over 4 hills inside the open top field chamber, taking care not to damage the plants. Flood water at the bottom of the assimilation chamber provided a seal from the outer atmosphere. For measuring assimilation in high-CO_2-grown plants, CO_2 rich air was pumped into the chamber. The CO_2

inside the chamber was then allowed to deplete for about 30 sec, and once a steady state was reached, assimilation was calculated from the slope of the CO_2 depletion curve when the CO_2 concentration was 700 ±10 μmol mol^{-1}. Assimilation was recorded from two locations inside each open-top chamber. No measurements of air temperature or humidity were made inside the canopy assimilation chamber, but the duration for each measurement was less than 60 s, so any change would have been small.

Respiration

Leaf respiration was measured between 2 and 2.5 h after sunset to avoid the higher CO_2 efflux usually found immediately after a period of irradiation. The procedure for measurements were similar to that used for measuring leaf CO_2 assimilation. Since leaf CO_2 efflux was small and the analyzer readability was low, two to three leaves were inserted into a leaf cuvette for each measurement and sampling time was increased to 30 s. Leaves used for each measurement were immediately detached and transferred to a labeled plastic bag and refrigerated until further analyses were done. Refrigerated leaves were analyzed for leaf area on the following morning. Leaf dry weight was measured after drying for 72 h at 70 ^{0}C. Dried leaves were ground and stored under refrigeration until the N and carbohydrate analyses were done.

Canopy respiration was measured using the same chambers used for measurement of canopy CO_2 uptake, with a sampling time of 30 s. Two to three measurements were made from each location after the CO_2 efflux rate was steady. In ambient CO_2 chambers, at low wind speeds, there was a build up of CO_2 in the field as a result of plant and human respiration. Therefore, we used pure N gas to flush the chambers to bring down the CO_2 concentration to ambient before recording those measurements.

Before each set of measurements for the day the Li-Cor 6200 gas analyzer was calibrated with a known CO_2 gas supplied by Li-Cor. Blank tests were carried out after every 3 - 4 chambers. The analyzer was periodically checked for accuracy.

Mesophyll resistance (r_m) was calculated using the equation ,

$$Assimilation=([CO_2]_{atmos}-[CO_2]_{chloroplast})/(r_m+r_{st}+r_{bl})$$

Stomatal resistance (r_s) was calculated based on flux of water vapor through stomata. Boundary layer resistance (r_{bl}) of the rice leaf was derived from evaporation rates from wet filter paper of the same size as the leaves. The CO_2 concentration inside the site of CO_2 fixation was assumed as the CO_2 compensation point for rice leaves which was about 75 µmol mol^{-1}. The r_m could then be calculated using the measured values for assimilation and $[CO_2]_{atmos}$. The r_m calculated in this way is a residual quantity which included all errors of measurement and cannot be related to any particular physical or biochemical process in the leaf.

Carbohydrate Analysis

For carbohydrate analysis approximately 2 g of dried, ground leaf was refluxed twice over a sand bed for about 15-20 minutes, using 40 ml of 80 % (v/v) ethanol each time. The supernatant containing total soluble sugars were combined, and leaf residues containing starch were oven-dried at 70^0 C overnight. An aliquot of the ethanol extract was then analyzed, after suitable dilution, for total soluble sugars. This was carried out using a modified anthrone reagent (Setter et al., 1989 a). Four-tenth g of Anthrone, 9-10-dihydro-9-oxoanthracene, was dissolved in 200 ml of concentrated sulfuric acid and mixed with 60 ml of 95 % ethanol. Ethyl alcohol was incorporated into the reagent to stabilize the colored product. Five ml of the Anthrone reagent was added to 0.5 ml of sugar extract. The color was developed by boiling in a water bath for 10 minutes. Absorbance was read at wave length of 620 nm. Total soluble sugar concentration was computed by comparing to the glucose standard curve run in conjunction with the samples.

Starch content was quantified by hydrolysis with amyloglucosidase and assayed using a purpurugallin-glucose oxidase (PGO) enzyme mixture (Setter et al., 1989 b). The ethanol insoluble residue was ground very finely and a 0.2 g subsample was placed into screw cap tubes with 2 ml of 25 mM acetate buffer at pH 6.0. Samples were boiled for 180 minutes, with occasional stirring. After subsequent cooling, 1 ml of amyloglucosidase (from Rhizopus, Sigma) solution containing 0.8 IU glucoamylase per 25 mM acetate buffer (pH 6.0) and 2 ml acetate buffer were added. Tubes were incubated for 24 h at 37 ^{0} C. Following incubation, centrifugation and dilution, 3 ml PGO-enzyme color reagent solution (PGO-enzyme; Ortho-Dianisidine dihydrocloride, Sigma) was added to a 0.5 ml aliquot. Samples were incubated in darkness at room temperature for 30 minutes for color development. Absorbance was read at wavelength of 450 nm. A glucose calibration curve was constructed to assess the efficiency of starch hydrolysis. Starch concentration was based on comparison of sample reading to a standard starch curve. Total non-structural carbohydrate was computed as the sum of total soluble sugars and starch.

Statistical analysis of variance (ANOVA) was performed using STATGRAPHICS statistical graphics system. F statistics were based on residual mean square error. The LSD at 95% probability was used for pair-wise comparisons between means.

Results and Discussion

Single Leaf CO_2 assimilation

To determine any acclimation of rice plant to prolonged exposure to high CO_2, CO_2 assimilation was measured at both 350 and 700 µmol mol^{-1}, using plants grown both at ambient and elevated CO_2 concentrations. Leaf CO_2 assimilation was measured on 19, 39, 64, and 74 DAP on plants grown at both ambient (350) and 700 µmol mol^{-1} of CO_2 and at 0, 90 or 200 kg ha^{-1} added fertilizer N. The results are given in Table 3.1. On all measure dates leaf CO_2 assimilation at all N fertilizer rates and all growth-CO_2 concentrations was significantly greater in 700 µmol mol^{-1} compared with ambient. Averaged over nitrogen treatments, the rate of assimilation of single leaves of plants grown at ambient CO_2 on the different sample dates increased by 60 to 83 % when the CO_2 concentration was increased from 350 to 700 µmol mol^{-1}. For leaves from plants grown at high CO_2, the corresponding increases ranged from 100 to 116%.

Since the assimilation response upon changing leaves from ambient to 700 µmol mol^{-1} CO_2 was so large in the leaves from plants grown at the high CO_2 concentration, one might interpret these data to indicate that rice adapts to being grown in high CO_2 by creating a leaf that is even more responsive to CO_2 increases than for leaves grown at ambient CO_2. In fact, however, the relative increases were large in those treatments because the rates of assimilation of leaves grown at high CO_2 but measured at ambient CO_2 (e/a) were less than were rates of leaves from plants both grown and measured at ambient CO_2 (a/a). Absolute rates of assimilation at high CO_2 were less than were rates of leaves grown at ambient CO_2 but measured at high CO_2.

Table 3.1. Average single leaf CO_2 assimilation (μmol m^{-2} sec^{-1}) and leaf N concentration for rice grown and measured at both ambient (350 μmol mol^{-1}) and enriched (700 μmol mol^{-1}) CO_2 at three different fertilizer N rates.

Sampling date	Nitrogen treatment	Plants grown at ambient CO_2			Plants grown at enriched CO_2		
		Assimilation measured at			Assimilation measured at		
		350(a/a)	700(a/e)	Leaf N %	350(e/a)	700(e/e)	Leaf N %
19 DAP	N_0	23.3±0.81	36.8±1.6	3.33	15.2±1.2	38.2±1.7	2.79
	N_{90}	25.1±0.8	42.8±1.3	3.40	16.9±1.08	36.4±1.1	2.62
	N_{200}	30.5±0.7	47.5±1.6	3.79	23.8±0.62	45.4±1.0	3.23
	Average	26.3	42.3		18.8	39.9	
39 DAP	N_0	17.3±1.4	30.3±1.2	1.86	8.5±1.2	22.7±1.2	1.35
	N_{90}	24.4±1.3	40.6±1.2	2.49	16.7±1.1	36.1±0.9	2.00
	N_{200}	25.3±1.0	43.5±0.8	3.46	18.8±1.0	36.6±1.1	2.91
	Average	22.3	38.1		14.7	31.7	
64 DAP	N_{90}	20.4±1.4	39.0±1.9	1.94	16.8±1.5	34.9±1.4	1.62
74 DAP	N_{200}	23.7±0.7	41.9±0.9	2.84	19.9±0.85	38.5±0.9	2.57
	Average	22.1	40.5		18.3	36.7	

Each mean ± SE is an average of a minimum of five measurements.

Hogan et al. (1991) proposed a hypothetical model to explain the acclimation of plants to increased CO_2 concentration. Acclimation would change the assimilatory response to intercellular CO_2 concentrations (C_i), showing either an up- or a down-regulation of assimilation with increased CO_2 concentration when compared with plants grown at ambient CO_2 concentration. We observed a lower rate of leaf CO_2 assimilation in rice grown at high CO_2 concentration, compared to rice grown at ambient CO_2 concentrations, when measured at a common CO_2 concentration, suggesting a down regulation of assimilation. Acclimation to high CO_2 was also observed by Baker et al. (1990 b) for rice grown in closed chambers.

Sink limitation and end product inhibition have being suggested as causes for photosynthetic acclimation (Azcon-Bieto, 1986 ; Neales and Incoll, 1978). Leaf starch accumulation in a high CO_2 concentration is a common phenomenon in field crops (Allen et al., 1988; Baker et al., 1989; Rowland-Bamford et al., 1990). However no conclusive evidence on photosynthetic inhibition by starch accumulation has been reported (Potter, 1980).

There was a nonlinear relationship between single leaf CO_2 assimilation, measured at its growth-CO_2 environment and average leaf N concentration (Fig. 3.1). The difference in assimilation between plants grown and measured at ambient CO_2 concentration (a/a) and plants grown and measured at elevated CO_2 concentration (e/e) increased as leaf N increased up to a leaf N concentration of about 2 - 2.5% N. The initial slope, which represents N use efficiency, was greater for leaves grown and measured at high CO_2, than for leaves grown and measured at ambient CO_2 (Fig. 3.1).

Some reports suggest that single leaf CO_2 assimilation in rice is linearly related to leaf N concentration per unit leaf area (Yoshida & Coronel 1976; Makino et al. 1988), but we observed a curvilinear relationship for rice grown at either elevated or ambient CO_2

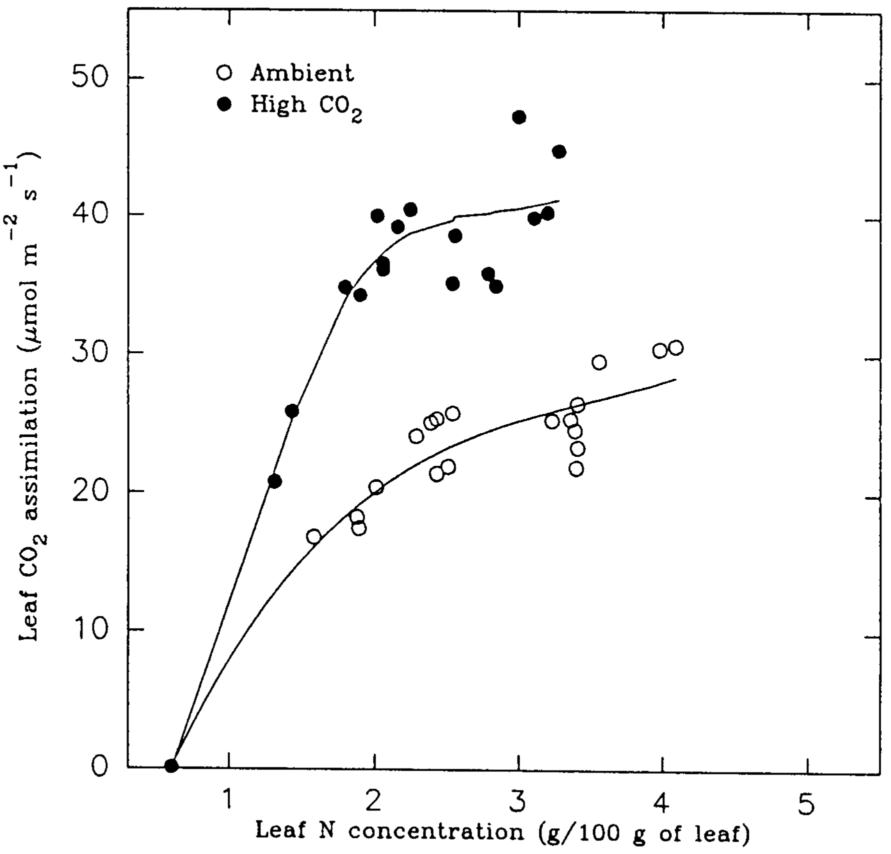

Figure 3.1. Light saturated single leaf CO_2 assimilation as a function of average leaf N for rice plants grown at high and ambient CO_2. Leaf N at zero assimilation was from Dingkuhn et al.(1992).

concentrations. This curvilinear relationship is similar to the relationship given in other reports for many species including rice (Sinclair and Horie, 1989; Takano and Tasunodo, 1977); *Spinacia oleracea* (Evans and Terashima, 1988); and wheat (*Triticum aestivum*, Evans, 1983). This relationship is possible because a substantial amount of leaf N is in the form of soluble chloroplast protein and thylakoid membrane proteins. Rice partitions about 28-37% of its leaf N into RuBP carboxylase (Makino et al., 1992). However, the exact percentage may vary with the growth environment. A strong correlation exists between RuBP carboxylase and pigment proteins with leaf N (Evans, 1989), which suggests that, under higher CO_2 concentrations, any increase in CO_2 assimilation will depend on the leaf N concentration. If leaf N concentration decreases below 2-2.5%, the decrease in leaf CO_2 assimilation was greater at high compared to ambient CO_2. Therefore, to achieve the full benefit of any future increases in CO_2 concentration, leaf N concentration in rice should be maintained at 2.5% or greater.

This also suggests that at lower leaf N, the biochemical limitations to CO_2 assimilation are greater at high than at ambient CO_2. If r_m is dependent on leaf N, then with an increase in leaf N, leaf CO_2 assimilation should increase and r_m should decrease. This was observed in this experiment as shown in Fig. 3.2. There was also a decrease in r_m with increased fertilizer N at all sampling days (Table 3.2). Therefore, it could be suggested that r_m is indeed dependent on leaf N.

A significant acclimation of rice leaves to prolonged exposure to high CO_2 should be an increase in leaf mesophyll resistance (r_m). Average r_m in this experiment was indeed greater in rice grown in high compared to ambient CO_2 concentrations (Table 3.2). The difference in r_m between treatments a/a and plants grown at ambient but measured at high CO_2 (a/e) gives the short term effects of CO_2 on biochemical and physical limitations. The difference in r_m between a/a and e/e gives the long term biochemical and physical limitations to CO_2 transfer after exposing to long term enrichment with CO_2. The difference between e/e and a/e should not be affected by short term effects. Thus, it should represent the long-term or adaptive effects of CO_2 enrichment on biochemical adjustments and limitations to CO_2 transfer. Therefore, it should be a measure of the amount of acclimation by rice to long term CO_2 enrichments. In this experiment, the r_m of e/e was significantly greater than that of a/e, suggesting a significant acclimation in rice to long term CO_2 enrichment. Mitchell and Hinckley (1993) observed a relationship between r_m and leaf N. Evans (1989) found that the activity of RuBP carboxylase decreased as r_m increased. Therefore, the increase in r_m which we observed at e/e could be a result of decreased RuBP carboxylase activity. Acclimation due to biochemical adjustments, therefore, could be partly due to a reduction in leaf protein complexes as decrease in leaf N with increased CO_2 concentration. As suggested by Ziska and Teramura (1992), if there is any up-regulation of RuBP and p_i at the expense of RuBP carboxylase under elevated CO_2 in an high CO_2 environment, where leaf N is lower, the activity of the RuBP carboxylase should decrease further, resulting in further down regulation of CO_2 assimilation with increased CO_2 concentration. Therefore, acclimation of rice plants to elevated CO_2 concentration could be mostly due to a decrease in leaf protein content with greater partitioning of plant N towards non-leafy parts and dilution of leaf N due to an increase in the non-structural carbohydrates which occurred after prolonged exposure to elevated CO_2 concentrations.

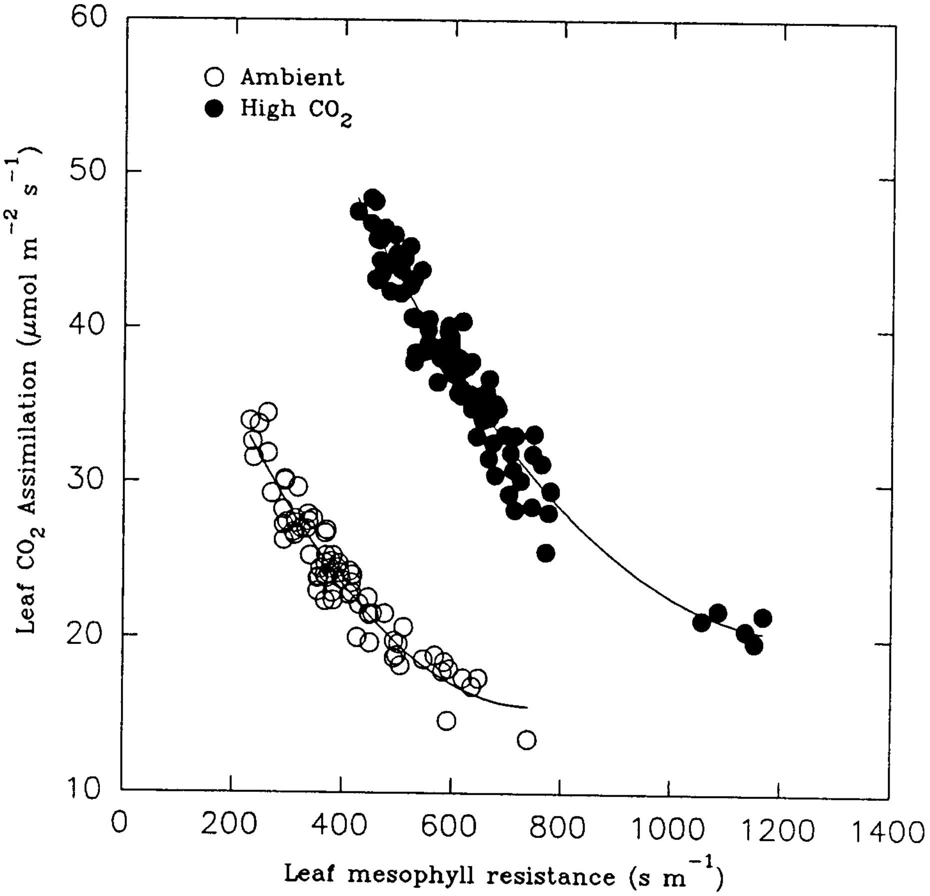

Figure 3.2. Relationship between leaf CO_2 assimilation and mesophyll resistance for rice plants grown at high and ambient CO_2 concentrations.

Table 3.2. Average leaf mesophyll resistance (r_m) and stomatal resistance (r_s) to CO_2 transfer for rice leaves. Stomatal resistance was measured from leaves grown and measured at both ambient (350 µmol mol^{-1}) and enriched (700 µmol mol^{-1}) CO_2 at different fertilizer nitrogen treatments. Mesophyll resistance was calculated using leaf CO_2 assimilation, boundary layer resistance (r_{bl}) and stomatal resistance for the same observations. Average boundary layer resistance for rice leaves inside the cuvette was measured as 1.03 s cm^{-1}.

Sampling Date	Nitrogen treatment	Mesophyll resistance (r_m, s cm^{-1})				Stomatal resistance (r_s, s cm^{-1})			
		grown at ambient CO_2		grown at enriched CO_2		grown at ambient CO_2		grown at enriched CO_2	
		measurement CO_2 (µmol mol^{-1})				measurement CO_2 (µmol mol^{-1})			
		350(a/a)	700(a/e)	350(e/a)	700(e/e)	350(a/a)	700(a/e)	350(e/a)	700(e/e)
19 DAP	N_0	4.34±0.30	6.27±0.24	7.65±0.46	5.36±0.26	0.29	0.41	0.62	0.37
	N_{90}	3.69±0.30	5.01±0.29	6.18±0.40	6.16±0.17	0.31	0.43	0.36	0.34
	N_{200}	2.82±0.28	4.48±0.24	3.81±0.23	4.80±0.15	0.37	0.34	0.50	0.45
39 DAP	N_0	6.17±0.83	7.92±0.34	14.5±0.73	10.4±0.36	0.62	0.53	1.41	0.91
	N_{90}	3.79±0.73	5.66±0.36	6.76±0.63	6.42±0.28	0.31	0.35	0.67	0.52
	N_{200}	3.66±0.58	5.23±0.23	5.45±0.58	6.19±0.31	0.33	0.38	0.65	0.58
64 DAP	N_{90}	4.72±0.43	5.74±0.39	6.48±0.49	6.55±0.28	0.30	0.42	0.49	0.40
74 DAP	N_{200}	3.91±0.23	5.11±0.18	4.78±0.26	5.82±0.19	0.40	0.51	0.57	0.46

Each mean ± SE (standard error) is an average of a minimum of five measurements.

Mesophyll resistance could also increase as a result of greater resistance of CO_2 transfer to the site of fixation. Increased CO_2 concentration increases leaf mesophyll thickness in soybean (Hofstra & Hesketh, 1975). Mesophyll resistance to CO_2 transfer is inversely proportional to the diffusion coefficient of CO_2 and the time to diffuse increases with the square of the distance (Parker, 1990). Therefore, apart from biochemical adjustments, physical barriers to CO_2 transfer could also result in a higher r_m in plants grown in high CO_2.

The increase in stomatal resistance (r_s) to CO_2 transfer with long-term enrichment of atmospheric CO_2 was negligible compared to the increase in mesophyll resistance (Table 3.2). However, this could have an important implication on rice grown under water scarce environments. Even under flooded conditions, it has been reported that canopy CO_2 assimilation of rice may decrease as a result of mid-day partial closure of stomates (Dingkuhn et al., 1990). O'Toole and Tomar (1982) have suggested that the transpiration in rice leaves is generally higher than in other upland species because of lower stomatal resistance. Therefore, increase r_s with increased atmospheric CO_2 could reduce excessive transpiration in lowland rice, thereby result in less mid-day closure of stomates.

Single Leaf Dark Respiration

Dark respiration rates measured at 2 h after sunset on the most recently fully expanded rice leaves at 49 and 57 DAP were significantly lower in plants in high compared to ambient CO_2 environments during vegetative growth (Table 3.3). Decrease in leaf respiration in rice during vegetative growth period with increased CO_2 concentration is consistent with the reports that prolonged exposure to elevated CO_2 decreases single leaf dark respiration (Amthor et al., 1992; Bunce, 1990; Gifford et al., 1985; Ziska and Bunce, 1994). However, at 66 and

74 DAP the differences in respiration between the growing environments were not significant (Table 3.3). The measurements on the 66 and 74 DAP were made on the fully emerged flag leaves. Plants were at early flowering stage at 66 DAP and grain filling stage at 74 DAP. There was no visible expansion growth of these leaves between these two periods. Thus the growth respiration could have been minimal.

The energy needed for resynthesis of protein on a leaf area basis may be reduced for plants grown under high compared to ambient CO_2 concentrations, if leaf N concentration on a leaf area basis decreases with increased CO_2 concentration. Therefore, with increased CO_2 concentration leaf respiration should decrease if there is a concomitant decrease in leaf N. In other words, leaf respiration may not be different for plants grown at ambient and high CO_2, when expressed on the basis of leaf N. We indeed observed that leaf respiration decreased with increased CO_2 concentration only when there was a significant decrease in leaf N. Furthermore, the respiration per g of leaf N was not different between high-and ambient CO_2-grown rice plants (Table 3.3). Leaf N was not measured at 49 DAP. However, measurements of leaf chlorophyll content using a leaf chlorophyll meter suggested a significant decrease in chlorophyll with increased CO_2 concentration, which indicates a decrease in leaf N. This further emphasizes that decreases in leaf dark respiration with increased CO_2 concentration were related to a decrease in leaf N. To further test that hypothesis, respiration of different leaves at 57 DAP were plotted against respective leaf N concentrations. There was a positive correlation between leaf dark respiration and leaf N concentration (Fig. 3.3), but there was no difference in the relationship between single leaf dark respiration and leaf N between the CO_2 environments at which plants were grown and measured. This suggests that any effect of CO_2 concentration on rice leaf respiration may be indirect, mediated by the CO_2 effect on leaf N.

Table 3.3. Average single leaf dark respiration for rice grown and measured at ambient (350 µmol mol^{-1}) and enriched (700 µmol mol^{-1}) CO_2 with N_{200}. Measurements were made about 2.5 hrs after sunset to avoid the higher initial CO_2 efflux.

Days after planting	Growth CO_2 conc.	Leaf dark respiration in µmol sec^{-1} on the basis of				
		m^{-2} leaf area	kg leaf dry weight	g leaf nitrogen	g leaf sugar	g leaf starch
49 DAP	350	0.745	-	-	-	-
	700	0.605	-	-	-	-
		*				
57 DAP	350	0.859	15.2	0.686	0.306	3.81
	700	0.662	11.1	0.613	0.163	0.92
		*	*	ns	*	*
66 DAP	350	0.691	12.8	0.392	0.190	2.15
	700	0.739	13.5	0.434	0.192	0.66
		ns	ns	ns	ns	*
74 DAP	350	0.642	11.2	0.389	0.195	1.42
	700	0.701	11.6	0.452	0.167	0.64
		ns	ns	ns	ns	ns

* The differences are statistically significant at $p<0.05$. ns - not significant.

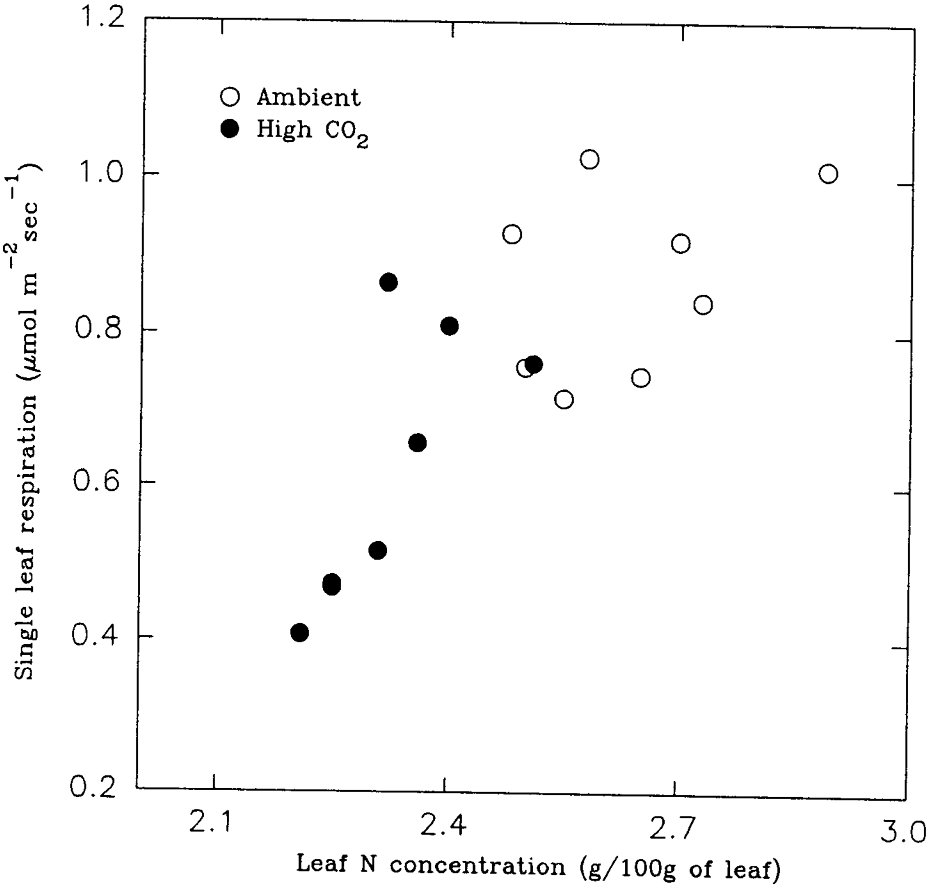

Figure 3.3. Single leaf dark respiration as a function of leaf N concentration at 57 DAP for rice plants grown at high and ambient CO_2 concentrations with high nitrogen fertilizer.

There was a significant increase in accumulation of starch and sugar in leaves of plants grown at high compared to ambient CO_2 (Table. 3.4). Accumulation of starch with increased CO_2 concentration has also been found in rice (Rowland-Bamford et al., 1990) and soybean (Allen et al. 1988). However, there was no observable relationship between leaf respiration of rice and the accumulation of starch or sugar concentration at either ambient or high CO_2. Despite the increase in leaf starch and sugar concentrations, leaf dark respiration decreased with increasing CO_2 concentration. Respiration on the basis of starch and sugar concentration of the leaves also decreased with increased CO_2 concentration (Table. 3.3), apparently due to very high buildup of these nonstructural carbohydrates at high CO_2. These findings contrast to some reports that plants grown at high CO_2 have higher leaf dark respiration because of increased availability of substrate. Thomas et al. (1993) found that, in Cotton (*Gossipium hirsutum*), with the enrichment of CO_2 the increase in leaf respiration appear to be related more closely to increase starch accumulation than to changes in leaf N concentration. Hrubec et al. (1985) and Thomas and Griffin (1994) observed a similar positive correlation between respiration rate and carbohydrate content in high-CO_2-adapted soybean plants.

The dependance of leaf respiration on leaf starch or total sugar content, in plants grown at high CO_2 concentration, as observed by many, could be an indirect effect. Amthor (1991) suggests that limitations imposed to *growth* respiration due to limited substrate levels diminishes with increasing CO_2 assimilation, while *maintenance* respiration is independent of the level of substrate. Azcon-Bieto and Osmand (1983) reported that, for wheat leaves, the rate of dark CO_2 efflux at ambient CO_2 was correlated with accumulated net CO_2 assimilation and increased leaf carbohydrate fraction. Leaf carbohydrate concentration is correlated with cumulative CO_2 assimilation for the day. Leaf CO_2 assimilation is also positively correlated

Table 3.4. Average leaf characteristics of rice leaves use for the respiratory measurements at both ambient (350 µmol mol^{-1}) and enriched (700 µmol mol^{-1}) CO_2 with N_{200}. Sampling to determine these leaf characteristics were done soon after the respiratory measurements.

Days after planting	Growth CO_2 concentration	Leaf N g m^{-2}	SLW g m^{-2}	Sugar mg g^{-1}	Starch mg g^{-1}	Leaf Temp. ^{0}C	Relative humidity (%)
57 DAP	350	1.25	56.2	49.8	4.0	26.8	70.5
	700	1.07	59.0	68.6	12.2	27.1	70.8
		*	ns	*	*	ns	ns
66 DAP	350	1.76	54.3	67.5	6.0	27.6	70.6
	700	1.70	55.2	70.6	20.6	27.4	70.9
		ns	ns	ns	*	ns	ns
74 DAP	350	1.65	57.9	57.2	7.9	26.8	72.0
	700	1.55	60.2	69.6	18.1	27.1	68.9
		ns	ns	*	*	ns	ns

* Differences are statistically significant $p<0.05$. ns-not significant.

with leaf N. If differences in carbohydrate content result from changing leaf N concentration, then the effect of carbohydrate on leaf dark respiration could be both direct and indirect. Direct effects would be through a limitation to respiration under conditions of reduced substrate. Indirect effects would be through lower leaf N concentration, which reduces the cost for synthesis since less synthesis occurs when leaf N content is low. However, if differences in substrate levels were achieved through different light intensities with the same level of N, then low substrate levels for respiration could be a direct limitation under lower light. Many growth chamber studies are done under lower photosynthetically active radiation, which could decrease the relative amount of substrate for subsequent dark respiration. Then leaf dark respiration could be related directly to the leaf carbohydrate concentration. Our study was conducted under natural sunlight in the field and leaf nonstructural carbohydrate increased as a result of increased CO_2 concentration. Thus, the level of substrate was not low enough to suppress the respiratory process at night.

Respiration and growth rates are positively correlated in many plant species. In our study, although respiration per unit leaf area decreased in high CO_2 grown plants, when respiration was expressed in terms of leaf N there was no difference, despite differences in growth rates between the growth-CO_2 environments. When substrate, O_2, and enzymes are not limiting, respiration is regulated by the regeneration of ADP or utilization of ATP (Amthor 1991). Increased CO_2 concentration increases the relative growth rate in rice, which requires more respiratory energy. The reason for observing a lower leaf respiration with increased relative growth rate at elevated CO_2 could be due to a decrease in leaf N. Increased CO_2 concentration increased buildup of carbohydrate rich compounds and caused the plant to partition a greater fraction of leaf N to less active stem and roots. Therefore, even when growth rate is high on a weight basis, the energy requirement is lower compared to a rice plant which has higher leaf N. This shows that leaf N concentrations could be the most important factor controlling leaf respiration. With the future increase in atmospheric CO_2 concentration, rice leaf dark respiration could possibly be higher, but only if leaves have ample N.

Canopy CO_2 assimilation

Canopy CO_2 assimilation was measured at 21, 43, 54 and 59 DAP. Canopy CO_2 assimilation was mainly dependent on leaf area, which in turn was dependent on absorbed N (Fig. 3.4). Unlike many other crop species, rice leaf area does not show any direct response to increased atmospheric CO_2 concentration. Increased N availability resulted in a larger LAI at initial stages of growth. However, that difference disappeared at latter stages of growth (Fig. 4.9 in Page 101). Therefore, the difference in canopy CO_2 assimilation with rice plants at high compare to ambient CO_2 was mainly dependent on the response at the single leaf level. Thus, it depends on leaf N and atmospheric CO_2 concentration. Therefore, any increase in canopy assimilation under high CO_2 is restricted to the plants which have higher leaf N. Dingkuhn et al. (1990) observed that rice canopy assimilation was limited by LAI during the vegetative stage, whereas leaf N concentration became limiting at full canopy closure. This was indeed what was observed at latter stages of growth in this experiment. Canopy CO_2 assimilation was greater at all N treatments in the high compared to ambient CO_2 at early stages of growth (Table 3.5). However, at later stages, increased canopy assimilation at high CO_2 was limited only to the N_{200} treatment. There was a limitation to assimilation by lower leaf N concentration at the lower N fertilizer rates. For example at 19 DAP we observed a significant increase in canopy CO_2 assimilation with increased CO_2 at all N levels, but at 43 and 54 DAP canopy CO_2 assimilation was not different between ambient and high CO_2 at N_0

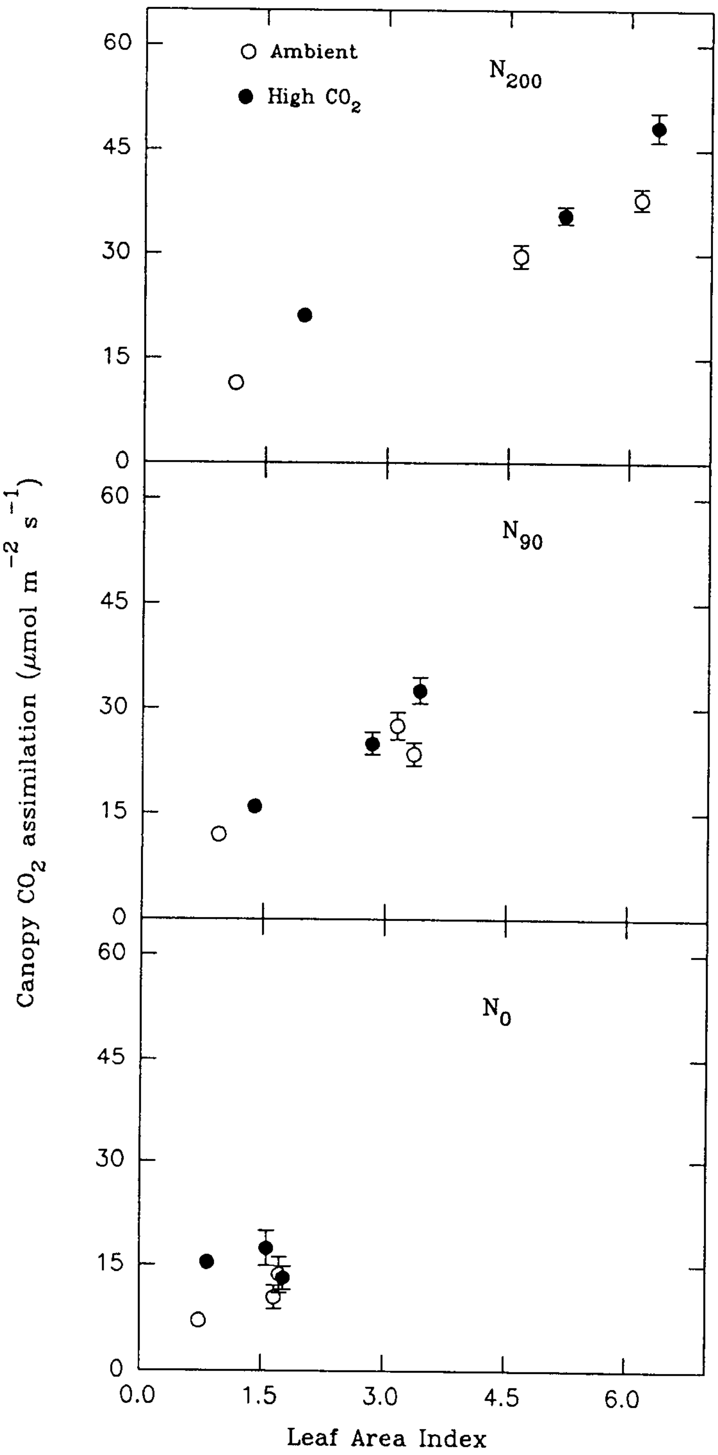

Figure 3.4. Canopy CO_2-assimilation as a function of LAI of rice plants grown continuously at high and ambient CO_2 concentration at three rates of N fertilizer.

