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Progress Report of Research: EFFECT OF ELEVATED LEVELS OF CO₂ ON
WINTER WHEAT UNDER TWO MOISTURE REGIMES

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EXECUTIVE SUMMARY

This report gives the findings during the second year (1985-86) of an on going field experiment with winter wheat (Triticum aestivum L.) at different carbon dioxide (CO_2) levels and grown under two moisture regimes. The purpose of the second year's experiment was to verify the results of 1984-85. The results for the first year's experiment are documented in the U.S. Department of Energy, Carbon Dioxide Research Division Response of Vegetation to Carbon Dioxide (Chaudhuri et al., 1986).

The study was conducted at the Evapotranspiration Research Site, Kansas State University. The site and the facilities used during the second year were the same as those used during the previous year. A few alterations and modifications were done in the second year based on the results of the first year's experiment. These included measurement of fluorescence from photosynthesis and water soluble carbohydrates, which were not measured in 1984-85.

Chlorophyll-fluorescence-induction-kinetic-characteristic curves and water soluble carbohydrates were studied to see how they were affected by CO_2 levels and water regimes. As in the previous report, this report also deals with the effects of CO_2 on wheat growth, which includes both roots and shoots, water use efficiency, and different physiological parameters (leaf water potential, canopy temperature, stomatal resistance). Net photosynthesis analysis and details of microclimatic differences have not been completed. No apparent trend in per cent protein content, as related to CO_2 level, was observed in 1984-85. Hence, protein content was not determined in 1985-86.

Preliminary results from the chlorophyll-fluorescence-induction-kinetics curves are also presented in this report. Changes in the induction curves due to CO_2 concentrations and soil moisture regimes were observed. Further analysis has yet to be completed.

Newton, a hard red winter wheat was planted inside the rhizotron boxes ($311,000 \text{ cm}^3$; 180 cm deep) on 7 October 1985. The plants in the rhizotron boxes were enclosed by plexiglas chambers (121 cm by 92 cm by 168 cm), which had an arc dome at the top. On 29 October 1985, the chambers were enriched with CO_2 at four different levels (340, 485, 660, and $825 \mu\text{LL}^{-1}$). On 11 November 1985 the chambers were removed and CO_2 injection was discontinued during the winter dormancy period. The experimental area was covered with straw (approximately 5 cm deep) during the winter months. The straw was removed and the chambers were reinstalled to continue the CO_2 injection on 8 March 1986 until harvest. This cultural operation (removing chambers during dormancy and using straw) prevented any winter damage as experienced during the 1984-85 cropping season. Therefore, no wheat was transplanted in 1986 as it was in 1985.

Soil moisture treatments started after 4 April 1986. In the stressed treatments, moisture was maintained between 14 to 25% by volume and in the well-watered treatment it was maintained at approximately 38% by volume. Wheat was harvested on 9 June 1986.

The results for 1985-86 indicated that all the vegetative and yield components of winter wheat were increased with increased CO_2 concentration, irrespective of moisture treatments. The trends were similar to those observed in 1984-85.

Grain yield increased more than 30% (293 g m^{-2}) when CO_2 level was

raised from ambient to $825 \mu\text{LL}^{-1}$ under well-watered conditions. However, under moisture-stressed conditions, the grain yield increased more than 63% (329 g m^{-2}) for similar CO_2 treatments. Similar trends were observed for the number of heads, head weight, and the test weight. However, the head length was least affected.

Leaf area, canopy height, the number of tillers, and root densities were increased with increased levels of CO_2 . Doubling of leaf area was observed 20 days after the date of CO_2 application. Dry weights of leaves, stems, heads and total tillers were also increased with increased levels of CO_2 concentration.

At harvest, tiller numbers were increased by 58% (556 m^{-2}) and 37% (277 m^{-2}) when CO_2 level was raised from ambient to $825 \mu\text{LL}^{-1}$ under well-watered and moisture-stressed conditions, respectively. Plants under moisture-stressed conditions had a higher per cent of infertile tillers than under well-watered conditions. The water required to produce a gram of any yield component for the 1985-86 cropping season was similar to that for the 1984-85 season.

The effect of CO_2 on the amount of water required to produce a gram of any yield component at harvest was more pronounced under water-stressed conditions compared to the well-watered conditions. Our results indicated that 14% and 23% less water was required to produce a gram of kernel, when CO_2 concentration was raised from ambient to $825 \mu\text{LL}^{-1}$, under well-watered and moisture-stressed conditions, respectively.

At harvest, the water soluble carbohydrate (WSC) increased from 16.6 to 26.6 mg g^{-1} dry weight of kernel when CO_2 levels were increased from ambient to $825 \mu\text{LL}^{-1}$ CO_2 under well-watered conditions. The trends were similar for stem and leaf under both the soil moisture

regimes. Under well-watered conditions, the canopy temperature of the plants exposed to high CO_2 concentration was warmer than the plants at ambient CO_2 . Under stressed conditions, the differences among the various CO_2 levels were not prominent. The water potential of the plants grown at high CO_2 was a few MPa lower (less negative) than those grown at ambient CO_2 .

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INTRODUCTION

This report deals with the second-year (1985-86) findings of an ongoing experiment with winter wheat (Triticum aestivum L.) at different carbon dioxide (CO₂) levels and under two moisture regimes. The results for the first year are given in the U.S. Department of Energy, Carbon Dioxide Research Division Response of Vegetation to Carbon Dioxide (Chaudhuri et al., 1986). The purpose of the second year's experiment was to verify the results of 1984-85. However, based on the performance and the results of 1984-85 experiments, a few modifications were made.

For example, in the 1984-85 cropping season, no apparent trend in per cent protein content, as related to CO₂ level, was observed; therefore, in the present experiment, protein content was not determined. Also, in 1985-86 (unlike 1984-85) chlorophyll - fluorescence - induction - kinetics -characteristic curves and water soluble carbohydrates were studied to see how they were affected by CO₂ levels and water regimes.

The chlorophyll fluorescence induction phenomenon has proved to be a sensitive indicator of reactions of photosynthesis and has been important in the understanding the photosynthetic processes (Papageorgious, 1975; Barber, 1976). Noticeable changes in the characteristics of the induction due to defects in photosynthesis result from environmental stress, such as chilling (Melcarek and Brown, 1977; Smillie, 1979), freezing (Klosson and Krause, 1981), and heat (Schreiber et al., 1976) have been reported.

Water stress is known to induce several specific changes at the level of photosynthetic light reactions, which find ultimate

expression in the intact leaf. Loss of variable fluorescence with decreasing water potential has been described by Govindjee (1981). Havaux and Lannoya (1983) found damage of the photosynthetic apparatus in maize caused by drought; and the condition was measurable by the chlorophyll-fluorescence technique. Working with wheat in another experiment, they also found that, in drought-sensitive varieties, water-stress resulted in a strong inhibition of the slow fluorescence induction transients. In contrast, leaves of drought-resistant varieties showed only minor changes in chlorophyll fluorescence.

Conroy et al. (1986) studied the chlorophyll-fluorescence-induction kinetics characteristic curves of Pinus radiata D. Don seedlings grown at 330 or 660 $\mu\text{LL}^{-1}\text{CO}_2$. They found that constant-yield fluorescence of the induction-kinetics characteristic curve was increased and induced fluorescence was reduced. The effect was greatest in the well-watered plants grown at 660 $\mu\text{LL}^{-1}\text{CO}_2$. In drought stressed plants grown at 330 $\mu\text{LL}^{-1}\text{CO}_2$, there was a reduction in the maximal rate of quenching of fluorescence after the major peak. Their results indicated that selection flow subsequent to photosystem II was affected by drought stress. At 660 $\mu\text{LL}^{-1}\text{CO}_2$ this response was eliminated showing that CO_2 enrichment improved the ability of the seedlings to acclimate to drought stress. The average growth increase with CO_2 enrichment was 37% in drought stresses plants and 19% in unstressed plants.

Sugar and carbohydrates are major constituents of many plant organs and tissues. Carbohydrates, the product of photosynthesis, are likely to be altered by CO_2 and the available soil water. In the 1985-86 cropping season, water soluble carbohydrates were determined from the various plant components at different growth stages. Zhanguo and Paulsen (1987)

reported that high-temperature stress severely alters carbohydrate metabolism in wheat during grain development. According to Rohrllich and Essner (1960), the glucose and fructose contents of mature wheat are 47 and 27 mg, respectively, per 100 g wheat on a dry-matter basis.

The goal of this study was to understand fundamental effects of enriched CO₂ on winter wheat and to determine responses that can be used to develop and test predictive models. In particular, the objectives of the work were to determine the effects of elevated levels of CO₂ on the following:

1. Agronomic factors of wheat (growth stage, height, leaves per plant, tillering, leaf area per plant, and reproductive yield);
2. Root growth, root distribution, and root:shoot ratios of wheat;
3. Transpiration rate and water use efficiency of wheat;
4. Photosynthesis, the kinetics of the chlorophyll fluorescence, water soluble carbohydrates, stomatal resistance, water potential, and canopy temperature of wheat.

