EFFECTS OF CARBON DIOXIDE, WATER AND NUTRIENT FLUXES ON LOBLOLLY PINE (*Pinus taeda* L.)

By

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Submitted to the Faculty of the
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in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
May, 1997

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NUTRIENT FLUXES ON LOBLOLLY

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ACKNOWLEDGMENTS

I wish to express my sincere appreciation to my major advisor, Dr. Thomas Hennessey for his constructive guidance, encouragement and friendship throughout my graduate program. I would like to thank Dr. Stephen Hallgren, Dr. Bjorn Martin and Dr. Edwin Miller for serving on my graduate committee, and for their helpful suggestions and guidance throughout my graduate program, and Dr. Mark Payton for formulating the statistical analysis for this study.

I would like to thank Mr. Keith Anderson for his wonderful assistance during data collection and friendship during the whole study period. I would like to extend my sincere appreciation to Mr. Robert Heinemann, Mr. Randal Holeman, and the rest of the Kiamichi Forest Research Staff for their excellent assistance during the whole study period. More over, I would like to express my sincere gratitude to those who provided suggestions and assistance during the study: Dr. Shangshan Zhang, Mr. Ed Lorenzi and Mr. Dave Ferris.

I would like to thank my wife Supreetha, for her suggestions, encouragement, friendship, love and understanding during the study period and I would also like to thank my parents Harinath Babu and Sushila Babu for their love, support and encouragement.

I would like to thank Dr. Thomas Hennessey and the Oklahoma State University Department of Forestry for providing me with this research opportunity and their generous financial support.

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CHAPTER I

INTRODUCTION

The presence of certain gases which trap long-wave radiation emitted from the Earth's surface has made our planet habitable. The presence of these gases has given a global mean temperature of 15^0C instead of the estimated -18^0C which would occur in the absence of an atmosphere. This phenomenon is called the 'Greenhouse Effect'. The most important greenhouse gas is water vapor. The other important greenhouse gases are carbon dioxide, nitrous oxide, methane and ozone (Mitchell 1989).

There is a consensus that the global atmospheric CO_2 concentration was about 270 $\mu l\ l^{-1}$ to 280 $\mu l\ l^{-1}$ prior to the industrial revolution about 130 years ago (Eamus and Jarvis 1989). At the present time the concentration is 350 $\mu l\ l^{-1}$ and is increasing at the rate of 1.2 $\mu l\ l^{-1}$ per year (Conway et al. 1988). The concentrations of other trace greenhouse gases such as methane, nitrous oxide, and ozone are also increasing. In recent years the concentration of chlorofluorocarbons has increased significantly. It has been projected that the carbon dioxide concentration will increase from 350 $\mu l\ l^{-1}$ to 700 $\mu l\ l^{-1}$ by the end of the next century (Eamus and Jarvis 1989). This increase in the concentration of the greenhouse gases could lead to an increase in the projected global mean temperature of about 4^0C by the end of the next century (Woodward 1993; Mohnen and Wang 1992; Mitchell 1989).

Analysis of the carbon dioxide and δ^{13} C in air locked in ice has clearly demonstrated that the carbon dioxide concentration has increased in the atmosphere. This increase in the concentration of the greenhouse gases has been attributed to the anthropogenic effects such as the burning of the fossil fuels and deforestation (Houghton et al. 1990). Forest clearing has decreased the total amount of carbon stored in the terrestrial ecosystems over recent centuries due to anthropogenic actions (Houghton et al. 1987). FAO has predicted that the global rate of forest clearance will increase for the rest of this century. This would result in the reduction of the present area of the forest by about 20% by the year 2000. This reduction in forest area is expected to increase CO_2 concentration in the atmosphere due to the oxidation of wood and wood products, and decrease the sink strength for CO_2 (Houghton et al., 1987).

Climate models have shown that an increase in temperature would affect the global climate and precipitation patterns. Some regions would receive higher precipitation compared to the other regions, but these changes in precipitation are not certain. Some of the other predicted consequences of the greenhouse effect include far-reaching climatic changes, such as an increase in the tropospheric air temperature (especially in the polar regions), and a gradual melting of the Greenland and Antarctic ice with a simultaneous rise of the seawater level (Beckmann and Klopries 1991). Some scientists feel carbon dioxide budgeting is a complex long-term dynamic behavior, and is not adequately addressed by current models being used which forecast future atmospheric carbon dioxide levels (Sundquist 1993).