Table 3.5. Average canopy CO_2 assimilation (μmol m^{-2} sec^{-1}) for rice grown and measured at ambient (350 μmol mol^{-1}) and enriched (700 μmol mol^{-1}) CO_2 with three different fertilizer nitrogen levels.

Date after planting	Growth CO_2 concentration	Canopy CO_2 assimilation (μmol m^{-2} sec^{-1})		
		N_0	N_{90}	N_{200}
21 DAP	350	7.12 a	11.3 a	11.4 a
	700	15.4 b	15.9 b	21.1 b
43 DAP	350	10.4 a	23.4 a	29.6 a
	700	12.7 a	24.6 a	34.3 b
54 DAP	350	13.6 a	26.9 a	35.8 a
59 DAP	700	17.4 a	32.6 a	48.3 b

Parameter values for a given N on the same day followed by a same letter are not significantly different at $P<0.05$ by DMRT.

and N_{90}. However, there was a difference at N_{200} (Table 3.5). At N_0 at high CO_2, there was no increase in canopy assimilation between 21 and 51 DAP, even with increased LAI from 0.83 to 1.56. However, leaf N concentration between these days decreased from 2.79 to 1.30. Therefore, at low N, despite increases in LAI, decreased leaf N impaired the canopy CO_2 assimilation. Thus, the response of rice canopy assimilation to high atmospheric CO_2 compared to ambient depends mainly on the level of N concentration of the plant.

Absolute values of the canopy CO_2 assimilation were consistent with data reported by Dingkuhn et al. (1990) for similar CO_2 concentration. However, there was a remarkable decrease in canopy assimilation when compared with single leaf assimilation. For example, with ambient CO_2 and N_0, canopy assimilation, on the basis of ground area at 43 DAP with LAI of 1.65 was 39% smaller than single leaf assimilation on the basis of leaf area at 39 DAP. This could be partly due to a limited LAI at that stage of plant growth and to decreased leaf N in the older leaves of the canopy. Our measurements on leaf assimilation were based on the most recently matured leaves, which were relatively higher in N. In the canopy however, leaves at the bottom layers might have no net CO_2 assimilation, due both to shade and aging. In fact, they could be parasitic to the plant. Respiration by the non leafy parts also contributed to the decrease in canopy assimilation, which was not included in the single leaf assimilation. We observed a similar response even at N_{200}, but the magnitude of the difference was small.

The percentage increase in leaf CO_2 assimilation at high compared to ambient CO_2 concentration was also greater when compared with the canopy assimilation. For example, at N_0 there was an increase in assimilation at high compared to ambient CO_2 at the leaf level of 31% at 39 DAP but at canopy level it was 22%. The corresponding values at N_{200} were 44% and 16%. This shows that the greater increase observed in single leaf CO_2 assimilation at high compared to ambient CO_2 may not be realized at the canopy level. It is certainly true that leaf assimilation cannot be directly compared with canopy assimilation, due to shading of leaves in the canopy, respiration by non leafy organs, and changes in the N profile of the canopy. However, it could be suggested that the potential increase in CO_2 assimilation with increased CO_2 concentration, which is observed in individual leaves at the top of the canopy may not be realized at whole canopy level.

Canopy respiration

Canopy dark respiration was measured at 42 DAP, in N_0 and N_{200} treatments, representing the stage of maximum tillering and at 58 DAP in N_{200} treatment, at the late booting stage, with high and ambient CO_2 concentrations. No canopy respiratory measurements were made after 58 DAP, to prevent any physical damage to the flowering and panicle bearing plants. From the single leaf dark respiration data, one may think that there will be a decrease in the dark respiration in rice canopies at high compared to ambient CO_2 environments. This was, however, not realized in this field experiment. We observed either a similar rate or an insignificant increase in canopy dark respiration at high compared to ambient CO_2, showing that an understanding of leaf respiration alone is not enough to predict the response of a rice crop canopy respiration to CO_2. With N_{200} there was a numerical increase in canopy dark respiration by 14-17 % with high compared to ambient CO_2 (Table. 3.6). Certainly there was no decrease at high CO_2 as observed at leaf level. Leaf respiration was 23% lower at high compared to ambient CO_2. Similar increases in canopy dark respiration with increased CO_2 concentration were reported by Baker et al. (1992). However, absolute

Table 3.6. Average canopy dark respiration (μmol m^{-2} sec^{-1}) for rice grown and measured at ambient (350 μmol mol^{-1}) and enriched (700 μmol mol^{-1}) CO_2 at 42 DAP and 58 DAP. Measurements were made about 2.5 hrs after sunset to avoid the high initial CO_2 efflux. The values were not corrected for the possible CO_2 efflux through the flood water which appears to be same and small for all treatments.

Days after planting	Growth CO_2 conc.	Applied N conc.	Basis of measurement					
			Area (μmol m^{-2} sec^{-1})		Nitrogen (μmol g^{-1} sec^{-1})		Dry weight (μmol kg^{-1} sec^{-1})	
			Ground	Leaf	Above ground	Leaf	Above ground	Leaf
42 DAP	350	low N	2.76	1.67	1.11	1.81	9.78	32.2
	700	low N	2.78	1.60	1.13	2.13	7.45	28.9
			ns	ns	ns	*	*	ns
42 DAP	350	High N	5.90	1.27	0.54	0.83	11.9	26.2
	700	High N	6.73	1.30	0.57	0.93	9.53	27.0
			ns	ns	ns	ns	*	ns
58 DAP	350	High N	6.79	1.10	0.59	0.85	8.98	23.3
	700	High N	7.93	1.25	0.68	1.12	8.19	26.0
			ns	ns	ns	*	ns	ns

* differences are statistically significant at $p<0.05$. ns- not significant

values reported by Baker et al. (1992) were greater than those we observed in our experiment. This could be partly due to the difference in canopy size and the growth environment.

When canopy dark respiration was expressed on the basis of total leaf area, leaf biomass and total above ground N there was also no significant increase in with increased CO_2 concentration (Table 3.6). This was possibly because increased atmospheric CO_2 concentration has little effect on those growth variables (Table 3.7). Canopy dark respiration on the basis of ground area, increased with the total above ground N, and growth CO_2 concentration had no influence on that relationship (Fig. 3.5). This further suggests that, even at the canopy level, CO_2 concentration has no direct influence on respiration.

When canopy respiration was expressed on the basis of total above ground biomass there was a decrease in respiration with increased CO_2 concentration (Table 3.6). Decreased canopy dark respiration at high CO_2 on the basis of above-ground dry matter in rice at high CO_2 concentrations resulted mainly from increases in leaf sheaths and stems, but with similar leaf biomass which had a lower N concentration. This emphasizes that interpretation of whole plant canopy respiration could vary depending on how the analysis is done. Our data suggest that it should be reported either on the basis of ground area or plant total N.

Canopy respiration increases as the canopy grows and with the change in physiological state of the canopy. Dingkuhn et al. (1990) found that the respiration of a rice canopy was less than 10% of the day time CO_2 uptake during vegetative growth, but increased up to 20-25% of the daytime assimilation during reproductive growth. Yamaguchi (1978) and Yoshida (1971) estimated that about 40% of the daily gross C gain for rice was lost through respiration during night and that was even higher during ripening. Our estimates of net CO_2 loss through dark respiration showed an increase with decreasing N, mainly because of decreased assimilation. At higher fertilizer N concentrations, the instantaneous respiration was about

Table 3.7. Characteristics of rice canopies used for measuring canopy respiration. Destructive measurements were made 2-4 days after the respiratory measurements.

Days after planting	Growth CO_2 concentration	Nitrogen concentration	Leaf area index	Total above ground biomass (g m^{-2})	Total above ground N (g m^{-2})	Total leaf N (g m^{-2})	N allocated to leaf (%)
42 DAP	350	N_0	1.65	282	2.5	1.52	61.2
	700	N_0	1.73	373	2.5	1.30	53.1
			ns	*	ns	ns	*
42 DAP	350	N_{200}	5.07	494	10.8	7.06	65.2
	700	N_{200}	5.19	706	12.0	7.28	60.6
			ns	*	ns	ns	*
58 DAP	350	N_{200}	6.13	756	11.4	8.00	69.9
	700	N_{200}	6.34	968	11.6	7.10	60.9
			ns	*	ns	ns	*

* differences are statistically significant at $p<0.05$. ns - not significant

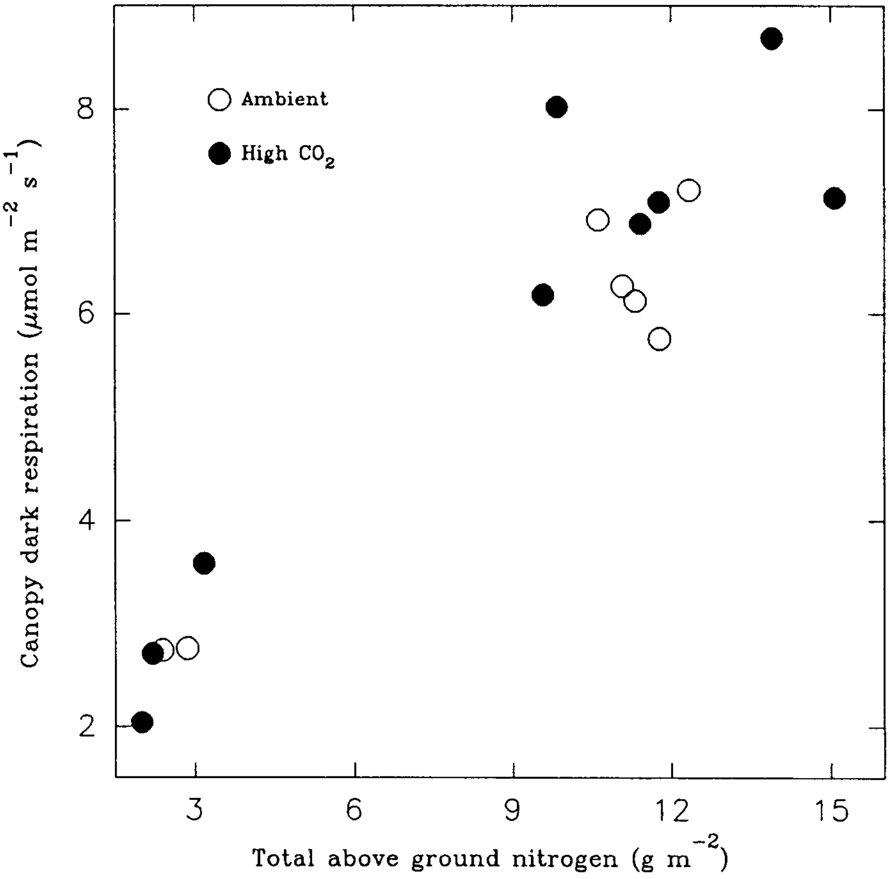

Figure 3.5. Canopy dark respiration as a function of total above ground N for rice plants grown continuously at high and ambient CO_2 concentration.

19% of mid day assimilation at 42 DAP and there was no difference between growth CO_2 concentrations. Despite the increase in respiration as a result of increased biomass and change in stage of development, which demands more translocation at 58 DAP, there was a decrease in relative respiration at high CO_2 concentration. Assimilate loss through respiration at ambient CO_2 remained 19%. This decrease in loss of assimilates through respiration just before flowering was due to greater assimilation compared to respiration in the high CO_2 compared to ambient.

Increase canopy dark respiration with increased CO_2 concentration was expected at high N treatments. Increased atmospheric CO_2 concentration increased plant growth rates, which required greater energy. Thus there should be an increase in canopy respiration. Surprisingly however, the increase in respiration was not proportional to increase in growth rate of plants at the high compared to ambient CO_2. When expressed on the basis of total leaf N, canopy dark respiration increased with increased CO_2 concentration. That means either there should be an increase in leaf respiration per unit leaf N or the respiration in other non-leafy parts increased. We observed no increase in single leaf respiration on the basis of leaf N and a decrease on the basis of leaf area. Therefore the respiration of non-leafy parts must have increased. This could be due to a change in partitioning of N. There was a numerical increase in total above-ground-plant N at high compared to ambient CO_2. However, the proportion of N allocated to leaves decreased, resulting in a decrease in the total leaf N pool. Nitrogen that is translocated is partly stored in the sheaths and stems which could lead to an increase in sheath and stem respiration. However, these reserves require less maintenance (Penning de vries et al., 1989). Therefore, the magnitude of increase in canopy respiration should be lower compared to a similar increases in leaf N. The ultimate response is a relatively similar canopy respiration rates at high and ambient CO_2 because respiratory needs have changed. Plants with high leaf N, and lower leaf sheath and culm biomass, such as plants grown at ambient CO_2, had relatively higher maintenance respiration requirements than plants with lower leaf N and higher leaf sheath and culm biomass grown in high CO_2. This shows that there could be a change in energy requirement for maintenance under higher CO_2 concentrations. Another possibility is that, with increased energy demand, the respiratory mechanism is more efficient in plants grown at high compared to ambient CO_2 concentration.

Summary and Conclusions

Single leaf CO_2 assimilation increased with increased atmospheric CO_2 concentration. However, there was an acclimation of leaves to prolong exposure to high atmospheric CO_2. Leaf mesophyll resistance of rice leaves grown at ambient and measured at high CO_2 was lower than leaves grown and measured at high $CO_{2,}$ suggesting acclimation at the biochemical level. Leaf mesophyll resistance decreased with increased fertilizer N. There was also a decrease in leaf N with increased CO_2 concentration. The acclimation of rice leaves to high atmospheric CO_2 was, therefore, mostly related to a decrease in leaf N at high CO_2 compared to ambient.

There was a curvilinear relationship between single leaf CO_2 assimilation and average leaf N concentration. N use efficiency in terms of leaf CO_2 assimilation increased with increased CO_2 concentration. The critical N concentration was about 2-2.5% , and any decrease in leaf N below critical limited the response of leaves to high CO_2. Therefore, with the increased CO_2 concentration, to maximize the leaf CO_2 assimilation dilution of leaf N should be minimized and it should be maintained above the critical.

Stomatal resistance increased with increased CO_2 concentration but the magnitude of difference was much less than that of mesophyll resistance. Therefore, increased stomatal resistance had an insignificant effect on leaf CO_2 assimilation. However, change in r_s due to CO_2 could have a significant effect on controlling leaf transpiration at midday in rice.

Canopy CO_2 assimilation increased with increased atmospheric CO_2. However, the magnitude of the response depended on the rates of fertilizer N. There was no increase in canopy CO_2 assimilation with increased atmospheric CO_2 at low N levels, suggesting that decreased leaf N at elevated CO_2 impaired the leaf photosynthetic functions, making leaves were less efficient in utilizing absorbed radiation. Therefore, the beneficial effects of increased CO_2 on rice may not be realized at lower rates of fertilizer N.

Single leaf respiration decreased with increased atmospheric CO_2 concentration when there was a decrease in leaf N. Also there was also no increase in single leaf respiration with increased total nonstructural carbohydrates, indicating that substrate for respiration was not limiting either in both ambient and high CO_2. There was no difference in single leaf respiration per gram of leaf N between high and ambient CO_2, suggesting that leaf respiration was dependent more on leaf N than on CO_2 concentration or substrate level. Therefore, the decrease in leaf respiration at high CO_2 compared to ambient could be related to the decrease in cost for maintenance and growth of leaves with decreased leaf N. However, this decrease in leaf respiration was not reflected at the canopy level. The canopy respiration was either not different or was greater at high compared to ambient CO_2, but it was not proportional to the growth enhancement at elevated CO_2. This suggests that there is a decrease in respiratory cost at high compared to ambient CO_2. This could be due to the decrease in partitioning of N to the leaves and increased partitioning to the metabolically less active stems and sheaths at high compared to ambient CO_2

The instantaneous respiratory loss was about 19% of the amount of assimilates fixed in mid day during the vegetative period. At late booting stage, because of greater uptake of CO_2 by plants grown at high CO_2 concentration, respiratory loss decreased at high CO_2, while it remained the same at ambient. Therefore, with the anticipated future increase in atmospheric CO_2 concentration there will not be a decrease in net CO_2 uptake by rice plans; rather, it will increase.

CHAPTER 4

THE EFFECTS OF INCREASED ATMOSPHERIC CO_2 CONCENTRATION ON GROWTH AND DEVELOPMENT OF RICE (*Oryza sativa* L.)

Introduction

The Mauna Loa observatory record shows a 12 % increase in mean annual atmospheric CO_2 concentration over the past 32 years, from 316 µmol mol^{-1} in 1959 to 354 µmol mol^{-1} in 1990 (Keeling and Whorf, 1992). Increased atmospheric CO_2 concentration is generally beneficial for terrestrial plants (Cure and Acock, 1986; Kimball, 1983; Lawlor and Mitchell, 1991), and the benefits are greater for C_3 than C_4 species (Lawlor and Mitchell, 1991). A substantial body of literature on the effect of CO_2 concentration on growth and development of crop species from green house and laboratory experiments exists. However, little attention has been directed at the response of tropical plants (Hogan et al., 1991). Few data are available on the response of rice to increased CO_2 concentration under tropical field conditions.

Temperature and photoperiod drive plant developmental process (Cao and Moss, 1994; Klepper et al., 1984; and Summerfield et al., 1992). Thermal-time requirements for successive leaf initiation on the main culm, the phyllochron, increase slightly with extreme water stress in wheat (*Triticum aestivum* L.; Cuforth et al., 1992; Schonfeld et al., 1989) or N deficiency in wheat (Longnecker et al., 1993) and barley (*Hordeum vulgare* L.; Dale and Wilson, 1978). However, Bauer et al. (1984) and Davidson and Campbell (1983) found no effect of N on phyllochron interval in wheat. Increased CO_2 concentrations have been reported to enhance the rate of leaf appearance in rice (Baker et al., 1992; Manalo et al., 1994), soybean (*Glycine max* L. Merr.; Baker et al., 1989; Cure et al., 1989), wheat (Schonfeld et al., 1989), and in some weed species (Tremmel and Patterson, 1994), and hasten flowering in wheat (Goudriaan and de Ruiter, 1983), cowpea (*Vigna unguiculata* L.; Biswas and Hileman, 1985), and rice (Imai et al., 1985; Seneweera et al., 1994). However, no direct effect of increased CO_2 concentration on timing of the developmental processes were reported in wheat (Mohapatra, 1990) or soybean (Havelka et al., 1984; Rogers et al., 1986). Tremmel and Patterson (1994) suggested that development response to increased CO_2 concentration depends on species.

Elevated CO_2 concentration decreases transpiration in rice (Baker et al., 1990a; Imai and Murata, 1976) and soybean (Valle et al., 1985), which could increase leaf temperature and thereby increase the rate of leaf initiation and emergence. Decreased leaf N, which is commonly observed in plants exposed to elevated CO_2 concentrations, could reduce the rate of leaf elongation within the leaf sheath after leaf initiation, and thus reduce the rate of leaf appearance. Increased canopy density through increased tillering in rice at high CO_2 concentrations could increase plant height (Imai et al., 1985; Manalo et al., 1994). Therefore, appearance of successive leaves may be delayed. Thus, reported changes in developmental rates with increased CO_2 concentration do not necessarily imply a direct effect of increased CO_2 concentration on developmental processes.

Productivity of field crops is seldom limited by a single factor, as is suggested by Liebig's law of the minimum. Rather, many factors affect production simultaneously and the marginal return from each limiting factor in combination gives the ultimate response (Sinclair, 1992). Therefore, factors such as availability of nutrients could limit the response of plants to increased CO_2 concentration.

Increased dry matter accumulation in plants grown under elevated CO_2 concentration is frequently accompanied by a lower concentration of tissue N (Allen et al., 1988; Baker et al., 1990; Wong, 1979). An increase in concentration of total nonstructural carbohydrate with an increase in CO_2 concentration has also been documented in soybean (Allen et al.,1988) and in rice (Rowland-Bamford et al., 1990). Therefore, structural growth under conditions of high atmospheric CO_2 may be limited by lack of N. Growth enhancement of many crop species at elevated CO_2 concentration occurs if the plants have ample N supply (Bazzaz et al., 1990; Imai and Murata, 1978; Williams et al., 1981; Wong, 1979). Moreover, increased root density with increased CO_2 concentration (Baker et al., 1990; Curtis et al., 1990; Imai et al., 1985; Ziska and Teramura, 1992) could exploit a greater soil volume. Therefore, fertilizer N recovery from the soil could be greater under high atmospheric CO_2 concentration, and the fertilizer N requirement per unit plant biomass at high CO_2 concentrations may not be as great as one might expect, because of more efficient recovery from soil.

Rice responds to superambient CO_2 concentration through increased tillering and more leaves per hill, with little or no increase in total leaf area, due to decrease size of individual leaves (Baker et al., 1990b; Imai et al., 1978; Ziska and Teramura, 1992). However, with limited N supply under tropical field situations, increase in tiller numbers may not increase panicle numbers, because N deficiency at latter stages of growth causes tiller abortion. Ample N and assimilate supply decrease the degradation of spikelets (Matsushima, 1980). An increased CO_2 concentration increases plant assimilate supply. However, at elevated CO_2 concentrations plant N content is diluted by greater biomass production and one may expect an interaction between CO_2 concentration and plant N content on final spikelet number.

No study has been reported on growth and development of rice at elevated CO_2 concentration in tropical field conditions. We studied the effects on rice of elevated CO_2 concentration at different levels of N nutrition in the field in the tropics with the objective of quantifying vegetative and reproductive development, fertilizer N recovery, and the partitioning of biomass and N among plant organs.

Materials and Methods.

Two field experiments were conducted, one during July to October 1993 ('93 wet season) and the second from March to June 1994 ('94 dry season) at the wetland research field of the International Rice Research Institute (IRRI), Los Banos, Philippines (15°N, 121°E). In both experiments, a randomized complete block design was used with three replications. Treatments consisted of factorial combination of two concentrations of CO_2, ambient and elevated (600 μmol mol^{-1} in the '93 wet season; 700 μmol mol^{-1} in the '94 dry season), and three rates of N fertilizer application, 0 (N_0), 50 (N_{50}), and 100 kg N ha^{-1} (N_{100}) in '93 wet season, and 0 N (N_0), 90 (N_{90}), and 200 (N_{200}) kg N ha^{-1} in the 94 dry season. The experimental unit was one open-top chamber, with a ground area of 3.3 m^2. The chamber, control systems and the data acquisition systems were described on page 34.

Plant culture

A short-stature rice cultivar, IR72, was transplanted in each chamber at 3 seedlings per hill, with a hill spacing of 20 by 20 cm. Seedlings for the 93 wet season were raised in a wetbed nursery and transplanted 21 days after seeding. In the 94 dry season, seedlings were raised at the treatment CO_2 concentration inside open top chambers on seedling trays and transplanted at 14 days. In both years, field was drained after planting for two days and there after water level was gradually raised to about 5-7 cm and kept throughout the study. Replanting of missing hills was done after 3 days in the 93 wet season. Replanting was not necessary for the 94 dry season.

Fertilizer N, P, and K applications are given in Table 4.1. Since the soil is rich in P and K no fertilizer P or K were given in the 93 wet season. In the 93 wet season leaf N became diluted in high CO_2 regimes. Therefore, N application for the 94 dry season was based on leaf chlorophyll values of intact leaves measured using a SPAD 502 (Soil-plant analysis development, Minolta Camera Co., Osaka, Japan). The SPAD 502 provides an indication of relative amount of chlorophyll present in leaves based on the transmission of radiation through leaves at approximately wavelengths of 650 nm and 940 nm. Leaf N concentration of rice is linearly related to SPAD values adjusted for specific leaf weight (Peng et al., 1993). Leaf SPAD readings were taken every 6-7 days, beginning 21 DAP. The minimum SPAD value for the highest N treatment (N_{200}) was set at 37 ± 1. When there was a decrease in average SPAD reading below the set value, fertilizer N was applied based on the following N uptake curve for IR72 for a typical dry season at IRRI (Cassman, unpublished 1994, IRRI).

$$Nuptake = 196 - 200 * \exp(-1.1(10^{-6}) * CUDD^{1.99})$$

CUDD = cumulative degree days.

We assumed that fertilizer N recovery by the rice crop is 50%. When there was a decrease in average SPAD reading, an amount of N to be applied for the N_{200} treatment for the next 14 d was calculated and applied, based on long-term temperature data for the same site. The N applied to the medium N treatment was half that applied to the N_{200} treatment, except at maximum tillering. At the maximum tillering we observed a large decrease in SPAD reading in the N_{200} treatment. Therefore, an additional application of 20 kg of N ha^{-1} was given. Weeds were controlled by hand pulling, and insect and decease control followed standard recommendations.

Table 4.1. Schedule of fertilizer nitrogen (N), phosphorus (P) and potassium (K) applied during 93 wet season and 94 dry season. No P and K fertilizer were applied during 93 wet season.

93 Wet season			94 Dry season				
Days after planting (DAP)	Nitrogen (kg ha^{-1})		Days after planting (DAP)	Nitrogen (kg ha^{-1})		Phosphorus (kg ha^{-1})	Potassium (kg ha^{-1})
	Medium	High		Medium	High		
0 DAP	25 (u)*	25 (u)	0 DAP	30 (a)	60 (a)	30	60
21 DAP	-	25 (a)	24 DAP	15 (a)	30 (a)	-	-
41 DAP	25 (a)	25 (a)	37 DAP	25 (u)	70 (u)	-	-
55 DAP	-	25 (a)	60 DAP	20 (a)	40 (a)	-	-
Total	50	100		90	200	-	-

*u=Urea, a=Ammonium sulphate.

Plant sampling

Plants were destructively sampled between 8:00 to 10:00 am at 19, 35, 49, 56, 67, 82, and 92 (final harvest) days after transplanting (DAP) in the 93 wet season and 22, 44, 56, 67, and 77 DAP in the 94 dry season. At least 4 hills were sampled each time, by manually pulling to recover as many roots as possible. Sampled hills were replaced immediately with similar sized plants taken from border plots outside chambers to minimize the shading effect on the remaining plants. Samples were kept in an ice chest until processing, which was done later on the same day.

Plant samples were analyzed for tiller number, leaf area (using an automatic leaf area meter, Hayashi Denko, Tokyo, Japan), and dry matter (leaf, sheath, culm, root, and panicle). Roots were washed carefully, separated, and dried. Tissue dry weights were determined after drying for 72 hrs at a constant temperature of 70^0 C. Tissue total N content was determined by the micro-Kjeldahl method. A root sampling devise was used on two hills per each chamber on one sampling date. The sampler was a 45 cm tall 20 cm diameter cylindrical tube with a beveled edge at the bottom. The sampler was placed on the soil encircling one hill and driven into the soil to a depth of 30 cm. The sampler was then removed carefully, with the soil, using a mechanical puller. Roots were separated by washing away the soil. Root dry weight from the sampler was always less than that recovered by pulling sowing no advantage of using the root sampler compared to manual pulling. Therefore, reported data are from the pulled samples.

In the '93 wet season, plants were damaged by a typhoon just before the harvest, which caused heavy shattering. During the 94 dry season, we removed the crop from the field at grain filling. However, a few hills were maintained inside each chamber until maturity.

Therefore, we do not have reliable yield data for either seasons. Grain N concentration for 94 dry season was measured on those selected hills left in each chamber.

Measurement of phenological development.

Leaf number on the main culm using the Haun scale (Haun, 1973) were recorded every 5-7 days, beginning 21 DAP. Three uniform, healthy plants from the middle of each chamber were labeled, and visual leaf appearance rate based on the previously fully developed leaf was recorded until maturation of the flag leaf. Flowering was determined using 12 hills in the middle of each chamber. Appearance of the first flower of each hill was recorded every morning until at least one plant in 50% of the hills had flowered.

Two way analysis of variance was performed using STATGRAPHICS statistical graphics system. Mean comparison were made using LSD at $P<0.05$.

Results and Discussion

Average day time CO_2 concentration inside the open top chambers for the 93 wet and 94 dry seasons are given in Fig. 4.1. Average daily CO_2 concentration in three of the nine high CO_2 chambers during the 93 wet season varied widely with a deviation above ± 40 µmol mol^{-1}. Therefore, those three chambers were treated as missing plots. Daily total solar radiation, maximum and minimum temperatures and vapor pressure deficit are given in Fig. 4.2. Cumulative solar radiation as a function of cumulative thermal time for the two growing seasons is given in Fig. 4.3.

N uptake

Total N uptake by rice plants grown at different concentrations of CO_2 and fertilizer N during the '93 wet and '94 dry seasons are given in Table 4.2. The N uptake increased with increased CO_2 concentration when fertilizer N was available, but not in the zero fertilizer N treatment. Interactions between CO_2 concentration and fertilizer N were significant only during early and latter stages of growth (Table 4.2). Decrease in total N uptake by rice plants during latter stages of growth in the N_0 treatment, at elevated CO_2 compared with ambient could be because of greater senescence during latter stages of growth in the high CO_2 atmosphere, leading to loss of plant tissue before sampling. Greater N uptake during initial stages of plant growth in the high CO_2 concentration resulted in higher biomass accumulation. In the N_0 treatment, there was a higher rate of senescence in elevated than in ambient CO_2 treatment could be due to greater depletion of soil N supply at high CO_2 during latter stage of growth. During the 93 wet season, total N uptake was much less than that during the 94 dry season. Therefore, the magnitude of difference in N uptake between ambient and high CO_2

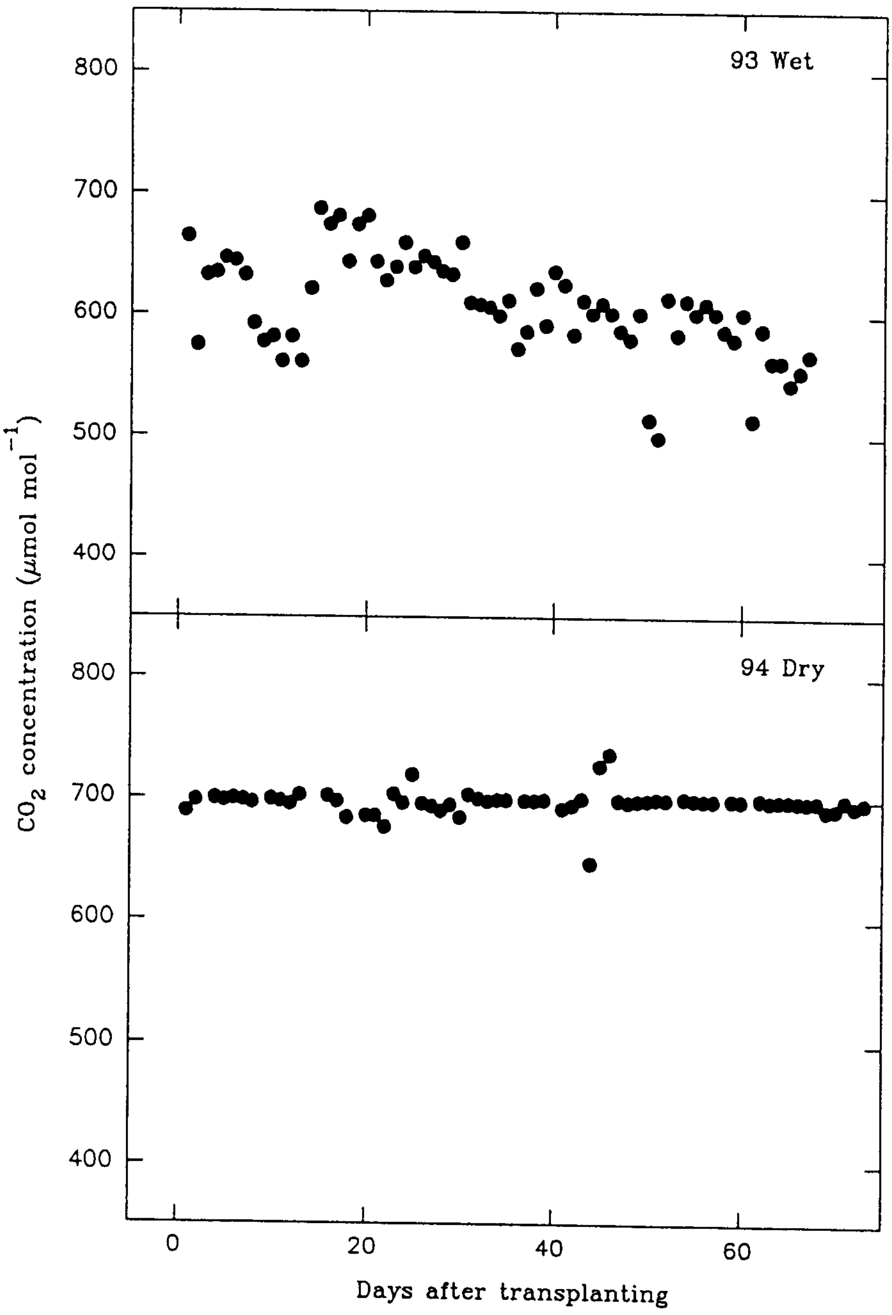

Figure 4.1. Daily average day time carbon dioxide concentration inside open top chambers during the 93 wet and 94 dry seasons.

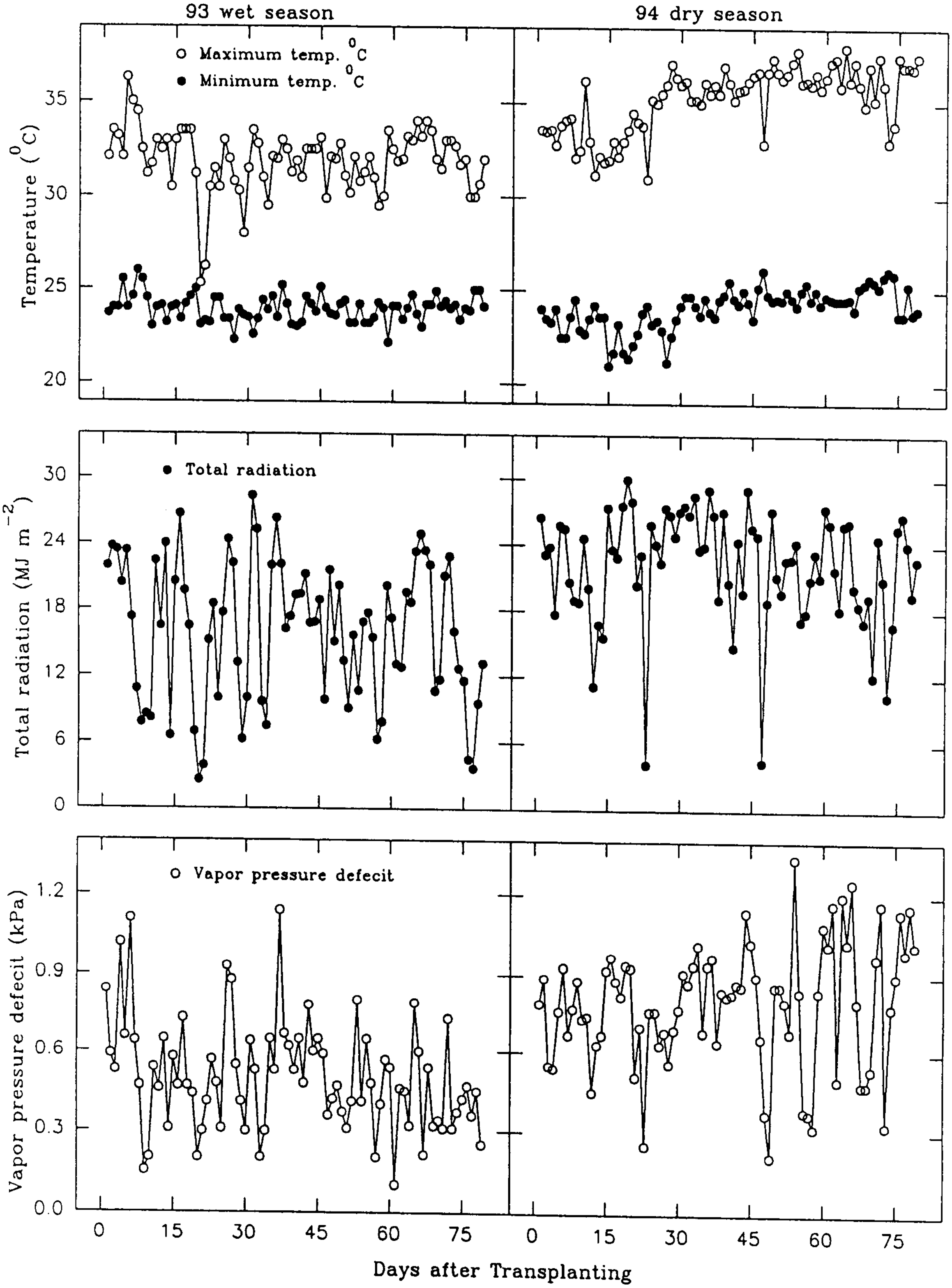

Figure 4.2. Daily maximum and minimum air temperature, solar radiation and vapor pressure deficit during the 93 wet and the 94 dry season.