MATERIALS AND METHODS

The experiment to study the performance of winter wheat (Triticum aestivum L.) at different carbon dioxide (CO₂) levels and two moisture regimes was conducted for the second year during the 1985-86 cropping season. It was conducted at the Evapotranspiration Research Site, 15 km southwest of Kansas State University, Manhattan. The site and the facilities used during the second year were the same as in 1984-85 (Chaudhuri et al., 1986). A few alterations and modifications were done in the second year based on the results of the first year's experiment. The materials and methods repeated during 1985-86 cropping season will be discussed only briefly, as they have already been documented in the U.S. Department of Energy, Carbon Dioxide Research Division: Response of Vegetation to Carbon Dioxide #29 (Chaudhuri et al., 1986). (From now on, this report will be referred to as "Green Book #29").

The underground rhizotron boxes were filled with loose, air dried, sieved soil during July and August 1985. Only a few centimeters of soil were added at a time. During the filling process, the layers were wetted slowly to saturation from top to bottom. Several wetting and drying cycles were carried out before planting. The soil used in the rhizotron boxes was a Muir silt loam (fine-silty, mixed, mesic Cumulic Haplustoll). The physical and chemical properties of the soil in the rhizotron are presented in Table 1. Soil water potential and the water content of the Muir silt loam used in for the experiment are presented in Table 2. The wheat variety used in the experiment was 'Newton' (Pitic 62/Chris sib 112* Sonara 64/Klein Randidor/4/Scout). Newton was planted on 7 October 1985, in an east-west row orientation, in two

Table 1. Physical and chemical properties of soil in the rhizotron.

Physical

Sand (%)	28%
Silt (%)	58%
Clay (%)	14%

Chemical

pH	7.9
Avl. P (kg ha^{-1})	77.0
Exch. K (kg ha^{-1})	67.0
Avl. N. (μLL^{-1})	
$\text{NH}_4 - \text{N}$	2.5
$\text{NO}_3 - \text{N}$	2.7
Organic Matter (%)	1.3
DTPA zinc (μLL^{-1})	5.0
DTPA Iron (μLL^{-1})	9.0
Exch. Ca (μLL^{-1})	1990.0
Exch. Mg (μLL^{-1})	165.0
Exch. Na (μLL^{-1})	8.0
Exch. Cu (μLL^{-1})	0.4
Avl. Mn (μLL^{-1})	2.9

Table 2. Values of soil water content, soil water potential, and bulk density of Muir Silt loam.

Soil Water Potential (-MPa)	Rep. 1	Rep. 2	Rep. 3	Rep. 4	Mean
	Soil Water Content $\text{cm}^3 \text{ cm}^{-3}$				
0.01	0.391	0.377	0.405	0.404	0.394
0.02	0.359	0.361	0.392	0.395	0.377
0.08	0.329	0.345	0.375	0.375	0.356
0.14	0.316	0.336	0.366	0.368	0.347
0.20	0.301	0.328	0.357	0.362	0.337
0.50	0.204	0.237	0.269	0.266	0.244
1.00	0.189	0.207	0.235	0.236	0.217
1.50	0.173	0.193	0.196	0.223	0.196
Bulk density (g cm^{-3})	1.37	1.29	1.38	1.30	1.34

rows (18 cm apart) in each box of the rhizotron. For comparison and to avoid border effects, approximately 0.1 hectare area was seeded around the boxes under ambient atmospheric conditions. The plant density, both inside and outside the boxes, was maintained at approximately 220 plants m^{-2} . The entire experimental area, including the boxes, received 160 Kg of nitrogen (34-0-0) per hectare.

The exposed soil-surface area of each box in the rhizotron was covered with black plastic to reduce evaporative loss of water from the soil. Therefore, total water loss from each rhizotron was primarily due to transpiration. For irrigation, 30 cm PVC pipe (3 cm radius) with several holes was placed 3 to 4 cm under the soil surface. One end of the pipe was attached with a hose to supply the required amount of water to irrigate the rhizotron box without lifting up the chamber.

Table 3 indicates the date of weighing the rhizotron boxes for calculation of transpiration rate and the irrigation schedule. The amount of water applied to each chamber was the amount necessary to bring the average soil water to approximately 38% by volume for the well-watered treatments. In the stressed treatments, moisture was maintained between 14 to 25% by volume. The moisture treatments started after 4 April 1986.

Canopy height was recorded throughout the growing season (1, 11, and 18 November 1985 and 24 March, 9, 23, and 28 April, and 6 May 1986). Five destructive plant samplings were done after the flag leaf appearance until physiological maturity (22 and 29 April and 5, 15, and 21 May 1986).

During each sampling, three main tillers were collected from each rhizotron box. The tillers were separated into stem, leaf, and head.

Table 3. Irrigation Treatment Scheduling.

<u>Date</u>	<u>Description of the treatments</u>
85.10.18	The boxes in the rhizotron were weighed.
85.11.1	The boxes in the rhizotron were weighed.
85.11.6	Approximately 3.0 L water box ⁻¹ was added.
85.11.11	Approximately 1.0 L water box ⁻¹ was added.
86.3.3	The boxes in the rhizotron were weighed. Approximately 2.8 L water box ⁻¹ was added.
86.3.24	The boxes in the rhizotron were weighed. Approximately 4.0 L water box ⁻¹ was added. The moisture treatments started.
86.4.11	6.0 L water box ⁻¹ for well-watered treatments was added.
86.4.22	8.0 L water box ⁻¹ for well-watered treatments was added.
86.4.25	The boxes in the rhizotron were weighed. Approximately 16.0 L water box ⁻¹ for well-watered treatments and 8.0 L water box ⁻¹ for stressed treatments were added.
86.5.1	10.0 L water box ⁻¹ for well-watered treatments was added.
86.5.6	6.0 L water box ⁻¹ for well-watered treatments was added.
86.5.9	17.0 water box ⁻¹ for well-watered treatments was added.

Table 3 (continued).

86.5.13	The boxes of the rhizotron were weighed. Approximately 12.0 L water box ⁻¹ for well-watered treatments and 4.0 L water box ⁻¹ for stressed treatments were added.
86.5.19	2.0 L water box ⁻¹ for well-watered treatments was added.

The area of the leaf samples was determined by using an LI-3100 Area meter (LI-COR, Inc. Lincoln, Nebraska)¹. Individual components were oven dried at 70°C for 3 days and dry weights were recorded. The dry samples were ground and a 20-mesh size screen was used for a sieve. The dry samples were stored in plastic containers for further analysis.

Stomatal resistance and leaf temperature of adaxial and abaxial surfaces of fully expanded top leaves were measured with a steady state porometer (Model LI 1600, LICOR, Inc., Lincoln, Nebraska). Five expanded leaves were measured at each observation. The average leaf stomatal resistance (r_s) was calculated by

$$1/r_s = 1/r_{ad} + 1/r_{ab}$$

where r_{ad} and r_{ab} are the resistances of the adaxial and abaxial surfaces, respectively.

Leaf water potential (γ_L) of the last fully expanded leaf was measured by means of a standard Scholander-type pressure chamber. Water potential measurements were made on 2, 6, 15 and 21 May 1986. Canopy temperatures were measured with an infrared thermometer (Teletemp Corp/Model AG-42, Fullerton, California).

Two undisturbed rows of 25 cm (each) long were harvested from the center of each rhizotron box to determine yield. Shoots of the wheat plants were harvested on 9 June 1986. The vegetative parts were separated from reproductive parts. Number of heads, head weights, head length, kernel weights, number of kernels per head, number of infertile heads, and total grain weights were recorded. Chaff weights

1. Mention of trademark or proprietary product in this report does not imply approval by the Kansas Agricultural Experiment Station to the exclusion of other products that may also be suitable.

and the straw weights were also recorded.

Grain moisture content was determined with the Burrows digital moisture meter (Model 700; Burrows Equipment Company, Evanston, Illinois). Grain yield and other plant components were adjusted to a 14 per cent moisture content by weight.

Water Soluble Carbohydrate:

Water soluble carbohydrates (WSC) of leaf, stem, kernel, and roots were determined at harvest. Carbohydrate assays were also carried out on samples collected on 22 April and 5 May 1986. Replicated dry plant samples (0.25 - 0.5 g) were shaken for 1 hour in 125-ml Erlenmeyer flasks containing 50 ml distilled water and filtered through Whatman #42 filter paper and 100-ml volume was made. An aliquot (0.1 to 0.5 ml) was added with 0.5 ml of 80% phenol and 1.0 N H_2SO_4 and 15 ml volume was made by adding water. The test tube was shaken for 20 minutes in a water bath at 28°C. Absorbance was measured at 490 nm in a Beckman spectrophotometer and tested against fructose as a standard.

Chlorophyll-Fluorescence Induction:

The kinetics of the induced chlorophyll-fluorescence rise were recorded by using a portable fluorometer (model SF-20, Richard Bramker Research, Ltd., Ottawa, Canada K1S 3Y7). The measuring sensor of the fluorometer, which was placed directly on the leaf, contained both a light-emitting diode (red light, $11.2 \mu\text{Em}^{-2}\text{s}^{-1}$) and a photodiode to detect chlorophyll-fluorescence emission. All readings were recorded during the dark hours (2100 to 0400 hours, CDT) on April 24-25, April 30-May 1, and May 15-16.