The increase in carbon dioxide concentration and a possible change in the global climate would affect the ecology of most living things. The productivity of forest trees and agricultural crops would be affected. An increase in carbon dioxide concentration would directly affect the growth of plants, crops and trees even if there is no change in the climatic patterns (Kimball et al. 1993). About one-third of the world land area is covered by forests which carry out about two-thirds of global photosynthesis. Hence, the information concerning the response of trees and forests to elevated carbon dioxide concentration is extremely important (Kramer 1981). Forests are widely distributed in the world and the major flux components such as carbon dioxide and water vapor from trees and forests needs to be quantified to develop reliable models to predict the effect of increased carbon dioxide on global climate. Also, the role of terrestrial ecosystems to act as carbon sinks to neutralize the increase in concentrations of carbon dioxide has been widely underestimated in global circulation models (Tans et al. 1990). Hence, fluxes of carbon dioxide and water vapor will be of pivotal significance to natural plant communities, agro-ecosystems and forest-ecosystems.

Due to the ecological and economic importance of forest communities, it is very important to characterize the gas exchange responses of these forest communities to a continued elevation in atmospheric carbon dioxide concentration and water availability. Also, understanding the response of photosynthesis to increasing atmospheric CO_2 concentration and water availability helps us to predict plant productivity and growth in a future environment.

A large number of experiments have been conducted to study the effects of elevated carbon dioxide on the response of photosynthesis. It has been shown that elevated carbon dioxide enhances the rate of carbon assimilation (Garcia et al. 1994, Mousseau 1993, Eamus 1993, Curtis and Teeri 1992, Samuelson and Seiler 1992, Eamus and Jarvis 1989, Conroy et al. 1988, Cure and Acock 1986, Higginbotham et al. 1985, Higginbotham 1983). In some experiments, it has been reported that nutrient availability increased the rate of carbon assimilation (El Kohen and Mousseau 1994, Wilkins et al. 1994, Conroy 1992, Conroy et al. 1990). A number of other studies reported that nutrient availability did not affect the rate of carbon assimilation (Conroy et al. 1988, Norby et al. 1986, Tolley and Strain 1985).

It has been reported that the availability of water affected the rate of carbon assimilation (Geuhl et al. 1994, Townend 1993, Miao et al. 1992, Tolley and Strain 1984). Other studies have reported the availability of water did not affect the rate of carbon assimilation (Cure and Acock 1986, Conroy et al. 1988, Conroy et al. 1990, Johnsen 1993). Some studies have shown stomatal conductance or stomatal sensitivity was not affected by elevated carbon dioxide concentration (Conroy et al. 1988, Higginbotham et al. 1985), while other studies have shown stomatal conductance was reduced in response to elevated carbon dioxide concentration (Tyree and Alexander 1993, Townend 1993, Eamus et al. 1993, Samuelson and Seiler 1992, Hollinger 1987).

It has also been shown that the total chlorophyll content decreased in response to elevated carbon dioxide concentration (El Kohen and Mousseau 1994, Wilkins et al. 1994, Drake 1992), while in other experiments it has been reported that elevated carbon

dioxide concentration did not affect the total chlorophyll content (Eamus et al. 1993). In some experiments it has been reported that downregulation of photosynthesis occurs after seedlings have been exposed to elevated concentrations of carbon dioxide (Johnsen 1993, Samuelson and Seiler 1992). The majority of these experiments have been conducted on seedlings of different species under conditions where nutrients or water are not limiting and these experiments were conducted in either pots or in greenhouses on a short-term basis.

The goal of this research was to determine the extent to which the theoretical carbon dioxide "fertilization effect" will occur when nitrogen and water sufficiency's and limitations co-occur with elevated carbon dioxide concentrations.

The objective of this study was to determine the extent to which elevated carbon dioxide, water and nutrients affect seasonal and long-term differences in light-saturated rate of photosynthesis (P_{max}), maximum stomatal conductance to water vapor (G_{max}) and total chlorophyll content in loblolly pine. The needles were also tested for acclimation to elevated concentrations of carbon dioxide.