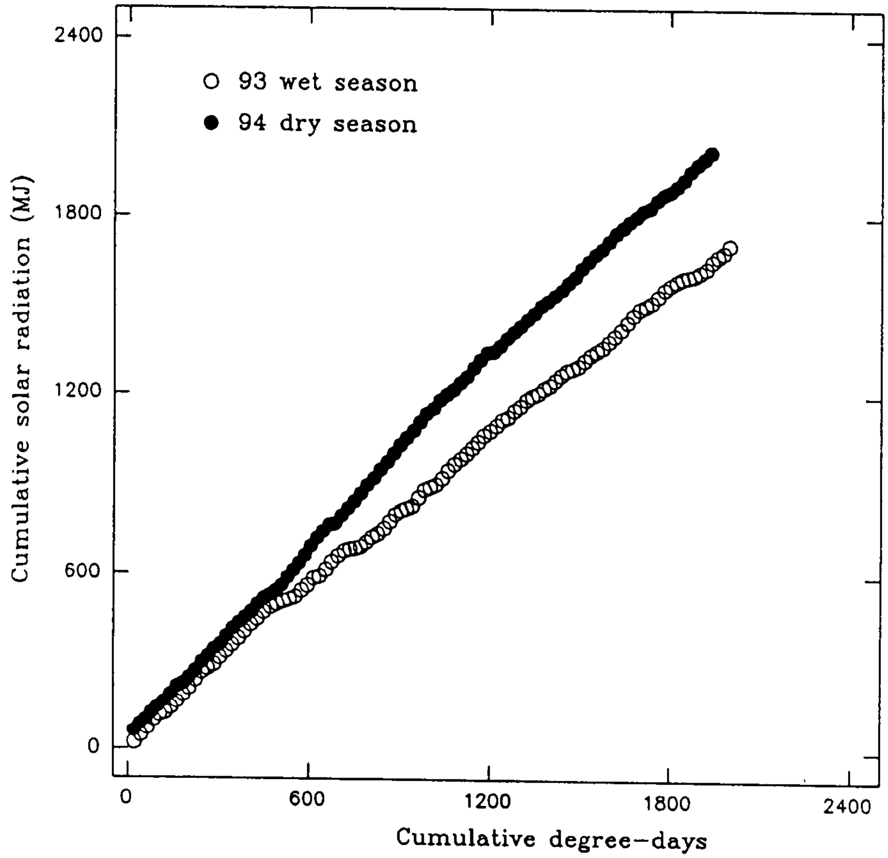

Figure 4.3. Cumulative solar radiation as a function of cumulative degree-days for the 93 wet and 94 dry seasons at the experimental site. Cumulative degree-days was calculated as the sum of average temperature minus base temperature (8° C).

Table 4.2. Total N uptake of rice IR72 grown in open top chambers during the 94 dry season at ambient or high CO_2 at varying rates of N fertilization.

CO_2 concentration	Fertilizer N	Total N uptake (g m^{-2})						
		94 Dry season				93 Wet season		
		22 DAP	42 DAP	55 DAP	67 DAP	19 DAP	49 DAP	82 DAP
Ambient	N_0	1.41	2.90	3.21	3.83	0.67	2.27	4.34
	N_{med}	1.77	6.46	5.67	7.90	0.55	4.38	6.00
	N_{high}	2.23	11.5	12.3	12.1	0.48	3.71	8.45
High CO_2	N_0	1.52	2.93	2.78	3.00	0.85	2.39	4.08
	N_{med}	2.38	6.39	6.41	8.84	0.77	4.28	5.63
	N_{high}	3.72	12.9	12.8	14.3	0.84	4.40	8.65
	SE_{CO2}	0.13	ns	ns	0.26	0.12	0.15	ns
	SE_N	0.10	0.61	0.35	0.33	ns	0.21	0.42
	SE_{CO2xN}	0.18	ns	ns	0.46	ns	0.28	ns

ns - not significant at $p<0.05$, SE-standard error for the difference in mean. N_0 - no applied N, N_{med}= N_{50} and N_{90} and N_{high}= N_{100} and N_{200} for the 93 wet and 94 dry seasons respectively.

was also less in the 93 wet season. This lower uptake could be related to lower radiation and temperature and lower N fertilizer inputs. Loss of fertilizer N from the soil also could have been high in the 93 wet season due to typhoons which may have caused runoff and leaching losses.

Relative N uptake rate (RNUR) in the 94 dry season increased with increased CO_2 concentration during the early exponential growth (planting to 22 DAP). However, from 22 to 43 DAP, RNUR at high CO_2 was lower than that at ambient CO_2 (Table 4.3). Decrease in RNUR at 22 to 43 DAP at high CO_2 suggests that soil N supply was limiting, and that rice plants grown at elevated CO_2 had a greater ability to extract soil N and deplete the soil N supply than that of ambient. Greater root density in the elevated CO_2 treatment would allow exploitation of a larger soil volume, and thereby increase RNUR. Rapid N uptake in high CO_2-grown rice had a significant effect on total fertilizer N recovery. Recovery of N from fertilizer was greater at high than at ambient CO_2. For example, the fertilizer N recovery at N_{200} treatment during 94 dry season was about 57% by plants at ambient CO_2 while it was to 62% by plants at high CO_2 (Fig. 4.4). Lower N recovery at ambient CO_2 could be mainly due to increased losses in fertilizer N because of delay in uptake compared to the plants at high CO_2. This supports the findings of Coleman and Bazzaz (1992) and Hocking and Meyer (1991) that plants at high CO_2 had higher N uptake.

Partitioning of nitrogen

Partitioning of N to different parts of the rice plant is given in Table 4.4. There was an increase in total leaf N at high compared to ambient CO_2 at 22 DAP. Thereafter, total leaf N in the high CO_2 treatment was lower than for plants in ambient CO_2 in the N_0 and N_{90} treatments. However, the difference was significant only at 67 DAP. This decreasing trend in

Table 4.3. Relative growth rate (g g^{-1}day^{-1}) of total biomass (RGR), leaf biomass (RLGR), sheath biomass (RSGR), root biomass (RRGR) and relative N uptake (RNUR) from planting to 22 DAP and 23 to 42 DAP during the 94 dry season. RGR for total biomass is reported for the 93 wet season for the period between planting to 20 DAP and 19 to 35 DAP.

		94 Dry										93 Wet	
Growth CO$_2$	N	Transplanting to 22 DAP					23 to 42 DAP					0-19	20-35
		RGR	RLGR	RSGR	RRGR	RNUR	RGR	RLGR	RSGR	RRGR	RNUR	RGR	RGR
Ambient CO$_2$	N_0	0.316	0.184	0.169	0.206	0.197	0.071	0.059	0.085	0.057	0.035	0.11	0.049
	N_{med}	0.325	0.194	0.176	0.215	0.207	0.083	0.078	0.097	0.062	0.064	0.10	0.094
	N_{high}	0.329	0.201	0.180	0.227	0.218	0.085	0.086	0.093	0.060	0.082	0.10	0.096
Average		0.323	0.193	0.175	0.216	0.207	0.080	0.075	0.092	0.060	0.060	0.10	0.080
High CO$_2$	N_0	0.321	0.191	0.174	0.206	0.198	0.073	0.056	0.090	0.055	0.032	0.13	0.043
	N_{med}	0.346	0.213	0.201	0.227	0.220	0.066	0.060	0.078	0.045	0.049	0.12	0.053
	N_{high}	0.355	0.227	0.209	0.248	0.240	0.068	0.065	0.078	0.048	0.061	0.12	0.066
Average		0.341	0.210	0.195	0.227	0.219	0.073	0.069	0.060	0.082	0.049	0.12	0.054
SE_{co2}		0.001	0.001	0.001	0.002	0.002	0.002	0.001	0.002	ns	0.002	0.005	0.005
SE_N		0.002	0.002	0.002	0.002	0.002	0.002	0.002	ns	ns	0.002	ns	0.006
SE_{CO2*N}		0.003	0.002	0.003	ns	ns	ns	0.002	ns	ns	ns	ns	ns

ns - not significant at $p<0.05$, SE-standard error for the difference in mean . N_0 - no applied N, N_{med}= N_{50} and N_{90} and N_{high} = N_{100} and N_{200} for the 93 wet and 94 dry seasons respectively.

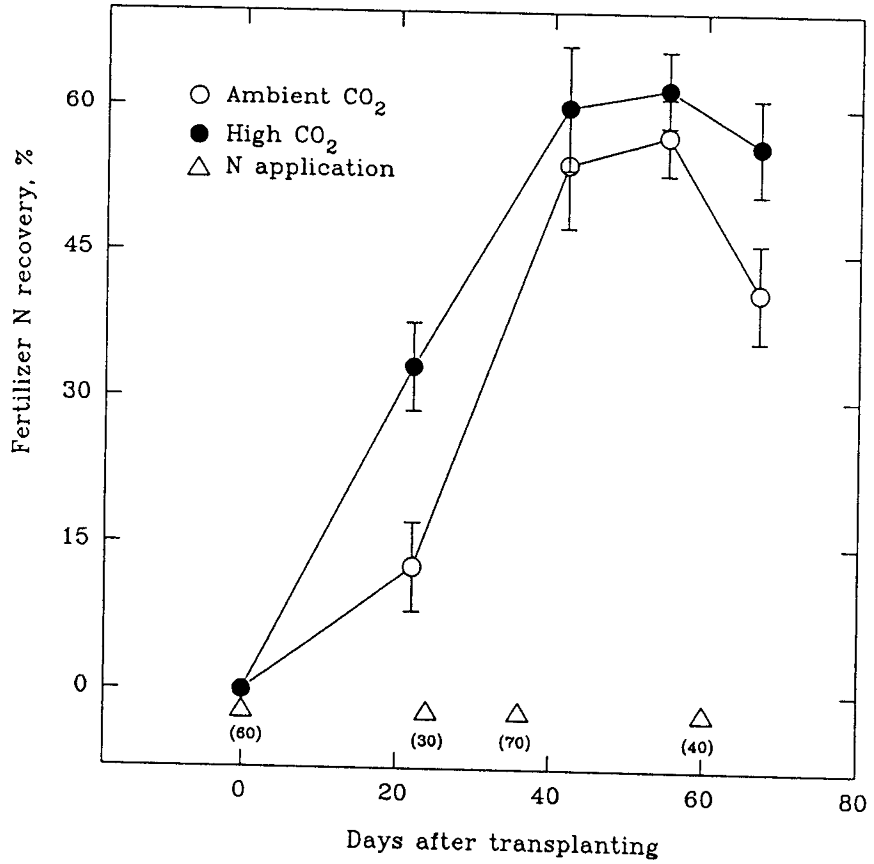

Figure 4.4. Recovery of fertilizer N in rice cultivar IR72 when grown continuously at ambient or high atmospheric CO_2 concentrations during the 94 dry season. N uptake by plants at no supplementary N was taken as soil N supply. Values inside parentheses are amounts of N applied. Error bars represent standard error of mean.

Table 4.4. Total nitrogen (g/m^2 ground area) partitioned among organs of rice plants grown at ambient or high CO_2 concentrations from planting to final harvest at different levels of applied N. The CO_2 x N interaction in the 93 wet season was not significant. Average N (g m^{-2}) across N treatments are reported.

CO_2 concentration	Fertilizer N	94 Dry season											
		Total leaf N (g m^{-2})				Total sheath N (g m^{-2})				Total root N (g m^{-2})			
		22	42	55	67	22	42	55	67	22	42	55	67
Ambient CO_2	N_0	0.82	1.52	1.56	1.44	0.42	0.96	1.16	1.00	0.17	0.42	0.39	0.41
	N_{90}	1.07	3.77	3.11	3.51	0.47	2.01	1.87	1.78	0.23	0.68	0.49	0.57
	N_{200}	1.31	7.06	8.00	5.83	0.62	3.77	3.45	2.73	0.24	0.73	0.62	0.54
High CO_2	N_0	0.86	1.30	1.25	0.73	0.44	1.15	1.15	0.78	0.21	0.47	0.34	0.41
	N_{90}	1.30	3.35	3.09	3.03	0.70	2.31	2.53	2.16	0.38	0.72	0.61	0.73
	N_{200}	2.18	7.28	7.10	6.06	1.08	4.73	4.56	3.37	0.47	0.90	0.74	0.94
	SE_{CO2}	0.07	ns	ns	0.11	0.03	ns	0.11	0.07	0.03	ns	ns	0.04
	SE_N	0.08	0.32	0.22	0.14	0.04	0.29	0.13	0.08	0.03	0.05	0.03	0.05
	SE_{CO2xN}	0.12	ns	ns	ns	0.06	ns	0.18	.012	ns	ns	0.04	0.07
		93 Wet season											
		19	49	56	67	19	49	56	67	19	49	56	67
Ambient	Average	0.33	2.42	2.56	2.25	0.13	0.80	1.24	1.47	0.06	0.24	0.29	0.26
High CO_2	Average	0.44	2.24	1.96	1.98	0.17	1.18	1.17	1.34	0.09	0.27	0.33	0.37
SE_{CO2}		ns	ns	0.12	0.19	ns	0.03	ns	ns	ns	ns	ns	ns

ns - not significant at $p<0.05$, SE- standard error for the difference in mean.

total leaf N in high CO_2 was also observed in the 93 wet season. The proportion of total N partitioned to leaves was lower at high than at ambient CO_2 concentration (Table 4.5).

Decrease in total leaf N at high CO_2 was in contrast to the N content of leaf sheaths and roots. Both total N content in leaf sheaths and roots (Table 4.4) and the N partitioned to the sheaths and roots (Table 4.5) increased with increased CO_2 concentration in both seasons. Increase in total N allocated to leaf sheaths could be due to increased tillering in the high CO_2 concentration, resulting in more sheath tissue. However, increased partitioning of N to leaf sheaths and roots with increased CO_2 concentration was not sufficient to maintain tissue N concentration of those organs in the high compared with ambient CO_2 atmosphere (Table 4.6), presumably due to greater accumulation of biomass in the high CO_2 atmosphere.

In all N treatments, there was less total N in leaf blades and sheaths at flowering (67 DAP) than at 55 DAP (Table 4.4). This decrease was greatest in the N_{200} treatments and especially in the high CO_2 treatment. This decrease in leaf sheath and leaf blade total N could have been because of the development of panicle as a sink for N and loss of N in leaves and sheaths through senescence.

Decreased partitioning of N to the leaves resulted in decreased leaf N concentration with long term exposure to high compared with ambient CO_2 (Fig. 4.5). Leaves in the high CO_2 treatment contained 16 to 19 % less N compared to ambient CO_2 in the 94 dry and 10 to 20% less in 93 wet season (Table 4.7). The difference in leaf N concentration was less on an leaf area (specific leaf N) than on a weight basis. Therefore decrease in leaf N was due not only to a decrease in partitioning of N to leaves at high CO_2, but also to dilution within leaves due to increased specific leaf weight. A decrease in leaf N content with increased CO_2 concentration was also reported for rice by Baker et al. (1990c), for wheat by Hocking and Meyer (1991), and Kentucky blue grass (*Pao pratensis* L.) by Owensby et al. (1993).

Table 4.5. Total plant canopy N and its allocation to different plant organs at ambient and high CO_2 concentration averaged for the three fertilizer N treatments in the '93 wet and the '94 dry season.

Plant organ	Allocated N to different organs 94 dry season							
	22 DAP		42 DAP		55 DAP		67 DAP	
	Ambient	High CO_2	Ambient	High CO_2	Ambient	High CO_2	Ambient	High CO_2
Total plant N (g m^{-2})	1.8 a	2.5 b	6.9 a	7.4 a	7.0 a	8.6 a	7.9 a	8.7 a
Allocation to: (%)								
Leaves	59.7 a	56.5 a	57.3 a	51.2 b	56.1 a	49.5 b	43.5 a	33.5 b
Sheaths and culms	28.1 a	29.2 a	32.3 a	37.2 b	32.4 a	38.9 b	33.1 a	35.5 a
Roots	12.1 a	14.2 a	10.4 a	11.5 a	8.6 a	9.1 a	7.50 a	9.5 b
Panicles	-	-	-	-	2.8 a	2.4 b	15.1 a	21.5 b
	1993 Wet season							
	19 DAP		49 DAP		56 DAP*		67 DAP*	
Total plant N (g m^{-2})	0.5 a	0.7 a	3.4 a	3.6 a	4.1 a	3.4 b	3.9 a	3.6 a
Allocation to: (%)								
Leaves	62.3 a	62.8 a	69.3 a	60.0 b	62.1 a	56.5 b	53.9 a	51.5 a
Sheaths and culms	25.5 a	23.9 a	23.7 a	32.3 b	30.7 a	34.1 b	39.4 a	38.8 a
Roots	12.2 a	13.1 a	6.9 a	7.6 a	7.1 a	9.3 b	6.6 a	9.6 b

- values for a given plant part on a given day followed by a common letter are not statistically significant at $p<0.05$ by DMRT. *Amount allocated to the panicle is not available for this date, thus the allocation of N was calculated excluding panicle N.

Table 4.6. N concentration (g 100 g^{-1}) of rice sheath and root exposed to different rates of fertilizer N and CO_2 concentrations during the '93 wet and the '94 dry season.

CO_2 concentration	Fertilizer N	Sheath N concentration (g per 100 g sheath dry weight)								
		'94 Dry season				'93 Wet season				
		22 DAP	42 DAP	55 DAP	67 DAP	19 DAP	49 DAP	56 DAP	67 DAP	82 DAP
Ambient	N_0	1.52	0.63	0.55	0.47	1.63	0.49	0.37	0.43	0.41
	N_{med}	1.51	0.90	0.65	0.59	1.68	0.81	0.55	0.50	0.41
	N_{high}	1.82	1.68	0.91	0.91	1.63	0.83	0.62	0.41	0.53
High CO_2	N_0	1.25	0.53	0.44	0.38	1.59	0.45	0.34	0.45	0.33
	N_{med}	1.11	0.76	0.59	0.56	1.47	0.96	0.50	0.33	0.38
	N_{high}	1.44	1.29	0.83	0.78	1.53	0.72	0.48	0.23	0.40
	SE_{CO2}	0.05	0.05	0.01	0.01	ns	ns	0.01	0.02	0.01
	SE_N	0.07	0.06	0.02	0.02	0.09	0.06	0.02	0.03	0.02
	$SE_{CO2\,N}$	ns	ns	ns	ns	ns	ns	ns	0.03	ns
		Root N concentration (g $100g^{-1}$ dry weight)								
Ambient	N_0	1.11	0.83	0.96	0.87	1.31	0.73	0.70	0.61	0.52
	N_{med}	1.21	1.00	0.94	0.94	1.45	0.81	0.81	0.66	0.61
	N_{high}	1.31	1.15	1.04	0.91	1.39	0.95	0.85	0.76	0.62
High CO_2	N_0	1.08	0.79	0.79	0.75	1.16	0.72	0.68	0.62	0.52
	N_{med}	1.08	0.84	0.85	0.75	1.33	0.87	0.77	0.72	0.50
	N_{high}	1.27	0.97	1.00	0.97	1.41	0.88	0.78	0.85	0.61
	SE_{CO2}	ns	0.04	0.03	0.02	ns	ns	ns	ns	ns
	SE_N	ns	0.04	0.03	0.03	ns	ns	ns	ns	ns
	SE_{CO2xN}	ns	ns	ns	ns	ns	ns	ns	ns	ns

ns-not significant at $p<0.05$,SE-standard error for the difference in mean. N_0 - no N, N_{med} = N_{50} and N_{90}, and N_{high}= N_{100} and N_{200} for the '93 wet and '94 dry seasons respectively.

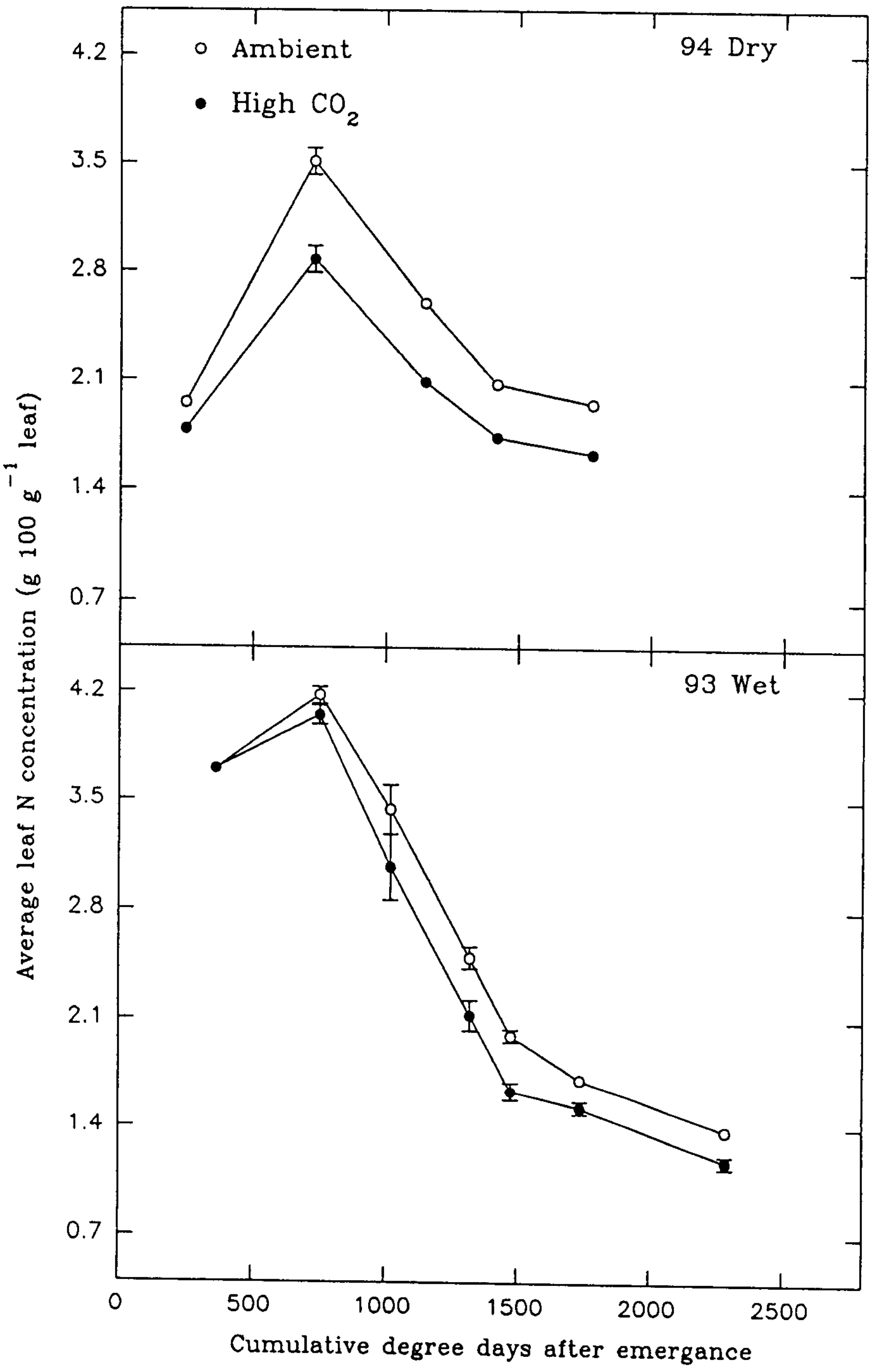

Figure 4.5. Average leaf N concentration in thermal-time of rice cultivar IR72, grown continuously at ambient or high atmospheric CO_2 concentration in the 93 wet and 94 dry seasons. Error bars represent standard error of mean.

Table 4.7. N concentration (g 100g^{-1}) and specific leaf N concentration (g m^{-2}) of rice leaf blades exposed to different N and CO_2 concentrations during the 93 wet and the 94 dry season.

CO_2 concentration	Fertilizer N	Leaf N concentration (g 100 g^{-1} leaf dry weight)								
		'94 Dry season				'93 Wet season				
		22 DAP	42 DAP	55 DAP	67 DAP	19 DAP	49 DAP	56 DAP	67 DAP	82 DAP
Ambient	N_0	3.33	1.86	1.66	1.51	4.12	1.89	1.71	1.38	1.05
	N_{med}	3.40	2.49	1.96	1.94	4.15	2.74	2.05	1.73	1.41
	N_{high}	3.79	3.46	2.62	2.40	4.28	2.87	2.24	2.06	1.69
High CO_2	N_0	2.79	1.35	1.30	1.10	3.87	1.65	1.36	1.23	1.00
	N_{med}	2.62	2.00	1.68	1.62	4.02	2.41	1.87	1.57	1.16
	N_{high}	3.23	2.91	2.22	2.17	4.06	2.32	1.68	1.79	1.35
	SE_{CO2}	0.08	0.03	0.02	0.02	ns	0.08	0.05	0.04	0.03
	SE_N	0.10	0.04	0.02	0.03	ns	0.10	0.06	0.04	0.04
	$SE_{CO2x\,N}$	0.12	ns	ns	ns	ns	ns	ns	ns	ns
		Specific leaf N concentration (g m^{-2} leaf)								
Ambient	N_0	1.13	0.91	0.86	0.84	1.84	1.37	1.12	0.92	0.70
	N_{med}	1.13	1.13	0.96	1.05	2.05	1.76	1.36	1.12	0.90
	N_{high}	1.21	1.52	1.23	1.24	2.11	1.85	1.35	1.30	1.03
High CO_2	N_0	1.02	0.74	0.75	0.66	1.22	1.16	0.97	0.89	0.71
	N_{med}	0.94	1.08	0.87	0.92	2.15	1.68	1.27	1.10	0.76
	N_{high}	1.11	1.40	1.08	1.22	2.05	1.58	1.13	1.16	0.90
	SE_{CO2}	ns	0.024	0.014	0.015	ns	0.04	0.035	ns	0.02
	SE_N	ns	0.029	0.017	0.019	0.12	0.04	0.040	0.03	0.02
	$SE_{CO2x\,N}$	ns	ns	ns	0.027	ns	ns	0.055	ns	ns

ns - not significant at $p<0.05$, SE-standard error for the difference in mean. N_0 - no applied N, N_{med} =N_{50} and N_{90} and N_{high} = N_{100} and N_{200} for the '93 wet and '94 dry season.

Decrease in leaf N at elevated CO_2 could have a significant effect on leaf CO_2 assimilation and radiation use efficiency of rice grown at high CO_2. For example in 94 dry season at 67 DAP, the N_{200} treatment had a leaf N concentration of only 2.2% at high CO_2 while at ambient CO_2 it was 2.4%. Single leaf CO_2 assimilation is curvilinearly related to leaf N concentration (Fig. 3.1 in page 44). We also observed that to sustain maximum light saturated leaf CO_2 assimilation, leaf N concentration should be greater than 2.5%. Thus rice may require additional N fertilization to assure that leaves maintain their ability to assimilate the additional CO_2 under elevated CO_2 conditions.

Vegetative and reproductive development

A plot of Haun scale leaf number as a function of cumulative degree-days revealed two different rates of leaf appearance, a higher rate earlier followed by a slower phase of leaf appearance, in both 93 wet and 94 dry seasons (Fig. 4.6). The change in rate of leaf appearance probably coincided initiation of reproductive development, but we do not have data on panicle initiation. A similar change in leaf appearance rate with the onset of reproductive development was observed for rice by Baker et al. (1990c), Yoshida (1977), and Vergara (1980); and for wheat by Baker et al. (1986) and Boone et al. 1990. Yoshida (1981) showed that phyllochron value (degree-day $leaf^{-1}$) increased from 100 to 170 degree-days $leaf^{-1}$ after the initiation of rice panicles. Because the graph between cumulative degree days and Haun scale leaf number does not show any observable difference in inflection point between ambient and elevated CO_2 in the 94 dry season, CO_2 concentration probably had no effect on time to panicle initiation of rice.

The phyllochron value before panicle initiation was 111 degree-days $leaf^{-1}$ for plants grown in ambient CO_2 and 114 degree-day $leaf^{-1}$ for the high CO_2 concentration in the '94 dry

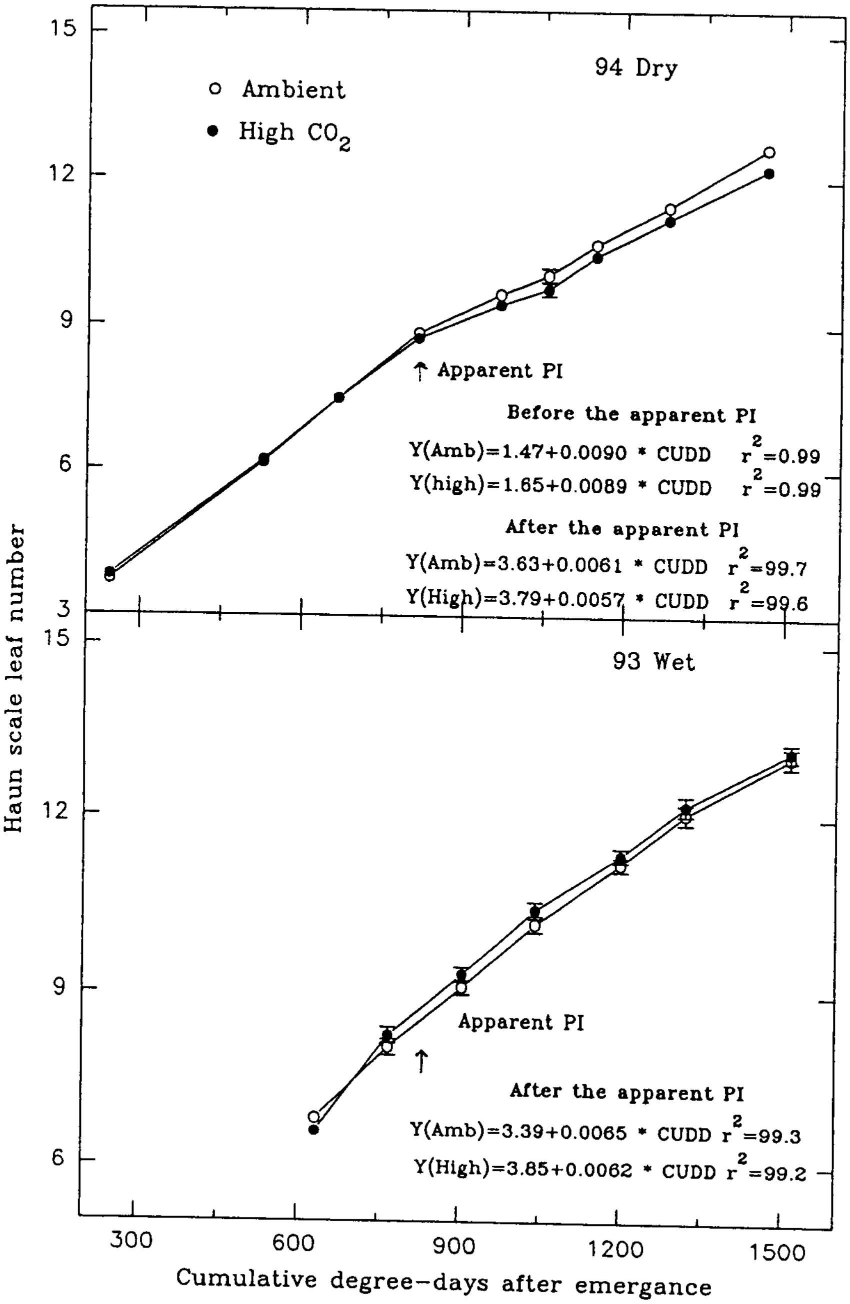

Figure 4.6. Haun scale leaf appearance in thermal-time of rice cultivar IR72 grown in ambient or high atmospheric CO_2 concentration. Regression equations for the 94 dry season were derived for both before and after apparent panicle initiation (PI) as indicated by the arrow. Regression equation by the 93 wet season was derived only for the data after the PI. Base temperature for calculation of degree-day was 8° C. Error bars represent standard error of mean.

season (Fig. 4.6). Phyllochron value before panicle initiation was not calculated for the '93 wet season due to insufficient data points. After panicle initiation, phyllochron increased to 163 degree-day leaf^{-1} at ambient CO_2 and 175 degree-day leaf^{-1} at high CO_2 during the '94 dry season. The phyllochron value after panicle initiation for the '93 wet season was 153 degree-day leaf^{-1} for ambient and 161 degree-day leaf^{-1} for high CO_2 (Fig. 4.6).

Haun scale leaf appearance is a combination of leaf initiation and leaf growth within the leaf sheath. Therefore, if leaf expansion rate decreased after leaf initiation we would observe a decrease in Haun scale leaf appearance rate. Panicle initiation would have shifted the priority of partitioning to panicles rather than to the leaves. Thus, there could be a decrease in rate of leaf growth and increase phyllochrone value after the panicle initiation.

The same theory could explain the small increase in phyllochron after panicle initiation at high compared to ambient CO_2. N concentration in rice leaves was significantly lower at high than at ambient CO_2. Therefore a greater N stress on the growing leaf at high compared to ambient CO_2 could decrease the rate of leaf emergence from the subtending leaf sheath. Although phyllochron value tended to be lower at N_0 compared with high fertilizer N treatments, we did not observe significant differences in phyllochron among fertilizer N treatments in either the 93 wet or 94 dry season.

Baker et al. (1990c) observed an increase in rate of leaf appearance in rice with increased CO_2 concentration when compared with subambient CO_2. However, their observations also show no change in leaf appearance between ambient and elevated CO_2. Manalo et al. (1994) observed an increased rate of leaf appearance in rice with increased CO_2, but only at low temperatures. Therefore, for rice under field conditions there should be no change in leaf phyllochron values due to increased CO_2 concentration.

The leaf appearance rate observed by Manalo et al. (1994) was much greater than that observed in this experiment. This could be due to fixed day and night temperatures in their outdoor glass house experiment compared to the diurnal variation observed in the field in this study. Phyllochron value in this study was higher in the 94 dry than the 93 wet season. This could have been due to higher mean air temperatures during the 94 dry season. Rate of leaf appearance per degree-day decreases when mean air temperature is above the optimum temperature for leaf growth (Kirby and Perry, 1987; Cao and Moss, 1989). The optimum mean air temperature for rice is about 30^0 C, above which development decreases (Kropff, 1993). In both seasons, mean air temperature exceeded the optimum on many days. Therefore the reason for the slightly greater phyllochron value in the 94 dry season compared to the 93 wet season could be because the mean air temperature was more often above the optimum temperature for development processes for rice.

Flowering of rice was not affected by the increased atmospheric CO_2 concentration. Accumulated thermal-time from germination to 50% flowering during the 93 wet season was 1591 and 1625 degree-days at ambient and high CO_2. In the 94 dry season it was 1606 and 1625 degree-days at ambient and elevated CO_2. Neither fertilizer N nor interaction between CO_2 concentration and N for 50% flowering were significant in either season. This suggests that CO_2 concentration has no effect on the developmental processes in rice cultivar IR72.

Tillering and leaf growth

Tiller number m^{-2} was significantly greater at high compared with ambient CO_2. There was a significant interaction between fertilizer N and CO_2 on tiller number in both early and later growth stages during the 94 dry season (Table 4.8). For example, in the 94 dry

Table 4.8 Tiller and panicle number of rice cultivar IR72 during the '94 dry and '93 wet season grown at ambient and elevated CO_2 concentration and with different rates of N fertilization.

CO_2 concentration	Fertilizer N	'94 Dry season Tiller number m^{-2}						Panicle number m^{-2}
		0 DAP	22 DAP	42 DAP	55 DAP	67 DAP	77 DAP	77 DAP
Ambient CO_2	N_0	75	345	431	336	337	254	226
	N_{90}	75	450	679	483	455	314	253
	N_{200}	75	481	875	854	401	334	278
	Average	75	425	661	557	398	301	252
High CO_2	N_0	75	416	497	370	245	294	245
	N_{90}	75	658	800	605	404	380	313
	N_{200}	75	813	1054	977	451	417	328
	Average	75	629	784	651	367	364	295
	SE_{CO2}		21.7	32.8	17.7	13.9	17.1	12.5
	SE_N		26.6	40.2	21.6	17.1	19.1	11.4
	SE_{CO2xN}		37.7	ns	ns	24.1	27.3	ns
		93 wet season						
		0 DAP	19 DAP	49 DAP	56 DAP	67 DAP	82 DAP	97 DAP
Ambient	Average	75	142	368	387	384	316	250
High CO_2	Average	75	213	382	418	375	343	265
	SE_{CO2}		12.4	ns	ns	ns	ns	ns

ns - not significant at $P<0.05$, SE-standard error for the difference in mean.

season at 22 DAP, tillering increased by 20% in N_0 and 69% in N_{200} with increased CO_2 concentration. In general, there was less tillering during the '93 wet than in '94 dry season. Tiller number m^{-2} at a given level of absorbed N from planting to 42 DAP in the 94 dry season was significantly higher at high than at ambient CO_2 (Fig. 4.7).