Root Measurement:

Methods of observing root distribution at different soil depths (35, 70, 104 and 135 cm) throughout the growing season and the calculations were similar to those reported in Green Book #29. Root distribution was determined on 1, 11, and 18 November 1985 and 24 April and 6 May 1986. Root sampling for total biomass was also determined, following the same procedures used in the previous year. The methods of root harvesting, cleaning, and drying were also reported in the earlier report.

Carbon Dioxide Treatment:

Wheat plants, grown inside the rhizotron boxes under enclosed plexiglas chambers (121 cm by 92 cm by 168 cm), had an arc dome at the top (Fig. 1). The chambers were enriched with CO₂ at four levels: 340, 485, 660, and 825 μLL^{-1} . Unlike the 1984-85 cropping season, CO₂ was not injected throughout the growing season. In 1985-86, the chambers were placed on the top of the rhizotron on 24-25 October 1985 and CO₂ was injected on 29 October 1985. On 11 November 1985 the chambers were removed and CO₂ injection was discontinued during the winter dormancy period. The experimental area was covered with straw (approximately 5 cm deep) during the winter months. The straw was removed and the chambers were reinstalled to continue the CO₂ injection on 8 March 1986 until harvest.

The details of the design of the air delivery systems, CO₂ enrichment systems, and CO₂ sampling systems have been documented in the Green Book #29 (Chaudhuri et al., 1986). Carbon dioxide was analyzed by an infrared gas analyzer (ADC 225 MK3 Analytical Development Co.,

CARBON DIOXIDE ENRICHMENT CHAMBER

Figure 1. CO₂ enrichment chamber.

Hoddesdon, England). One gas analyzer was operating in an absolute mode to determine the CO_2 concentration and the another gas analyzer was operating in a differential mode to determine the net change in CO_2 concentration between the inlet and outlet streams. From this, and the calculation of the flow rate, a mass balance of CO_2 can be used to determine photosynthetic rates. The air velocity profile in the system was measured by using a portable velocity meter (Teledyne Hastings - Raydist Model AAB-27, Hampton, Virginia).

Mass transfer rates of water vapor through the chamber were measured with two shielded wet-dry psychrometers. One psychrometer was placed in the outlet tube of the chamber and the other outside the chamber. Temperatures, measured with thermocouples, were monitored by the CR-5 recorder (Campbell Scientific, Logan, Utah).

Soil temperature at different depths (2, 10, 20, 60, 90 cm) were measured inside each rhizotron box. A wooden dowel with copper-constantan thermocouples taped on the side was buried in the ground to measure the soil temperature. A Campbell CR-5 (Campbell Scientific Co., Logan, Utah) data logger recorded the temperature of the thermocouples at 15 minute intervals.

Several light interception measurements of the canopies in the rhizotron boxes were made with a light bar (LI-COR Inc, Model Line Quantum, Li-Cor Instruments, Lincoln, NE). The results were recorded with a polycorder (Model 516A, Omni International, Logan, Utah). Li-Cor sensors were installed in the field to measure the total incoming radiation, photosynthetically active radiation, and canopy and soil reflection throughout the growing season. These reading were recorded by a polycorder and the Cambell CR-5.

Statistics:

The study was performed as a factorial experiment in a completely randomized design. Initially there were four levels of CO₂ with four observations for each treatment. Two levels of water treatments were introduced after winter dormancy for each level of CO₂, and, hence, the experiment was treated as a 2 x 4 factorial study with two observations for each treatment. However, all the 8 treatments were assigned to 16 rhizotron boxes randomly before seeding.

Analysis of variance before the initiation of the moisture treatments:

<u>Source of variance</u>	<u>df</u>
CO ₂	3
Within CO ₂ levels	12
total	<u>15</u>

Analysis of variance after the initiation of the moisture treatments:

<u>Source of variance</u>	<u>df</u>
CO ₂	3
Water	1
CO ₂ X Water	3
Error	8
total	<u>15</u>

Results were compared by analysis of variance and LSD (0.05) values were calculated when F values were significant.

RESULTS AND DISCUSSION

In this chapter we will present and discuss the results of the effect of elevated levels of CO₂ on wheat plants grown under two soil moisture regimes during the 1985-86 cropping season. The performance of wheat in the 1985-86 season will also be compared with the results of the 1984-85 cropping season. Performance of the CO₂ enrichment system and of the air and CO₂ delivery system has been documented in the Green Book #29.

It was stated in Methods and Materials that the entire experimental area was covered with straw during the winter dormancy period. Unlike the 1984-85 cropping season, chambers were removed during the winter dormancy period in 1985-86. It is assumed that discontinuing CO₂ enrichment during the winter months did not affect the performance of wheat, since little growth occurs during the dormant period. Damage of the wheat plants in the rhizotron boxes was associated with ice and snow cover and the high conductance of the metal rhizotron structure in the 1984-85 season. Such damage did not occur in 1985-86, presumably because of the straw cover, and, hence, no transplanting was needed for the 1985-86 wheat.

Physiological Growth Stages:

In the present experiment, four different growth-stage scales were used, namely Feekes (Large, 1954), Robertson (1968), Haun (1973), and Zadoks *et al.* (1974). Due to physical limitations of the experiment (difficulty in removing the chamber often and limited plant population),

certain growth stages (double-ridge and milk-development stages) could not be determined with great accuracy for all of the treatments.

Wheat was planted 12 days earlier in 1985 compared to 1984 (7 Oct. 1985 vs. 19 Oct. 1984). The two-leaf stage was 10 days earlier in 1985-86 compared to the previous year. Similarly, first tillering started on 27 October for the 1985-86 wheat compared to 7 November for the 1984-85 wheat. Table 4 shows the approximate dates and thermal units from germination for the appearance of different growth stages.

The thermal units (T_u) were calculated from daily maximum ($T_{\max}$) and minimum ($T_{\min}$) air temperatures as follows.

$$T_u = [(T_{\max} + T_{\min})/2] - T_b.$$

$$\text{if } T_{\max} > 30, T_{\max} = 30$$

$$\text{if } T_u < 0, T_u = 0$$

$$T_b = \text{Base temperature at which growth ceased} = 0^{\circ}\text{C}$$

$T_{\max}$ and $T_{\min}$ were recorded from the air temperature inside the chamber when the plants were enclosed. Otherwise air temperature were collected from the surrounding area. Total T_u required until harvest was about 2450. It required 209 T_u for first tillering.

The leaf growth rate expressed in numbers using the Haun scale was observed on a tagged leaf of the main stem. The Haun scale was recorded after injection of CO_2 until the completion of flag leaf emergence (Table 5).

The other 2-digit numerical system, known as Zadoks-Chang-Konzak scale (Table 6), was used between 25 April to 27 May. Under well-watered conditions different elevated levels of CO_2 did not show

Table 4. The approximate dates and thermal units from germination for the appearance of commonly known growth stages of winter wheat (1985-86).

<u>Date</u>	<u>Stages</u>	<u>Approx. thermal units</u> <u>after germination</u>
<u>1985</u>		
7 Oct.	Planting	---
14 Oct.	Germination	---
20 Oct.	2-leaf stage	87
23 Oct.	2.5 leaf stage	120
27 Oct.	Tillering started	209
26-27 Feb.	Double ridge	809
<u>1986</u>		
26-27 Feb.	Double ridge	809
2-3 April	Jointing	1200
19 April	Appearance of flag leaf	1450
25 April	Booting	1550
4 May	Anthesis appearance	1730
13 May	Milk	2000
5 June	Ripe	2350
9 June	Harvest	2445

Table 5. Leaf growth of winter wheat as affected by enriched CO₂ (Haun Scale).

CO ₂ conc.	10.28	11.1	11.5	11.11	11.18	4.9	4.15	4.22
(μLL ⁻¹)	-----1985-----					-----1986-----		
----- HAUN SCALE -----								
340	4.6	5.4	5.7	6.3	8.1	9.9	10.9	12.0
485	4.5	5.7	6.2	8.1	9.5	11.7	12.8	13.5
660	4.3	5.7	6.3	8.7	10.0	11.9	12.9	13.7
825	4.7	5.8	6.7	9.2	10.7	12.1	13.2	13.9

Table 6. Growth stages of winter wheat as affected by enriched CO₂
(Zadoks-Chang-Konzak scale).

CO ₂ Conc.	Moist.	4.25	4.28	5.2	5.5	5.15	5.20	5.27
(μLL^{-1})	Levels	-----1986-----						
----- (Zadoks-Chang-Konzak Scale) -----								
340	Well-watered	44	47	56	59	72	75	86
485	"	43	44	54	57	71	76	81
660	"	43	45	53	55	71	76	82
825	"	42	44	52	54	68	75	80
340	Stressed	44	54	57	61	78	78	95
485	"	45	53	57	60	76	77	92
660	"	46	51	58	59	74	77	88
825	"	48	50	57	58	74	76	85

any effects on the growth stages. However, the plants exposed to the ambient level of CO_2 were slightly advanced compared to the plants exposed to elevated levels of CO_2 . Similar trends were observed for the plants under the moisture-stressed conditions. Plants under moisture-stressed conditions were slightly advanced compared to the well-watered plants. Like 1984-85 cropping season, the emergence and appearance of the leaves and tillers for the plants grown inside the chamber were ahead by a few days compared to the plants in the surrounding open field. The other growth stages were also a few days ahead for the plants inside the rhizotron compared to the open field irrespective of moisture and CO_2 treatments.