CHAPTER II

MATERIALS AND METHODS

Site description

This field study site is located in southeastern Oklahoma near Antlers, Pushmatha County, OK, USA (34°13' N, 95°42' W). This area represents the northwestern edge of the natural range of loblolly pine in the USA. The climate of the study area is hotter and drier than that currently found across the range of loblolly pine. Since our research site was located on the edge of the range, changes in climate may be clearly expressed. Miller et al. (1987) have stated that the western edge of the loblolly pine range is an extremely significant area where in climate change may lead to harmful effects on productivity leading to a decrease in the geographical distribution of loblolly pine forests.

The average annual precipitation at the study site is 120 cm. Drought periods are commonly experienced during the summer months and early fall. The average annual temperature is 17°C. Mean daytime summer and winter temperatures are 33.6°C and 13.3°C, respectively. The total number of growing days is 200.

The soil at the study site is a deep loamy fine sand belonging to the Glenpool series, described as sandy, siliceous, thermic psammentic paleudalf (USDA Soil Classification System). The soil has poor water holding capacity. The low

nutrient availability, of the soil is reflected in the site index of a nearby stand, which at 14.9 m at age 25, is low for the region (Woods et al. 1988).

The site was planted in 1990 with a mixture of unimproved Arkansas-Oklahoma families of loblolly pine (*Pinus taeda* L.). In 1994, at age four the average tree height was 2.1 m and the average ground line diameter was 6.2 cm. The density of the stand was 498 trees/hectare. The understory herbaceous vegetation was controlled using a mixture of Roundup (glyphosate) and Oust (Sulfometuron methyl), and hardwoods were controlled using Garlon (triclopyr) as a basal spray.

Study design and layout

The study design was a 2 x 2 factorial split plot with a combination of irrigation and fertilization treatments (Figure 83). The study included two levels of irrigation and two levels of fertilization. The four main plot treatment combinations were: (1) control (C-no irrigation and no fertilization), (2) irrigated (I-irrigation only), (3) fertilized (F-fertilization only), and (4) irrigated and fertilized (IF). The treatment combinations were established as a randomized complete block design. The four treatment combinations were assigned at random to the four treatment plots in one block and replicated in the other three blocks. The treatment plots were 50 x 50 m and the measurement plots within the treatment plots were 30 x 30 m. Fertilizer was applied in April 1994 at a rate of 200 lbs/ha of nitrogen. An additional application of fertilizer, based on foliar nutrient analysis, was made in August 1994, and consisted of 200 lbs/ha of nitrogen, 50 lbs/ha of phosphorus, 100 lbs/ha of potassium, 120 lbs/ha of calcium, 50 lbs/ha of magnesium and

1.5 lbs/ha of boron. Irrigation was initiated in July 1994 and continued throughout the study period. Irrigated plots were watered with a sprinkler irrigation system. Xylem pressure potential was used as an indirect measure of soil moisture. An additional application of fertilizer, based on foliar nutrient analysis, was made in May 1995, and consisted of 18 lbs/ha of nitrogen, 20 lbs/ha of phosphorus, 50 lbs/ha of magnesium 65.5 lbs/ha of sulfur and 1.5 lbs/ha of boron. The subplot treatments were three levels of carbon dioxide. The three levels of carbon dioxide were: (1) ambient CO2 (350 $\mu l\ l^{-1}$), (2) ambient CO2 + 175 $\mu l\ l^{-1}$ (525 $\mu l\ l^{-1}$) and (3) ambient CO2 + 350 $\mu l\ l^{-1}$ (700 $\mu l\ l^{-1}$).