Tillers initiate from the leaf axil at each unelongated node of a main shoot or a tiller in synchrony with the leaf (Yoshida, 1981). However, competition for assimilates may prevent these initiated tillers from developing into autotrophic tillers. High CO_2 increased assimilate supply, which may explain increased tillering. High N fertilizer further increased tillering. Increased tillering in rice during early growth stages often increases in panicle number (Matsushima, 1980). Although, there was a significant increase in panicle number with increased CO_2, that increase was not proportional to the increase observed in tillering at early stages of growth at high CO_2 compared with ambient.

The high N treatment initiated far more tillers, but tiller abortion also increased as N fertilization increased in this study. Tiller abortion was similar for both ambient and high CO_2 treatments. On average, 62% of the tillers did not produce panicles. Panicle density was 6% and 17% greater at high compared with ambient CO_2 during the '93 wet and '94 dry seasons respectively. This low response of panicle number to high CO_2 could be a result of excessive tillering during early growth stages. This appeared to be true for the 94 dry season. Tillers may die because of decreased N availability and competition for assimilates, or competition for light. However, the decrease in panicle number in 93 wet season could be partly due to increased transplanting shock coupled with lower radiation and lower N absorption, which delayed tillering. Most late tillers are unproductive. Therefore, judging by the 94 dry season, in the field with adequate fertilizer N and radiation, excessive tillering at high CO_2 may not result in greater final panicle numbers in rice. It is also evident from the wet season, that

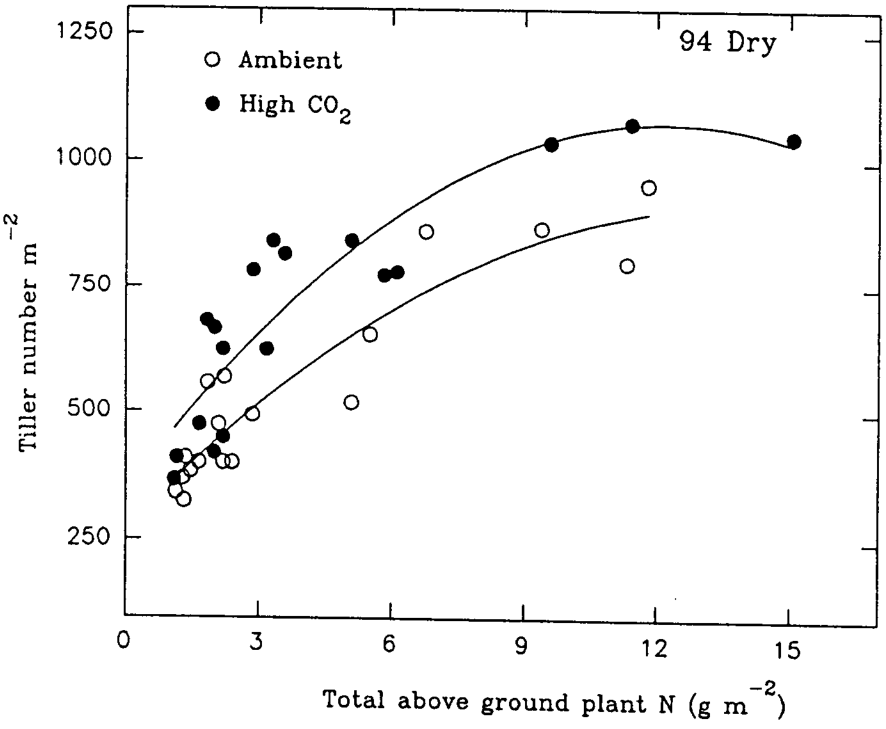

Figure 4.7. Tillering from transplanting to 42 DAP as a function of total above ground plant N, of the rice cultivar IR72, grown in ambient or high atmospheric CO_2 concentration with different rates of fertilizer N during the 94 dry season.

increased tillering and thereby increased panicle number, at high compared with ambient CO_2 concentration greatly depends on N fertilizer absorption and solar radiation.

Leaf growth

The relationship between LAI and total above-ground plant N was linear from planting to flowering for both the '93 wet and '94 dry seasons (Fig. 4.8). There was a slight nonlinearity after flowering, which could be a result of leaf senescence at higher LAI. Growth CO_2 concentration had no direct effect on this relationship. Yoshida (1981) and Dingkuhn et al. (1990) also showed that plant N and leaf area were closely related in ambient CO_2 environments. Leaf area index in the '94 dry season at 22 DAP was 75% greater in high CO_2 in N_{200}, but increase in LAI at N_0 was 15% (Table 4.9). This increase in LAI at early vegetative growth could be due to greater absorption of N at high CO_2. As plots approached canopy closure, differences in LAI between high and low CO_2 concentrations gradually disappeared in both the 93 wet and 94 dry seasons (Fig. 4.9).

However, in contrast to rice many upland crops, including cotton (*Gossipium hirsutum* L.) Mauney et al. (1978); soybean, Baker et al. (1989) and Jones et al. (1985), and Wheat, Hocking and Meyer (1991), responded positively to elevated CO_2 concentration by increasing leaf area. In this study we did not observe an increase in LAI with increased CO_2 concentration in the absence of a significant increase in total above-ground plant N. The greater response of leaf area to increased CO_2 concentration in upland crops, compared to lowland rice, could be related to the greater N uptake. We suggest that increased atmospheric CO_2 concentration affect leaf area only when ample soil N is available.

Increased CO_2 concentration increased number of leaves per hill, due to increased tillering (Fig. 4.10). However there were fewer leaves per tiller and individual leaves were

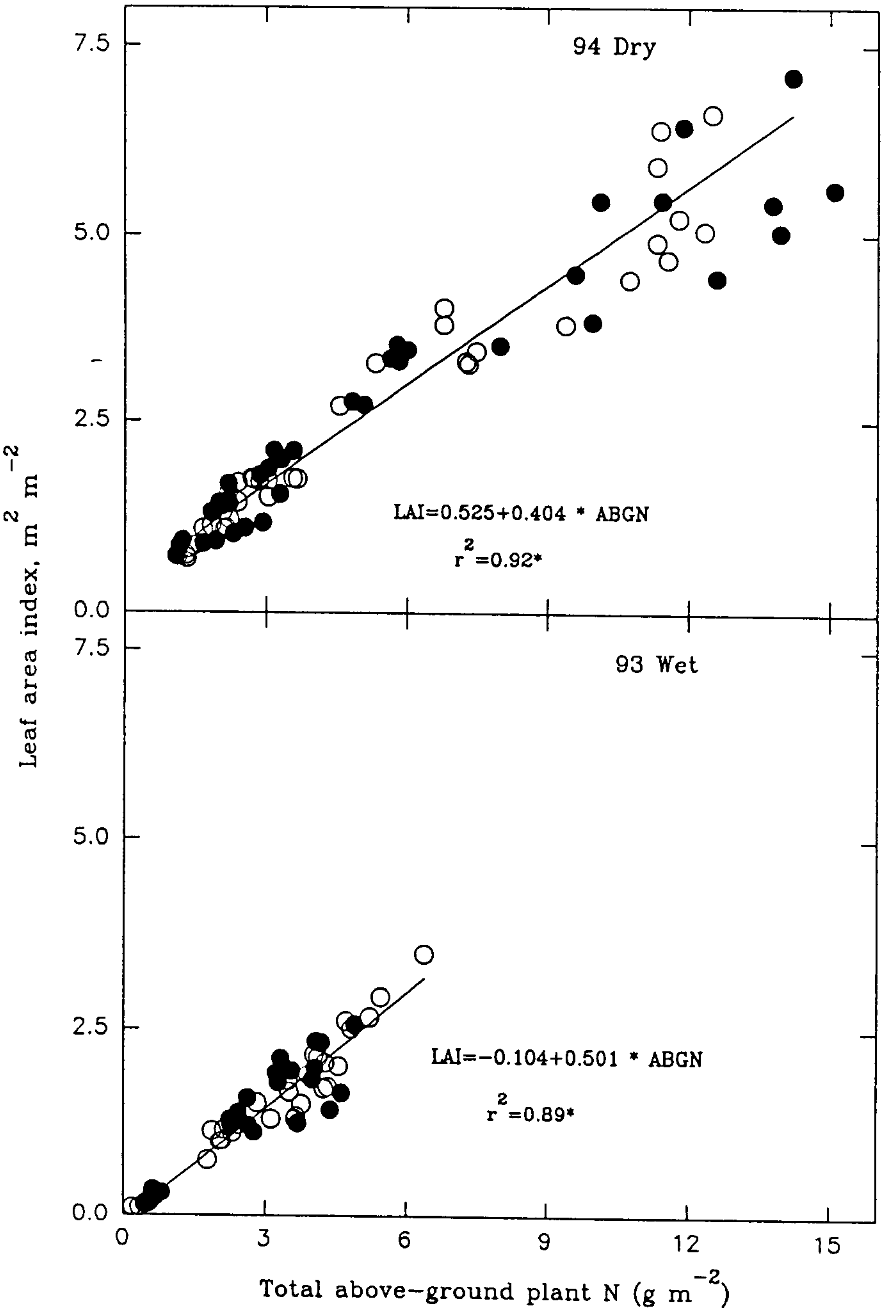

Figure 4.8. Leaf area index from transplanting to flowering as a function of total above-ground plant N (ABGN) of rice cultivar IR72 grown in ambient or high atmospheric CO_2 concentration in the 93 wet and 94 dry seasons.

Table 4.9. Leaf area index of rice grown at ambient and high CO_2 concentration at different fertilizer N rates during the '93 wet and the '94 dry seasons.

CO_2 conc.	N	93 Wet season						94 Dry season				
		19 DAP	35 DAP	49 DAP	56 DAP	67 DAP	82 DAP	22 DAP	42 DAP	56 DAP	67 DAP	77 DAP
Ambient	N_0	0.185	0.596	1.00	1.30	1.10	0.78	0.72	1.65	1.73	1.66	1.28
	N_{med}	0.150	0.861	1.60	1.95	2.00	1.25	0.94	3.35	3.14	3.32	2.23
	N_{high}	0.151	0.849	1.38	2.68	2.68	1.87	1.12	4.63	6.31	4.71	3.59
	Average	0.162	0.769	1.33	1.98	1.93	1.30	0.93	3.21	3.73	3.23	2.36
High CO_2	N_0	0.291	0.810	1.18	1.29	1.18	0.84	0.83	1.73	1.56	1.09	1.13
	N_{med}	0.202	0.576	1.37	1.77	2.18	1.66	1.38	2.83	3.42	3.27	2.58
	N_{high}	0.234	0.889	1.55	2.12	2.01	2.04	1.96	5.18	6.34	4.96	3.94
	Average	0.243	0.758	1.37	1.73	1.79	1.51	1.39	3.25	3.77	3.11	2.55
	SE_{CO2}	0.025	ns	ns	ns	ns	ns	0.03	ns	ns	ns	0.15
	SE_N	ns	ns	0.08	0.15	0.11	0.11	0.04	0.23	0.15	0.13	0.18
	SE_{CO2xN}	ns	ns	ns	ns	ns	ns	0.06	ns	ns	ns	0.25

ns - not significant at $p<0.05$, SE-standard error for the difference in mean. N_0 - no applied N, N_{med}= N_{50} and N_{90} and N_{high}= N_{100} and N_{200} for the '93 wet and '94 dry seasons respectively.

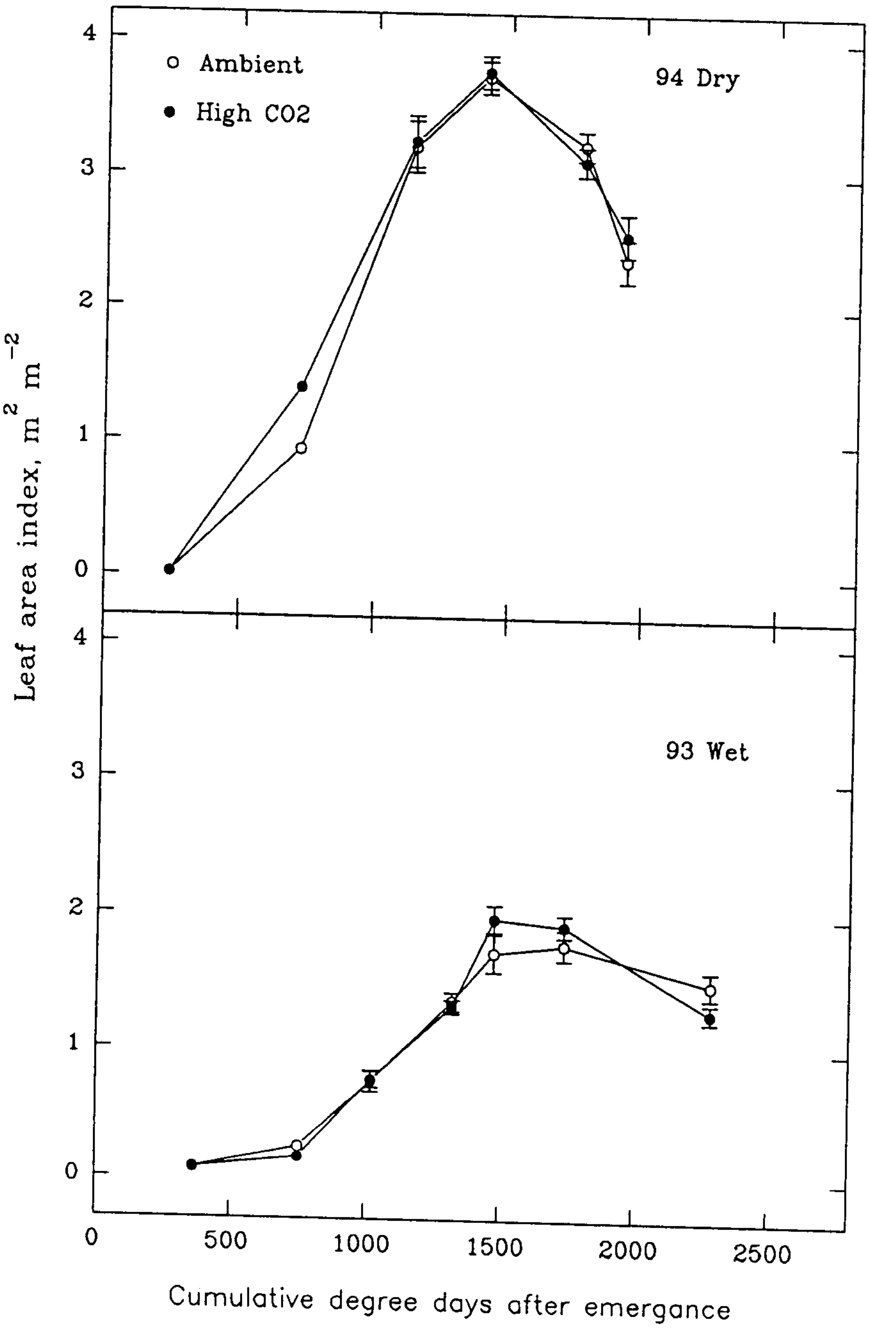

Figure 4.9. Leaf area index as a function in thermal-time of rice cultivar IR72 grown in ambient or high atmospheric CO_2 concentration.

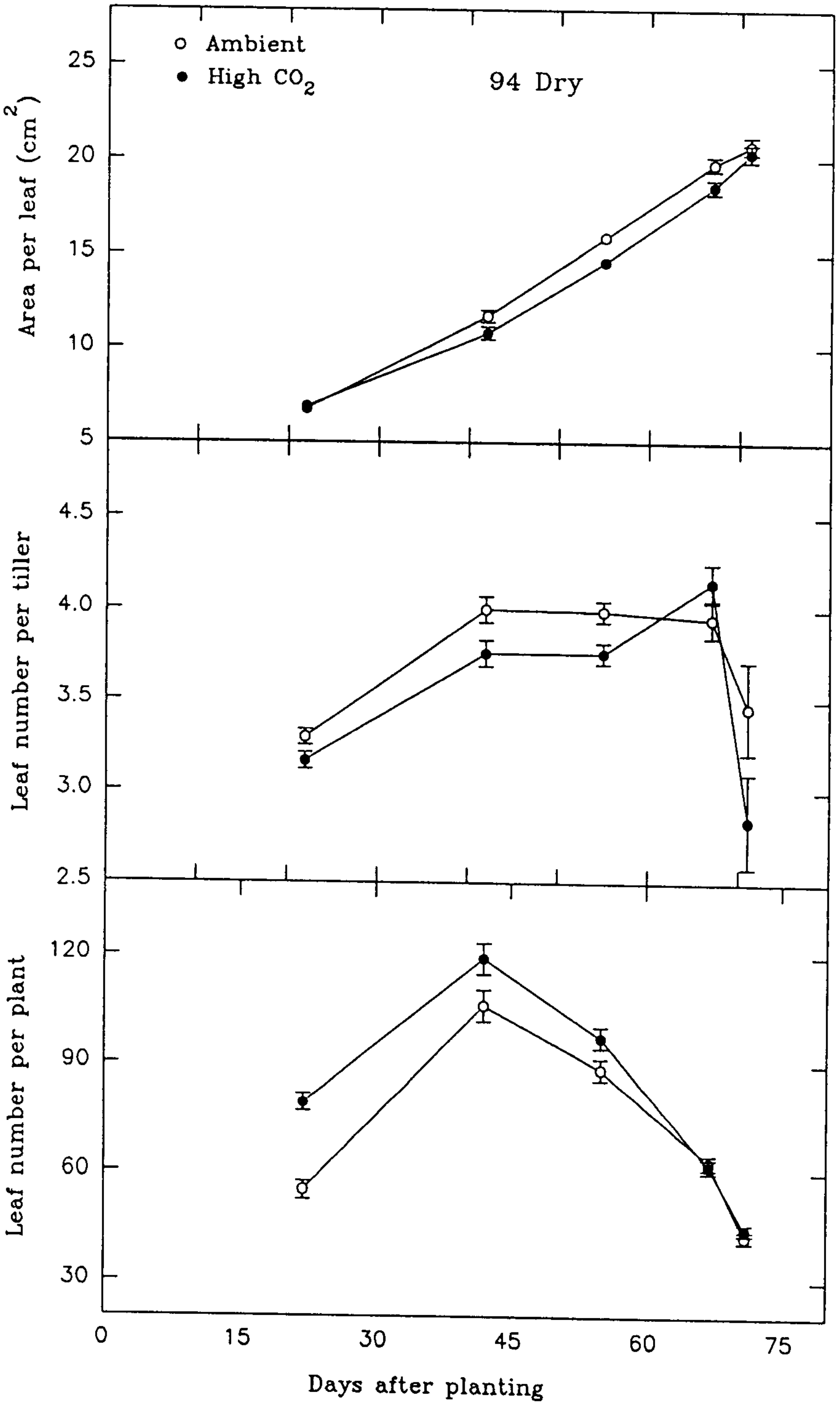

Figure 4.10. Mean individual leaf area, Leaf number per tiller, and leaf number per hill of rice cultivar IR72 grown in ambient or high atmospheric CO_2 concentration in the 94 dry season.

smaller in the high CO_2 treatment. This could have been due to an increased number of small tillers and to a decrease in leaf N. Cultivar IR72 produced greater number of small tillers with smaller leaves with no change in LAI in high compared with ambient CO_2. These findings suggest that a cultivar with fewer unproductive tillers with larger leaves and similar LAI should be developed to maximize the benefits of elevated atmospheric CO_2.

Biomass production and partitioning

Total dry matter of rice increased with increased CO_2 concentration in all plots that received N fertilizer. Total dry weight at N_0 did not increase with increased CO_2 concentration during latter growth stages while at N_{90} and N_{200} it increased with increased CO_2 concentration in the 94 dry season (Table 4.10). There was no significant interaction between CO_2 concentration and fertilizer N for total biomass during the 93 wet season. This was supported by Griffin et al. (1993) that increased CO_2 concentration increased seedling growth of *Pinus taeda* L. only when soil N was high, however differs from the findings of Mitchell et al. (1993) and Sionit et al. (1991), that high CO_2 stimulated dry matter production even with lower N concentration. At N_0, initial growth of rice in high CO_2 was greater, resulting a larger canopy. However, with no fertilizer input, the soil N supply was quickly depleted because of greater uptake at high CO_2 treatment, causing increased senescence, reduced assimilation and low growth rates at latter stages of growth, resulting in no increase in total biomass due to the increased CO_2.

Average relative growth rate for total biomass (RGR), relative leaf mass growth rate (RLGR), relative sheath and culm mass growth rate (RSGR), and relative root mass growth rate (RRGR), were significantly greater at elevated than at ambient CO_2 concentration from planting to 22 DAP (Table 4.3). However, from 23 to 42 DAP, except RRGR, all other

Table 4.10 Total biomass production (g m^{-2}) of rice cultivar IR72 during the '94 dry and '93 wet seasons grown at ambient and elevated CO_2 concentration and with different rates of N fertilization.

CO_2 concentration	Fertilizer N	Total Dry weight (g m^{-2})				
		22 DAP	42 DAP	55 DAP	67 DAP	77 DAP
Ambient CO_2	N_0	67	282	367	517	546
	N_{90}	82	442	514	807	802
	N_{200}	89	494	756	878	833
	Average	79	406	546	734	727
High CO_2	N_0	85	373	409	504	587
	N_{90}	147	559	700	1060	1161
	N_{200}	179	706	968	1238	1183
	Average	137	546	692	934	1008
	SE_{CO2}	7.9	45.9	41.3	46.5	72.0
	SE_N	4.5	26.5	23.8	26.9	45.5
	SE_{CO2xN}	5.6	32.4	29.2	32.9	50.9
		93 wet season				
		19 DAP	49 DAP	56 DAP	67 DAP	82 DAP
Ambient	Average	20.4 a	243 a	423 a	615 a	702 a
High CO_2	Average	28.4 b	315 b	458 a	674 a	856 b

Values for a given day followed by a common letter are not statistically significant at $p<0.05$ by DMRT. ns - not significant SE-standard error for the difference in mean.

relative growth rates were lower at high than at ambient CO_2. When calculating relative growth rates we assumed that growth from planting to 42 DAP was exponential for both high and ambient CO_2 grown rice plants. One reason for the decrease in relative growth rate at high CO_2 could be a decrease in N supplying capacity of the soil due to greater N uptake from planting to 22 DAP in those plots. It could also be that our assumption of exponential growth was invalid. This would mean that the growth rate at high CO_2 was not less than at ambient. Rather, it shifted from exponential growth to linear phase more quickly at high than at ambient CO_2.

Partitioning of total biomass among organs of the rice plants is given in Fig. 4.11. At high CO_2 leaves got a smaller fraction of total biomass, while sheath and culm received a greater portion, compared to ambient. This suggest that with increased CO_2 concentration there will be a change in partitioning of biomass in rice.

Average leaf dry weight in the N fertilized treatments during '94 dry season were greater in the high CO_2 than ambient treatment however during '93 wet season, it was limited to early stages of growth (Table 4.11). This increase in leaf dry weight at high CO_2 was partly due to accumulation of non structural carbohydrates due to increased assimilation. Because there was no increase in leaf area with increased CO_2 concentration, accumulation of non structural carbohydrates increased specific leaf weight (Fig. 4.12).

Leaf sheaths and culms were the heaviest plant organs and the greatest effect of CO_2 on vegetative growth was also on sheath and culms (Fig. 4.13). Increase in sheath and culm weight with high CO_2 was greatest in high N treatments (Table 4.11). For example, at 22 DAP, sheath and culm dry weight in the N_0 treatment was 30% greater in high compared with ambient CO_2 concentration, while in the N_{90} and N_{200} they were 100% and 118% greater. This

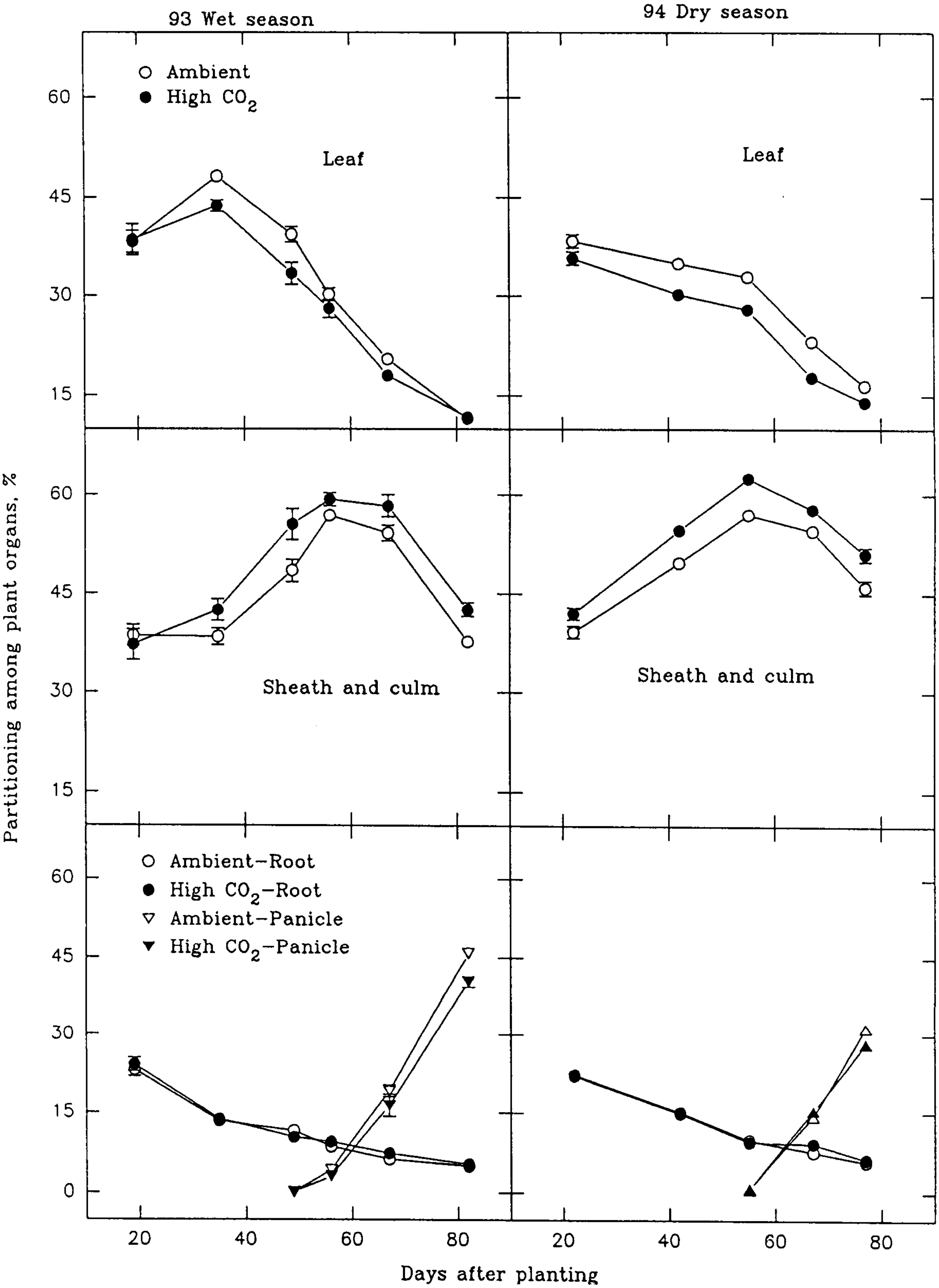

Figure 4.11. Dry matter partitioning to plant organs of rice cultivar IR72 grown in ambient or high atmospheric CO_2 concentration during the 93 wet and 94 dry seasons.

Table 4.11. Dry weight of green leaf blade and sheath and culm (g hill^{-1}) of rice cultivar IR72 exposed to different N and CO_2 concentrations during the '94 dry and '93 wet seasons.

CO_2 conc.	N	Leaf dry weight (g hill^{-1})									
		94 Dry season					93 Wet season				
		22 DAP	42 DAP	55 DAP	67 DAP	77 DAP	19 DAP	49 DAP	56 DAP	67 DAP	82 DAP
Ambient	N_0	0.98	3.27	3.60	3.82	3.90	0.33	3.09	3.49	2.93	2.09
	N_{med}	1.25	6.06	6.21	7.23	5.24	0.30	4.40	5.37	5.16	3.20
	N_{high}	1.43	8.18	11.8	9.74	7.22	0.29	3.85	6.52	6.76	4.59
High CO_2	N_0	1.22	3.81	3.61	2.62	2.25	0.40	3.45	3.84	3.44	2.40
	N_{med}	1.98	6.70	7.14	7.39	6.34	0.44	4.12	5.16	6.09	4.35
	N_{high}	2.68	9.97	12.4	11.1	8.89	0.47	4.89	5.99	5.23	5.40
	SE_{CO2}	0.05	0.35	ns	ns	0.03	0.03	ns	ns	0.25	0.22
	SE_N	0.06	0.42	0.36	0.25	0.40	ns	0.16	0.31	0.32	0.26
	SE_{Co2xN}	0.09	ns	ns	ns	0.57	ns	ns	ns	ns	ns
		Sheath and culm weight (g hill^{-1})									
Ambient	N_0	1.09	6.02	8.46	12.1	10.3	0.42	5.26	8.74	10.4	8.75
	N_{med}	1.26	8.94	11.5	17.8	14.6	0.26	5.30	9.36	14.4	10.6
	N_{high}	1.37	9.05	15.3	17.6	17.0	0.26	3.69	10.7	14.7	12.3
High CO_2	N_0	1.41	8.70	10.5	12.4	13.5	0.48	7.25	11.8	14.0	10.63
	N_{med}	2.52	12.2	17.2	24.3	22.8	0.38	6.56	9.40	18.6	15.9
	N_{high}	3.00	14.5	22.1	26.6	22.6	0.38	7.33	11.9	14.4	17.0
	SE_{CO2}	0.08	0.60	0.60	0.52	0.80	ns	0.35	ns	0.64	0.57
	SE_N	0.09	0.74	0.74	0.63	0.99	ns	0.43	ns	0.64	0.67
	SE_{CO2XN}	0.14	ns	ns	0.89	1.41	ns	ns	ns	ns	ns

ns - not significant at $p<0.05$, SE-standard error for the difference in mean. N_0 - no applied N, N_{med}= N_{50} and N_{90} and N_{high}= N_{100} and N_{200} for the '93 wet and '94 dry seasons.

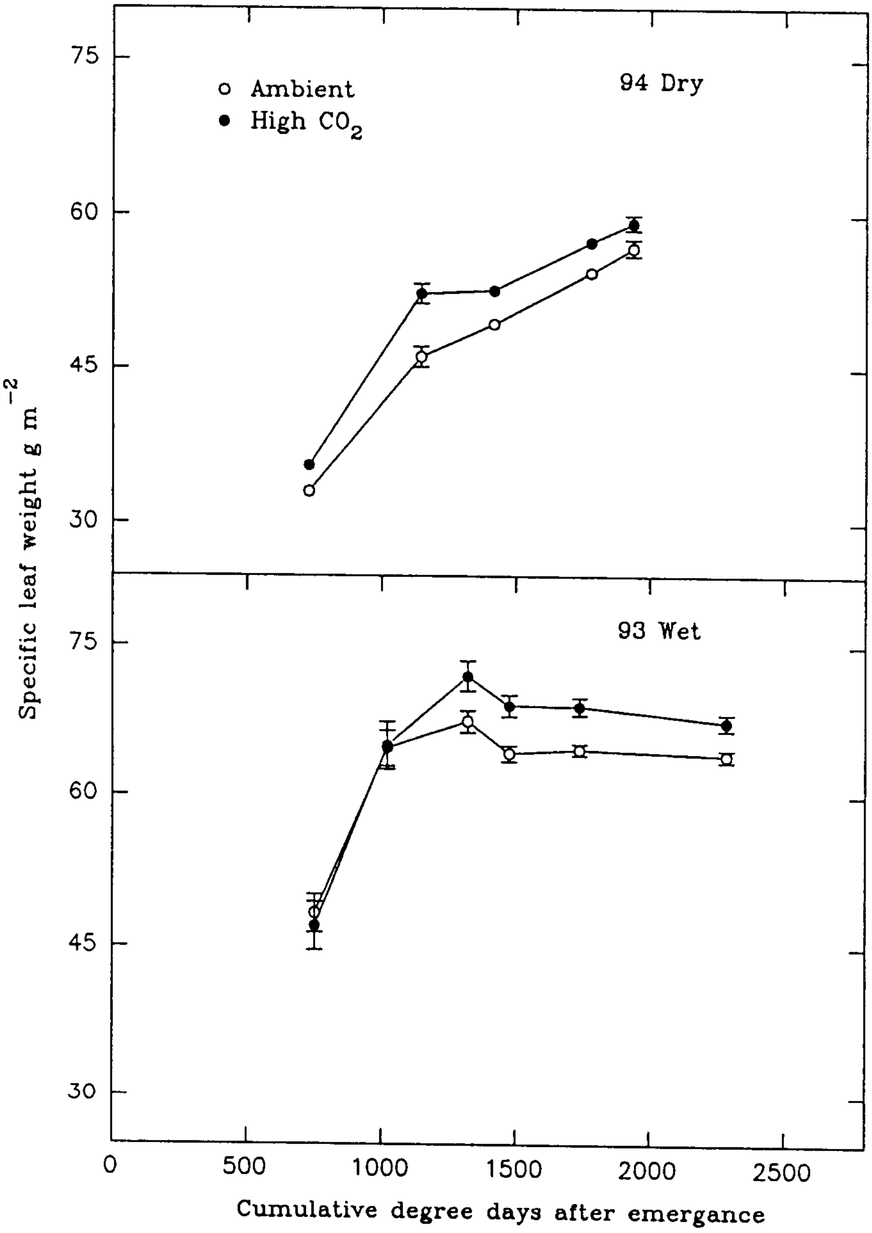

Figure 4.12. Specific leaf weight in thermal-time of rice cultivar IR72 grown in ambient or high atmospheric CO_2 concentration.

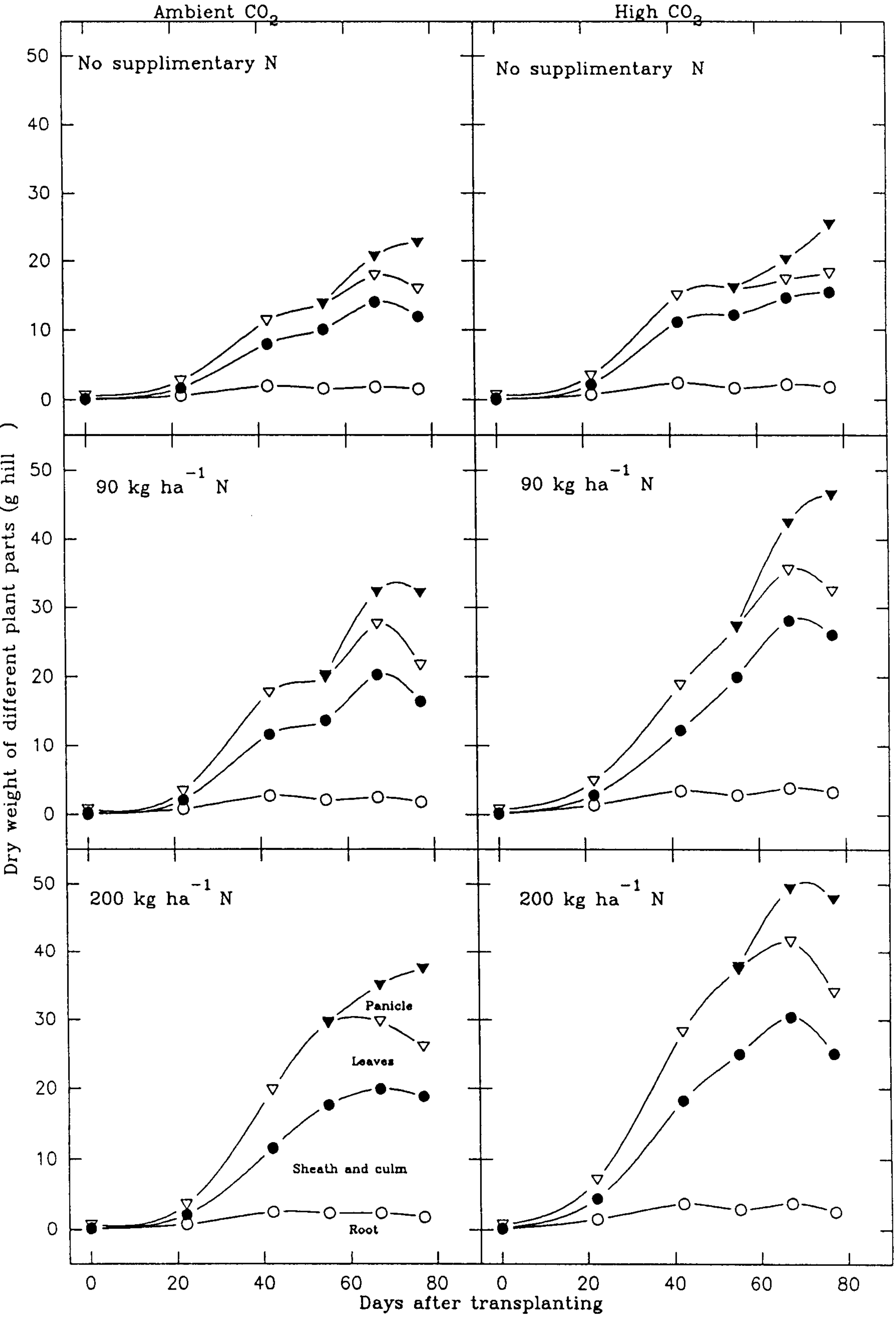

Figure 4.13. Partitioning of dry matter to different parts of the rice plant grown at ambient or high atmospheric CO_2 concentration and different rates of fertilizer N during the 94 dry season.

increase in sheath and culm weight at high CO_2 resulted from increase in tillering at high compared with ambient CO_2.