Agronomic Parameters:

Canopy height and root length density were measured throughout the growing season. Number of leaves, leaf area per plant, and the number of tillers per plant were measured before winter dormancy. Flag leaf area, periodic dry matter production, and leaf area on the main stem were recorded post-dormancy.

Canopy Height:

Table 7 indicates that, during the early growth stages, the different levels of enriched CO_2 did not affect canopy height. The effect of CO_2 level and soil moisture on canopy height was visible before the appearance of the flag leaf (Table 8). Canopy height was increased under enriched CO_2 levels for both soil moisture regimes. Wheat grown under well-watered conditions was taller than moisture-stressed plants at any CO_2 level.

Table 7. Canopy height of wheat as affected by different levels of CO₂
(1985-86).

CO ₂ Conc. (μLL^{-1})	1 Nov. '85	18 Nov. '85	24 March '86
<hr/>			
	<hr/> cm <hr/>		
340	11.2	12.5	12.3
485	11.3	13.4	13.9
660	12.0	12.9	13.8
825	11.3	13.3	13.7
LSD _(0.05)	NS	NS	NS

Table 8. Canopy height of winter wheat as affected by enriched
CO₂ for two moisture regimes (1985-86).

CO ₂ Conc. (μLL^{-1})	Moist. Level	9.4.86	23.4.86	28.4.86	6.5.86
		(cm)			
340	Well-Watered	34	56	63	73
485	"	39	61	72	78
660	"	40	65	75	79
825	"	39	65	79	82
340	Stressed	32	52	60	65
485	"	36	54	69	73
660	"	36	54	67	72
825	"	36	57	69	73
Well-Watered		38	62	72	78
Stressed		35	54	66	71
LSD _(0.05)		NS	3.5	3.0	2.6
340		33	54	61	69
485		38	58	70	76
660		38	59	71	76
825		38	61	74	77
LSD _(0.05)		4.3	4.9	4.3	3.6

Number of Leaves per Plant:

The number of leaves per treatment in Table 9 represents the mean of 16 plants. Carbon dioxide was injected at the five-leaf-growth stage. The effect of different levels of CO_2 on the number of leaves per plant appeared 13 days (1 Nov. 1985) after the injection of CO_2 into the chamber. However, significant differences were found on 18 Nov. Plants enriched with the highest level of CO_2 had the greatest number of leaves and leaf number gradually declined with decreasing rate of CO_2 . It was lowest at the ambient level of CO_2 .

Number of Tillers:

Table 10 gives the number of tillers per plant as affected by different CO_2 levels before winter dormancy. Plants had 1.5 tillers when a significant effect of CO_2 enrichment on the number of tillers was observed 13 days after the CO_2 was injected (11 Nov. 1985). Plants injected with the highest level of CO_2 had the maximum number of tillers per plant and the plants in the ambient CO_2 concentration had the lowest number of tillers. Total number of tillers at harvest will be discussed later.

Leaf Area:

Leaf area of the plants was measured by multiplying the length and the width of each leaf of the tagged plant. The leaf area of each treatment represents the mean of 16 plants. The effect of enriched CO_2 on leaf area was rapid. The leaf area was doubled when CO_2 levels were raised from ambient to $825 \mu\text{LL}^{-1}$. Doubling of leaf area was observed 20 days from the date of CO_2 application (Table 11).

Table 9. Number of leaves per wheat plant as affected by different levels of CO₂ before winter dormancy (1985).

CO ₂ Conc. (μLL^{-1})	1 Nov.	11 Nov.	18 Nov.
	-----Leaves plant ⁻¹ -----		
340	5.5	9.9	10.9
485	6.7	11.4	13.9
660	5.6	11.2	14.6
825	5.7	11.4	15.7
LSD (0.05)	0.8	NS	1.2

Table 10. Number of tillers per wheat plant as affected by different CO_2 levels before winter dormancy (1985).

CO_2 Conc. (μLL^{-1})	1 Nov.	11 Nov.	18 Nov.
	-----Tillers plant ⁻¹ -----		
340	1.69	3.12	3.44
485	1.88	3.69	4.12
660	1.62	3.87	4.31
825	1.81	3.94	5.06
LSD (0.05)	NS	0.46	0.51

Table 11. Leaf area of winter wheat as affected by enriched CO₂ levels (1985).

CO ₂ Conc. (μLL^{-1})	1 Nov.	11 Nov.	18 Nov.
	$\text{cm}^2 \text{ plant}^{-1}$		
340	30	70	77
485	39	89	97
660	29	94	118
825	32	107	152
LSD _(0.05)	7	28	21

Leaf area of tillers was also measured five times after the appearance of the flag leaf until the milk stage (i.e., between growth stages 40 and 75 according to Zadok's scale). These measurements were made 28 days after moisture-stress treatments were initiated (Table 12). The effect of different levels of CO_2 and soil moisture on leaf area per tiller were observed throughout the measurement period. Increased levels of CO_2 increased the leaf area under both moisture levels. After late booting (6 May), leaf area of the moisture-stressed treatments was reduced substantially compared to the leaf area of the well-watered plots. During the milk stage, the green leaf area of the stressed plots was less than one-third of the well-watered plots. The rate of decrease in leaf area was less for plants grown at higher CO_2 levels compared to the ambient ones. During the early stages of measurements, leaf area of the plants grown under ambient conditions and which were well-watered had comparable values with the plants grown under moisture-stressed conditions and which had higher levels of CO_2 .

King, Wardlaw, and Evans (1967) found that wheat flag leaf photosynthetic rate was regulated by the demands upon the leaf for photosynthate. Flag leaf assimilates are the most important contributor to dry weight accumulation in grain (Makunga et al, 1978; Austin et al., 1977; Morgan and Austin, 1983). Measurements made of the green part of the flag leaf of the main stem tiller indicate that the plants grown in enriched CO_2 were larger compared to those grown in at ambient CO_2 (Table 13). Under well-watered conditions, the effect of CO_2 on plants was more pronounced compared to the effect on plants grown under water-stressed conditions. The trends were similar to those observed in 1984-85.

Table 12. Leaf area per tiller as affected by different CO₂ concentration at two moisture levels (1986).

CO ₂ Conc. (μLL^{-1})	Moist. Level.	4.22	4.29	5.6	5.15	5.21
<hr/>						
		<hr/> (cm ² tiller ⁻¹) <hr/>				
340	Well-Watered	44.9	55.1	50.4	44.5	40.9
485	"	56.0	66.0	63.3	53.4	46.8
660	"	58.4	66.2	66.2	54.8	54.0
825	"	66.0	78.2	68.8	60.3	60.0
340	Stressed	37.7	43.1	42.0	17.2	11.6
485	"	45.5	55.4	43.6	32.8	14.7
660	"	51.2	61.4	49.9	30.9	17.5
825	"	51.7	58.7	58.4	32.7	21.9
<hr/>						
	Well-Watered	56.3	65.9	62.2	53.3	50.4
	Stressed	46.5	54.7	48.5	28.4	16.4
	LSD _(0.05)	8.1	5.9	6.1	5.5	4.9
<hr/>						
340		41.3	48.1	46.2	30.9	26.2
485		50.8	60.7	53.5	43.1	30.8
660		54.8	63.8	58.1	42.9	35.6
825		58.9	68.4	63.6	46.5	41.0
	LSD _(0.05)	11.5	8.4	8.6	7.8	6.9
<hr/>						

Table 13. Leaf area of the flag leaf as affected by different
CO₂ concentrations at two moisture levels (1986).

CO ₂ Conc. (μLL^{-1})	Moist. Levels	6 May	15 May	21 May
-----cm ² flag leaf ⁻¹ -----				
340	Well-Watered	9.8	14.3	11.4
485	"	13.8	17.2	17.7
660	"	20.3	17.2	16.9
825	"	21.4	19.4	19.6
340	Stressed	8.3	7.3	6.5
485	"	9.1	8.4	7.5
660	"	9.8	9.8	8.3
825	"	10.1	10.3	9.6
	Well-Watered	16.3	17.1	16.4
	Stressed	9.8	9.0	8.0
	LSD _(0.05)	2.6	2.3	1.5
340		9.0	10.8	8.9
485		11.4	12.8	12.6
660		15.1	13.5	12.6
825		16.8	14.9	14.6
	LSD _(0.05)	3.7	3.2	2.1

Tiller Weight:

Dry weights of leaf, stem, head, and total tillers weight of winter wheat as affected by enriched CO₂ for two moisture regimes were measured (Table 14). Five measurements were made between the appearance of the flag leaf and the milk stage. The effect of different levels of CO₂ and soil moisture on different components of tillers were observed throughout the measurement period. Increased levels of CO₂ increased the different components of tillers under both moisture levels.

Root measurements:

Non-destructive monitoring of root growth and development throughout the growing season was made possible by using the rhizotron boxes. Root length density per unit area was measured at four soil profile depths (0-44, 45-88, 88-132 and 133-176 cm) on 1, 11, and 18 Nov. 1985 (Table 15). The first root count was made four days after the injection of CO₂ into the chamber (21 days after germination). At this time, roots were observed between 0-44 cm soil-profile depth, and the root length density was less than 0.5 cm cm⁻². Within 10 days, the roots grew profusely at all the soil-profile depths and effects of different CO₂ enrichment levels started to appear. The root length density per unit area was higher for the enriched CO₂ plants compared to the ambient plants. Table 16 indicates root length density at different CO₂ levels for the two moisture regimes. No definite trend was observed for the root distribution pattern at different soil profile depths. Overall, root density for CO₂ enriched plants was higher compared to the ambient level. However, the change in the root length density per unit area due to enriched CO₂ levels was not as pronounced as in the case of shoots.