A single tree was selected from each of the sixteen treatment plots and carbon dioxide treatments were individually assigned at random to three branches on each tree, for a total of 48 branches. Four towers were erected and connected by walkways to form a square around each tree. These walkways were used to reach the canopy of the trees. These towers and walkways also held the experimental branch chambers. Carbon dioxide fumigation was started in April 1994. Branches were exposed to the different levels of carbon dioxide for 24 hrs/day throughout the study period using branch chamber technology. Branch chambers have been shown to satisfactorily allow the fumigation of tissue from mature trees while maintaining adequate control of the microenvironment within the chamber so treatment effects can be distinguished (Teskey et al. 1991). Thus, long term manipulative studies on large trees can be easily conducted using branch chambers. Chambers consisted of a cylindrical aluminum frame (1.5 by 0.5 m) covered by a clear polyvinyl plastic film. Access to the foliage in the chamber was provided by a 1.5 m long zipper which was sewn to the polyvinyl plastic film. The plenum at the top of

the chamber had a number of holes which helped in the uniform distribution of air throughout the chamber. The chamber was completely open at the bottom. Air flow through each chamber was supplied by a blower which provided for ten air exchanges per minute to minimize heat gain within the chamber. Liquid carbon dioxide was vaporized and injected into the air stream to produce elevated concentrations of carbon dioxide. Elevated concentrations of carbon dioxide were dispensed to selected branch chambers using a mass flow controller connected to flow meters (one per chamber). Blowers mixed the known amount of carbon dioxide with ambient air and this mixture was then delivered to each branch chamber. The distribution and sampling of carbon dioxide to each of the chambers was done using a computer based control system. A data logger (Keithley 500A, Keithley Inc., Data Systems, Ohio, USA) was connected to the computer. The data logger controlled the opening and closing of the solenoid valves which directed the sample air coming from the branch chambers sequentially to an infrared gas analyzer (LI-6262, LiCor Inc., Lincoln, NE, USA). The infrared gas analyzer measured the carbon dioxide and water vapor concentration in the sample air from each branch chamber. All 48 branch chambers were sampled within thirty minutes. Chamber air temperature was not regulated.

Photosynthetic photon flux density (PPFD) and air temperature were measured inside each branch chamber. The PPFD was measured using photodiodes (G1118, Hamamatsu Corp., Bridgewater, NJ, USA). Light sensors were located above and below sample branches and were individually calibrated against a quantum sensor (LI-190SA, LiCor Inc, Lincoln, NE, USA). Air temperature was measured using a 0.8 mm diameter

copper-constantan thermocouple. The output from each of these sensors was measured every 6 s, averaged over each hour and stored in dataloggers (CR-7, Campbell Scientific Inc., Logan, UT, USA). An on-site weather station measured ambient weather conditions.

Physiological Measurements

Gas exchange data was collected with a portable CI-301 PS photosynthesis system (CID Inc., Vancouver, WA, USA). Light-saturated rate of photosynthesis (P_{max}), maximum stomatal conductance to water vapor (G_{max}) and total chlorophyll content were determined once a month on the first flush of the current-year foliage and on the first flush of the one-year old foliage on branches within each chamber. The P_{max} and G_{max} measurements were obtained under saturating light intensities. A source of artificial light (CI-301 LA, CID Inc., Vancouver, WA, USA) was used during measurements. Light-saturated rate of photosynthesis is an index of photosynthetic capacity and is designated as P_{max}. Stomatal conductance is defined as the maximum stomatal conductance to water vapor and designated as G_{max}. The light-saturated rate of photosynthesis (P_{max}) and maximum stomatal conductance to water vapor (G_{max}) measurements were determined at carbon dioxide concentrations similar to the fumigation concentrations. These concentrations of carbon dioxide were generated using a portable CI-301 AD adjustable humidity and CO_2 control unit (CID Inc., Vancouver, WA, USA). Using a standard carbon dioxide gas, the CI-301 PS was calibrated before each measurement day. Gas exchange measurements were obtained between 0800 and 1600 h Central Standard Time

from July 94 to March 96. It took approximately 5-6 minutes to obtain each measurement. The gas exchange measurements were made on attached needles inside the branch chamber. Light intensity was maintained at >1400 μmol $m^{-2}s^{-1}$ during all the gas measurements. During the months of July and August the measurements were obtained between 0100 and 0800 h Central Standard Time. These times were chosen in July and August to reduce the temperature and water stress. Prior to gas exchange measurements in July and August, the needles were exposed to a source of artificial light for a period of about 90 minutes using tungsten-halogen lamps (Osram Corp., NY, USA) placed in the branch chambers. This was done to ensure that the needles would more quickly reach equilibrium with the high light intensity (>1400 μmol $m^{-2}s^{-1}$) provided during gas exchange measurements. Three fascicles (9 needles) were enclosed in the leaf chamber during gas exchange measurements. An equation was used to determine the total needle surface area:

$$A\ (cm^2) = 2RFL\ (N + \pi) \qquad \text{Equation (1)}$$

where R is the average radius of the fascicles, F is the number of fascicles, L is the total fascicle or average fascicle length, and N is the number of needles per fascicle (Bingham, 1983). The radius was measured using a magnifying glass. After the gas exchange measurements were completed the needles were harvested and used to determine the chlorophyll content using the acetone method (Arnon, 1949).

Also, during the study needles were tested for acclimation. This was done by developing A/C_i curves, which plot internal carbon dioxide concentration (C_i) versus assimilation (A). A/C_i curves were obtained twice during the study. The A/C_i curves

were made using a portable CI-301 PS photosynthesis system, a portable CI-301 AD adjustable humidity, and a CO_2 control unit (CID Inc., Vancouver, WA, USA). A source of artificial light CI-301 LA (CID Inc., Vancouver, WA, USA) was used during measurements. The time to gather data to construct each A/C_i curve was about 2 to 2.5 hr. The carbon dioxide concentrations ranged from 0 to 2000 ppm. The measurements were obtained starting from the lowest and moving to the highest concentration. During each measurement the data was saved only after a steady-state value was reached. Each measurement took about 12 minutes. A/C_i curves were determined once in June 95 (for the first flush of one-year foliage), which was 14 months after the needles had been exposed to elevated concentrations of carbon dioxide, and again in October 95 (for the first flush of current-year foliage), which was 8 months after the needles had developed and grown under elevated concentrations of carbon dioxide. In June 95 the A/C_i curves were constructed between 0100 and 0800 h Central Standard Time. This was done to reduce needle temperature and water stress. In October 95 the A/C_i curves were constructed between 0900 and 1500 h Central Standard Time. Due to time constraints blocks I, II and IV were only used in gathering data to construct the A/C_i curves in June 95 and October 95.

Gas exchange data was collected for one-year old foliage (developed in 1994) from July 1994 to September 1995. Due to instrument malfunctioning data collection was not possible in the months of October, November and December in 1994 and January, February, March and August in 1995. The needles started to senesce after September. Gas exchange data was collected for current-year foliage (developed in 1995)

from June 95 to March 96. Data was collected for the current-year foliage starting in June because the needles were very fragile and their short length prevented their use in the foliage chamber of the CI-301 PS system before this period. Data was not collected in August due to instrument malfunctioning. In February 96 data was not collected because of bad weather conditions.

Statistical Analysis

The main effects of carbon dioxide, water and nutrient fluxes on light-saturated rate of photosynthesis (P_{max}), maximum stomatal conductance to water vapor (G_{max}) and total chlorophyll content were analyzed using the standard split plot analysis. The proc GLM procedure was used for analysis. Fischer's LSD was used for separation of the means of the dependent variables. All the analyses were interpreted at the $P = 0.05$ probability level. The Statistical Analysis System (SAS, 1988) was used for the analysis.

The A/C_i curves were fitted to an empirical non-linear regression model of the form: $A_{net} = A_{sat} [1-(1-R_d/A_{sat})^{(1-Ci/\Gamma)}]$ Equation (2)

where A_{sat} is the light and CO_2-saturated rate of photosynthesis, R_d is the rate of dark respiration at 0 ppm carbon dioxide concentration and Γ is the carbon dioxide compensation point for photosynthesis (Taylor and Gunderson 1988). The A/C_i data was fitted by the Marquardt-Levenberg iterative least-square method available in Sigma Plot software (Jandel Scientific, San Rafael, CA). The carboxylation efficiency was determined using the first four points of the A/C_i curve. The differences in the estimates of parameters such as A_{sat}, R_d, Γ, and carboxylation efficiency due to treatment (in this

case comparison was made between the 350 and 700 $\mu l\ l^{-1}$ treated needles in each block) was done by using the dummy variable technique. All the analysis were interpreted at the P = 0.05 probability level.