Root dry weight was generally less than other parts of the rice plant (Fig. 4.13). We recovered only a portion of the root biomass, but we believe that the recovery was about 80% and same for all treatments. Root dry weight was greater at high compared with ambient CO_2 in both seasons, but the response was generally less during '93 wet season (Fig 4.14). There was no difference in root:shoot ratio between high and ambient CO_2. This suggests that assimilate partitioning between above-and below-ground was the same in high and ambient CO_2.

There was no difference in spikelet number per panicle at high compared with ambient CO_2 in either season, but the 94 dry season had a greater average spikelet number per panicle than in the 93 wet season (Table 4.12). In both seasons, increased N increased spikelet number per panicle. Thus, spikelet number per panicle was not directly dependent on CO_2 concentration, but rather depended on N. N deficiency after panicle initiation influences spikelet degeneration (Wada and Matsushima, 1962; Schnier et al., 1990). Therefore, differentiation of spikelets would have been favored through increased N absorption during early growth stages at high compared with ambient CO_2. However, spikelet degeneration would have been higher with greater dilution of plant N at high compared to ambient CO_2.

Filled grains per panicle increased with increased CO_2 concentration and there was a small, but significant, increase in seed weight at high compared with ambient CO_2 in the 93 wet season. There was a decrease in grain N concentration with increased CO_2 suggesting a decrease in rice grain quality with increased CO_2 concentration (Table 4.12). Therefore, it could be suggested that with increased CO_2 concentration, positive effects observed on vegetative growth may not be fully transferred to reproductive growth in rice cultivar IR72.

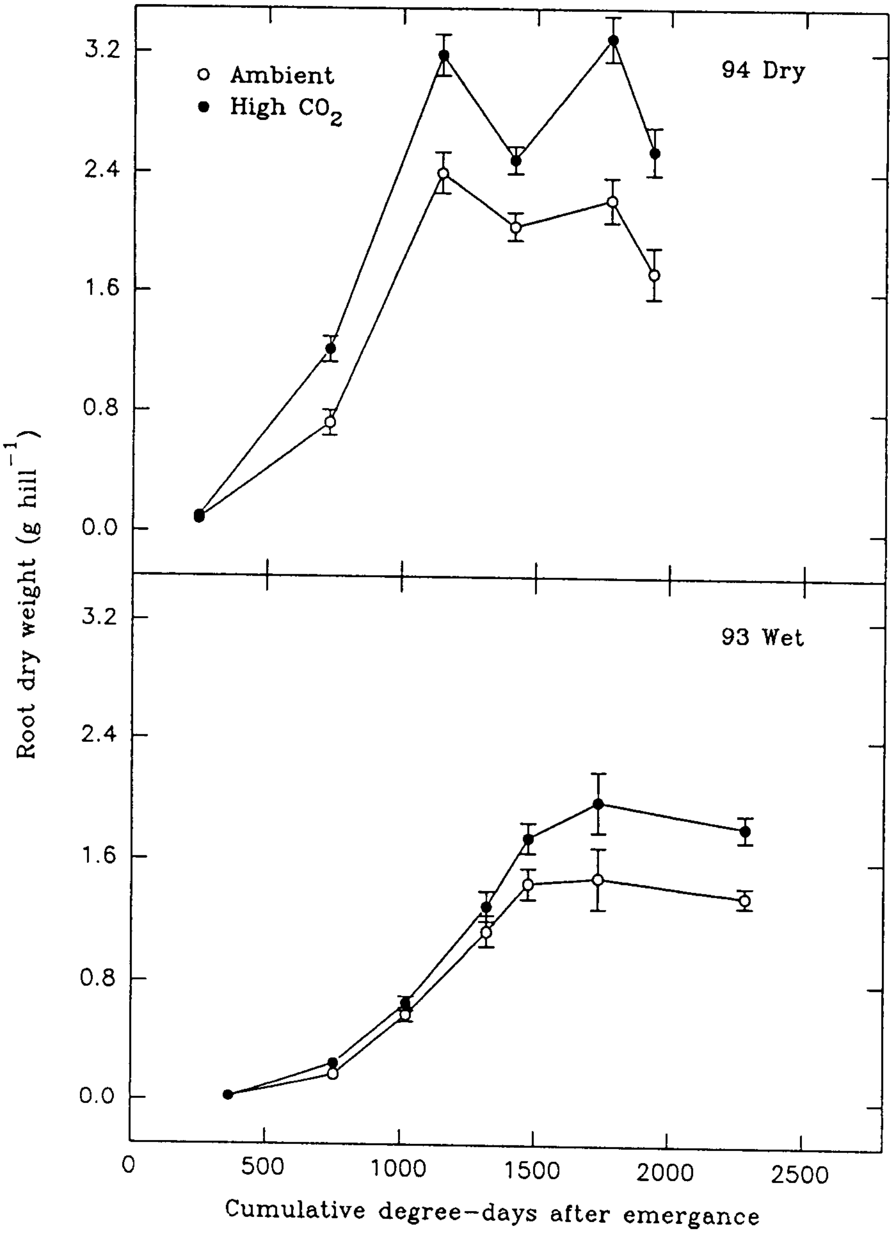

Figure 4.14 Root dry weight in thermal-time of rice cultivar IR72 grown in ambient or high atmospheric CO_2 concentration during the 93 wet and 94 dry seasons.

Table 4.12 Panicle and mature grain characteristics in response to CO_2 concentration and N nutrition for the '93 wet and '94 dry seasons. Filled grain and grain weight were not recorded for the '94 dry season.

Growth CO_2	Fertilizer N	Spikelet Number per panicle		Filled grain %	Grain weight g/100 grains	Developing panicle N (%) 94 Dry			Grain N (%)	
		93 Wet (93)*	94 Dry (77)	93 Wet (93)	93 Wet (93)	94 Dry (55)	94 Dry (67)	93 Wet (82)	94Dry (90)	93 wet (93)
Ambient	N_0	76.3	86.3	78.63	2.28	3.52	0.86	0.98	1.21	1.00
	N_{med}	91.6	116.6	76.06	2.31	3.68	0.98	1.06	1.30	1.10
	N_{high}	91.0	127.4	70.07	2.33	3.65	1.33	1.29	1.36	1.45
	Average	86.3	110.1	75.13	2.31	3.62	1.06	1.11	1.29	1.18
High CO_2	N_0	80.4	90.8	85.74	2.37	4.40	1.05	0.85	0.98	0.87
	N_{med}	90.7	111.4	77.68	2.36	3.75	1.13	0.81	1.07	1.09
	N_{high}	94.6	133.3	79.28	2.39	3.39	1.19	1.08	1.49	1.08
	Average	88.6	111.8	80.9	2.37	3.85	1.13	0.91	1.18	1.01
	SE_{CO2}	ns	ns	1.50	0.01	ns	ns	0.02	0.03	0.02
	SE_N	4.06	6.92	1.83	ns	ns	0.04	0.03	0.04	0.03
	$SE_{CO2 \cdot N}$	ns	ns	ns	ns	ns	ns	0.03	0.05	0.05

ns - not significant at $p<0.05$, SE-standard error for the difference in mean. N_0 - no applied N, N_{med} = N_{50} and N_{90} and N_{high}= N_{100} and N_{200} for the '93 wet and '94 dry seasons respectively. * Values within parenthesis in this row are DAP.

Summary and Conclusions

Increased atmospheric CO_2 concentration has no direct effect on phenological development of rice. There was no effect on the rate of leaf initiation, but leaf growth may be reduced by a change in leaf N at elevated compared to ambient CO_2. Leaf phyllochron value decreased with the initiation of panicle. Based on the inflection point for leaf number in thermal-time, the thermal-time to panicle initiation did not change with increased CO_2 concentration. Thermal-time to flowering also remained unchanged with increased CO_2 concentration.

Recovery of fertilizer N increased with increased CO_2 concentration. However, the change in partitioning of N within the plant and increased specific leaf weight decreased leaf N concentration at high compared with ambient CO_2. Sheath and root N concentration also reduced at high CO_2, despite increases in allocation of N towards those plant parts.

Increased tillering at high compared with ambient CO_2 was a result of greater availability of photoassimilates for tiller growth. However, this increase in tiller number at early stages of growth did not result in increased numbers of panicles. Even though there was an increase in panicle number with high compared to ambient CO_2, it was not proportional to the increase in tillering with increased CO_2 concentration. The increase in tillering caused smaller tillers, fewer panicle bearing tillers, and reduced the panicle size. Increasing fertilizer N to increase leaf N may induce further unproductive tillering which will compete for radiation. Therefore, further increases in fertilizer N may not be an option. This suggests that an unfavorable balance exists between vegetative and reproductive growth at high compared with ambient CO_2 in rice cultivar IR72. Excess tillering should be reduced and stem reserves should be increased through optimum number of healthy tillers, to sustain a high leaf N content. Hence cultivar IR72 used in this study may not be suitable for future high CO_2 environments, even with higher fertilizer N.

Leaf area index of rice has no direct relationship with atmospheric CO_2 and depends mainly on the absorbed N. Increased atmospheric CO_2 increased recovery of N from fertilizer. Therefore, in terms of increasing LAI, N fertilizer requirement for high CO_2 environments should be less than for present ambient conditions, provided that unproductive excessive tillering is reduced, thereby reducing the N dilution.

Rice grain quality could decrease in a high CO_2 environment. Spikelet number and filled spikelet percentage should increase with high CO_2, if adequate N is supplied during reproductive phase to prevent spikelet degeneration. Therefore to sustain higher yield at elevated CO_2 a rice cultivar should be developed with less tillering ability and high foliar N through the season.

CHAPTER 5

LIGHT INTERCEPTION AND RADIATION USE EFFICIENCY WITH INCREASED ATMOSPHERIC CO_2 CONCENTRATION AND N NUTRITION IN RICE (*Oryza sativa* L.)

Introduction

Biomass accumulation of many species grown in nonstress environments can be estimated in terms of the amount of intercepted solar radiation (Monteith, 1977). Radiation use efficiency (RUE) is defined as the efficiency of conversion of radiation energy into dry matter (Monteith, 1977). The relationship between intercepted solar radiation by the canopy and dry matter production are linear for many crops such as soybean *(Glycine max* L. merr.; Shibles and Weber, 1965), maize (*Zea mays* L.; Williams et al., 1965) and guar (*Cyamopois tetragonoloba;* Charles-Edwards et al., 1986). This relationship suggests that at the whole canopy level the nonlinear response of single leaf CO_2 assimilation rate to irradiance (Hesketh and Baker, 1967) is compensated for by other leaves. Linearity between canopy CO_2 assimilation rate and intercepted radiation is supported by Baker and Meyer, (1966), Baker et al. (1990a), Biscoe et al. (1975), and Hesketh and Baker, (1967).

Nitrogen nutrition can strongly affect crop growth through its effect on leaf area and CO_2 assimilation. The latter can affect RUE, since leaf N concentration is strongly correlated with leaf CO_2 assimilation (Evans, 1989; Keulen and Seligman, 1987). Sinclair and Horie (1989) proposed that RUE depends on specific leaf N (SLN), with a greater sensitivity at lower ranges of SLN. Subsequent field experiments for peanut (*Arachis hypogaea* L.) by Hammer and Wright (1994) and Wright et al. (1993), for maize and sorghum (*Sorghum bicolor* L.) by Muchow and Sinclair (1994) and for tall fescue (*Festuca arundinacea*) by

Belanger et al. (1992) confirmed that RUE is indeed dependent on SLN. Further, Sinclair and Shiraiwa (1993) and Wright and Hammer (1994) also showed that a canopy gradient in SLN had a small, but significant, effect on RUE.

With an increase in atmospheric CO_2 concentration there could be an increase in radiation use efficiency (RUE) in rice (*Oryza sativa* L.). Rice responds to increased atmospheric CO_2 concentration through increased biomass production, even without a significant increase in leaf area index (LAI) (Baker et al., 1990b; Imai et al., 1985). However, increased CO_2 concentration also causes a decrease in leaf N concentration in rice (Baker et al., 1992); hence, the effect of CO_2 concentration on RUE could be either positive or negative, depending on the relative magnitude of these two opposing responses.

The RUE may also be affected by the mean daily temperature (Andrade et al., 1993), vapor pressure deficit (Manrique et al., 1991), radiation levels, and the proportion of diffuse radiation (Sinclair et al., 1992; Sinclair and Shiraiwa, 1993).

If the linear relationship between biomass accumulation and intercepted solar radiation in rice under ambient CO_2 concentration is also valid under elevated CO_2 concentration, it would be a significant concept for modeling crop performance. No reports are available on the effect of increased atmospheric CO_2 concentration on RUE of rice under tropical field conditions, where climatic factors are highly variable during the cropping season. Therefore, the objectives of this study were to: a) quantify the relationship between biomass accumulation and intercepted radiation for rice at elevated CO_2 concentration in the tropical field conditions; b) determine the optimum LAI for maximum radiation interception and to relate that to canopy nitrogen content at elevated CO_2; and c) determine the quantitative relationship between radiation use efficiency and leaf N for rice under ambient and elevated CO_2 concentration.

Materials and Methods

Field experiments were conducted during July to October 1993 (93 wet season) and March to May 1994 (94 dry season) in the wetland research site of the International Rice Research Institute (IRRI), Los Banos, Philippines (15^0 N, 121^0 E). The soil was an Andaqueptic Haplaquoll. The experimental unit was a octagonal chamber covered with mylar film with a ground area of 3.3 m^2. The chamber is described on page 34.

Treatments were factorial combinations of two concentrations of CO_2, the current ambient (about 350 to 360 μmol mol^{-1} during day time) and enriched CO_2 (700 μmol mol^{-1} in 94 dry season and about 600 μmol mol^{-1} in 93 wet season) and three fertilizer N levels in a randomized complete block design with three replications. Fertilizer N rates were zero (N_0), 50 (N_{50}), and 100 (N_{100}) kg ha^{-1} N during the 93 wet season and zero (N_0), 90 (N_{90}), and 200 (N_{200}) kg ha^{-1} N during the 94 dry season. Details of the rates, date of applications of fertilizer N and the average CO_2 concentrations inside chambers at each season are given on page 74. and 78 respectively. Diurnal variation in total radiation, temperature, and CO_2 concentration were measured using a computer controlled data acquisition system as described in Fig. 4.2 on page 79. Ambient vapor pressure deficit was obtained from a weather station about 200 m from the experimental site.

Prior to transplanting, the soil was puddled to a depth of about 15 cm. One day before transplanting, 60 kg ha^{-1} of P and 30 kg ha^{-1} of K were applied. Rice cultivar IR72 was transplanted, with three seedlings per hill at 20 cm by 20 cm hill spacing, inside the open top chambers. Plots outside chambers were planted at the same time using the same plant density. Pests and diseases were chemically controlled. Plots were weeded manually.

Crop canopy interception of radiation was measured using tube solarimeters (Type TSL, Delta-T Devices, Cambridge, UK). Tubes were calibrated prior to each experiment using a standard pyranometer (Rimco integrating pyranometer, Selby's Scientific Ltd, Australia). All tubes used for the experiment had an accuracy greater than 97% of the standard reading. Chamber interception of radiation was measured by placing a tube solarimeter in each chamber and comparing with outside radiation before planting of rice seedlings. Chamber walls intercepted about 15% of the radiation in the 93 wet season and 20% in the 94 dry season. One day after transplanting, tube solarimeters were placed midway between plant hills at 5 cm above ground level, oriented in an east-west direction. Dead leaves on plants around solarimeters were removed. Tubes were cleaned at weekly intervals. Solarimeter outputs were read every 60 s, averaged over a 300 s interval, and the 300 s average was recorded throughout the season using CR 10T dataloggers (Campbell Scientific). Cumulated daily total radiation from tube solarimeters were subtracted from total radiation above the canopy inside the chamber to calculate radiation intercepted by the rice canopy.

Biomass sampling was done at 19, 35, 49, 56, 67 DAP in 93 wet season and 22, 42, 56, and 67 DAP in 94 dry season, without disturbing the plants used for radiation measurements. Samples were analyzed for leaf area using an electronic leaf area meter (Hayashi Denko Co., Tokyo, Japan). After measuring the area, leaves and other parts of the plant were dried at 70^0 C for 72 h. Nitrogen concentration of plant tissues were determined using the micro Kjeldahl procedure. Canopy net assimilation was measured with the Li-Cor 6200 photosynthetic gas exchange system (Li-Cor, Lincoln, NE, USA) in conjunction with a 0.4 by 0.4 by 0.6 m Mylar-covered chamber. Description of measurements and specifications are given on page 37.

Analysis of variance, linear and non linear regression analysis was performed using STATGRAPHICS statistical graphics system . Mean comparisons were made using LSD test at $P<0.05$.

Results and Discussion

Radiation interception by the canopy

Early in the growth of the crop there was significantly more interception of radiation in the higher CO_2 treatments. That difference disappeared as the canopy grew. It persisted only a short while in the N_0 treatment and had disappeared in all N treatments by 32 DAP (Table 5.1). This suggests that higher CO_2 stimulated new leaf production, as is shown from the leaf area index (LAI) data in Table 5.2. It also suggest that, for enhanced CO_2 to stimulate leaf production, the plant must have an adequate N supply.

This latter point is supported by the relationship of radiation interception to total above-ground plant N shown in Fig. 5.1. There was no difference in radiation interception between ambient and enhanced atmospheric CO_2 treatments when expressed on the basis of plant N. Figure 5.1 also shows the relationship between LAI and total above-ground plant nitrogen, which was linear and identical for both CO_2 concentrations. Although the LAI was greater as plant above-ground N content increased, radiation interception changed only slightly with LAI at higher LAI values. That was true because at LAI values greater than 5 more than 80% of the radiation was already intercepted. Therefore, as LAI increased above 5 there was relatively little additional radiation to be intercepted.

These results suggest that, if sufficient N is available within the plant, an increase in atmospheric CO_2 will result in greater assimilation and greater biomass production. This enhanced growth should result in an enlarged root system which is capable of taking up more N if it is available in the soil volume occupied by the roots. Greater N uptake lead to greater top growth, greater leaf area, and greater interception of solar radiation. In the absence of added N fertilizer (N_0 treatments in both seasons) or when less radiation is available (the 93

Table 5.1 Radiation interception during the exponential phase of growth of rice variety IR72 grown at ambient or enriched atmospheric CO_2 at different rates of fertilizer nitrogen during the 94 dry season.

CO_2 concentration	Applied Nitrogen	Radiation interception (%)			
		17 DAP	22 DAP	27 DAP	32 DAP
Ambient	N_0	15.9	24.0	30.9	36.4
	N_{90}	23.7	33.3	42.6	50.9
	N_{200}	21.6	33.0	45.2	56.6
High CO_2	N_0	18.2	24.1	29.5	34.1
	N_{90}	26.7	36.2	44.7	52.0
	N_{200}	26.6	41.9	53.2	62.6
SE_{CO2}		0.8	0.9	ns	ns
SE_N		0.9	1.2	1.5	1.5
$SE_{CO2 \times N}$		1.5	1.8	1.7	ns

SE-standard error for the difference in mean at 95% probability. ns - differences were statistically not significant at 5% probability

Table 5.2 Leaf area index of rice grown at ambient and enriched atmospheric CO_2 at different rates of fertilizer N during the '93 wet and '94 dry seasons.

CO_2 concentration	N	93 Wet season					94 Dry season			
		19 DAP	35 DAP	49 DAP	56 DAP	67 DAP	22 DAP	42 DAP	56 DAP	67 DAP
Ambient	N_0	0.185	0.596	1.00	1.30	1.10	0.72	1.65	1.73	1.66
	N_{med}	0.150	0.861	1.60	1.95	2.00	0.94	3.35	3.14	3.32
	N_{high}	0.151	0.849	1.38	2.68	2.68	1.12	4.63	6.31	4.71
Average		0.162	0.769	1.33	1.98	1.93	0.93	3.21	3.73	3.23
High CO_2	N_0	0.291	0.810	1.18	1.29	1.18	0.83	1.73	1.56	1.09
	N_{med}	0.202	0.576	1.37	1.77	2.18	1.38	2.83	3.42	3.27
	N_{high}	0.234	0.889	1.55	2.12	2.01	1.96	5.18	6.34	4.96
Average		0.243	0.758	1.37	1.73	1.79	1.39	3.25	3.77	3.11
SE_{CO2}		0.025	ns	ns	ns	ns	0.03	ns	ns	ns
SE_N		ns	ns	0.08	0.15	0.11	0.04	0.23	0.15	0.13
$SE_{CO2 \times N}$		ns	ns	ns	ns	ns	0.06	ns	ns	ns

ns - not significant at $P<0.05$, SE-standard error for the difference in mean. N_0 - no applied N, N_{med} = N_{50} and N_{90} and N_{high}= N_{100} and N_{200} for the 93 wet and 94 dry seasons respectively.

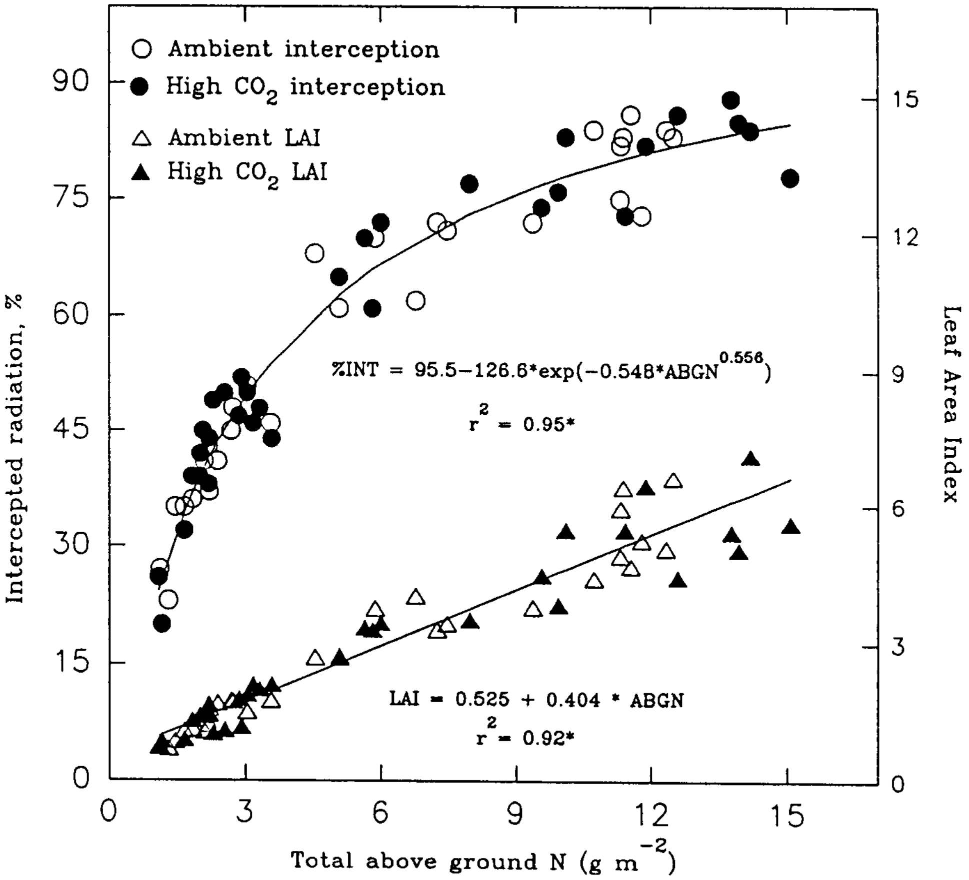

Figure 5.1. Intercepted radiation (% INT) and leaf area index (LAI) as a function of total above ground nitrogen (ABGN) for rice cultivar IR72 grown at ambient and high CO_2 concentration during the '94 dry season. The linear regression between LAI and ABGN for the '93 wet season was; LAI=-0.104+0.501*ABGN, r^2=0.89.

wet season, for example; Fig 4.2 in page 79) that enhanced growth is small, and therefore there was only a small effect of super-ambient CO_2 on radiation interception.

Leaf senescence and, thereby, a reduction in LAI after 55 DAP, had only a small effect on intercepted radiation in either season. This suggests that there was an excessive buildup of leaf area in rice during the latter part of vegetative growth. Stems and panicles also intercept significant amounts of radiation in the later stages of growth. For example in 94 dry season radiation interception reached to its maximum at 50 DAP, at which time about 83% of the total radiation was intercepted by the canopy at an LAI of 6 and 13 g m^{-2} of total above-ground leaf N (Fig. 5.1). At either ambient or high CO_2 concentration, LAI of 6 was achieved at similar level of canopy N. This suggests that, at both ambient and high CO_2, rice has a similar N requirement for optimum light interception. As pointed out earlier (Fig 4.4 in page 84), fertilizer N recovery was greater for rice plants grown at high CO_2 concentration than at ambient CO_2, perhaps because of roots in the higher CO_2 treatment exploited a greater soil volume. Therefore, the actual *fertilizer* N requirement to achieve optimum light interception or LAI for rice should be lower at high than at ambient CO_2. However, with increased CO_2 concentration there was a dilution of leaf N (Fig. 5.2). Thus, high CO_2 plants actually may need more N to compensate for leaf N dilution.

Biomass accumulation and leaf N

There was a large and significant increase in rice plant total-above-ground dry weight with increased CO_2 concentration in the 94 dry season (Fig. 5.3). There was also an increase in above-ground dry weight with increase CO_2 concentration in the 93 wet season. However, differences in dry weight between CO_2 concentrations in the 93 wet season were small and were statistically significant only on two sampling dates. This emphasizes that enhanced

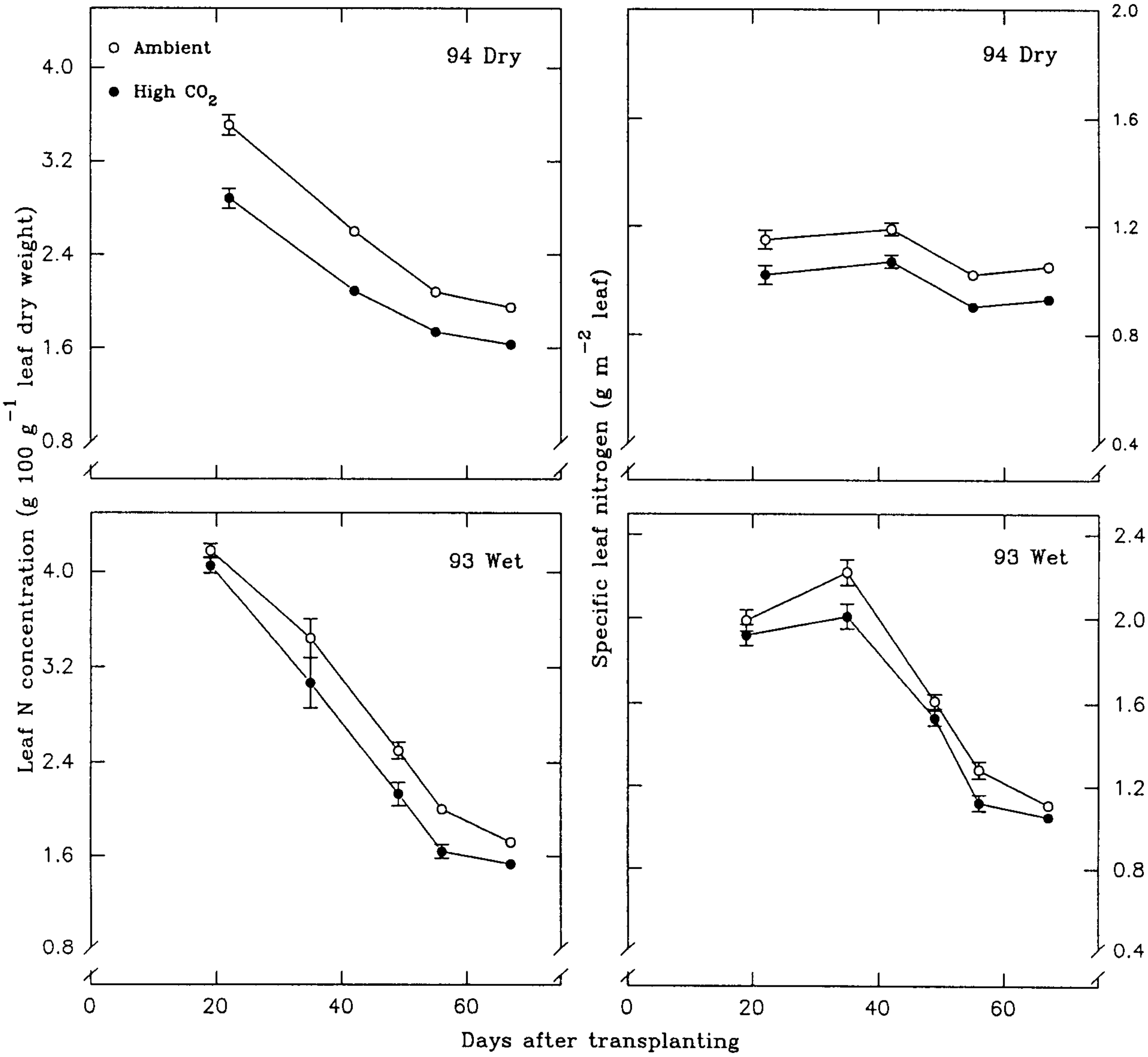

Figure 5.2. Leaf nitrogen concentration on the leaf dry weight and leaf area basis (specific leaf nitrogen) for rice cultivar IR72 grown at ambient and high CO_2 concentration during '93 wet and '94 dry season. Error bar represent standard error of mean.

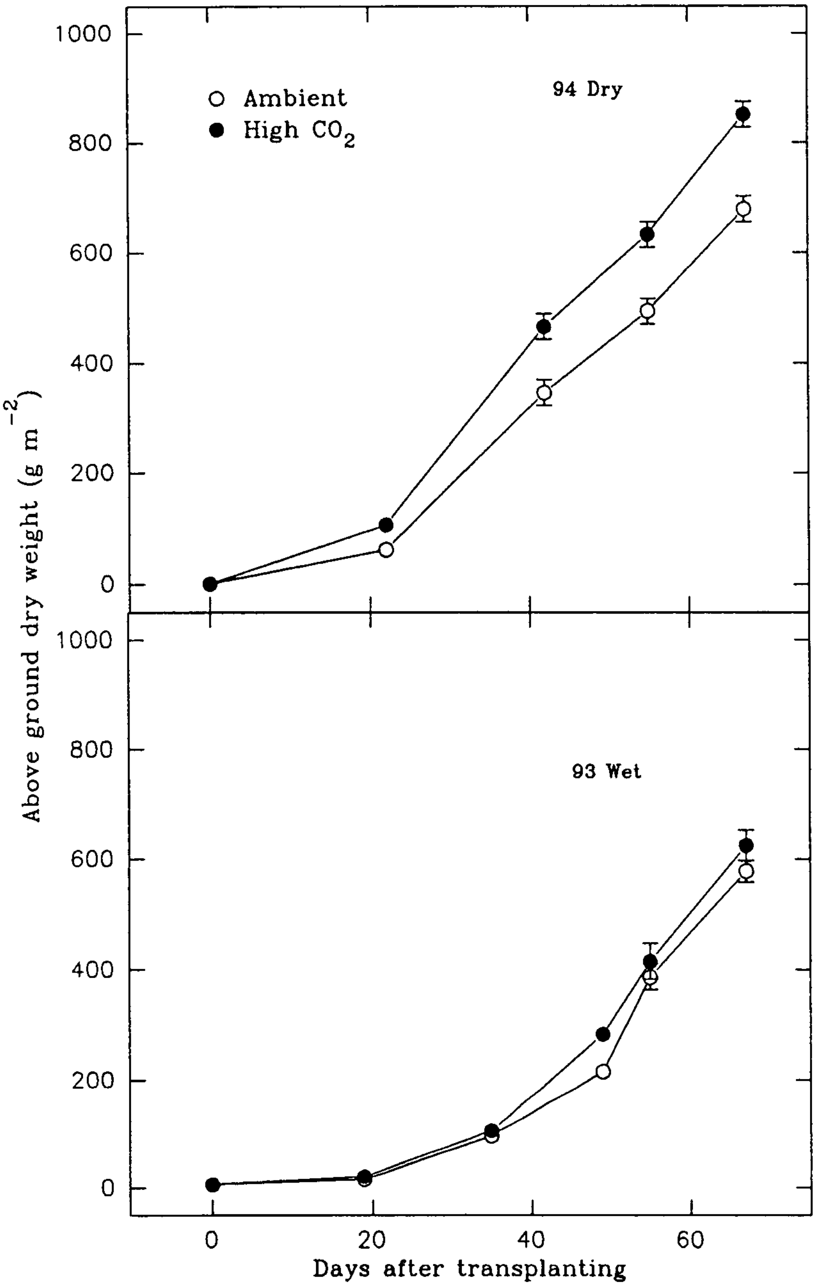

Figure 5.3. Total above-ground dry weight of rice cultivar IR72 grown at ambient and high CO_2 concentration during the '93 wet and '94 dry season. Error bar represent standard error of mean.

atmospheric CO_2 stimulates biomass production only when there is ample radiation intercepted.

Average canopy green leaf N concentration, both on a leaf dry weight and leaf area basis, decreased with time and with increased CO_2 concentration in all N treatments (Fig. 5.2). The average decrease in leaf N on a leaf dry weight basis was 16-19%, while on a leaf area basis it was about 10%. This difference was partly due to an increase in specific leaf weight with increased CO_2 concentration. Even though there were differences in total applied N, N uptake, and other environmental factors, leaf N concentration on dry weight basis was similar in both seasons.

Canopy CO_2 assimilation and radiation interception

Although biomass production had a linear relationship with intercepted solar radiation, the relationship of instantaneous canopy CO_2 assimilation with radiation interception, measured near solar noon on clear days, was nonlinear (Fig. 5.4). This could be because, at lower LAI, the leaves get light saturated with high radiation at noon. After full canopy closure there is less tendency for the canopy to get light saturated. However, the time of exposure to very high irradiance during the diurnal cycle is limited. Thus light saturation has a minor effect on daily total net CO_2 accumulation by the canopy and thereby production of dry matter.

When canopy CO_2 uptake was analyzed on the basis of intercepted radiation, differences in assimilation were due only to concentrations of leaf N and atmospheric CO_2. Canopy assimilation did not respond to increased CO_2 concentration at N_0 (Fig. 5.4) and even at N_{90} the increase was not significant. The increase at N_{200} therefore suggests, that canopy assimilation at a given radiation interception is dependent on leaf N status. Sinclair and Horie (1989) and Schnier et al. (1990) also showed that maximum canopy CO_2 assimilation in rice

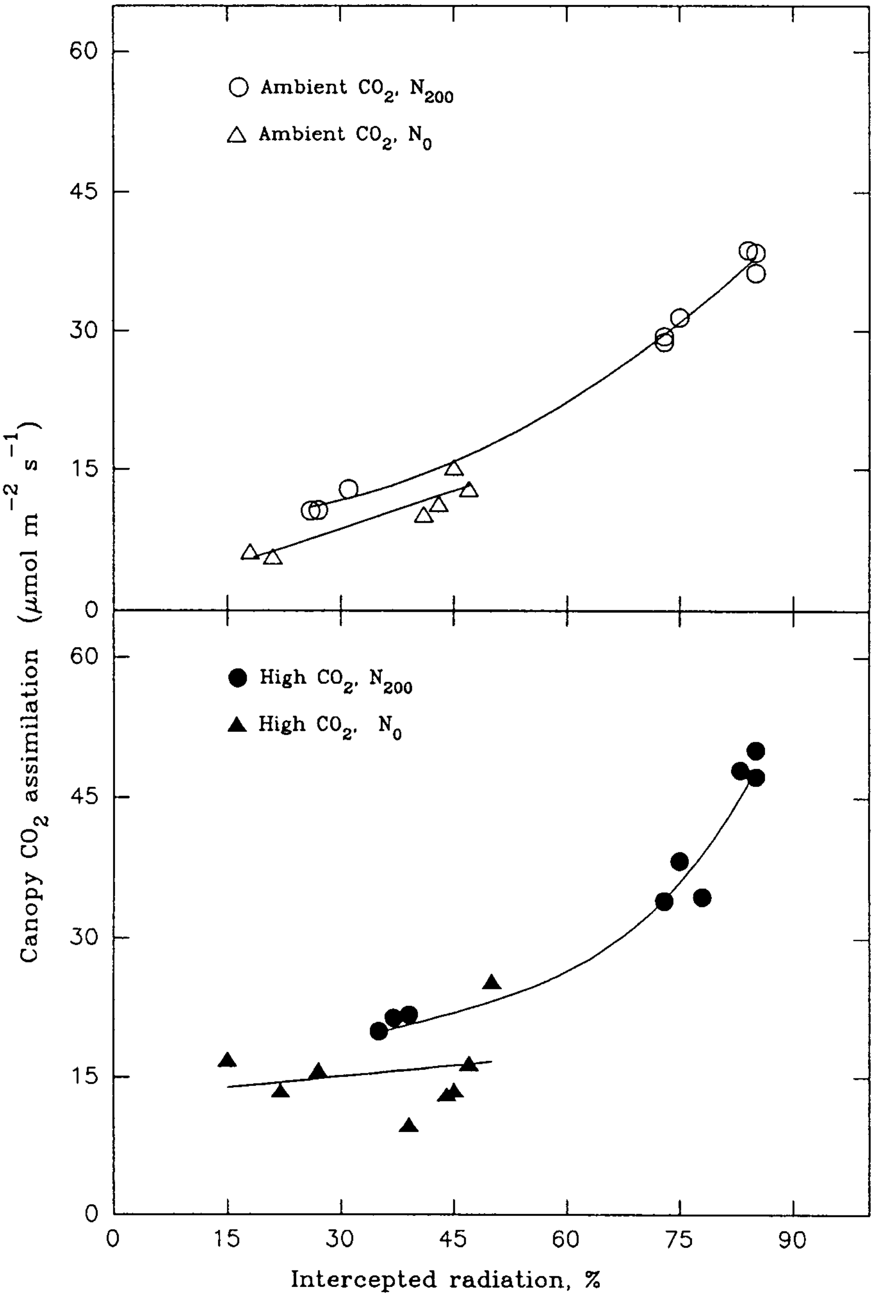

Figure 5.4. Canopy CO_2 assimilation as a function of intercepted radiation for cultivar IR72 grown at ambient and high CO_2 concentration with zero and 200 kg ha^{-1} of fertilizer N in '94 dry season.

depends on leaf N at a given LAI and the increase in assimilation with increased CO_2 concentration was greater at higher LAI. Therefore, the potential benefit of increased CO_2 concentration decreases with dilution of leaf N. These results are further evidence that one of the results of higher atmospheric CO_2 is to dilute leaf N concentration. In the N_0 treatment, that dilution appeared to be to the point where leaf photosynthetic functions were impaired and therefore, leaves were less efficient at utilizing absorbed radiation. Therefore, to maximize Canopy CO_2 assimilation of rice at high CO_2 concentration, dilution of leaf N should be minimized.