Table 14. Leaf, stem, head and total dry weight of winter wheat as affected by enriched CO₂ for two moisture regimes.

CO ₂ Conc. (μLL^{-1})	Moist. Levels	Date	Leaf	Stem	Head	Total
			g tiller ⁻¹			
340	Well-watered	4.22.86	0.30	0.69	-	0.99
485	"	"	0.34	0.82	-	1.15
660	"	"	0.40	0.78	-	1.18
825	"	"	0.41	0.81	-	1.36
340	Stressed	"	0.24	0.50	-	0.74
485	"	"	0.27	0.46	-	0.73
660	"	"	0.30	0.86	-	1.17
825	"	"	0.30	0.81	-	1.11
340	Well-watered	4.29.86	0.32	0.69	0.26	1.26
485	"	"	0.37	0.98	0.26	1.61
660	"	"	0.40	0.72	0.20	1.32
825	"	"	0.36	0.81	0.22	1.56
340	Stressed	"	0.38	0.66	0.00	0.94
485	"	"	0.33	0.72	0.31	1.36
660	"	"	0.31	0.74	0.24	1.28
825	"	"	0.31	0.83	0.31	1.43

Table 14 (Continued).

340	Well-watered	5.6.86	0.34	0.96	0.40	1.70
485	"	"	0.39	1.16	0.49	2.04
660	"	"	0.30	0.98	0.42	1.71
825	"	"	0.42	1.11	0.46	2.09
340	Stressed	"	0.22	0.59	0.23	1.04
485	"	"	0.26	0.76	0.37	1.38
660	"	"	0.30	0.91	0.41	1.62
825	"	"	0.29	1.18	0.42	1.88
340	Well-watered	5.15.86	0.32	1.04	0.87	2.23
485	"	"	0.35	1.13	1.00	2.48
660	"	"	0.34	1.12	0.95	2.40
825	"	"	0.37	1.22	0.76	2.35
340	Stressed	"	0.20	0.63	0.82	1.27
485	"	"	0.30	1.08	0.71	1.90
660	"	"	0.19	1.02	0.92	1.03
825	"	"	0.28	1.19	1.16	2.43
340	Well-watered	5.21.86	0.24	0.85	0.95	2.04
485	"	"	0.35	1.14	1.00	2.47
660	"	"	0.32	0.83	1.05	2.19
825	"	"	0.33	1.20	1.31	2.84
340	Stressed	"	0.18	0.89	0.80	1.88
485	"	"	0.18	0.64	0.71	1.52
660	"	"	0.15	0.72	0.92	1.78
825	"	"	0.18	1.03	1.16	2.37

Table 15. Winter wheat root length density per unit area as affected by enriched CO₂ at different soil profile depths.

Date	CO ₂ Conc. (μLL^{-1})	Soil profile (cm)			
		0-44	45-88	89-132	133-176
<hr/>					
----- Root density (cm cm^{-2}) -----					
11.1.85	340	0.35	-	-	-
	485	0.20	-	-	-
	660	0.16	-	-	-
	825	0.23	-	-	-
<hr/>					
11.11.85	340	0.59	1.08	0.61	0.14
	485	0.80	1.69	0.82	0.24
	660	0.73	1.80	0.54	0.40
	825	0.82	1.66	0.28	0.23
<hr/>					
11.18.85	340	0.68	1.66	1.31	1.93
	485	0.86	2.41	1.70	1.84
	660	1.14	2.31	1.17	1.77
	825	1.09	1.94	0.97	0.96

Table 16. Winter wheat root length density per unit area as affected by enriched CO₂ for two soil moisture regimes at different depths.

Date	CO ₂ Conc. (μLL^{-1})	Moist. Level	Soil Profile (cm)			
			0-44	45-88	89-132	133-176
			----- Root Density (cm cm ²) -----			
4.22.86	340	Well-watered	1.78	2.07	1.83	1.98
	485	"	3.23	2.53	2.46	1.79
	660	"	2.78	4.07	4.22	2.16
	825	"	4.02	3.99	3.20	1.90
	340	Stressed	3.39	2.90	2.05	2.04
	485	"	3.36	2.62	1.96	2.07
	660	"	2.42	1.58	1.24	1.26
	825	"	2.98	1.47	1.39	1.46
5.6.86	340	Well-watered	2.77	4.18	4.11	5.46
	485	"	4.63	4.32	2.91	3.82
	660	"	3.60	6.14	5.76	5.97
	825	"	8.39	5.80	5.54	4.04
	340	Stressed	4.44	2.46	3.82	2.73
	485	"	3.66	2.57	2.30	2.83
	660	"	2.58	2.73	2.97	4.29
	825	"	4.14	2.34	2.40	2.24

Primarily, roots are much less efficient than are the shoots in attracting carbohydrates from the general pool. The values in the table probably represent an underestimate of the total root length because minute root hairs were not visible through the thick glass.

In the 1984-85 cropping season, only flag leaf area was measured. The results of the effect of CO_2 on flag leaf area were similar to those in 1984-85. In both cropping seasons, differences in flag leaf sizes, due to different CO_2 concentrations, were more visible in well-watered plants than in water-stressed plants.

Wheat Yield and Yield Components:

Different yield parameters (Table 17) were measured at harvest to study the effect of enriched CO_2 on winter wheat under two soil moisture regimes. We also calculated the reduction of different yield components between the well-watered and moisture-stressed rhizotron boxes at different CO_2 levels.

The values were obtained by calculating the differences between the well-watered and moisture-stressed rhizotron boxes experiencing identical CO_2 concentrations. The percentage reduction was calculated based on the well-watered results. For example, the calculation for the reduction of heads between the well-watered and moisture-stressed treatments at ambient conditions is as follows:

At $340 \mu\text{LL}^{-1} \text{CO}_2$, the number of heads m^{-2}	
under well-watered conditions	= 885
under moisture-stressed conditions	= 577
Actual Reduction	= 308
% Reduction	= $308/885 \times 100 = 34.8$

Table 17. Tillers and chaff of winter wheat as affected by enriched CO₂ for two moisture levels (1985-86).

CO ₂ Conc. (μLL^{-1})	Moist. Level	No. Tillers m^{-2}	No. Infertile Tillers m^{-2}	% Infertile Tillers	Tiller Weight without head g m^{-2}	Chaff Weight g m^{-2}
340	Well-watered	964	79	8.3	1072	312
485	"	1252	144	11.6	1203	393
660	"	1366	157	11.5	1115	502
825	"	1520	181	12.0	1448	532
340	Stressed	759	181	24.2	770	292
485	"	848	163	19.2	847	316
660	"	1009	236	23.5	977	282
825	"	1036	215	20.7	1075	315
	Well-watered	1276	141	10.8	1210	435
	Stressed	913	199	21.9	923	302
	LSD (0.05)	103	22	-	101	38
340		862	130	16.2	921	302
485		1050	154	15.4	1025	355
660		1187	197	17.5	1056	393
825		1278	198	16.3	1262	424
	LSD (0.05)	146	31	N.S.	142	53

Similarly the reduction of different wheat yield components between the ambient and different CO_2 levels for two moisture conditions was also calculated as follows:

Under well-watered conditions, the number of heads m^{-2}

At 485 μLL^{-1} CO_2 level	=	1107
At 340 μLL^{-1} CO_2 level	=	885
Actual Reduction	=	222
% Reduction	=	$222/885 \times 100 = 25.1$

Tillers and Chaff:

Table 17 gives the number of total tillers and infertile tillers and their weights without heads and chaff weight (g m^{-2}) at harvest as affected by enriched CO_2 concentrations under two soil moisture regimes. Number of total tillers and infertile tillers at harvest were affected both by the different levels of CO_2 concentration and soil moisture regimes. Number of tillers m^{-2} was increased with increased CO_2 concentration, irrespective of soil moisture regimes. Tiller numbers were increased by 58% (556 m^{-2}) and 37% (277 m^{-2}) when CO_2 level was raised from ambient ($340 \mu\text{LL}^{-1}$) to $825 \mu\text{LL}^{-1}$ under well-watered and moisture-stressed conditions (Table 18), respectively. There were increased numbers of infertile tillers with the increased number of total tillers. Plants under moisture-stressed conditions had a higher per cent of infertile tillers than under well-watered conditions.

Tiller weights without the head and chaff weight were increased with CO_2 concentration, irrespective of soil moisture regimes. Total

Table 18. Reduction of tillers and chaff of winter wheat between ambient ($340 \mu\text{LL}^{-1}$) and different CO_2 levels under two soil moisture regimes (1985-86).

CO_2 Conc. (μLL^{-1})	<u>Total tillers</u>		<u>Tiller Wt.</u> <u>without heads</u>		<u>Chaff Wt.</u>	
	No	%	g m^{-2}	%	g m^{-2}	%
----- Well-Watered -----						
485	288	29.9	131	12.2	81	26.0
660	402	41.7	43	4.0	190	60.9
825	556	57.7	376	35.1	220	60.5
----- Stressed -----						
485	89	11.7	77	10.0	24	3.1
660	250	32.9	207	26.9	-10	-3.4
825	277	36.5	305	29.6	23	7.9

Table 19. Reduction of tillers and chaff weight of winter wheat between the well-watered and moisture-stressed rhizotron boxes at different CO₂ levels (1985-86).