The dummy variable technique for making treatment comparison. For example, if we were trying to determine the differences in A_{sat} between the 350 and 700 $\mu l\ l^{-1}$ treated needles, equation (2) is modified as follows:

$$A_{net} = [A_{sat} + (dv) \times A_{satdiff}] [1-(1-R_d/(A_{sat} + (dv) \times A_{satdiff}))^{(1-Ci/T)}] \quad \text{Equation (3)}$$

The x and y columns in the spreadsheet were assigned to C_i and A_{net}. The dummy variables (dv, 0 or 1) were assigned to the needles treated with 350 and 700 $\mu l\ l^{-1}$ carbon dioxide. Sixteen data points for each carbon dioxide level was fitted to equation (3) using the iterative non-linear regression procedure. This procedure gave an estimate of the parameter and the standard error of the estimate. The Z-value was obtained by dividing the estimate of the parameter with the standard error of the estimate. The P-value was obtained by multiplying the area by 2. The above procedure was repeated for the other parameters.

The relative measure of stomatal limitation was calculated according to Farquhar and Sharkey (1982) using the data obtained from the A/C_i curves. In this simple method of assessing stomatal limitation, the actual assimilation rate that occurs, A, is subtracted from A_0, the rate which would occur if resistance to carbon dioxide diffusion was zero, and then divided by A_0 to give a relative measure of stomatal limitation, L_s. Thus

$$L_s = (1 - A/A_0) \times 100 \quad \text{Equation (4)}$$

The main effects of carbon dioxide, water and nutrient fluxes on stomatal limitations were analyzed using the ANOVA procedure. Fischer's LSD was used for separation of the means. All the analyses were interpreted at the $P = 0.05$.

CHAPTER III

RESULTS

Environmental Conditions

The total amount of precipitation received during the study period (121.8 cm) was slightly greater than the thirty year average for the region (114.8 cm) (Oklahoma Climatological Survey, Norman, OK). The amount of precipitation received in the months of July and November of 1994 was 7.5 and 10.4 cm, greater than the monthly average received in the region. During the month of September 1994 the amount of precipitation received was 11.1 cm less than the monthly average received in the region. The amount of precipitation received in the months of April and September of 1995 was 7.1 and 8.1 cm greater than the monthly average received in the region, respectively. During the month of February 1995 and 1996 the amount of precipitation received was 5.79 and 6.2 cm less than the monthly average received in the region (Figure 1).

Within the branch chambers the average daytime temperature ranged from 5.2 to 36.2^{0}C throughout the study period. The average daytime temperature within the branch chambers differed only slightly from the ambient temperature (Figure 2). The average PPFD in the lower part of the branch chambers during the daytime ranged from 150 to 600 μmol $m^{-2}s^{-1}$. The average PPFD in the upper part of the branch chambers during the

daytime ranged from 200 to 800 μmol $m^{-2}s^{-1}$ (Figure 3). The average CO_2 concentration within the branch chambers during the study period was 366.3, 543.0 and 714.2 μl l^{-1} for the three treatment levels , with standard errors of 10.8, 13.0 and 68.4, respectively (Figure 4).

Physiological Responses

The seasonal data for the light-saturated rate of photosynthesis (P_{max}), maximum stomatal conductance to water vapor (G_{max}) and total chlorophyll content of the one-year old needles and current-year needles are presented in figures 5 to 10. All the A/C_i curves obtained in July and October 1995 are presented in figures 11 and 12. The monthly data for the light-saturated rate of photosynthesis (P_{max}), maximum stomatal conductance to water vapor (G_{max}), total chlorophyll content and the complete set of A/C_i curves are presented in detail in figures 13 to 82.