Radiation use Efficiency.

Mean above-ground biomass accumulation for all N treatments combined had a linear relationship with cumulative intercepted radiation at both ambient and high CO_2 concentration in both the '93 wet and '94 dry seasons (Fig. 5.5). Average radiation use efficiency was 1.32 g MJ^{-1} at ambient and 1.74 g MJ^{-1} at high CO_2 concentration for the '94 dry season and 1.42 g MJ^{-1} and 1.69 g MJ^{-1} at ambient and high CO_2 respectively for the '93 wet season. Reported RUE values agree well with the values found in this experiment for ambient CO_2. Kiniry et al. (1989) summarized the reported RUE values for rice under ambient CO_2 concentration and found that values varied between locations, with a mean of 2.7 g MJ^{-1} intercepted photosynthetically active radiation. Horie and Sakurtani (1985) reported that the RUE for Japonica rice, on the basis of total crop dry weight, was about 1.9 g MJ^{-1} from planting to 20 days after heading. There was a difference in RUE by about 20% between cultivars and they suggested that it was mainly due to higher soil fertility associated with high yielding cultivars compared to low yielding cultivars. Sinclair and Horie (1989) suggested

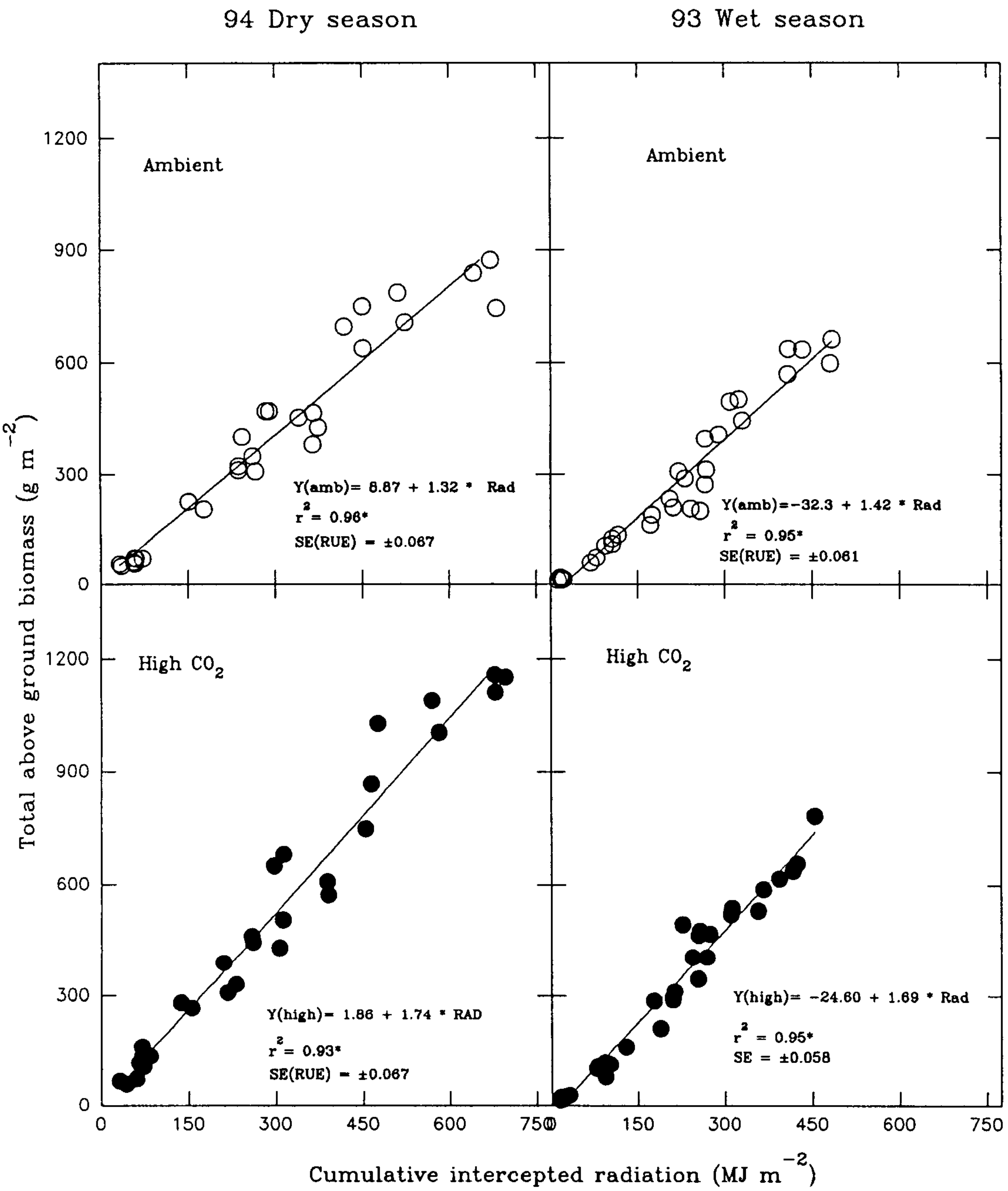

Figure 5.5. Total above-ground biomass as a function of cumulative intercepted total radiation of the rice cultivar IR72 grown at ambient and high CO_2 concentration during 93 wet and 94 dry season.

that RUE of rice at ambient CO_2 concentration could be approximately 1.4 g MJ^{-1} when there is no N stress.

The relationships between total above-ground biomass and cumulative intercepted radiation at different N levels for the 94 dry season are given in Fig. 5.6. The slight nonlinearity in these relationship could be because of differences in plant N, due to different timings of fertilizer N application, and dilution of N with increased CO_2 concentration. Because of the nonlinearity of the relationship between biomass and intercepted radiation, the RUE was calculated for each sample period from planting to flowering by taking the slopes of linear regressions between biomass harvests. Those RUE values are given in Table 5.3. Radiation use efficiency decreased with age at all N levels. However, this is not consistent with the calculations by Sinclair and Horie (1989) that RUE at low LAI was lower because leaves tended toward light saturation. Higher RUE at lower LAI in this study was because of high leaf N at early growth stages, compared to lower leaf N with higher LAI during latter stages. The RUE was highest with N_{200}, in both ambient and high CO_2 concentration. However, differences of RUE at flowering among N treatments was slight in the ambient CO_2 and there was no difference in the RUE between CO_2 concentrations at flowering with N_0. These data suggest that RUE depends on plant N status.

Light saturated single leaf CO_2 assimilation in rice was dependent on leaf N concentration. Canopy CO_2 assimilation at a given level of radiation interception also increased with increased fertilizer N. Therefore, biomass accumulation at a given level of intercepted radiation should depend on leaf N concentration. Thus, RUE in rice should depend on leaf N concentration as is shown in Fig. 5.7. The relationship between RUE and average leaf N was nonlinear. Since leaf CO_2 assimilation has a curvilinear relationship with leaf N concentration, accumulation of very high leaf N results in no advantage to RUE.

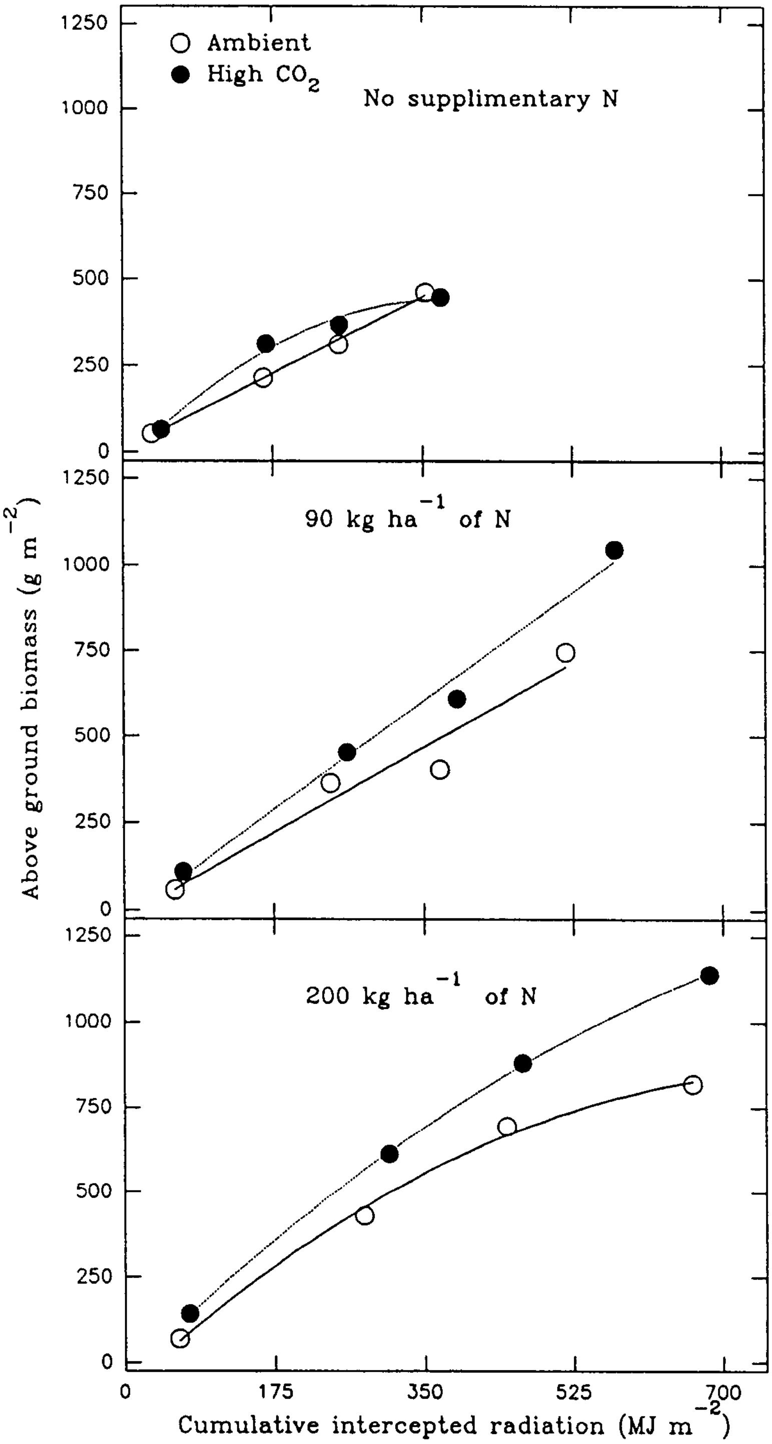

Figure 5.6. Mean total above-ground biomass as a function of cumulative intercepted total radiation for rice cultivar IR72 grown at ambient and high CO_2 concentration at three different rates of fertilizer N during 94 dry season.

Table 5.3 Radiation use efficiency (g MJ^{-1}) of rice variety IR72 for different periods of growth, grown under ambient or enriched CO_2 at different rates of fertilizer N in the 94 dry season.

Time period	Applied treatment	Radiation use efficiency (g MJ^{-1})			
		Ambient	r^2	High CO_2	r^2
22 - 42 DAP	N_0	1.30 ± 0.10	0.93*	1.82 ± 0.08	0.96*
42 - 55 DAP	N_0	1.24 ± 0.06	0.73*	1.55 ± 0.05	0.36
55 - 67 DAP	N_0	1.27 ± 1.55	0.93*	1.26 ± 0.05	0.65
22 - 42 DAP	N_{90}	1.47 ± 0.11	0.95*	1.74 ± 0.04	0.99*
42 - 55 DAP	N_{90}	1.21 ± 0.11	0.45	1.58 ± 0.06	0.67
55 - 67 DAP	N_{90}	1.32 ± 0.11	0.77*	1.72 ± 0.09	0.87*
22 - 42 DAP	N_{200}	1.52 ± 0.07	0.97*	1.98 ± 0.11	0.93*
42 - 55 DAP	N_{200}	1.56 ± 0.05	0.89*	1.92 ± 0.10	0.69*
55 - 67 DAP	N_{200}	1.33 ± 0.08	0.82	1.74 ± 0.07	0.62*

* significant at $P<0.05$.

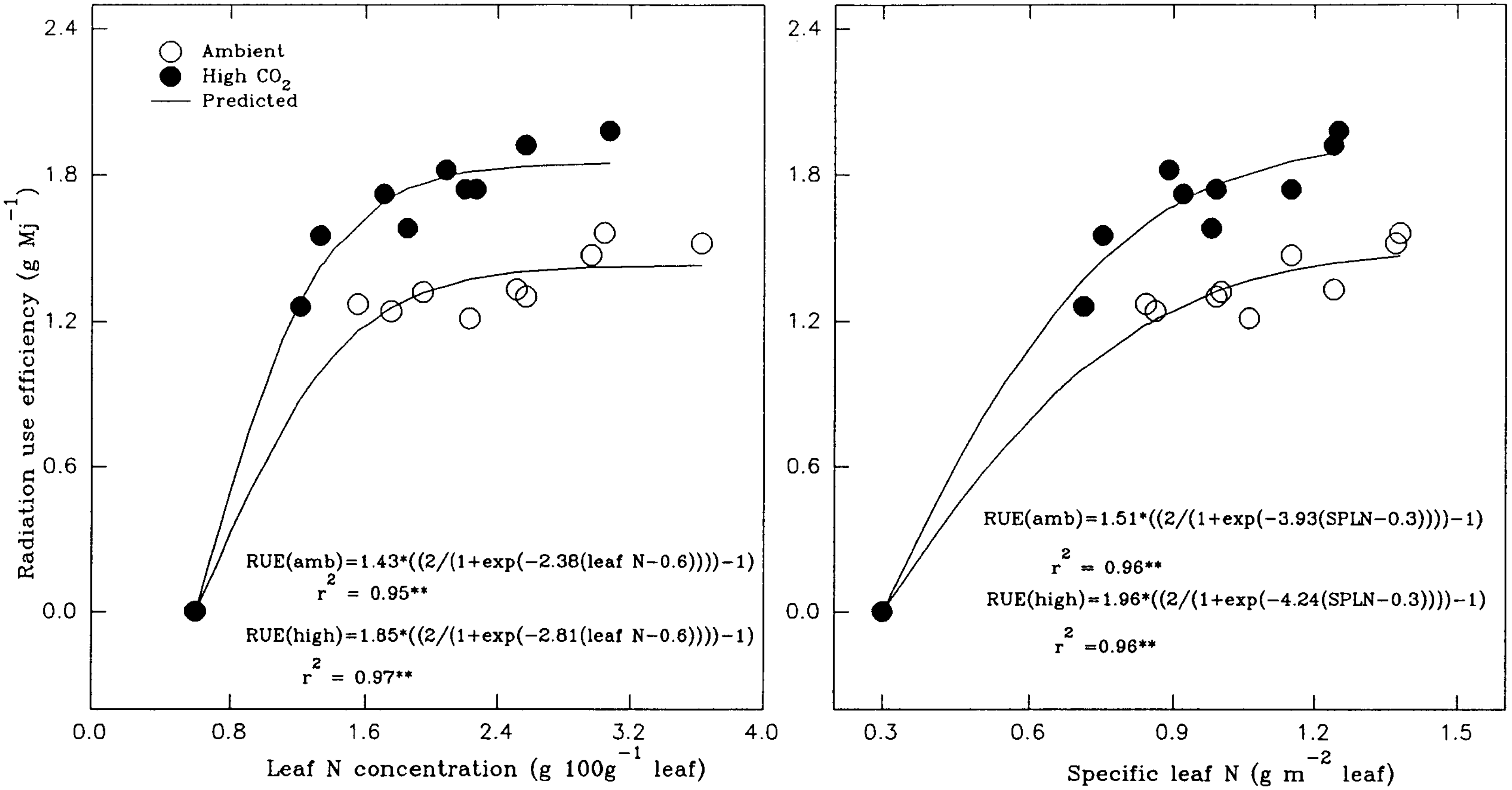

Figure 5.7. Radiation use efficiency (RUE) as a function of average canopy leaf N for rice cultivar IR72 grown at ambient and high CO$_2$ concentration. RUE for different growth periods were determined by linear regression between total biomass and cumulative intercepted total radiation. Average leaf N between two consecutive growth periods were taken as the corresponding leaf N. Leaf N concentration at zero leaf assimilation reported by Dingkuhn et al. (1992) was taken as the N concentration at zero RUE. The data were fitted to the logistic equation derived by Sinclair and Horie (1989).

A decrease in leaf N concentration below the optimum should also reduce potential RUE. This was observed in our field experiments. Radiation use efficiency increased with increased leaf N concentration. Sensitivity of RUE to leaf N increased at lower values of leaf N. Sensitivity of RUE to leaf N concentration also increased with an increase in CO_2 concentration. In general, RUE at ambient CO_2 was relatively stable across leaf N, but at high CO_2 concentration some canopies had very low leaf N and low RUE. These observations are consistent with findings for tall fescue by Belanger et al. (1992), peanut by Wright et al., (1993), Hammer and Wright (1994), and rice by Sinclair and Horie (1989).

Even though there was a similar trend for RUE to decrease with a decrease in leaf N with age in the '93 wet season, we did not observe a clear relationship. This could be as a result of frequent changes in weather during the wet season, resulting in greater heterogeneity of plants within a treatment, and thus making it difficult to find any significant relationship.

Average RUE at ambient CO_2 in the '93 wet season was slightly higher than the 94 dry season. The RUE between seasons at high CO_2 was similar, however. There were large differences in growing environment between the '93 wet and the '94 dry season. The '93 wet season had less incident radiation, a lower maximum temperature and a lower vapor pressure deficit than did the '94 dry season (Fig. 4.2. in page 79). Furthermore, there was a significantly lower average daily CO_2 concentration inside elevated CO_2 chambers in '93 wet season than in '94 dry season as shown in Fig. 4.1 on page 78. However, leaf N concentration was relatively similar for the two seasons.

Evaluation of RUE of many species has shown great stability within a species in nonstressed environments. Therefore RUE is regarded as a stable quantity, in the absence of limitations due to water deficit, nutrition, pest, and disease (Monteith and Elston 1983). Stable RUE in unstable environments have been observed for rice by Horie and Sakurtani (1985), soybean (*Glycine max* L. merr.), mung bean (*Vigna radiata*), and cowpea (*Vigna unguiculata*) by Muchow et al. (1993), and pearl millet by Ong and Monteith (1985). However, Stockle and Kiniry (1990) reported a decline in RUE under high vapor pressure deficit. Sinclair et al. (1992) suggested that RUE may increase with increased diffuse radiation coupled with decreased total irradiance. Therefore, the small increase in RUE (about 2.5%) in this experiment at ambient CO_2 in the '93 wet season compared to the '94 dry season could be due to decreased vapor pressure deficit and increased diffuse radiation with greater cloud cover in during the '93 wet season. Surprisingly, there was no effect of differences in CO_2 concentration inside elevated CO_2 chambers between seasons on RUE. Rice seedlings did not respond to elevated CO_2 concentration of above 545 μmol mol^{-1} as shown earlier in Fig. 2.1 on page 25. This was also supported by findings of Baker et al. 1990a. Therefore it could be suggested that, even under field conditions, RUE of rice cultivar IR72 may not respond to an increased in atmospheric CO_2 concentration above 550 μmol mol^{-1}.

Summary and Conclusions

Increased atmospheric CO_2 concentration stimulated increased radiation interception at early stages of growth. This effect became non significant as the canopy grew. Radiation interception was curvilinearly related to total above-ground N. LAI was linearly related to total above-ground N. Interception of radiation and LAI per unit of total above-ground nitrogen was not different for rice plants grown at ambient and elevated CO_2. This shows that the plant N requirement for radiation interception was similar for rice grown in ambient or high CO_2.

Increased biomass accumulation with high CO_2 differed between seasons, suggesting that the effect of CO_2 concentration depends on level of radiation. There was a decrease in leaf N concentration with increase CO_2 concentration.

Canopy CO_2 assimilation had a nonlinear relationship with radiation interception presumably because of light saturation of leaves at lower LAI. Increased canopy assimilation with increased atmospheric CO_2 concentration was dependent on level of fertilizer N.

Average RUE for ambient CO_2 was 1.4 g MJ^{-1}. RUE at high CO_2 was 1.7 g MJ^{-1}. Radiation use efficiency was curvilinearly related to the canopy leaf N concentration and the sensitivity of RUE to leaf N concentration increased with increased CO_2 concentration. Dilution of leaf N at high CO_2 could have a significant effect on RUE. Therefore, in modeling rice crop responses, decrease in leaf N with increase CO_2 concentration should be considered in terms of RUE, as it could have a significant effect on the ultimate simulated biomass. Radiation use efficiency should be adjusted for changing leaf N, especially at high atmospheric CO_2 concentrations.

The average CO_2 concentration in the high CO_2 treatment was about 100 μmol mol^{-1} lower in the '93 wet season than in the '94 dry season. However, the difference in average RUE between the two seasons was not significant. This insignificant difference in RUE at elevated CO_2 between the '93 wet and '94 dry seasons confirms that rice plant may saturate with atmospheric CO_2 before the predicted doubling of current atmospheric CO_2.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Global atmospheric carbon dioxide (CO_2) concentration is increasing mainly due to emission from fossil fuel combustion and change in land use patterns. The current rate of carbon emission from fossil fuel is about 6.0 ± 0.5 Gt per year, and estimates of release as a result of land use changes are in the range of 1.6 ± 0.5 Gt C per year. The Mauna Loa observatory records shows a 12% increase in mean annual atmospheric concentration of CO_2, from 316 μmol mol^{-1} in 1959 to 354 μmol mol^{-1} in 1990. Along with this increase in CO_2, other green house gases, such as methane, nitrous oxide, and chlorofluorocarbons (CFCs) are increasing. The atmospheric residence times for these gases range from several decades to centuries, thus ruling out any sudden decreases of their atmospheric concentrations.

The primary direct effect of increased CO_2 concentration on plants which have the C_3 pathway of photosynthesis is to increase net CO_2 assimilation. In C_3 plants, increased CO_2 concentration increases assimilation by providing more substrate for assimilation and by suppressing photorespiration.

Productivity of field crops is seldom limited by a single factor, as is suggested by Liebig's law of the minimum. Rather, many factors affect production simultaneously and the marginal return from each limiting factor in combination gives the ultimate response. Productivity of crops under field conditions depends on the interaction of many environmental factors, such as temperature, radiation, moisture, humidity, wind, and edaphic factors, especially nutrient availability. These factors will interact with increased atmospheric CO_2 concentration. Therefore, factors such as the availability of nutrients could limit the response of plants to increased CO_2 concentration.

Rice (*Oryza sativa* L.) is the only major cereal grain used almost exclusively for human consumption. Globally, rice ranks second to wheat in area harvested with 147 million ha in 1991. Eighty five percent of all rice produced is consumed directly by humans, compared with 60% for wheat and 25% for maize (*Zea mays* L.). Of the 25 top rice producing nations, 17 are located within South, Southeast and East Asia. The world rice requirements are predicted to increase at a compound rate of 1.7% per year between now and year 2025. This means that by year 2025, the world needs an additional 13 million tons of rough rice each year. Much of that increase must come from additional production in Asia.

Increased atmospheric CO_2 could be of great advantage in achieving that goal. However, improvements of agronomic and cultural management of rice to suit a new environment is vital in realizing the maximum benefit. Thus, understanding the rice plants behavior to increased CO_2 concentration under tropical environments is of primary importance. This work was undertaken to evaluate the combine effect of increased atmospheric CO_2 concentration and fertilizer N on rice plant growth and development.

Preliminary work was done in controlled environment chambers in the U.S. Environmental Protection Agency's Environmental Research Laboratory in Corvallis, Oregon to evaluate the response of rice seedlings, cultivars IR72 and KDML 105, to different concentrations of CO_2 and N nutrition. Four concentrations of atmospheric CO_2 (373, 545, 723, and 895 μmol mol^{-1}) and three fertilizer N rates (12, 24, and 36 mg N per plant) were tested, inside 1 m^3 chambers, located inside a glass house exposed to natural sunlight. Response of rice seedlings to increased atmospheric CO_2 in both cultivars were limited to concentrations of 545 μmol mol^{-1}. The response to increased atmospheric CO_2 concentration depended on N nutrition. There were no cultivar differences for any agronomic trait tested in this study. Root and shoot biomass, root:shoot biomass ratio, leaf and tiller number increased with CO_2 and N, with greatest increase occurring between 373 to 545 µmol mol^{-1}. An increase in total seedling dry weight with increased CO_2 concentration suggests, that seedling vigor increases with increased atmospheric CO_2. Leaf CO_2 assimilation increased with increased CO_2, however, the response was limited to concentrations of 545 µmol mol^{-1} and was dependent on leaf N. With increased CO_2 concentration there was a dilution of leaf N. Leaf C:N ratio decreased with increased CO_2 concentration. This should decrease both leaf CO_2 assimilation and leaf dark respiration. Therefore, there could be an acclimation of rice leaves to increased CO_2, due to dilution of N. These results also suggest that, when interpreting data on rice plant growth under different concentrations of atmospheric CO_2, dilution of leaf N at higher CO_2 concentration must be considered as it can affect the overall growth and development. Dilution effects cannot be ignored even on rice seedlings as young as 21 days.

Pot experiments in controlled environment chambers are criticized for their inability to simulate the natural environments. Smaller rhizosphere volume, lower radiation, increased temperatures and increased vapor pressure deficits might interact with treatments to alter plant responses. Therefore, our next objective was to simulate the high CO_2 environment in rice fields in Asia, where most rice grows. However, controlling CO_2 concentrations in the field is costly and difficult. Thus the field experiment was limited to two concentrations of CO_2.

Rice cultivar IR72 was tested at ambient and elevated CO_2 concentrations with three rates of fertilizer N. Eighteen, octagonal, 2 m tall, open top chambers with a cross sectional area of 3.3 m^2 were built on rice fields at IRRI, Philippines. Nine chambers were maintained at high CO_2 and nine at ambient CO_2. Controlling of CO_2 concentration, monitoring and recording of environmental variables such as, temperature and radiation inside the chambers were done by a computer controlled data acquisition system. The objectives were to understand the CO_2 fluxes at both leaf and canopy levels, phenological development, plant growth and N dynamics, and fertilizer N recovery, and to relate these responses in terms of light interception and radiation use efficiency for rice plants exposed to long-term high CO_2 concentrations.

Single leaf CO_2 assimilation increased with increased atmospheric CO_2 concentration. However, there was an acclimation of leaves to prolonged exposure to high atmospheric CO_2. Leaf mesophyll resistance increased at high CO_2, suggesting a leaf acclimation at the biochemical level. Leaf mesophyll resistance decreased with increased fertilizer N. There was also a decrease in leaf N with increased CO_2 concentration. Thus, acclimation of rice leaves to high atmospheric CO_2 could be due to a decrease in leaf N.

There was a curvilinear relationship between single leaf CO_2 assimilation and average leaf N concentration. leaf CO_2 assimilation per unit leaf N increased with increased CO_2 concentration. The critical N concentration for CO_2 assimilation was about 2-2.5%, and any decrease in leaf N below critical limited response of leaves to high CO_2. Therefore, with increased CO_2 concentration, to maximize leaf CO_2 assimilation dilution of leaf N should be avoided, and leaf N should be maintained above 2.5%.

Stomatal resistance increased with increased CO_2 concentration, but the effect of CO_2 on stomatal resistance was much less than that on mesophyll resistance. Therefore, the increased stomatal resistance had an insignificant effect on leaf CO_2 assimilation, but it could have a significant effect on rice leaf transpiration at midday.

Canopy CO_2 assimilation also increased with increased atmospheric CO_2, but the magnitude of response depended on the of fertilizer N. There was no increase in canopy CO_2 assimilation with increased atmospheric CO_2 at low N, levels suggesting that decreased leaf N at elevated CO_2 impaired leaf photosynthetic functions making leaves were less efficient in utilizing absorbed radiation. Therefore, beneficial effects of increased CO_2 on rice may not be realized at lower rates of fertilizer N.

Single leaf respiration decreased with increased atmospheric CO_2 concentration when there was a decrease in leaf N. Also there was also no increase in single leaf respiration with increased total nonstructural carbohydrates, indicating that substrate for respiration was not limited in either ambient and high CO_2. There was no difference in single leaf respiration per unit of leaf N between high and ambient CO_2, suggesting leaf respiration depended more on leaf N than on CO_2 concentration or substrate level. Therefore, decrease in leaf respiration at high compared to ambient CO_2 during vegetative growth could be related to the decrease in cost for maintenance and growth of leaves with decreased leaf N. However, this decrease in leaf respiration was not reflected at the canopy level. Canopy respiration was either not different or was greater at high compared with ambient CO_2, but it was not proportional to growth enhancement at elevated CO_2. This suggests that there is a decrease in respiratory cost per unit of biomass at high compared to ambient CO_2. This was due to the decrease in partitioning of N to leaves and increased partitioning to less metabolically active stems and sheaths at high compared with ambient CO_2. Respiratory CO_2 loss was about 19% of CO_2 assimilation during midday with high fertilizer N during the vegetative period. At late booting stage, because of greater uptake of CO_2 by plants grown at high CO_2 concentrations, respiratory loss decreased to 16% of midday assimilation, while it remained the same at ambient CO_2. Therefore, with anticipated future increase in atmospheric CO_2 concentration there will be a relative decrease in respiratory loss by rice plants.

Atmospheric CO_2 concentration had no direct effect on phenological development on rice cultivar IR72. There was no effect on rate of leaf initiation, but leaf growth may be reduced by a change in leaf N at elevated compared to ambient CO_2. The leaf phyllochron value decreased after panicle initiation. Thermal time to panicle initiation and flowering remained unchanged with increased CO_2 concentration with rice cultivar IR72. This suggests that, with a future increase in atmospheric CO_2, phenological development of rice will not be changed.

Recovery of fertilizer N increased with increased CO_2 concentration, which could be due to a greater rate of N uptake and a larger root density, which prevented leaching losses of N fertilizer. Under elevated CO_2 partitioning of N to leaves decreased, while it increased towards sheath and root. The change in partitioning of N and increase specific leaf weight decreased leaf N concentration at high compared with ambient CO_2. Despite increases in allocation of N towards sheaths and roots, N concentration of those organs also decreased at high CO_2.

Increased tillering at high compared with ambient CO_2 was a result of greater availability of photoassimilates for tiller growth. However, this huge increase in tiller number at early growth stages did not proportionally increase panicle number with increased CO_2 concentration. Increased tillering caused smaller tillers, fewer panicle-bearing tillers, and reduced panicle size. Further increases in fertilizer N above 200 kg ha^{-1} to increase leaf N and to prevent tiller death may induce further unproductive tillering, which would compete for light. Therefore, further increases in fertilizer N may not be an option. This suggests that an unfavorable balance exists between vegetative and reproductive growth at high compared to ambient CO_2 in rice cultivar IR72. Excess tillering should be reduced and stem reserves should be increased through optimum number of healthy tillers, to sustain a higher leaf N content. Hence, cultivar IR72 used in this study may not be suitable for future high CO_2 environments, even with higher fertilizer N.

Increased atmospheric CO_2 concentration stimulated new leaf production and increased radiation interception at early growth stages due to increased tillering. This effect disappeared as the canopy grew. The LAI of rice had no direct relationship with atmospheric CO_2 concentration, but was linearly related to the above-ground total N. Radiation interception was curvilinearly related to total above-ground N and was identical in rice plants grown at ambient and elevated CO_2, when expressed on the basis of total above-ground N. Therefore, in terms of increasing LAI and interception of radiation, N fertilizer requirement for rice grown at high CO_2 should be less than that of ambient, provided that unproductive excessive tillering is reduced, thereby reducing leaf N dilution.

Increased biomass accumulation with high CO_2 differed between the seasons, suggesting that the effect of CO_2 concentration also depends on radiation level. Average radiation use efficiency (RUE) for ambient CO_2 was 1.37 g MJ^{-1}. Average RUE for high CO_2 was 1.71 g MJ^{-1}, an increase of about 25% over ambient. Radiation use efficiency was curvilinearly related to average canopy leaf N concentration and sensitivity of RUE to leaf N concentration increased with increased CO_2 concentration. Therefore, in modeling rice crop responses, the decrease in leaf N with increase CO_2 concentration should be considered in terms of RUE, as it could have a significant effect on the ultimate simulated biomass. Radiation use efficiency should be adjusted for changing leaf N, especially at high atmospheric CO_2 concentrations.

Rice grain N could decrease in a high CO_2 environment. Spikelet number and filled spikelet percentage should increase with high CO_2 if adequate N is supplied during reproductive growth to prevent spikelet degeneration. Therefore, to sustain higher production at elevated CO_2 a rice cultivar with less tillering and high foliar N through the season should be developed.

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APPENDIX

Appendix Table 1. Daily maximum and minimum air temperature and total radiation at the experimental site during the 93 wet and 94 dry seasons.