CO ₂ Conc. (μLL^{-1})	<u>No. Tillers</u>		Tiller wt. <u>without head</u>		<u>Chaff wt.</u>	
	m ⁻²	%	g m ⁻²	%	g m ⁻²	%
340	205	21.2	302	39.2	20	6.8
485	404	47.6	356	42.0	76	24.1
660	357	35.4	138	14.1	220	78.0
825	484	46.7	373	34.7	217	68.9

tiller weight for the high CO_2 treatment ($825 \mu\text{LL}^{-1}$ under moisture-stressed conditions was similar to that of the total tiller weight at ambient CO_2 levels under well-watered conditions. Present results indicate that high CO_2 concentration can compensate for low soil moisture in maintaining tiller numbers and weight.

Head:

Number of heads, head weight per unit area, and individual head lengths were increased with increased CO_2 concentration, irrespective of soil moisture treatments (Table 20). The effect of CO_2 and water treatments was more visible for the number of heads and head weights compared to the head length.

The number of heads per unit area increased more than 55% (489 m^{-2}) when the CO_2 level was increased from the ambient level to $825 \mu\text{LL}^{-1}$ under well watered conditions.

However, under moisture-stressed conditions, the number of heads m^{-2} increased 42% (243 m^{-2}) at $825 \mu\text{LL}^{-1}$ CO_2 compared to the ambient CO_2 level. Head weight was increased by 242 (18.9%), 390 (30.5%), and 512 g m^{-2} (40.0%) when the CO_2 levels were increased from ambient to 485, 660, and $825 \mu\text{LL}^{-1}$, respectively, under well-watered conditions.

The reduction of number of heads, head weight (g m^{-2}), and head length due moisture stress at different CO_2 concentrations is presented in Table 21. The reduction in the number of heads m^{-2} at any CO_2 level was more than 50% due to moisture stress. The percentage reduction was also high for the head weight. However, head length reduction was less than 10% at any CO_2 level.

Table 20. Winter wheat heads as affected by enriched CO₂ for two moisture levels (1985-86).

CO ₂ Conc. (μLL^{-1})	Moist. level	No. Heads m^{-2}	Head Wt. g m^{-2}	Head length cm
340	Well- Watered	885	1280	8.8
485	"	1107	1522	9.2
660	"	1209	1670	9.2
825	"	1374	1792	9.3
340	Stressed	577	816	8.1
485	"	685	1115	8.4
660	"	772	1118	8.7
825	"	820	1168	8.8
	Well-Watered	1144	1566	9.2
	Stressed	714	1054	8.5
	LSD (0.05)	83	102	0.18
340		731	1084	8.5
485		896	1319	8.8
660		991	1394	9.0
825		1097	1480	9.1
	LSD (0.05)	118	145	0.26

Table 21. Reduction of different head components of winter wheat between the well-watered and moisture-stressed rhizotron boxes at different CO₂ levels (1985-86).

CO ₂ Conc. (μLL^{-1})	No. Head		Head Weight		Head Length	
	No. m ⁻²	%	g m ⁻²	%	cm	%
340	308	53.4	464	56.9	0.7	8.6
485	422	61.6	407	36.5	0.8	9.5
660	437	56.6	552	49.4	0.5	5.7
825	554	67.6	624	53.4	0.5	5.7

Table 22. Reduction of different components of winter wheat heads between ambient (340 μLL^{-1}) and different CO_2 levels under two moisture regimes (1985-86).

CO_2 Conc. (μLL^{-1})	<u>No. of Heads</u>		<u>Head weight</u>		<u>Head length</u>	
	No. m^{-2}	%	g m^{-2}	%	cm	%
<hr/>						
	<hr/> Well-Watered <hr/>					
485	222	25.1	242	18.9	0.4	4.5
660	324	36.6	390	30.5	0.4	4.5
825	489	55.3	512	40.0	0.5	5.7
	<hr/> Stressed <hr/>					
485	108	18.7	299	36.6	0.3	3.7
660	195	33.8	302	37.0	0.6	6.9
825	243	42.1	352	43.1	0.7	8.6
<hr/>						

Kernel:

Kernel number per head, 100 kernel weight (test weight) and grain yield m^{-2} , as shown in Table 23, were affected both by enriched CO_2 and soil moisture. All the parameters mentioned above were increased with increased levels of CO_2 . Grain yield per unit area, test weight, and number of kernels per head were highest for wheat grown at $825 \mu\text{LL}^{-1}$, CO_2 under well-watered conditions. Well-watered wheat produced significantly greater grain yield compared to moisture-stressed wheat.

Grain yield increased more than 30% (293 g m^{-2}) when CO_2 level was raised from ambient to $825 \mu\text{LL}^{-1}$ under well-watered conditions (Table 24). However, under moisture-stressed conditions, the grain yield increased more than 63% (329 g m^{-2}) for similar CO_2 treatments. Grain yield under soil-moisture-stressed conditions, for any increase in CO_2 level, was more pronounced than under well-watered treatments. Similar trends were observed for the number of kernels per head and the test weight.

Results for the 1985-86 wheat crop indicated that all the yield components were increased with increased CO_2 concentration, irrespective of moisture treatments. The trends were similar to those of the 1984-85 wheat. However, the grain yields during 1985-86 for any individual treatment were greater than in the previous experiment. Lower yield in 1984-85 compared to 1985-86 may be due to transplanting, which occurred in 1984-85 because the crop originally planted was winter-killed. The yield of kernels or other yield components found in this experiment appears to be high compared to others reported for wheat. Such high-yield results may be partly due to the small sampling area and to the well-controlled environment inside the chambers.

Table 23. Kernels of winter wheat as affected by enriched CO₂ for two moisture levels (1985-86)

CO ₂ Conc. (μLL^{-1})	Moist. level	No. kernel head ⁻¹	Kernel wt. g/100	Grain yield g m ⁻²
340	Well-watered	38.4	3.51	967
485	"	40.8	3.60	1129
660	"	41.5	3.67	1168
825	"	43.9	4.09	1260
340	Stressed	24.8	2.50	524
485	"	34.2	3.17	799
660	"	35.0	3.40	835
825	"	34.9	3.54	853
	Well-watered	41.2	3.71	1131
	Stressed	32.3	3.15	753
	LSD (0.05)	4.0	0.24	73
340		31.6	3.00	746
485		37.5	3.38	964
660		38.3	3.53	1002
825		39.4	3.82	1056
	LSD (0.05)	5.7	0.33	104

Table 24 Reduction in different components (m^{-2}) of winter wheat kernels between ambient ($340 \mu LL^{-1}$) and different CO_2 levels for two moisture regimes (1985-86).

CO ₂ Conc. (μLL^{-1})	No. Kernel/head		100 Kernel wt.		Grain Yield m^{-2}	
	No.	%	Wt. (g)	%	Wt. (g)	%
----- Well-watered -----						
485	2.4	6.3	0.09	2.6	162	16.8
660	3.1	8.1	0.16	4.6	201	20.8
825	5.5	14.3	0.58	16.5	293	30.3
----- Moisture-stressed -----						
485	9.4	37.9	0.67	26.8	275	52.5
660	10.2	41.1	0.90	36.0	311	59.4
825	10.1	40.7	1.04	41.6	329	62.8

Table 25. Reduction in different kernel components of winter wheat (m^{-2}) between the well-watered and moisture-stressed rhizotron boxes at different CO_2 levels (1985-86).

CO_2 Conc. (μLL^{-1})	<u>No. Kernel/head</u>		<u>100 Kernel wt.</u>		<u>Grain Yield</u>	
	No.	%	g	%	$g\ m^{-2}$	%
----- Per rhizotron box -----						
340	13.6	14.8	1.01	40.4	44.3	45.8
485	6.6	19.3	0.43	13.6	33.0	29.2
660	6.5	18.6	0.27	7.9	33.3	28.5
825	9.0	25.8	0.55	15.5	40.7	32.3

Root and Shoot Weight:

Table 26 gives the dry root and vegetative shoot weight, root:shoot ratio, and harvest index at harvest. Total shoot weight includes the total vegetative weight and the grain yield. Harvest index was calculated by dividing grain weight by the total vegetative weight, which includes the root and vegetative shoot weight.

Root dry weights were affected by different CO_2 levels and soil-moisture regimes. At harvest, dry-root weight was increased with increased levels of CO_2 under both soil moisture regimes. Increased in dry root mass due to increased levels of CO_2 , compared to the ambient CO_2 level, were of similar magnitudes under both soil moisture regimes (Table 27). Like the dry root weights, the vegetative-shoot weight at harvest was increased with increased CO_2 levels. Under well-watered conditions, vegetative shoot weight was increased 43% (597 g m^{-2}) when the CO_2 level was increased from ambient to $825 \mu\text{LL}^{-1}$. Under water-stressed conditions, for a similar CO_2 increment, the total vegetative shoot increased by 31% (328 g m^{-2}).