Light-saturated rate of photosynthesis (P_{max})

One-year old needles

The results from the split-plot analysis on a monthly basis indicated that the carbon dioxide concentration had a substantial effect on the light-saturated rate of photosynthesis (P_{max}) of the needles growing at elevated carbon dioxide compared to the needles growing at ambient carbon dioxide concentration (Table 1 and Figure 5). This means that the elevated carbon dioxide concentration significantly increased the light-saturated rate of photosynthesis. Based on the split-plot analysis the irrigation and

fertilization treatments did not have any effect on the light-saturated rate of photosynthesis (Table 1 and Figure 5). In general, the light-saturated rate of photosynthesis of the 700 $\mu l\ l^{-1}$ carbon dioxide treated needles were higher than the light-saturated rate of photosynthesis of 525 and 350 $\mu l\ l^{-1}$ carbon dioxide treated needles. When averaged across the main plot treatments for the whole study period, the light-saturated rate of photosynthesis was 2.7, 4.6 and 5.4 $\mu mol\ m^{-2}s^{-1}$ for the 350 $\mu l\ l^{-1}$, 525 $\mu l\ l^{-1}$ and 700 $\mu l\ l^{-1}$ treatments, respectively. In other words, the light-saturated rate of photosynthesis was about 70 and 100% greater for the 525 $\mu l\ l^{-1}$ and 700 $\mu l\ l^{-1}$ treated needles, respectively compared to the 350 $\mu l\ l^{-1}$ treated branches for the whole study period. Interactions were not significant for carbon dioxide, irrigation and fertilization treatments during the study period except in the month of September 95 (Table 1).

Current-year needles

The light-saturated rate of photosynthesis for the current-year needles was obtained only from June 95 onward because prior to this date the needles would not accommodate the CI-301 PS foliage chamber. The results from the split-plot analysis on a monthly basis indicated the carbon dioxide concentration significantly increased the light-saturated rate of photosynthesis (P_{max}) of the needles growing at elevated carbon dioxide compared to the needles growing at ambient carbon dioxide concentration (Table 2 and Figure 6). Irrigation and fertilization treatments did not have any effect on the light-saturated rate of photosynthesis of the current-year needles during the study period except in the month of December 95, wherein the light-saturated rate of photosynthesis

was significantly affected by fertilization (Table 2 and Figure 6). During this month the light-saturated rate of photosynthesis of the fertilized plot was less than the non-fertilized plot (3.6 μmol $m^{-2}s^{-1}$ to 4.5 μmol $m^{-2}s^{-1}$, respectively).

Elevated carbon dioxide concentration had a significant effect on the light-saturated rate of photosynthesis even in the month of January (Table 2 and Figure 6). The light-saturated rate of photosynthesis increased with an increase in the carbon dioxide concentration even though the maximum stomatal conductance to water vapor was at its lowest. During this month, when averaged across the main plot treatments, the light-saturated rate of photosynthesis was 2.6, 3.5 and 3.8 μmol $m^{-2}s^{-1}$ for the 350 μl l^{-1}, 525 μl l^{-1} and 700 μl l^{-1} treatments, respectively.

When averaged across the main plot treatments for the whole study period, the light-saturated rate of photosynthesis was 3.4, 4.6 and 5.6 μmol $m^{-2}s^{-1}$ for the 350 μl l^{-1}, 525 μl l^{-1} and 700 μl l^{-1} treatments, respectively for foliage which developed under elevated carbon dioxide treatments. In other words, the light-saturated rate of photosynthesis was about 35 and 65% greater for the 525 μl l^{-1} and 700 μl l^{-1} treated needles, respectively compared to the 350 μl l^{-1} treated needles for the whole study period. Interactions were not significant for carbon dioxide, irrigation and fertilization treatments during the study period (Table 2).

Maximum stomatal conductance to water vapor (G_{max})

One-year old needles

In general, the needles growing under 525 µl l^{-1} carbon dioxide concentration had a slightly higher maximum stomatal conductance to water vapor compared to the 350 µl l^{-1} and 700 µl l^{-1} carbon dioxide concentration. When averaged across the main plot treatments for the whole study period, the maximum stomatal conductance was 83.8, 94.0 and 83.2 mmol $m^{-2}s^{-1}$ for the 350 µl l^{-1}, 525 µl l^{-1} and 700 µl l^{-1} treated needles, respectively. Interactions were not significant for carbon dioxide, irrigation and fertilization treatments during the study period (Table 3).