	1993 Wet season				1994 Dry season		
J Day	Max. T	Min T	Radiation Mj/day	J Day	Max. T	Min T	Radiation Mj/day
182	30.1	25.6	19.4	60	32.6	21.0	26.2
183	34.6	25.8	18.4	61	31.6	21.6	17.3
184	33.0	24.5	19.0	62	32.0	21.4	20.4
185	32.7	25.0	22.8	63	32.4	22.0	23.7
186	33.5	25.7	21.9	64	31.7	22.5	15.4
187	34.0	24.0	26.9	65	32.5	23.3	23.0
188	33.5	24.8	29.0	66	32.6	22.7	18.5
189	31.5	25.0	19.4	67	36.6	24.4	23.3
190	29.0	23.5	6.6	68	34.5	24.9	25.8
191	30.6	23.6	17.2	69	34.2	23.4	25.2
192	32.0	23.7	21.0	70	32.2	24.7	12.1
193	32.2	24.0	24.0	71	33.5	23.5	18.2
194	32.8	23.5	24.8	72	34.1	23.8	25.0
195	34.0	24.8	26.4	73	33.6	24.0	26.5
196	33.0	24.6	27.8	74	33.5	23.5	23.1
197	31.0	24.3	11.6	75	33.6	23.3	23.8
198	32.7	25.3	14.0	76	32.8	24.0	17.7
199	32.0	23.5	23.9	77	33.8	22.5	25.8
200	32.1	24.1	20.8	78	34.1	22.5	25.5
201	32.2	23.4	21.6	79	34.2	23.6	20.6
202	32.1	23.7	21.9	80	32.1	24.5	19.0
203	33.5	24.0	23.7	81	32.5	22.9	18.8
204	33.2	24.0	23.4	82	36.2	22.7	24.6
205	32.1	25.5	20.4	83	33.0	23.5	20.1
206	36.3	24.0	23.3	84	31.2	24.2	11.2
207	35.0	24.6	17.3	85	32.2	23.6	16.8
208	34.5	26.0	10.8	86	31.9	23.6	15.6
209	32.5	25.5	7.8	87	32.0	21.0	27.4
210	31.2	24.5	8.5	88	33.0	21.7	23.6
211	31.7	23.0	8.2	89	32.2	23.2	22.9
212	33.0	24.0	22.4	90	33.0	21.7	27.6
213	32.5	24.1	16.5	91	33.6	21.4	30.0
214	33.0	23.2	24.0	92	34.5	22.1	28.0
215	30.5	24.0	6.6	93	34.0	22.7	20.4
216	33.0	24.1	20.5	94	33.8	23.8	23.1
217	33.5	23.4	26.7	95	31.0	24.2	4.2
218	33.5	24.2	19.7	96	35.2	23.2	25.9
219	33.5	24.6	16.5	97	35.0	23.4	24.1
220	31.2	25.0	7.0	98	35.5	22.9	22.4
221	25.3	23.1	2.6	99	36.0	21.2	27.4
222	26.2	23.3	3.9	100	37.1	22.6	26.8
223	30.5	23.2	15.2	101	36.4	23.5	24.8
224	31.5	24.5	18.5	102	36.0	24.2	27.1
225	30.5	24.5	10.0	103	36.2	24.7	27.6

226	33.0	23.4	17.7
227	32.0	23.4	24.4
228	30.8	22.3	22.2
229	30.3	23.9	13.2
230	28.0	23.6	6.3
231	31.5	23.5	10.0
232	33.5	22.6	28.4
233	32.8	23.4	25.3
234	31.0	24.4	9.7
235	29.5	23.9	7.5
236	32.1	24.6	22.0
237	32.0	23.5	26.3
238	33.0	25.2	22.1
239	32.5	24.2	16.3
240	31.3	23.1	17.4
241	31.9	23.0	19.3
242	31.0	23.2	19.4
243	32.5	24.6	21.2
244	32.5	24.2	16.8
245	32.5	23.8	16.9
246	33.1	25.1	18.9
247	29.9	24.0	9.9
248	32.1	23.7	21.6
249	32.0	23.6	15.1
250	32.8	24.2	20.2
251	31.1	24.4	13.4
252	30.2	23.2	9.1
253	32.1	23.2	15.7
254	30.8	24.2	10.7
255	31.3	23.2	16.9
256	32.1	23.2	17.7
257	31.0	23.5	15.5
258	29.5	24.3	6.3
259	30.0	24.0	7.9
260	33.5	22.2	20.2
261	32.5	24.1	17.3
262	31.9	24.1	13.1
263	32.0	23.4	12.8
264	33.2	24.0	19.6
265	33.0	24.7	18.7
266	34.0	23.7	23.3
267	33.2	23.0	24.9
268	34.0	24.2	23.4
269	33.5	24.2	22.1
270	32.0	24.9	10.7
271	31.5	24.1	11.7
272	33.0	24.4	21.1
273	33.0	24.0	22.9
274	32.7	24.2	16.1
275	31.7	23.4	12.7
276	32.0	24.0	11.6

104	35.2	24.7	26.8
105	35.2	24.2	28.5
106	35.0	23.7	23.6
107	36.1	24.6	23.9
108	35.5	23.9	29.1
109	36.0	23.6	26.8
110	35.5	24.5	19.1
111	37.0	24.8	27.1
112	36.1	25.5	20.6
113	35.2	24.6	14.8
114	35.7	24.3	24.4
115	35.8	25.0	19.7
116	36.2	24.4	29.1
117	36.5	23.5	25.6
118	36.7	25.2	24.9
119	32.9	26.1	4.4
120	36.7	24.8	18.9
121	37.4	24.5	27.2
122	36.7	24.6	21.2
123	36.3	24.5	19.7
124	36.6	25.0	22.7
125	37.2	24.6	22.8
126	37.8	24.2	24.3
127	36.1	25.0	17.2
128	36.2	25.4	17.9
129	36.0	24.5	20.9
130	36.6	25.0	23.3
131	35.8	24.3	21.1
132	36.4	24.7	27.4
133	37.2	24.6	26.0
134	37.4	24.5	21.8
135	35.9	24.5	18.2
136	38.0	24.5	25.9
137	36.2	24.6	26.1
138	37.2	24.0	20.2
139	36.0	25.2	18.6
140	34.9	25.4	17.1
141	37.0	25.7	19.3
142	35.2	25.5	12.2
143	37.5	25.2	24.7
144	36.0	25.8	20.9
145	33.0	26.1	10.4
146	33.9	25.9	16.8
147	37.5	23.7	25.6
148	37.0	23.7	26.7
149	37.0	25.3	24.1
150	36.9	23.8	19.5
151	37.5	24.0	22.7

Appendix Table 1. contd...

277	30.0	23.9	4.5
278	30.0	25.0	3.7
279	30.7	25.0	9.6
280	32.0	24.1	13.2
281	33.0	23.7	24.4
282	32.6	21.1	18.1
283	31.6	23.1	13.5
284	34.2	21.5	23.1
285	32.5	23.2	20.8
286	31.2	23.5	12.1
287	30.3	23.4	13.1
288	30.7	23.2	11.8
289	30.5	23.7	14.0
290	31.4	24.0	11.5
291	31.0	24.6	8.2
292	32.1	23.9	16.3
293	33.6	23.7	23.7
294	32.6	23.4	19.4
295	30.0	23.9	7.0
296	30.5	24.2	13.2
297	29.5	23.7	6.4
298	28.2	23.2	5.2
299	29.2	23.5	9.1
300	31.9	23.5	22.9
301	32.0	22.9	18.6
302	30.0	24.2	10.3
303	31.6	23.6	13.1
304	32.5	22.5	19.2

Appendix Table 2. Haun Scale leaf number of rice cultivar IR72 grown at ambient or elevated CO_2 and different levels of N nutrition during the 93 wet and 94 dry seasons.

Chamber number	CO2	N	REP	Haun Scale Leaf Number							
				1993 Wet Season							
				215 *	222	229	236	244	250	260	
				633 **	769	905	1041	1201	1321	1515	
1	0	0	1	6.8	7.6	8.6	9.5	10.6	11.3	12.7	
5	0	0	2	6.6	7.7	9.1	10.3	11.2	12.0	12.8	
17	0	0	3	6.9	8.4	9.4	10.3	11.1	11.9	12.7	
3	0	1	1	7.0	8.1	9.2	10.6	11.4	12.3	13.4	
14	0	1	2	6.8	8.5	9.2	10.2	11.3	12.3	12.8	
7	0	1	3	6.6	7.3	8.5	9.7	10.8	11.6	12.9	
12	0	2	1	6.5	8.1	9.1	10.1	11.2	12.1	13.0	
4	0	2	2	6.9	9.0	10.0	11.1	12.1	13.1	14.1	
8	0	2	3	7.2	8.0	9.0	10.1	11.3	12.2	13.2	
13	1	0	1	6.5	8.2	9.2	10.1	11.1	11.7	12.9	
16	1	0	2	6.9	8.6	9.7	10.8	11.8	12.6	13.3	
18	1	0	3	6.9	8.5	9.5	10.4	11.3	11.9	12.3	
11	1	1	1	6.6	8.1	9.1	10.3	11.3	12.3	13.3	
15	1	1	2	6.2	8.0	9.1	10.3	11.2	12.0	13.0	
9	1	1	3	6.6	8.6	9.7	11.0	11.9	12.9	14.0	
2	1	2	1	6.3	8.2	9.3	10.5	11.4	12.4	13.4	
6	1	2	2	6.9	8.4	9.5	10.4	11.3	12.2	13.2	
19	1	2	3	6.7	8.1	9.1	10.1	11.1	12.0	13.0	
				1994 - Dry Season							
				73 *	87	94	101	108	112	116	122
				244 **	526	665	813	967	1056	1145	1280
1	0	0	1	3.7	4.6	5.4	6.7	7.5	7.9	8.5	9.2
4	0	0	2	3.7	4.0		6.6	7.3	7.6	8.1	9.3
17	0	0	3	3.7	4.3	5.6	7.0	7.5	7.9	8.5	9.2
3	0	1	1	3.7	4.2	5.8	7.0	7.8	8.2	8.8	9.5
14	0	1	2	3.7	4.2	5.3	6.7	7.5	8.0	8.5	9.4
7	0	1	3	3.7	4.1	5.8	7.1	8.0	8.3	8.9	9.8
12	0	2	1	3.7	4.0	5.3	6.9	7.9	8.3	8.9	9.6
5	0	2	2	3.7	4.2	5.6	6.8	7.5	8.0	9.1	9.7
8	0	2	3	3.7	4.0	5.5	7.0	8.1	8.5	9.3	10.0
11	1	0	1	3.8	4.1	5.7	7.0	7.8	7.8	8.5	9.2
16	1	0	2	3.8	4.2	5.6	6.8	7.3	7.6	8.2	8.9
19	1	0	3	3.8	4.0	5.5	6.6	7.2	7.6	8.0	9.2
2	1	1	1	3.8	4.3	5.4	7.1	7.9	8.2	9.0	9.6
15	1	1	2	3.8	4.1	5.3	6.4	7.1	7.4	8.1	8.8
9	1	1	3	3.8	4.0	5.6	6.8	7.3	7.8	8.4	9.2
13	1	2	1	3.8	4.3	5.7	7.0	7.8	8.2	9.0	9.8
6	1	2	2	3.8	4.4	6.3	7.4	8.3	8.6	9.3	10.1
18	1	2	3	3.8	4.5	5.4	6.7	7.5	7.9	8.7	9.3

Appendix Table 3. Effects of increased atmospheric CO_2 and N nutrition on growth of rice cultivar IR72 during, 94 dry season.

Days after planting	Treatment			Plant Height (cm)	Number of			Green leaf area (cm^2)	Dry weight				Total N Conc.			
	CO2	N	REP		Tillers /hill	Panicles /hill	Leaves /hill		Leaf (g/hill)	Sheath (g/hill)	Root (g/hill)	Panicle (g/hill)	Leaf N (%)	Sheath N (%)	Root N (%)	Panicle N (%)
22	0	0	1	40.55	14.75		52	297	1.05	1.00	0.65		3.40	1.61	1.10	
22	0	0	2	42.60	14.25		50	292	1.01	0.95	0.62		3.23	1.31	0.96	
22	0	0	3	43.80	12.50		43	280	0.90	1.35	0.59		3.36	1.64	1.29	
22	0	1	1	42.63	15.75		50	333	1.10	1.12	0.59		3.36	1.50	1.29	
22	0	1	2	42.23	15.00		49	345	1.20	1.22	0.68		3.39	1.47	1.32	
22	0	1	3	44.25	20.50		66	452	1.46	1.45	1.12		3.48	1.57	1.02	
22	0	2	1	45.58	18.00		55	430	1.42	1.34	0.70		4.09	1.94	1.54	
22	0	2	2	45.48	23.33		72	486	1.52	1.37	0.69		3.98	2.05	1.34	
22	0	2	3	42.78	17.00		60	434	1.37	1.40	0.88		3.32	1.48	1.06	
22	1	0	1	44.70	18.75		59	360	1.40	1.54	0.92		3.17	1.43	1.17	
22	1	0	2	42.18	15.00		49	296	1.05	1.26	0.64		2.71	1.21	1.12	
22	1	0	3	42.55	16.75		58	344	1.21	1.43	0.80		2.52	1.10	0.97	
22	1	1	1	42.48	27.00		88	565	2.02	2.57	1.33		2.56	1.12	1.04	
22	1	1	2	42.68	25.75		78	523	1.87	2.38	1.49		2.54	1.09	1.13	
22	1	1	3	44.80	24.75		79	580	2.08	2.62	1.34		2.78	1.14	1.08	
22	1	2	1	48.38	29.50		94	717	2.46	2.92	1.73		3.01	1.40	1.24	
22	1	2	2	47.78	35.00		105	841	2.89	3.46	1.77		3.28	1.40	1.38	
22	1	2	3	47.68	34.00		103	799	2.72	2.63	0.93		3.41	1.52	1.20	
42	0	0	1	56.30	19.75		79	686	3.67	7.02	2.46		1.88	0.65	0.91	
42	0	0	2	53.98	16.00		64	626	2.93	5.21	1.84		1.89	0.62	0.83	
42	0	0	3	57.50	16.00		61	675	3.20	5.83	1.68		1.81	0.65	0.76	
42	0	1	1	66.68	26.25		108	1340	5.75	7.98	2.57		2.51	0.95	0.98	
42	0	1	2	67.35	20.75		84	1081	5.20	7.70	2.36		2.54	0.93	1.02	
42	0	1	3	68.35	34.50		125	1606	7.25	11.14	3.17		2.43	0.85	1.01	
42	0	2	1	69.15	32.00		144	1960	8.80	10.04	2.82		3.41	1.52	1.18	
42	0	2	2	68.60	38.25		158	2093	9.19	9.66	2.67		3.41	1.64	1.15	
42	0	2	3	65.70	34.75		133	1512	6.56	7.46	2.08		3.56	1.89	1.12	
42	1	0	1	56.83	25.00		85	843	4.84	10.79	2.83		1.43	0.54	0.74	

Appendix table 3. contd..

42	1	0	2	53.73	16.75		59	571	3.20	7.50	2.35		1.32	0.50	0.91	
42	1	0	3	54.45	18.00		68	667	3.41	7.84	2.05		1.33	0.55	0.68	
42	1	1	1	59.43	33.75		123	1088	6.45	12.03	3.59		1.90	0.67	0.77	
42	1	1	2	60.55	31.00		116	1319	6.46	11.46	3.41		2.08	0.86	0.96	
42	1	1	3	66.63	31.25		120	1326	7.19	13.20	3.30		2.02	0.75	0.80	
42	1	2	1	69.25	41.50		161	1790	8.67	11.57	3.31		2.84	1.18	1.01	
42	1	2	2	74.25	43.00		179	2187	10.38	15.62	4.39		2.79	1.07	0.79	
42	1	2	3	73.65	42.00		168	2249	10.87	16.40	3.56		3.11	1.61	1.12	
55	0	0	1	60.48	12.33		55	688	3.68	8.10	1.56	0.21	1.73	0.61	0.94	2.91
55	0	0	2	58.48	14.50		57	699	3.56	8.64	1.77	0.09	1.66	0.51	0.97	3.43
55	0	0	3	61.83	13.50		53	692	3.57	8.67	1.61	0.05	1.62	0.53	0.96	4.24
55	0	1	1	74.87	19.00		75	1195	6.00	10.77	2.05	0.21	1.96	0.71	1.03	3.84
55	0	1	2	74.40	17.17		70	1080	5.23	9.71	1.66	0.13	2.07	0.67	0.94	3.82
55	0	1	3	79.95	21.83		87	1501	7.42	14.19	2.56	0.28	1.86	0.59	0.87	3.42
55	0	2	1	92.60	34.00		134	2646	12.38	17.03	2.48	0.35	2.67	0.89	1.01	3.28
55	0	2	2	88.08	34.00		131	2370	11.21	13.73	2.24	0.23	2.71	0.95	1.04	3.80
55	0	2	3	89.33	34.50		134	2559	12.01	15.01	2.44	0.32	2.48	0.89	1.09	3.88
55	1	0	1	60.48	18.50		67	752	4.49	12.61	2.01	0.03	1.35	0.46	0.84	4.55
55	1	0	2	56.32	12.83		49	568	3.27	9.77	1.66	0.04	1.27	0.44	0.78	4.25
55	1	0	3	57.53	13.17		53	561	3.08	8.99	1.43	0.04	1.31	0.42	0.75	4.40
55	1	1	1	72.45	25.17		99	1377	7.21	16.74	2.99	0.14	1.74	0.62	0.87	4.41
55	1	1	2	71.27	24.17		93	1333	6.83	15.73	2.62	0.15	1.70	0.64	0.75	3.20
55	1	1	3	74.93	23.33		91	1405	7.38	19.08	2.86	0.28	1.61	0.51	0.95	3.65
55	1	2	1	91.03	39.00		141	2578	12.36	21.80	3.45	0.40	2.27	0.81	0.91	3.11
55	1	2	2	88.63	36.00		123	2184	10.33	18.81	2.53	0.38	2.17	0.84	1.18	3.28
55	1	2	3	93.37	42.33		160	2848	14.45	25.60	2.91	0.58	2.23	0.83	0.92	3.81
71	0	0	1	76.70	14.33	10.83	53	696	4.08	12.50	2.04	3.01	1.58	0.46	0.83	0.90
71	0	0	2	70.77	13.33	10.17	52	700	3.94	11.92	2.03	2.78	1.56	0.46	0.94	0.99
71	0	0	3	70.80	12.83	9.50	43	599	3.45	11.99	1.55	2.70	1.38	0.49	0.87	0.71
71	0	1	1	83.40	20.17	12.17	67	1302	7.05	16.72	2.25	4.32	2.01	0.67	0.85	1.00
71	0	1	2	83.23	18.17	12.67	71	1371	7.59	18.67	2.58	5.15	1.96	0.56	0.96	0.86
71	0	1	3	85.13	16.33	12.50	62	1316	7.04	18.23	2.49	4.56	1.88	0.57	1.00	1.11
71	0	2	1	105.13	15.67	13.67	73	2023	10.39	18.58	2.63	5.97	2.39	0.97	0.93	1.30
71	0	2	2	100.70	17.00	11.17	70	1761	9.03	16.17	1.97	4.62	2.57	0.87	0.94	1.21
71	0	2	3	97.63	15.50	13.33	76	1868	9.82	18.02	2.50	5.49	2.25	0.89	0.90	1.50

Appendix table 3. contd..

71	1	0	1	78.12	10.17	9.33	35	467	2.82	13.63	2.65	3.39	1.21	0.36	0.72	1.19
71	1	0	2	69.82	10.33	9.50	38	411	2.40	11.54	1.94	2.61	1.08	0.39	0.71	0.92
71	1	0	3	74.40	9.00	8.80	37	441	2.65	11.97	2.04	2.91	1.04	0.39	0.83	1.07
71	1	1	1	95.80	20.00	15.50	77	1532	8.60	26.90	4.53	8.10	1.80	0.59	0.69	1.16
71	1	1	2	90.87	15.83	14.83	71	1399	7.66	25.15	4.34	7.38	1.60	0.53	0.85	1.02
71	1	1	3	91.10	12.67	11.17	57	998	5.92	20.85	2.68	5.08	1.47	0.55	0.72	1.22
71	1	2	1	109.43	17.17	14.00	78	2017	11.28	26.51	4.04	8.50	2.16	0.79	1.04	1.29
71	1	2	2	107.80	20.83	14.00	92	2169	11.60	26.07	3.98	6.85	2.30	0.83	0.99	1.08
71	1	2	3	104.54	16.20	14.40	73	1773	10.45	27.32	3.52	8.19	2.08	0.70	0.89	1.23
77	0	0	1	80.60	10.33	10.00	40	574	3.53	11.40	1.80	8.16	1.04	0.22	0.81	0.36
77	0	0	2	77.52	10.67	8.33	39	526	3.01	9.87	1.64	5.48	0.89	0.34	0.82	0.40
77	0	0	3	78.92	9.50	8.83	32	437	2.73	9.88	1.26	6.82	0.80	0.24	0.99	0.56
77	0	1	1	93.70	12.50	9.83	42	926	5.03	13.14	1.47	8.92	1.30	0.34	0.72	0.79
77	0	1	2	93.93	13.00	10.83	43	915	4.99	13.87	1.72	10.63	1.26	0.30	0.92	1.06
77	0	1	3	97.05	12.25	9.75	37	826	5.70	16.86	2.24	11.78	1.35	0.35	0.88	0.69
77	0	2	1	107.76	13.40	12.20	55	1512	6.69	16.81	1.76	10.03	1.39	0.46	0.86	0.93
77	0	2	2	100.63	12.75	10.50	52	1306	7.19	16.06	1.88	3.66	1.13	0.45	0.86	1.40
77	1	0	1	77.98	13.50	12.83	44	618	3.65	19.14	2.56	9.38	0.52	0.31	0.82	0.59
77	1	0	2	77.40	11.67	9.50	29	373	2.10	13.45	1.38	7.45	0.43	0.33	0.57	0.44
77	1	0	3	78.38	10.17	7.17	33	373	2.42	13.72	1.59	4.91	0.62	0.24	0.58	0.17
77	1	1	1	99.00	14.20	12.60	54	1105	6.73	20.89	4.02	15.02	0.76	0.36	0.66	0.47
77	1	1	2	94.12	14.33	11.67	44	826	5.20	19.88	2.65	10.48	0.66	0.60	0.70	0.92
77	1	1	3	101.73	17.17	13.33	50	1168	7.10	27.82	3.02	16.60	0.89	0.34	0.66	0.81
77	1	2	1	108.45	14.00	14.33	50	1434	7.92	21.74	2.40	13.43		0.45	0.95	0.58
77	1	2	2	105.55	15.75	11.50	51	1331	7.53	22.36	2.33	10.54	1.06	0.22	0.78	0.38
77	1	2	3	109.58	20.40	13.60		1964	11.23	23.57	3.02	15.92		0.49	0.88	0.61

Appendix Table 4. Effects of increased atmospheric CO_2 and N nutrition on growth of rice cultivar IR72, during 93 wet season.

Days After Planting	Treatment CO2	N	Rep	Plant height (cm)	Number of Tiller /hill	Panicle /hill	Leaf area cm^2/hill	Dry weight Leaf g/hill	Root g/hill	Sheath g/hill	Panicle g/hill	Unopen g/hill	Total N conc. Leaf %	Sheath %	Root %	Panicle %
19	0	0	1	39.38	4.5		60.69	0.291	0.157	0.471			4.22	1.66	1.44	
19	0	0	2	43.10	6.8		42.25	0.182	0.177	0.317			4.12	1.64	1.30	
19	0	0	3	45.90	7.8		120.12	0.522	0.200	0.474			4.03	1.60	1.19	
19	0	1	1	37.18	4.8		42.30	0.229	0.167	0.194						
19	0	1	2	40.53	5.0		64.41	0.318	0.202	0.257			4.06	1.86	1.40	
19	0	1	3	44.38	5.5		74.44	0.360	0.228	0.315			4.22	1.52	1.46	
19	0	2	1	39.78	5.5		67.31	0.320	0.159	0.313			4.32	1.67	1.40	
19	0	2	2	42.43	6.0		71.19	0.315	0.179	0.262			4.48	1.70	1.43	
19	0	2	3	39.40	5.5		43.64	0.249	0.157	0.216			4.05	1.54	1.35	
19	1	0	1	41.93	8.8		120.55	0.467	0.345	0.446			3.88	1.45	1.17	
19	1	0	2	46.60	9.3		140.69	0.329	0.332	0.641			3.96	1.84	1.20	
19	1	0	3													
19	1	1	1	40.00	8.8		97.33	0.485	0.248	0.450			4.01	1.56	1.34	
19	1	1	2	42.45	6.5		60.89	0.336	0.191	0.328			4.14	1.50	1.39	
19	1	1	3													
19	1	2	1	35.85	6.5		60.67	0.322	0.242	0.268			4.10	1.49	1.54	
19	1	2	2	43.38	9.8		123.37	0.570	0.310	0.512			4.12	1.68	1.35	
19	1	2	3													
35	0	0	1	60.53	11.5		214.67	1.493	0.533	1.264		0.126	3.37	1.26	1.10	
35	0	0	2	59.85	13.5		264.07	1.531	0.489	1.218		0.186	3.49	0.59	1.17	
35	0	0	3	57.68	10.5		237.48	1.530	0.479	1.682		0.134	2.58	0.88	1.74	
35	0	1	1													
35	0	1	2	63.83	15.5		377.51	2.428	0.806	2.229		0.227	3.26	1.18	1.05	
35	0	1	3	64.43	13.8		295.73	2.096	0.607	1.883		0.184	3.42	1.36	1.08	
35	0	2	1	59.65	16.3		400.18	2.251	0.415	1.887		0.166	3.96	1.72	1.14	

Appendix Table 4. contd...

35	0	2	2	66.80	17.5		432.63	2.766	0.799	2.358		0.292	3.27	1.42	1.25
35	0	2	3	56.68	11.5		186.23	1.290	0.449	0.963		0.108	3.96	1.60	1.43
35	1	0	1	55.43	15.8		350.56	2.006	0.802	2.212		0.199	2.90	1.10	1.04
35	1	0	2	63.90	15.8		365.56	2.320	0.735	2.675		0.205	2.91	1.08	1.06
35	1	0	3												
35	1	1	1	56.05	18.5		291.34	2.062	0.658	2.039		0.154	3.18	1.27	1.03
35	1	1	2	53.48	14.0		237.97	1.524	0.559	1.408		0.156	3.52	1.35	1.29
35	1	1	3												
35	1	2	1	60.33	15.3		311.54	1.947	0.605	1.842		0.164	3.70	1.52	1.23
35	1	2	2	63.85	20.3		467.95	2.890	0.835	3.159		0.214	2.62	0.94	1.01
35	1	2	3												
49	0	0	1	67.62	12.0		411.19	2.665	0.896	4.512	0.040	0.273	2.03	0.52	0.77
49	0	0	2	68.75	14.5		497.78	3.255	1.056	5.659	0.012	0.211	2.00	0.48	0.76
49	0	0	3	65.80	10.2		302.34	2.711	1.150	5.626	0.021	0.178	1.66	0.41	0.66
49	0	1	1	65.66	22.0		699.77	4.200	2.057	4.676	0.000	0.421	2.83	0.91	0.96
49	0	1	2	70.53	16.8		687.02	4.459	1.602	6.820	0.051	0.235	2.63	0.68	0.64
49	0	1	3	69.75	14.3		541.47	3.658	0.858	4.421	0.009	0.252	2.78	0.85	0.83
49	0	2	1	69.64	16.2		608.61	3.806	0.906	4.122	0.004	0.276	2.87	0.81	0.88
49	0	2	2	77.05	12.0		529.21	3.654	0.945	4.072	0.005	0.242	2.60	0.59	0.87
49	0	2	3	67.54	14.8		529.52	3.326	0.847	2.897	0.000	0.248	3.16	1.11	1.12
49	1	0	1	65.15	12.3		501.28	3.488	1.556	7.931	0.023	0.191	1.57	0.42	0.62
49	1	0	2	67.53	13.8		524.63	3.388	1.350	7.019	0.042	0.168	1.72	0.41	0.79
49	1	0	3												
49	1	1	1	64.16	15.4		506.73	3.292	0.911	7.032	0.001	0.254	2.39	0.89	0.78
49	1	1	2	67.28	21.4		668.53	4.668	1.520	6.540	0.000	0.365	2.42	0.95	0.93
49	1	1	3												
49	1	2	1	65.37	16.7		578.84	4.612	1.751	6.474	0.000	0.330	2.56	0.75	0.96
49	1	2	2	73.15	17.3		740.21	4.880	1.300	8.633	0.010	0.307	2.06	0.61	0.77
49	1	2	3												
56	0	0	1	69.88	13	7.8	612.05	3.898	1.123	9.892	0.951	0.066	1.89	0.40	0.72
56	0	0	2	67.40	13	7.3	494.08	3.314	1.116	8.142	0.348	0.055	1.70	0.40	0.76
56	0	0	3	68.03	10	6.3	462.57	3.119	1.008	8.216	0.732	0.048	1.55	0.32	0.64

Appendix Table 4. contd...

56	0	1	1	75.18	19	8.8	851.69	5.728	1.849	9.711	0.175	0.296	1.97	0.53	0.82
56	0	1	2	74.40	18	7.5	824.70	5.399	1.825	10.596	1.207	0.103	2.06	0.56	0.86
56	0	1	3	75.15	16	7.0	669.82	4.489	1.147	7.776	0.544	0.111	2.12	0.58	0.75
56	0	2	1	80.43	16	10.0	1064.39	6.628	1.939	11.391	1.135	0.090	2.12	0.60	0.78
56	0	2	2	81.33	20	11.5	1394.11	8.010	2.012	14.513	1.696	0.108	2.15	0.57	0.79
56	0	2	3	80.03	16	6.8	758.10	4.588	1.046	6.108	0.120	0.175	2.47	0.70	0.99
56	1	0	1	69.78	12	7.8	561.85	4.132	1.819	13.012	1.099	0.107	1.28	0.34	0.65
56	1	0	2	70.85	12	8.5	637.33	4.375	1.528	12.847	1.761	0.046	1.41	0.34	0.73
56	1	0	3												
56	1	1	1	75.20	19	6.8	783.72	5.185	1.991	10.681	0.234	0.268	1.78	0.47	0.65
56	1	1	2	77.60	23	8.0	796.83	5.539	2.056	10.355	0.121	0.292	1.93	0.53	0.91
56	1	1	3												
56	1	2	1	64.25	21	8.8	929.11	6.441	2.461	11.572	0.215	0.349	1.64	0.54	0.87
56	1	2	2	75.68	19	8.8	937.11	6.051	1.816	14.385	0.888	0.122	1.69	0.42	0.70
56	1	2	3												
69	0	0	1	75.83	13	7.3	469.08	3.068	1.278	9.934	3.239	0.809	1.44	0.41	0.58
69	0	0	2	75.25	12	6.8	452.39	3.016	1.084	10.990	2.862	0.085	1.35	0.46	0.58
69	0	0	3	74.85	11	7.8	406.08	2.730	0.965	10.525	4.021	0.019	1.36	0.42	0.69
69	0	1	1	75.45	18	8.8	863.78	5.310	1.585	13.639	2.948	0.067	1.65	0.54	0.62
69	0	1	2	88.10	16	7.5	808.58	5.202	2.011	14.264	5.255	0.059	1.80	0.62	0.69
69	0	1	3	90.38	15	9.8	732.05	4.997	1.380	15.443	8.767	0.056	1.75	0.34	0.68
69	0	2	1	89.63	17	11.7	1004.00	6.262	2.046	12.845	4.459	0.073	2.12	0.47	0.89
69	0	2	2	89.58	17	9.0	1043.64	6.464	1.372	15.506	6.950	0.054	1.93	0.42	0.65
69	0	2	3	85.55	21	12.0	1169.28	7.556	1.729	15.744	4.971	0.063	2.15	0.35	0.77
69	1	0	1	72.00	14	7.8	459.51	3.384	1.866	13.323	2.712	0.031	1.21	0.52	0.58
69	1	0	2	81.88	10	8.5	494.46	3.370	1.598	14.009	6.179	0.030	1.25	0.46	0.63
69	1	0	3												
69	1	1	1	77.00	17	8.8	722.96	4.909	1.462	15.008	3.079	0.085	1.45	0.40	0.65
69	1	1	2	84.15	20	12.3	1024.49	7.141	3.575	21.446	4.575	0.108	1.68	0.35	0.77
69	1	1	3												
69	1	2	1	80.43	16	8.0	844.61	5.414	2.050	12.592	2.849	0.052	1.82	0.27	0.81
69	1	2	2	82.00	14	9.0	769.21	4.927	1.771	15.603	3.672	0.018	1.74	0.28	0.86

Appendix Table 4. contd...

69	1	2	3													
82	0	0	1	77.96	8.80	8.0	282.34	1.944	1.067	9.036	12.165	0.019	1.05	0.46	0.51	1.00
82	0	0	2	77.60	12.20	9.6	389.53	2.580	1.328	9.856	11.805	0.015	1.09	0.42	0.55	0.98
82	0	0	3	74.28	9.60	7.4	269.97	1.756	0.875	7.379	9.172	0.019	1.01	0.37	0.51	0.97
82	0	1	1	82.22	15.17	10.3	549.32	3.496	1.794	11.826	11.761	0.051	1.34	0.38	0.62	0.97
82	0	1	2	86.47	11.33	10.0	529.99	3.364	1.936	10.451	15.458	0.025	1.56	0.43	0.71	1.19
82	0	1	3	84.38	11.00	8.8	424.56	2.760	1.093	9.683	11.826	0.030	1.33	0.44	0.51	1.05
82	0	2	1	86.35	15.50	12.5	794.78	4.690	1.569	11.776	12.340	0.021	1.85	0.57	0.70	1.34
82	0	2	2	88.16	12.00	9.8	596.68	3.678	1.377	10.863	14.819	0.012	1.57	0.49	0.62	1.35
82	0	2	3	87.20	18.33	13.8	853.07	5.413	1.319	14.342	16.045	0.029	1.66	0.53	0.55	1.20
82	1	0	1	81.26	12.20	8.8	345.49	2.473	1.499	10.795	8.776	0.055	1.09	0.34	0.55	0.88
82	1	0	2	79.50	10.33	8.8	337.05	2.327	1.360	10.589	14.474	0.049	0.97	0.32	0.56	0.87
82	1	0	3													
82	1	1	1	85.76	13.20	11.4	695.06	4.464	1.724	16.876	13.153	0.089	1.19	0.35	0.56	0.85
82	1	1	2	86.22	13.33	10.7	640.46	4.231	2.073	14.988	13.072	0.067	1.20	0.42	0.51	0.82
82	1	1	3													
82	1	2	1	89.87	15.33	10.8	786.07	5.240	2.488	16.457	12.955	0.071	1.41	0.38	0.68	1.13
82	1	2	2	91.63	17.17	13.3	852.50	5.562	2.661	17.717	21.750	0.081	1.36	0.43	0.61	1.09
82	1	2	3													
																kernal N
97	0	0	1	76.33	10	8.3	153.50	1.065	1.191	8.796	13.307		1.31	0.58	0.47	1.10
97	0	0	2	76.40	10	8.8	163.94	1.160	1.237	8.725	11.562		1.29	0.76	0.47	0.96
97	0	0	3	75.33	7	6.7	133.11	0.986	0.809	6.875	10.754		1.09	0.60	0.50	0.95
97	0	1	1	81.02	10	9.8	217.14	1.432	1.461	10.147	12.600		1.30	0.69	0.44	1.10
97	0	1	2	84.75	12	11.5	242.20	2.019	1.560	14.504	20.700		1.08	0.64	0.47	1.02
97	0	1	3	84.00	10	9.7	216.64	1.457	1.070	10.739	17.699		1.24	0.66	0.50	1.19
97	0	2	1	84.22	15	13.3	319.40	2.046	2.000	7.669	22.496		1.26	0.76	0.66	1.49
97	0	2	2	87.15	13	9.8	324.94	2.245	1.378	12.445	17.553		1.18	0.74	0.65	1.41
97	0	2	3	81.82	10	9.0	121.40	0.739	1.413	8.502	13.631		1.46	0.78	0.65	1.45
97	1	0	1	73.80	10.17	8.8	210.78	1.652	1.426	10.163	13.817		0.87	0.57	0.38	
97	1	0	2	77.75	10	8.7	204.13	1.614	1.714	10.549	15.343		0.93	0.72	0.37	0.83
97	1	0	3													0.90

Appendix Table 4. contd...

97	1	1	1	86.23	11	10.0	242.57	1.883	1.547	12.368	18.531	1.27	0.69	0.49	1.16
97	1	1	2	85.15	11	10.0	280.91	2.628	2.234	14.615	18.141	1.00	0.85	0.47	1.03
97	1	1	3												0.96
97	1	2	1	86.98	12	12.7	333.17	1.936	2.711	16.121	22.217	0.98	0.87	0.54	1.00
97	1	2	2	88.45	13	10.3	305.56	1.887	1.921	14.049	20.179	1.12	0.79	0.52	1.16
97	1	2	3												

Appendix Table 5. Light saturated leaf CO_2 assimilation of rice cultivar IR72 grown at ambient or elevated CO_2 and different levels of N nutrition during the 94 dry seasons.

Days After Planting	Cham. #	Growth CO2	Measured CO2	N	Rep	Assimilation µmol/m^2/sec	PAR mean	CO2 conc.	Temp leaf	RH (%)	Stomatal resistance	Internal CO2
19	1	0	1	0	1	22.55	2026	363	38.01	62.18	0.212	322
19	1	0	1	0	1	16.89	1897	366	38.83	59.48	0.297	325
19	1	0	1	0	1	24.04	1988	368	35.41	64.41	0.234	325
19	1	0	1	0	1	24.00	2005	366	36.53	62.46	0.202	325
19	4	0	1	0	2	27.38	1854	351	36.33	51.93	0.323	289
19	4	0	1	0	2	24.27	1690	376	39.57	48.28	0.383	308
19	4	0	1	0	2	24.14	1713	366	39.81	47.76	0.408	296
19	1	0	2	0	1	37.31	2014	680	38.16	62.80	0.263	599
19	1	0	2	0	1	33.12	1992	701	36.61	60.47	0.259	628
19	1	0	2	0	1	32.49	1946	713	40.13	59.26	0.408	612
19	4	0	2	0	2	41.28	1726	736	38.93	47.48	0.546	586
19	4	0	2	0	2	36.65	1580	695	39.23	44.65	0.439	575
19	4	0	2	0	2	39.81	1750	713	39.21	47.08	0.562	565
19	3	0	1	1	1	24.47	1916	354	36.72	59.12	0.178	316
19	3	0	1	1	1	22.89	1953	351	36.32	61.03	0.188	313
19	3	0	1	1	1	27.51	1922	357	36.60	60.22	0.170	316
19	3	0	1	1	1	26.95	1968	371	37.24	61.50	0.171	330
19	14	0	1	1	2	24.90	1705	373	37.66	51.86	0.526	293
19	14	0	1	1	2	25.25	1838	354	38.78	50.55	0.500	274
19	14	0	1	1	2	23.83	1792	346	38.23	50.52	0.499	271
19	3	0	2	1	1	40.45	1914	704	37.86	59.15	0.201	627
19	3	0	2	1	1	45.74	1951	706	38.30	58.07	0.299	603
19	3	0	2	1	1	48.05	1904	704	37.19	60.69	0.223	617
19	3	0	2	1	1	42.21	1973	705	37.51	62.96	0.250	620
19	3	0	2	1	1	44.23	1951	685	38.59	58.06	0.279	589
19	14	0	2	1	2	40.60	1806	632	40.57	47.55	0.685	461
19	14	0	2	1	2	40.41	1825	718	39.08	48.24	0.616	561
19	14	0	2	1	2	42.42	1715	744	38.96	48.51	0.661	572
19	14	0	2	1	2	41.38	1808	655	40.37	47.94	0.695	480
19	12	0	1	2	1	34.48	2043	371	35.26	62.74	0.186	320
19	12	0	1	2	1	30.10	1773	359	36.06	63.74	0.231	308
19	12	0	1	2	1	27.68	2029	370	36.83	61.28	0.267	318
19	5	0	1	2	2	28.26	1765	361	38.13	51.32	0.581	266
19	5	0	1	2	2	30.25	1764	381	37.93	51.74	0.545	284
19	5	0	1	2	2	31.62	1782	343	36.42	58.82	0.378	268
19	5	0	1	2	2	31.92	1769	363	35.94	59.15	0.368	288
19	5	0	1	2	2	29.32	1950	349	37.58	55.15	0.430	270
19	12	0	2	2	1	51.14	2045	712	36.41	62.36	0.249	616
19	12	0	2	2	1	52.31	1812	705	36.80	64.19	0.273	601
19	12	0	2	2	1	45.46	1914	706	36.36	62.87	0.281	612
19	5	0	2	2	2	47.29	1791	709	36.34	55.33	0.352	594
19	5	0	2	2	2	45.39	1805	714	38.52	51.74	0.550	557
19	5	0	2	2	2	43.37	1724	636	37.18	53.37	0.368	513
19	16	1	1	0	2	13.16	1480	386	41.88	48.00	0.683	321
19	16	1	1	0	2	12.75	1536	394	41.78	47.91	0.687	329
19	16	1	1	0	2	19.62	1570	348	39.94	50.55	0.512	281
19	11	1	2	0	1	37.28	1902	702	37.60	61.97	0.345	608

Appendix Table 5. contd...