Moisture -stressed wheat had higher root:shoot ratios compared to well-watered wheat. However, the root:shoot ratios were not affected by different CO_2 levels. At harvest, 35 to 40 per cent of the total phytomass was grain, irrespective of CO_2 or soil moisture treatments.

Root:shoot ratio results indicated that during both cropping seasons, water-stressed plants had higher ratios compared to the well-watered plants. Higher root:shoot ratios under water-stressed conditions may be due to the delay in inducing moisture stress. By the first of April, when soil-moisture stress started, the plants had already developed a large amount of roots. Restricted amount of water

Table 26. Root and shoot weight and harvest index of winter wheat as affected by enriched CO₂ for two soil moisture regimes (1985-86).

CO ₂ Conc. (μLL^{-1})	Moist. level	Root wt. -----g m ⁻² -----	Veg-shoot wt.	Root:shoot ratio	Harvest index
340	Well-watered	129	1384	0.055	0.39
485	"	146	1596	0.053	0.40
660	"	165	1612	0.059	0.42
825	"	170	1981	0.052	0.38
340	Stressed	100	1062	0.063	0.28
485	"	122	1164	0.064	0.40
660	"	131	1280	0.061	0.37
825	"	140	1390	0.062	0.35
	Well-watered	153	1210	0.055	0.40
	Stressed	129	923	0.062	0.35
	LSD _(0.05)	7.0	100.7	0.003	0.04
340		114	921	0.059	0.34
485		134	1025	0.058	0.40
660		148	1056	0.061	0.40
825		153	1262	0.057	0.36
	LSD _(0.05)	9.9	142	NS	0.05

Table 27. Reduction of root and shoot weight between the well-watered and moisture-stressed rhizotron boxes at different CO₂ levels (1985-86).

CO ₂ Conc. (μLL^{-1})	<u>Root Weight</u>		<u>Veg-Shoot Weight</u>	
	(g m ⁻²)	%	(g m ⁻²)	%
340	29	29	322	30.3
485	24	19.7	432	45.7
660	34	26.0	332	25.9
825	30	21.4	591	42.5

Table 28. Reduction of root and shoot weight between ambient and different CO₂ levels for two soil moisture regimes (1985-86).

CO ₂ Conc. (μLL^{-1})	<u>Root weight</u>		<u>Veg-shoot wt.</u>	
	g m^{-2}	%	g m^{-2}	%
----- Well-watered -----				
485	17	13.2	212	15.3
660	36	27.9	228	16.5
825	41	31.8	597	43.1
----- Stressed -----				
485	22	22	102	9.6
660	31	31	218	20.5
825	40	40	328	30.9

slows shoot growth more, and sooner, than it does root growth. Generally, the stress on a plant results in a decrease in the growth at the opposite end of the plant (furthest away from the stress). Thus moisture stress in the root zone results in decreased shoot growth and the proportion of roots is increased.

Transpiration:

The plastic cover on the surface of each box in the rhizotron kept the evaporative loss from the soil to a minimum. Therefore, total water loss from each rhizotron box was primarily due to transpiration.

Table 29 shows the total water loss through transpiration from the rhizotron boxes from planting to physiological maturity (18 Oct. 1985 to 2 June 1986). It ranged from 2.27-2.37 mm day⁻¹ and 1.56-1.70 mm day⁻¹ of water from planting to maturity under well-watered and water-stressed treatments, respectively. Moisture-stressed treatments were initiated on 4 April 1986 and lasted until physiological maturity. Before that, differences measured for the amount of water transpired were due to the CO₂ treatments. Approximately 66-80 mm of water per rhizotron box was used before jointing. Increased amount of transpiration after jointing was primarily due to rapid vegetative growth and increased environmental evaporative demand. A rapid decline in the transpiration amount from ripening to physiological maturity occurred in the stressed treatment compared to the well-watered treatment. This may have been due to rapid senescence of the leaves of the moisture-stressed plants compared to the well-watered plants. The majority of the leaves under well-watered conditions were green. The possibility of a gradual adjustment of the plants to low soil moisture can not be ruled out.

Table 29. Transpiration of wheat as affected by enriched CO₂
and two moisture levels (1985-86).

CO ₂ Conc. (μLL^{-1})	Moist. level	Date						
		from	10.18	11.1	3.3	3.24	4.23	5.6
		to	11.1	11.11	3.24	4.23	5.6	6.2
(mm/day)								
340	Well-watered		1.43	1.87	0.11	5.17	11.53	5.46
485	"		1.55	1.97	0.18	5.06	10.80	5.88
660	"		1.27	1.94	0.15	5.04	12.22	5.65
825	"		1.36	2.20	0.15	4.82	12.32	5.90
340	Stressed		1.53	1.91	0.13	3.76	9.46	1.85
485	"		1.57	2.07	0.15	3.87	8.60	2.13
660	"		1.55	1.84	0.16	3.69	9.56	2.30
825	"		1.43	2.37	0.19	3.83	9.03	2.64

Water requirements and yield components:

Table 30 shows the amount of water required to produce a gram of kernel, root, and total phytomass as affected by enriched CO₂ and variable moisture regimes. Total water used throughout the growing season ranged from 157 to 164 L per rhizotron box in well-watered treatments compared to 108 to 118 L per rhizotron box under water-stressed conditions.

Amount of water required to produce a yield component was calculated as follows:

Amount of water required for root (g g^{-1}) =

$$\frac{[\text{Seasonal water used per rhizotron box (g)}]}{[\text{Total root weight at harvest per rhizotron box (g)}]}$$

The results indicated that less water was required to produce a gram of kernel, root, or total phytomass at higher CO₂ concentrations than at lower concentrations. Water required to produce a gram of any component was less under moisture-stressed conditions compared to the well-watered treatment. The effect of CO₂ on the amount of water required to produce a gram of any yield component at harvest was more pronounced under water-stressed conditions compared to the well-watered conditions. Carbon dioxide can compensate for water required to produce a gram of kernel or phytomass. The results indicated that 14% less water was required to produce a gram of kernel under well watered conditions, when CO₂ concentration was raised from ambient to 825 μLL^{-1} , whereas 23% less water was required under moisture-stressed conditions. Under similar

Table 30. Summary of water used to produce a gram of different yield components of winter wheat as affected by enriched CO₂ for two moisture levels (1985-86).

CO ₂ Conc. (μLL^{-1})	Moist. levels	Kernel -----	Root (g g ⁻¹)-----	Total phytomass
340	Well-watered	474	3796	197
485	"	446	3448	175
660	"	432	3057	171
825	"	406	3007	150
340	Stressed	451	3366	200
485	"	355	2807	164
660	"	352	2693	157
825	"	348	2623	155

CO₂ enrichment level, water required to produce a gram of total phytomass was similar for the two soil-moisture regimes. There was about a 23% reduction in total water used to produce a gram of total phytomass, when CO₂ concentration was raised to 825 LL⁻¹ from ambient for both soil-moisture regimes.

The water required to produce a gram of any yield component for the 1985-86 cropping season was similar to that for the 1984-85 season. Total seasonal water used by winter wheat in 1985-86 was more than in 1984-85. However, the amount of water used to produce a gram of any yield component was less in 1985-86 compared to 1984-85 season. This may be primarily due to higher yields in 1985-86 season compared to 1984-85.

Water Soluble Carbohydrates:

Water Soluble Carbohydrates (WSC) were measured during flag leaf appearance (20 April), just before anthesis (May 1), and at harvest (Tables 31 and 32). Leaf WSC decreased with the progress of the growth stages. From flag-leaf appearance to harvest, WSC of the leaves decreased from 22.4 mg g⁻¹ to 10.7 mg g⁻¹ at ambient levels (340 mg g⁻¹ CO₂), whereas in the enriched CO₂ level (825 mg g⁻¹), leaf-WSC decreased from 24.7 mg g⁻¹ to 17.4 mg g⁻¹ during the same period. The differences in the amount of decrease in WSC may be primarily due to delayed senescence of the CO₂-enriched plants compared to the plants grown at ambient levels of CO₂. However, the plants in ambient level had attained physiological maturity. Significant differences in the leaf-WSC were found only at harvest among the plants enriched with different levels CO₂. Rapid reduction of WSC of the stem was found with advance

Table 31. Water soluble carbohydrates as affected by enriched CO₂ in winter wheat under two moisture regimes at harvest (1985-86).

CO ₂ Conc. (μLL^{-1})	Moist. level	Leaf	Stem	Kernel
----- (mg g ⁻¹ dry weight) -----				
340	Well-watered	11.8	16.3	16.6
485	"	13.1	16.9	21.9
660	"	17.9	22.8	25.9
825	"	17.1	23.9	26.9
340	Stressed	9.6	20.4	20.6
485	"	12.7	17.4	24.1
660	"	16.3	24.5	22.4
825	"	17.6	26.5	25.4
Well-watered		15.0	20.0	22.8
Stressed		14.0	22.2	23.2
LSD _(0.05)		NS	NS	NS
340		10.7	18.3	18.6
485		12.9	17.2	23.0
660		17.1	23.7	24.2
825		17.4	25.2	26.2
LSD _(0.05)		5.2	3.7	3.7

Table 32. Water soluble carbohydrates in winter wheat at two growth stages as affected by enriched CO₂ and two moisture levels (1985-86).