19	11	1	2	0	1	43.17	1988	649	37.97	59.45	0.330	547
19	11	1	2	0	1	38.08	1988	686	37.96	61.60	0.367	587
19	11	1	2	0	1	42.73	1980	708	37.78	59.24	0.375	597
19	16	1	2	0	2	29.97	1646	520	38.83	51.68	0.445	429
19	2	1	1	1	1	16.27	1952	367	38.04	59.40	0.256	331
19	2	1	1	1	1	15.10	1993	350	38.52	57.27	0.226	324
19	15	1	1	1	2	17.86	1443	358	39.63	52.71	0.517	296
19	15	1	1	1	2	18.42	1459	367	39.47	52.75	0.473	306
19	2	1	2	1	1	39.04	1953	672	37.27	62.09	0.257	589
19	2	1	2	1	1	37.26	1958	691	36.71	61.52	0.224	616
19	2	1	2	1	1	38.39	2017	688	38.57	61.03	0.275	602
19	2	1	2	1	1	39.72	2012	715	38.24	60.96	0.267	628
19	15	1	2	1	2	31.59	1342	662	39.37	52.69	0.597	539
19	15	1	2	1	2	30.53	1395	641	37.98	54.01	0.464	543
19	15	1	2	1	2	37.81	1836	720	36.32	56.28	0.253	638
19	15	1	2	1	2	45.70	1008	677	34.45	63.25	0.200	599
19	15	1	2	1	2	43.14	1120	701	33.99	64.33	0.183	630
19	15	1	2	1	2	28.14	1381	655	37.66	54.49	0.418	569
19	15	1	2	1	2	29.32	1266	645	39.56	52.52	0.620	526
19	13	1	1	2	1	23.91	1905	383	39.12	57.40	0.497	311
19	13	1	1	2	1	24.12	1887	370	39.24	57.67	0.484	299
19	13	1	1	2	1	24.95	1926	365	38.98	60.37	0.432	298
19	13	1	1	2	1	23.13	1935	344	37.65	61.01	0.434	283
19	6	1	1	2	2	23.77	1712	365	38.02	53.64	0.662	275
19	6	1	1	2	2	24.01	1685	342	38.04	52.35	0.544	264
19	6	1	1	2	2	23.03	1703	331	38.29	52.37	0.573	252
19	6	1	1	2	2	23.20	1718	380	38.22	50.33	0.641	293
19	6	1	1	2	2	24.86	1689	355	38.37	63.00	0.237	306
19	6	1	1	2	2	26.53	1683	369	38.18	63.83	0.249	316
19	6	1	1	2	2	21.93	1733	366	38.47	49.79	0.655	282
19	6	1	1	2	2	22.66	1727	354	38.11	53.76	0.653	268
19	13	1	2	2	1	47.55	1902	680	36.75	62.41	0.407	556
19	13	1	2	2	1	48.20	1860	724	38.00	61.76	0.422	593
19	13	1	2	2	1	48.40	1970	712	36.11	61.28	0.353	596
19	13	1	2	2	1	39.90	1897	716	40.23	55.97	0.603	566
19	13	1	2	2	1	45.72	1954	694	38.59	57.78	0.417	568
19	13	1	2	2	1	46.79	1871	698	38.28	61.51	0.417	571
19	6	1	2	2	2	45.26	1691	752	36.94	53.25	0.449	620
19	6	1	2	2	2	44.81	1702	726	37.18	52.95	0.510	584
19	6	1	2	2	2	46.48	1633	702	39.32	58.98	0.262	600
19	6	1	2	2	2	46.03	1688	739	37.31	55.57	0.492	596
19	6	1	2	2	2	44.05	1694	717	37.50	55.02	0.527	573
19	6	1	2	2	2	43.09	1342	644	36.34	65.17	0.273	555
19	6	1	2	2	2	44.48	1619	749	36.92	55.57	0.628	582
19	6	1	2	2	2	44.23	1626	723	37.27	55.23	0.646	554
39	1	1	0	0	1	18.01	1740	370	36.53	57.76	0.344	322
39	1	1	0	0	1	18.49	1705	372	33.82	61.90	0.277	331
39	1	1	0	0	1	17.86	1727	360	34.46	61.71	0.279	320
39	1	1	0	0	1	18.65	1682	362	37.32	55.26	0.361	311
39	4	1	0	0	2	17.45	1657	387	38.14	52.40	0.473	327
39	4	1	0	0	2	17.45	1704	374	36.13	53.53	0.411	321
39	4	1	0	0	2	13.51	1628	349	40.85	48.71	0.627	285
39	1	2	0	0	1	32.84	1745	772	35.99	59.82	0.372	677
39	1	2	0	0	1	30.66	1745	752	36.54	58.48	0.411	656
39	1	2	0	0	1	32.76	1689	693	39.09	52.31	0.506	573

39	1	2	0	0	1	31.36	1676	700	38.59	54.05	0.497	587
39	1	2	0	0	1	30.70	1739	743	38.52	52.73	0.566	619
39	1	2	0	0	1	32.84	1683	674	39.45	52.05	0.547	548
39	4	2	0	0	2	27.30	1667	746	40.12	50.78	0.618	621
39	4	2	0	0	2	24.37	1667	762	39.81	51.25	0.586	650
39	4	2	0	0	2	30.62	1627	749	41.99	50.95	0.746	590
39	4	2	0	0	2	30.05	1519	748	37.62	53.94	0.463	643
39	3	1	0	1	1	22.13	1700	355	35.75	58.58	0.329	303
39	3	1	0	1	1	20.68	1824	372	34.19	60.39	0.266	329
39	3	1	0	1	1	22.90	1719	340	37.22	57.84	0.321	285
39	14	1	0	1	2	23.89	1998	338	35.86	60.05	0.308	285
39	14	1	0	1	2	26.80	1922	341	35.39	59.65	0.295	285
39	14	1	0	1	2	26.74	2046	383	37.50	58.68	0.434	306
39	7	1	0	1	3	22.35	1770	327	36.93	56.43	0.321	274
39	7	1	0	1	3	24.11	1908	345	35.49	58.71	0.227	300
39	7	1	0	1	3	29.70	2091	371	34.72	65.58	0.246	316
39	3	2	0	1	1	42.72	1730	720	36.82	59.28	0.383	607
39	3	2	0	1	1	45.09	1720	739	38.23	57.65	0.419	608
39	3	2	0	1	1	38.05	1778	714	35.78	59.99	0.333	620
39	14	2	0	1	2	42.52	1752	712	36.83	64.24	0.315	615
39	14	2	0	1	2	41.50	1944	708	37.12	62.63	0.328	609
39	7	2	0	1	3	37.65	1625	742	38.31	57.74	0.341	642
39	7	2	0	1	3	40.57	1891	703	36.58	57.24	0.277	611
39	7	2	0	1	3	42.93	2034	684	37.18	57.09	0.295	584
39	7	2	0	1	3	34.63	1904	688	35.71	58.49	0.424	586
39	12	1	0	2	1	23.53	1317	369	36.12	60.18	0.388	307
39	12	1	0	2	1	23.73	1699	360	36.32	58.91	0.368	300
39	12	1	0	2	1	32.64	1767	343	33.99	58.57	0.284	278
39	5	1	0	2	2	33.75	1883	359	34.01	65.58	0.260	296
39	5	1	0	2	2	21.47	1508	353	36.76	54.99	0.259	308
39	5	1	0	2	2	25.26	1549	356	36.43	55.85	0.239	307
39	5	1	0	2	2	24.45	1631	356	34.65	51.66	0.319	299
39	5	1	0	2	2	18.24	1736	340	35.39	57.41	0.389	290
39	5	1	0	2	2	19.68	1585	341	37.44	54.92	0.496	277
39	5	1	0	2	2	18.74	1607	345	37.64	55.10	0.444	287
39	5	1	0	2	2	23.98	1822	346	34.95	56.68	0.350	289
39	8	1	0	2	3	27.26	2194	331	37.65	60.43	0.239	279
39	8	1	0	2	3	33.97	2182	350	38.31	62.15	0.280	279
39	8	1	0	2	3	27.48	2144	338	35.36	64.64	0.255	285
39	12	2	0	2	1	41.63	1689	765	37.14	58.19	0.475	634
39	12	2	0	2	1	40.09	1712	736	37.50	57.67	0.512	603
39	12	2	0	2	1	51.94	1765	715	35.78	61.46	0.319	600
39	12	2	0	2	1	40.56	1716	727	37.28	60.39	0.472	600
39	12	2	0	2	1	40.16	1724	703	37.52	59.82	0.513	571
39	5	2	0	2	2	41.42	*1500	731	37.25	63.13	0.464	605
39	5	2	0	2	2	38.54	1733	743	36.58	59.52	0.421	631
39	5	2	0	2	2	34.79	1611	656	38.13	57.48	0.503	540
39	5	2	0	2	2	40.23	1520	678	37.53	57.90	0.269	592
39	5	2	0	2	2	38.66	1748	693	36.77	62.45	0.420	585
39	5	2	0	2	2	43.56	1493	717	37.39	56.77	0.333	612
39	5	2	0	2	2	44.69	1423	703	36.01	63.12	0.353	592
39	5	2	0	2	2	40.49	1639	728	36.72	53.75	0.499	597
39	5	2	0	2	2	43.78	1547	701	37.32	57.72	0.253	611
39	5	2	0	2	2	43.75	*1500	759	37.02	63.46	0.447	631
39	8	2	0	2	3	49.40	2192	711	38.71	60.93	0.255	608

39	8	2	0	2	3	50.47	2179	738	39.28	62.34	0.339	610
39	8	2	0	2	3	51.91	2146	744	38.41	60.84	0.242	640
39	8	2	0	2	3	43.76	2164	681	36.58	62.19	0.259	590
39	8	2	0	2	3	47.64	2198	701	39.71	62.20	0.359	576
39	8	2	0	2	3	45.83	2167	706	36.29	62.33	0.263	611
39	11	1	1	0	1	5.83	2082	377	43.70	40.35	1.358	309
39	11	1	1	0	1	10.00	1686	377	41.86	41.52	1.107	298
39	11	1	1	0	1	9.82	1704	371	42.38	41.47	1.191	289
39	11	1	1	0	1	14.82	1680	366	39.97	48.07	0.754	291
39	16	1	1	0	3	9.38	1778	375	41.42	43.58	0.864	310
39	16	1	1	0	3	7.43	1791	376	42.83	42.11	0.829	317
39	16	1	1	0	3	7.02	1808	383	44.53	51.34	4.690	213
39	16	1	1	0	3	7.74	1807	381	43.07	43.54	0.831	320
39	11	2	1	0	1	21.54	1723	745	41.11	42.85	1.184	576
39	11	2	1	0	1	28.53	1585	664	38.32	50.57	0.738	527
39	11	2	1	0	1	25.55	1727	625	41.25	43.75	0.874	477
39	11	2	1	0	1	28.31	1623	640	38.96	50.39	0.737	504
39	16	2	1	0	3	19.82	1824	672	42.92	42.46	0.873	537
39	16	2	1	0	3	21.24	1769	667	40.30	44.97	0.845	538
39	16	2	1	0	3	21.85	1738	698	42.13	42.70	0.840	559
39	16	2	1	0	3	20.55	1830	680	42.41	43.73	0.748	555
39	2	1	1	1	1	12.25	1771	380	41.44	46.45	1.185	288
39	2	1	1	1	1	10.18	1729	365	40.12	40.33	1.048	289
39	2	1	1	1	1	16.59	1784	367	40.68	50.01	0.731	286
39	2	1	1	1	1	9.33	1723	374	40.32	40.30	1.144	297
39	2	1	1	1	1	12.95	1807	355	40.46	46.66	0.856	280
39	15	1	1	1	2	22.14	1741	367	38.64	51.94	0.361	306
39	15	1	1	1	2	18.08	1791	365	39.30	53.07	0.534	298
39	15	1	1	1	2	21.75	1727	380	36.43	54.95	0.359	322
39	15	1	1	1	2	18.61	1782	376	39.12	53.21	0.520	308
39	15	1	1	1	2	20.05	1701	367	36.65	54.47	0.380	311
39	15	1	1	1	2	20.59	1747	356	38.80	52.34	0.335	301
39	9	1	1	1	3	18.26	2218	358	40.47	49.60	0.589	283
39	2	2	1	1	1	30.83	1812	680	39.30	49.55	0.635	548
39	2	2	1	1	1	30.17	1754	688	39.56	50.11	0.798	537
39	2	2	1	1	1	40.43	1718	776	38.89	49.79	0.544	624
39	2	2	1	1	1	35.89	1763	741	39.53	50.67	0.649	586
39	15	2	1	1	2	40.17	1751	719	34.92	64.66	0.219	643
39	15	2	1	1	2	33.19	1735	736	37.66	57.67	0.369	640
39	15	2	1	1	2	33.06	1762	712	38.09	57.23	0.420	608
39	15	2	1	1	2	38.05	1756	692	35.26	62.64	0.241	615
39	15	2	1	1	2	38.86	1769	710	38.38	55.31	0.305	612
39	9	2	1	1	3	33.14	2097	723	42.61	45.30	0.747	550
39	9	2	1	1	3	34.07	2128	706	41.68	50.48	0.696	545
39	9	2	1	1	3	42.26	2066	693	39.03	53.54	0.464	556
39	9	2	1	1	3	37.82	2186	646	38.42	53.50	0.424	529
39	9	2	1	1	3	34.79	2252	744	42.11	45.53	0.726	568
39	9	2	1	1	3	38.08	2133	738	40.93	51.28	0.624	576
39	13	1	1	2	1	14.43	1498	362	37.20	50.44	0.812	289
39	13	1	1	2	1	17.92	2224	370	38.53	54.74	0.620	298
39	13	1	1	2	1	17.74	1659	348	36.02	54.56	0.472	291
39	13	1	1	2	1	13.23	1488	360	40.50	48.67	1.024	274
39	6	1	1	2	2	17.38	1730	359	38.90	54.83	0.640	288
39	6	1	1	2	2	13.43	1951	371	38.56	50.75	1.055	286
39	6	1	1	2	2	18.49	1463	353	39.65	55.81	0.592	281

39	6	1	1	2	2	18.49	1463	353	39.65	55.81	0.592	281
39	18	1	1	2	3	21.33	1632	378	37.71	56.12	0.614	296
39	18	1	1	2	3	22.13	1825	379	37.99	56.32	0.533	302
39	18	1	1	2	3	24.93	1679	378	36.60	55.23	0.430	306
39	18	1	1	2	3	19.74	1509	352	38.44	54.96	0.571	280
39	18	1	1	2	3	22.09	1730	369	38.23	54.65	0.515	294
39	13	2	1	2	1	34.22	1403	707	36.63	53.98	0.542	584
39	13	2	1	2	1	34.83	2223	687	37.23	56.80	0.478	574
39	13	2	1	2	1	32.61	1526	712	39.87	51.23	0.961	525
39	13	2	1	2	1	35.44	1648	735	39.29	51.36	0.824	556
39	13	2	1	2	1	38.11	1758	716	34.45	57.17	0.417	607
39	6	2	1	2	2	31.89	1722	739	37.25	55.61	0.791	586
39	6	2	1	2	2	40.60	1531	701	39.14	56.21	0.545	556
39	6	2	1	2	2	35.80	1777	689	37.87	55.63	0.544	563
39	6	2	1	2	2	35.64	1804	718	37.45	53.57	0.536	592
39	18	2	1	2	3	37.61	1749	695	36.56	56.71	0.415	585
39	18	2	1	2	3	43.74	1633	749	36.96	55.73	0.435	617
39	18	2	1	2	3	38.41	1753	658	37.18	57.10	0.433	544
64	3	0	1	1	1	19.63	590.4	355	38.50	64.57	0.315	309
64	3	0	1	1	1	18.88	1526	374	37.95	67.84	0.339	327
64	3	0	1	1	1	20.00	1680	327	37.48	69.12	0.330	281
64	3	0	1	1	1	23.80	1621	342	37.51	68.24	0.276	294
64	3	0	1	1	1	19.81	1688	353	36.98	69.41	0.284	310
64	3	0	2	1	1	35.54	1657	708	39.23	64.70	0.447	600
64	3	0	2	1	1	35.71	1493	739	39.03	65.15	0.430	633
64	3	0	2	1	1	46.11	1682	658	38.96	64.81	0.400	536
64	3	0	2	1	1	38.74	1656	674	39.57	62.81	0.411	564
74	5	0	1	2	1	21.57	1699	373	39.28	65.42	0.373	317
74	5	0	1	2	1	21.54	1650	356	38.47	67.91	0.326	306
74	5	0	1	2	1	18.89	1614	342	37.71	69.21	0.285	301
74	12	0	1	2	1	22.75	1828	366	39.40	70.85	0.560	289
74	12	0	1	2	1	21.54	1685	363	39.43	66.27	0.402	305
74	12	0	1	2	1	24.44	1959	361	39.85	62.80	0.603	273
74	12	0	1	2	1	27.03	1913	372	37.62	68.42	0.534	286
74	12	0	1	2	1	26.27	2317	331	38.37	67.13	0.400	263
74	12	0	1	2	1	27.96	1856	370	35.66	72.87	0.316	311
74	12	0	1	2	1	22.96	2212	338	39.54	64.33	0.544	262
74	12	0	1	2	1	27.68	2311	352	36.24	74.41	0.304	294
74	12	0	1	2	1	24.78	1604	354	36.50	73.59	0.312	301
74	12	0	1	2	1	26.61	1998	353	38.72	65.01	0.505	271
74	12	0	1	2	1	27.08	1920	356	38.93	69.31	0.360	291
74	8	0	1	2	3	22.41	1729	339	38.72	70.35	0.406	280
74	8	0	1	2	3	24.76	1503	370	36.30	74.03	0.355	312
74	8	0	1	2	3	25.27	1208	369	36.68	69.78	0.344	311
74	5	0	2	2	1	41.73	1706	726	39.00	66.97	0.376	618
74	5	0	2	2	1	40.23	1724	701	38.12	73.89	0.439	587
74	5	0	2	2	1	35.35	1699	695	39.71	63.87	0.487	581
74	5	0	2	2	1	37.50	1654	703	38.36	68.59	0.332	614
74	5	0	2	2	1	38.56	1651	722	39.44	70.57	0.478	601
74	12	0	2	2	1	41.28	1420	656	36.48	69.68	0.345	559
74	12	0	2	2	1	41.70	1943	695	39.63	64.63	0.775	511
74	12	0	2	2	1	50.33	2584	685	39.72	65.02	0.558	517
74	12	0	2	2	1	40.83	1685	689	40.32	69.06	0.616	538
74	12	0	2	2	1	44.57	1949	685	39.84	62.11	0.699	505
74	12	0	2	2	1	43.05	2010	686	40.56	61.22	0.756	498

74	12	0	2	2	1	44.42	1849	681	38.58	70.14	0.469	551
74	12	0	2	2	1	38.23	1805	680	40.13	64.75	0.531	553
74	12	0	2	2	1	49.21	2402	679	37.33	73.33	0.397	555
74	12	0	2	2	1	43.10	1798	707	39.03	70.86	0.548	564
74	12	0	2	2	1	50.46	2060	711	39.42	61.91	0.591	535
74	8	0	2	2	3	37.40	1344	695	37.22	70.76	0.447	587
74	8	0	2	2	3	38.38	1024	694	36.81	69.04	0.359	600
74	8	0	2	2	3	41.28	1653	694	40.00	71.73	0.453	574
64	2	1	1	1	1	20.54	1564	368	38.91	65.11	0.386	313
64	2	1	1	1	1	17.86	1541	357	39.76	62.85	0.438	303
64	2	1	1	1	1	11.01	1815	356	41.80	59.42	0.652	302
64	2	1	1	1	1	17.69	1571	362	40.84	61.76	0.499	301
64	2	1	2	1	1	37.55	1577	719	39.66	63.72	0.374	617
64	2	1	2	1	1	36.18	1550	689	39.92	63.31	0.421	583
64	2	1	2	1	1	31.27	1873	718	40.50	61.93	0.526	604
64	2	1	2	1	1	36.55	1622	652	37.63	67.42	0.301	570
64	2	1	2	1	1	35.79	1597	695	39.06	64.66	0.395	596
64	2	1	2	1	1	29.53	1896	697	40.95	61.18	0.586	579
64	2	1	2	1	1	37.93	1825	706	39.90	64.25	0.371	602
64	2	1	2	1	1	35.03	1626	692	37.09	68.15	0.251	620
74	13	1	1	2	1	22.77	1614	356	39.33	62.60	0.541	280
74	13	1	1	2	1	20.93	1264	366	41.88	61.20	0.683	278
74	13	1	1	2	1	21.45	2211	370	40.24	66.87	0.563	294
74	13	1	1	2	1	20.72	1752	375	41.20	60.30	0.604	297
74	13	1	1	2	1	17.80	1076	343	38.58	61.52	0.601	277
74	13	1	1	2	1	21.15	2231	367	42.23	61.98	0.818	265
74	13	1	1	2	1	19.38	2098	327	42.04	60.61	0.729	243
74	6	1	1	2	2	20.40	1766	341	39.85	62.64	0.533	272
74	6	1	1	2	2	26.24	1688	368	38.63	66.47	0.440	295
74	18	1	1	2	3	13.48	1993	326	40.51	71.25	0.424	284
74	18	1	1	2	3	19.43	1916	367	42.28	68.55	0.562	298
74	18	1	1	2	3	19.29	2017	378	42.53	67.76	0.599	304
74	18	1	1	2	3	19.82	1835	364	38.52	74.78	0.312	319
74	18	1	1	2	3	16.43	2091	335	41.69	70.04	0.528	278
74	13	1	2	2	1	35.11	1624	741	38.81	62.74	0.658	599
74	13	1	2	2	1	43.76	2195	709	38.15	66.55	0.405	589
74	13	1	2	2	1	40.58	1977	714	40.46	61.27	0.451	591
74	13	1	2	2	1	44.37	1847	694	40.50	62.83	0.551	543
74	13	1	2	2	1	42.38	2218	695	41.35	64.70	0.669	525
74	13	1	2	2	1	37.06	1419	697	38.05	62.97	0.462	584
74	13	1	2	2	1	31.99	1442	686	38.14	63.23	0.431	591
74	6	1	2	2	2	38.48	1688	678	39.21	64.27	0.486	556
74	6	1	2	2	2	40.69	1708	692	39.86	63.62	0.491	562
74	6	1	2	2	2	39.39	1661	731	38.86	64.88	0.439	614
74	6	1	2	2	2	43.50	1729	670	37.59	68.37	0.391	559
74	18	1	2	2	3	36.72	1943	731	36.75	74.68	0.287	652
74	18	1	2	2	3	34.75	1820	709	39.50	73.69	0.382	616
74	18	1	2	2	3	38.78	1963	706	41.52	68.68	0.480	584
74	18	1	2	2	3	35.66	1855	670	37.55	76.42	0.275	596
74	18	1	2	2	3	38.19	2030	718	40.82	71.71	0.453	603
74	18	1	2	2	3	33.03	2125	659	41.23	68.55	0.427	559

Appendix Table 6. Canopy CO_2 assimilation of rice cultivar IR72 grown at ambient or elevated CO_2 and different levels of N nutrition during the 94 dry seasons.

DAP	Chamber #	CO2	N	A µ mol/mol	PAR MEAN	PAR RANGE	[CO2] PPM
21	1	0	0	9.39	1279	16.4	350.2
21	4	0	0	5.74	1720	158.6	346.8
21	17	0	0	6.28	1521	19.2	344.0
21	3	0	1	9.81	1464	24.6	342.7
21	14	0	1	11.12	1714	38.3	345.4
21	7	0	1	13.09	1808	13.7	354.1
21	12	0	2	12.90	1853	16.4	349.8
21	5	0	2	10.71	1908	19.2	345.5
21	8	0	2	10.60	1843	10.9	352.3
21	11	1	0	15.78	1774	19.2	719.4
21	16	1	0	13.54	1814	27.4	718.5
21	19	1	0	16.95	2024	5.5	779.4
21	2	1	1	16.51	1279	32.9	691.2
21	15	1	1	12.77	1430	27.4	719.7
21	9	1	1	18.57	1948	15.5	689.5
21	13	1	2	21.80	1846	30.1	665.9
21	6	1	2	20.03	1724	41.0	737.1
21	18	1	2	21.43	1869	106.7	692.9
43	1	0	0	9.23	2155	22.8	355.0
43	1	0	0	10.64	2152	42.4	370.1
43	1	0	0	10.47	2168	65.2	362.0
43	4	0	0	12.11	2255	6.5	345.9
43	4	0	0	10.04	2259	9.8	364.3
43	4	0	0	13.21	2248	9.8	363.9
43	3	0	1	22.91	2220	16.3	338.0
43	3	0	1	24.73	2227	8.7	335.3
43	3	0	1	25.09	2229	16.3	338.1
43	14	0	1	25.05	2224	9.8	342.3
43	14	0	1	22.94	2277	22.8	359.0
43	14	0	1	22.14	1701	11.5	349.6
43	12	0	2	31.82	2239	75.0	336.7
43	12	0	2	30.79	2214	6.5	345.1
43	12	0	2	31.93	2324	339.0	344.9
43	5	0	2	25.89	2394	68.5	317.9
43	5	0	2	30.19	2393	22.8	346.8
43	5	0	2	23.69	2311	6.5	336.2
43	5	0	2	23.13	2317	19.6	343.3
43	5	0	2	28.69	2293	3.3	371.7
43	8	0	2	27.80	2160	3.3	364.3
43	8	0	2	28.35	2186	9.8	342.6
43	8	0	2	23.88	2190	3.3	327.2
43	11	1	0	14.04	2311	19.6	666.4
43	11	1	0	15.69	2308	9.8	699.8
43	11	1	0	17.66	2279	16.3	735.9
43	11	1	0	15.06	2310	32.6	880.8

Appendix table 6 contd..

43	11	1	0	13.77	2289	9.8	672.3
43	11	1	0	18.45	2286	6.5	700.4
43	11	1	0	17.15	2329	16.3	856.6
43	11	1	0	17.69	2295	32.6	828.2
43	16	1	0	10.18	2195	9.8	704.7
43	16	1	0	9.26	2170	6.5	782.0
43	16	1	0	9.40	2261	39.1	750.3
43	2	1	1	23.75	2206	12.0	690.8
43	2	1	1	25.01	2205	9.8	731.6
43	2	1	1	26.22	2173	94.6	828.4
43	2	1	1	25.95	2137	3.3	882.4
43	2	1	1	22.95	2221	6.5	666.4
43	15	1	1	23.98	2160	9.8	736.5
43	15	1	1	22.81	2153	16.3	697.3
43	15	1	1	29.43	2155	6.5	682.3
43	13	1	2	41.81	2246	19.6	669.9
43	6	1	2	33.56	2356	9.8	629.8
43	6	1	2	36.21	2206	453.1	691.7
43	6	1	2	32.76	2343	9.8	633.3
43	13	1	2	35.49	1993	22.8	697.7
43	13	1	2	36.40	1937	9.8	749.3
43	18	1	2	32.23	1974	3.3	701.1
43	13	1	2	37.72	2073	13.0	738.3
43	18	1	2	38.86	1934	19.6	665.8
54	1	0	0	14.46	2051	16.3	363.3
54	1	0	0	15.88	2005	6.5	356.9
54	2	1	1	22.74	2059	9.8	619.2
54	2	1	1	31.45	2099	6.5	726.2
54	2	1	1	27.02	2125	22.8	685.9
54	2	1	1	30.09	2054	13.0	729.0
54	2	1	1	27.03	2060	9.8	682.7
54	3	0	1	23.93	2096	78.2	352.0
54	3	0	1	26.99	2019	48.9	369.0
54	11	1	0	25.55	2073	6.5	690.3
54	11	1	0	25.31	2018	9.8	713.1
54	14	0	1	26.57	1977	6.5	336.0
54	14	0	1	27.71	2061	6.5	340.8
54	14	0	1	28.16	2052	9.8	349.6
54	15	1	1	31.27	1683	6.5	861.6
54	15	1	1	35.26	1712	26.1	680.3
54	16	1	0	13.13	2032	6.5	719.7
54	16	1	0	13.00	1774	39.1	826.4
54	17	0	0	14.23	1946	52.2	334.7
54	17	0	0	13.74	1879	6.5	351.9
54	17	0	0	10.99	1865	52.2	351.6
54	19	1	0	13.62	1131	264.0	784.2
59	5	0	2	39.01	2002	9.8	354.0
59	5	0	2	38.54	1997	13.0	357.6
59	6	1	2	48.34	1938	3.3	709.4
59	6	1	2	46.23	1938	13.0	657.9
59	7	0	1	23.97	2127	9.8	406.2

59	7	0	1	21.78	2118	3.3	379.5
59	7	0	1	24.93	2100	6.5	334.0
59	7	0	1	29.49	2145	48.9	338.7
59	7	0	1	35.29	2119	26.1	364.2
59	8	0	2	36.07		3.3	330.4
59	8	0	2	40.97		6.5	351.1
59	9	1	1	44.20	2113	6.5	704.3
59	9	1	1	41.64	2113	9.8	651.7
59	9	1	1	26.72	2129	13.0	666.2
59	9	1	1	30.38	2125	6.5	793.2
59	9	1	1	36.75	2140	19.6	822.3
59	12	0	2	35.24	2008	39.1	328.2
59	12	0	2	34.35	1984	3.3	328.4
59	12	0	2	44.66	1997	3.3	367.5
59	12	0	2	37.55	2017	39.1	378.6
59	12	0	2	34.15	2010	35.9	342.0
59	12	0	2	31.61	1987	6.5	346.9
59	13	1	2	46.09	2089	6.5	665.5
59	13	1	2	48.68	2095	3.3	694.3
59	13	1	2	49.26	2074	6.5	667.5
59	18	1	2	48.21	2172	3.3	692.0
59	18	1	2	50.53	2163	3.3	720.4
59	18	1	2	57.67	2172	6.5	673.6

Appendix Table 7. Interception of radiation and biomass accumulation of rice cultivar IR72 grown at ambient or elevated CO_2 and different levels of N nutrition.

1993 Wet Season							1994 Dry Season						
DAP	Chamber No.	Treatment REP	CO2	N	Intercepted Radiation Mj/m^2	Above Ground wt g/M^2	DAP	Chamber No.	Treatment REP	CO2	N	Intercepted Radiation Mj/m^2	Above Ground wt g/M^2
19	1	1	0	0	6	19.2	22	4	0	0	2	36	48.8
19	5	2	0	0	5	8.5	22	17	0	0	3	33	56.3
19	17	3	0	0	10	25.4	22	14	0	1	2	57	60.2
19	14	2	0	1	8	14.7	22	7	0	1	3	59	55.4
19	7	3	0	1	9	17.3	22	12	0	2	1	71	69.1
19	12	1	0	2	7	16.6	22	5	0	2	2	58	72.3
19	4	2	0	2	8	14.9	22	8	0	2	3	60	69.2
19	8	3	0	2	6	11.6	22	11	1	0	1	60	73.4
19	13	1	1	0	8	23.0	22	16	1	0	2	43	57.8
19	16	2	1	0	8	19.4	22	19	1	0	3	32	66.1
19	11	1	1	1	7	23.6	22	2	1	1	1	65	114.6
19	15	2	1	1	7	17.1	22	15	1	1	2	72	106.2
19	9	3	1	1	7	19.7	22	13	1	2	1	83	134.5
19	2	1	1	2	8	14.7	22	6	1	2	2	70	158.6
19	6	2	1	2	8	27.6	22	18	1	2	3	70	133.8
35	1	1	0	0	58	73.6	42	4	0	0	2	177	203.5
35	5	2	0	0	62	74.3	42	17	0	0	3	151	225.9
35	17	3	0	0	75	84.1	42	14	0	1	2	238	322.0
35	14	2	0	1	69	123.4	42	7	0	1	3	244	401.0
35	7	3	0	1	83	105.5	42	12	0	2	1	290	471.0
35	12	1	0	2	73	108.9	42	5	0	2	2	284	471.0
35	4	2	0	2	88	135.7	42	8	0	2	3	262	350.0
35	8	3	0	2	47	59.0	42	11	1	0	1	210	390.0
35	13	1	1	0	77	111.5	42	16	1	0	2	155	267.0
35	16	2	1	0	83	132.9	42	19	1	0	3	137	281.0
35	11	1	1	1	69	107.2	42	2	1	1	1	259	462.0

Appendix Table 7. contd..

35	15	2	1	1	59	78.5	42	15	1	1	2	261	448.0
35	9	3	1	1	69	135.0	42	13	1	2	1	312	506.0
35	2	1	1	2	49	100.4	42	6	1	2	2	297	650.0
35	6	2	1	2	78	160.1	42	18	1	2	3	314	681.0
49	1	1	0	0	149	188.4	55	4	0	0	2	267	309.0
49	5	2	0	0	149	231.2	55	17	0	0	3	238	312.0
49	17	3	0	0	158	217.0	55	14	0	1	2	365	381.0
49	14	2	0	1	169	289.6	55	7	0	1	3	374	427.0
49	7	3	0	1	192	209.0	55	12	0	2	1	450	749.0
49	12	1	0	2	182	206.1	55	5	0	2	2	451	638.0
49	4	2	0	2	210	199.7	55	8	0	2	3	419	695.0
49	8	3	0	2	134	162.2	55	11	1	0	1	306	431.0
49	13	1	1	0	167	296.7	55	16	1	0	2	231	331.0
49	16	2	1	0	182	269.3	55	19	1	0	3	217	309.0
49	11	1	1	1	172	210.4	55	2	1	1	1	388	607.0
49	15	2	1	1	153	289.7	55	15	1	1	2	391	573.0
49	9	3	1	1	165	312.5	55	13	1	2	1	465	868.0
49	2	1	1	2	136	286.4	55	6	1	2	2	455	749.0
49	6	2	1	2	193	347.6	55	18	1	2	3	476	1028.0
56	1	1	0	0	197	308.6	71	4	0	0	2	366	466.0
56	5	2	0	0	186	293.3	71	17	0	0	3	341	454.0
56	17	3	0	0	195	253.5	71	14	0	1	2	511	786.0
56	14	2	0	1	217	408.0	71	7	0	1	3	524	707.0
56	7	3	0	1	244	313.3	71	12	0	2	1	672	873.0
56	12	1	0	2	236	496.5	71	5	0	2	2	682	745.0
56	4	2	0	2	267	503.9	71	8	0	2	3	642	839.0
56	8	3	0	2	183	273.4	71	11	1	0	1	438	495.0
56	13	1	1	0	204	476.8	71	16	1	0	2	340	413.0
56	16	2	1	0	217	495.2	71	19	1	0	3	336	438.0
56	11	1	1	1	223	407.8	71	2	1	1	1	569	1090.0
56	15	2	1	1	200	407.5	71	15	1	1	2	581	1004.0
56	9	3	1	1	213	469.5	71	13	1	2	1	678	1159.0
56	2	1	1	2	183	495.4	71	6	1	2	2	679	1112.0
56	6	2	1	2	246	521.1	71	18	1	2	3	696	1153.0

Appendix Table 7. contd..

67	7	3	0	1	355	637.3
67	4	2	0	2	390	662.3
67	8	3	0	2	296	718.0
67	15	2	1	1	305	637.0
67	9	3	1	1	315	657.6
67	6	2	1	2	365	515.3