CO ₂ Conc. (μLL^{-1})	Moist. level	<u>Leaf</u>		<u>Stem</u>		<u>Head</u>
		4.20	5.1	4.20	5.1	5.1
<hr/>						
----- mg g ⁻¹ dry weight -----						
340	Well-watered	22.9	21.7	60.0	28.9	6.3
485	"	24.8	17.7	75.5	37.9	3.1
660	"	27.0	21.2	65.0	36.6	6.1
825	"	26.5	21.4	69.8	31.8	5.7
340	Stressed	22.9	19.1	55.5	30.8	5.0
485	"	22.8	18.7	72.9	34.3	5.2
660	"	22.3	16.7	81.6	38.0	4.0
825	"	22.9	18.0	71.8	41.8	5.0
<hr/>						
	Well-watered	25.1	20.5	67.6	33.8	5.3
	Stressed	22.7	18.2	70.5	36.2	4.8
	LSD _(0.05)	NS	NS	NS	NS	NS
<hr/>						
340		22.4	20.4	57.8	29.8	5.7
485		23.8	18.2	74.2	36.9	4.2
660		24.7	20.0	73.3	37.3	5.0
825		24.7	19.7	70.8	36.8	5.3
	LSD _(0.05)	NS	NS	9.8	8.9	NS

in maturity. There was a 50% about reduction of stem-WSC from flag leaf appearance to anthesis; CO₂-enriched plants had significantly (0.05) higher stem-WSC compared to plants at the ambient level at CO₂. Sum of the total water soluble carbohydrate was highest at the flag leaf stage and decreased at harvest. This may be due to formation of other complex sugars at advanced stages of growth.

Total WSC for the CO₂ enriched wheat was higher compared to WSC in wheat at ambient CO₂. This was primarily due to higher WSC in all the plant components. The two moisture regimes had no effect on water soluble carbohydrates.

Canopy temperature:

Canopy temperature of any treatment was a few degrees warmer than the open air temperature. This was probably due to higher air temperature (2-3°C) inside the chamber compared to the open field. Canopy temperature was measured on three different days at around midnight (April 25-26; April 30-May 1; May 15-16). Differences between the canopy temperature inside the chamber and the outside were greater at night than during day time (Table 33). The greatest difference was found between the canopy temperature of the plants inside the chamber compared to outside when the inside air temperature was lowest (6.7°C).

Differences in canopy temperature among the different CO₂ treatments under the two moisture regimes were also great. Under well-watered conditions, the plants exposed to high CO₂ concentration were warmer than the plants at the ambient concentration of CO₂. Under water-stressed conditions, the differences among the various CO₂ levels were

Table 33. Wheat canopy temperature as affected by enriched CO₂ and two moisture levels (1985-86).

CO ₂ Conc. Moist.	April	April	April/May	May	May	May	May	May	May	Avg.
(μ LL ⁻¹) level	24/25	29	30/1	6	13	15	15/16	21		
<hr/>										
	<hr/>									
	°C									
340 Well-Watered	17.2	26.6	13.7	27.2	25.8	24.4	16.9	24.2	22.0	
485 "	17.1	26.9	13.3	27.3	25.0	26.6	17.5	26.9	22.6	
660 "	16.8	27.6	14.6	28.0	26.1	27.6	17.0	27.3	23.1	
825 "	16.3	28.0	13.8	27.8	26.0	27.4	17.0	28.0	23.0	
340 Stressed	17.4	28.4	15.7	30.2	30.1	30.5	19.4	29.9	25.2	
485 "	17.6	28.5	15.6	29.3	27.9	29.7	17.1	30.4	24.5	
660 "	17.1	28.6	14.6	30.1	28.6	27.5	18.5	30.8	24.5	
825 "	16.8	28.7	14.4	30.8	29.1	29.7	18.3	31.0	24.9	
Obs. Time	2330	1350	0130	1500	1230	1400	0100	1500		
(CDT)										
Avg. Air Temp.	14.4	28.6	6.7	31.0	25.3	26.5	15.7	28.3	22.1	

not prominent.

Leaf Water Potential:

The leaf water potential (γ_L) of the last fully expanded leaf was recorded four times during the cropping season (Table 34). The γ_L of plants grown at high CO_2 was always a few MPa higher than those grown at ambient CO_2 . Irrespective of the soil moisture content, lowest γ_L was found for plants at the ambient level of CO_2 and decreased with increase in CO_2 concentration.

Stomatal Resistance:

Summarized in Table 35 are estimates of stomatal resistance (r_s) of the last extended leaf. The general trend was a increase in value with increasing CO_2 . Higher r_s was observed for the moisture-stressed treatments, compared to the well-watered. Like 1985, the lowest mean r_s was found for the well-watered plants under ambient conditions. Elevated CO_2 increased the mean r_s of the wheat leaves under well-watered conditions, whereas under moisture-stressed conditions different levels of CO_2 has little effect on the mean r_s of plants.

Chlorophyll Fluorescence:

It has been reported that fluorescence-kinetic curves may provide insight into some important phenomena of photosynthesis, primarily, those involving the state of e^- (electron) transfer due to H_2O -oxidation and the transport of the e^- . It may also tell, indirectly, the time required to reach the interface between e^- transport and the start up of carbon fixation.

Table 34. Leaf water potential as affected by enriched CO₂ and two moisture levels (1985-86).

CO ₂ Conc. ($\mu\text{L L}^{-1}$)	Moist. level	2 May		6 May		15 May		21 May		Grand
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean
----- (-MPa) -----										
340	Well-Watered	2.39	0.00	2.53	0.05	2.29	0.12	2.70	0.13	2.48
485	"	2.21	0.07	2.24	0.03	2.23	0.21	2.30	0.16	2.24
660	"	2.13	0.03	2.04	0.22	1.94	0.10	2.07	0.23	2.04
825	"	1.83	0.41	2.15	0.14	2.01	0.17	2.10	0.28	2.02
340	Stressed	2.62	0.05	2.86	0.08	3.07	0.11	3.04	0.33	2.90
485	"	2.36	0.25	2.81	0.13	2.94	0.09	2.88	0.08	2.75
660	"	2.30	0.16	2.64	0.10	2.72	0.29	2.52	0.26	2.55
825	"	2.14	0.03	2.36	0.05	2.24	0.08	2.38	0.24	2.28
Air temp. ($^{\circ}\text{C}$)		26.5		28.0		26.5		28.3		
Time (CDT)		1400-1600		1300-1530		1335-1510		1300-1430		

Table 35. Wheat stomatal resistance as affected by enriched CO₂ and two moisture levels (1985-86).

CO ₂ Conc. (μLL^{-1})	Moist. Level	April 29	May 6	May 15	May 20	May 21	Grand Mean
-----s cm ⁻¹ -----							
340	well-watered	0.23	0.24	0.39	0.49	0.46	0.36
485	"	0.24	0.27	0.45	0.50	0.55	0.40
660	"	0.23	0.30	0.48	0.51	0.53	0.41
825	"	0.30	0.32	0.47	0.50	0.60	0.43
340	stressed	0.29	0.34	0.66	0.70	0.74	0.55
485	"	0.26	0.36	0.64	0.67	0.78	0.54
660	"	0.26	0.40	0.65	0.88	0.68	0.53
825	"	0.38	0.49	0.66	0.67	0.69	0.58

Transfer of electrons from water to CO_2 takes place in photosynthesis. Chlorophyll a fluorescence, associated with primary photochemical events, is emitted by the chlorophyll in the thylakoids, and CO_2 is reduced in the stroma. Figure 2 reported by Lavoniel and Etienne (1977) describes the general chlorophyll fluorescence-induction-kinetic curve (PSMT). In the nomenclature, 0 represents the onset of illumination to a peak (P). From P, the fluorescence falls to the quasistate (S), entering the domain of carbon assimilation. Following the quasistate, fluorescence produces a secondary maximum (M) peak, which then falls to a terminal value (T). The effect of increased levels of CO_2 for two moisture regimes on chlorophyll-fluorescence-induction-kinetic curves will be studied in detail later. In the present report, we give preliminary results for the curve (Figure 3). The points 0 to P were measured and interphases between 0 to P were skipped, as those phases are short, and our intention was to observe the entire curve for a large number of treatments. Some of the curves presented in this report show times required to reach the different peaks, viz., P, S, M and T phases, and the height of the peaks of the curves. We have also measured the different slopes (highest) from one phase to another phase of the curves. The heights in mm, times in seconds, and the slopes in angles were plotted as functions of canopy temperature and different CO_2 levels. Changes in the induction curves due to CO_2 concentrations and soil moisture regimes were observed. Further analysis is yet to be completed.

Figure 2. Schematic representation of fast (left) and slow (right) fluorescence-induction kinetic characteristic curves during a dark to light transition showing the use of the nomenclature adopted by Lavorel and Etienne (1977).

Figure 3. Chlorophyll fluorescence induction transients in wheat leaves as affected by enriched CO_2 for two soil moisture regimes. (a) Well-Watered, $340 \mu\text{L}^{-1} \text{CO}_2$ (b) Stressed, $340 \mu\text{L}^{-1} \text{CO}_2$ (c) Well-Watered, $825 \mu\text{L}^{-1} \text{CO}_2$ (d) Stressed, $825 \mu\text{L}^{-1} \text{CO}_2$.

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