The results from the split-plot analysis on a monthly basis indicated maximum stomatal conductance to water vapor (G_{max}) was not affected by carbon dioxide concentration, irrigation or fertilization in any of the months during the study period except for July 94, August 94 and June 95(Table 3 and Figure 7).

In the month of July 94, with increasing carbon dioxide concentration, the maximum stomatal conductance to water vapor decreased. During this month, when averaged across the main plot treatments, the maximum stomatal conductance to water vapor (G_{max}) was 108.9, 109.0 and 65.1 mmol $m^{-2}s^{-1}$ for the 350 µl l^{-1}, 525 µl l^{-1} and 700 µl l^{-1} treatments, respectively. In this case, the maximum stomatal conductance to water vapor did not differ between the 350 and 525 µl l^{-1} treated needles but the G_{max} differed significantly between the 350 µl l^{-1} and 700 µl l^{-1} treated needles and also between the 525 and 700 µl l^{-1} treated needles.

In the month of August 94, with increasing carbon dioxide concentration, the maximum stomatal conductance to water vapor increased. During this month, when averaged across the main plot treatments, the maximum stomatal conductance to water vapor (G_{max}) was 71.0, 106.0 and 93.0 mmol $m^{-2}s^{-1}$ for the 350 $\mu l\ l^{-1}$, 525 $\mu l\ l^{-1}$ and 700 $\mu l\ l^{-1}$ treatments, respectively. In this case, the maximum stomatal conductance to water vapor did not differ between the 525 and 700 $\mu l\ l^{-1}$ treated needles but the G_{max} differed significantly between the 350 $\mu l\ l^{-1}$ and 525 $\mu l\ l^{-1}$ treated needles and also between the 350 and 700 $\mu l\ l^{-1}$ treated needles.

The maximum stomatal conductance to water vapor was at its highest in the month of June 95. During this month, when averaged across the main plot treatments, the maximum stomatal conductance to water vapor (G_{max}) was 139.4, 156.6 and 174.0 mmol $m^{-2}s^{-1}$ for the 350 $\mu l\ l^{-1}$, 525 $\mu l\ l^{-1}$ and 700 $\mu l\ l^{-1}$ treatments, respectively. In this case the maximum stomatal conductance to water vapor did not differ between the 350 and 525 $\mu l\ l^{-1}$ treated needles and 525 and 700 $\mu l\ l^{-1}$ needles but the G_{max} differed significantly between the 350 and 700 $\mu l\ l^{-1}$ treated needles.

Current-year needles

When averaged across the main plot treatments for the whole study period, the maximum stomatal conductance was 84.1, 81.5 and 83.3 mmol $m^{-2}s^{-1}$ for the 350 $\mu l\ l^{-1}$, 525 $\mu l\ l^{-1}$ and 700 $\mu l\ l^{-1}$ treated needles, respectively.

The results from the split-plot analysis on a monthly basis indicated that the maximum stomatal conductance to water vapor (G_{max}) was significantly affected by either

one of these treatments such as carbon dioxide, irrigation or fertilization in the months of September 95, October 95, December 95 and March 96 during the study period. In the months of June 95, July 95, November 95 and January 96 the maximum stomatal conductance to water vapor was not affected by carbon dioxide, irrigation and fertilization treatments. During these months interactions were not significant for carbon dioxide, irrigation and fertilization treatments (Table 4 and Figure 8).

The maximum stomatal conductance to water vapor was at its highest in the month of June 95. During this month, when averaged across the main plot treatments, the maximum stomatal conductance to water vapor (G_{max}) was 211.4, 213.0 and 236.4 mmol $m^{-2}s^{-1}$ for the the 350 $\mu l\ l^{-1}$, 525 $\mu l\ l^{-1}$ and 700 $\mu l\ l^{-1}$ treated needles, respectively (Figure 8).

In the month of September 95, irrigation and fertilization significantly affected the maximum stomatal conductance to water vapor. The maximum stomatal conductance to water vapor of the irrigated plot was significantly greater than the non-irrigated plot. The average G_{max} for the irrigated plot was 104.4 mmol $m^{-2}s^{-1}$ and for the non-irrigated plot it was 85.2 mmol $m^{-2}s^{-1}$. The maximum stomatal conductance to water vapor of the fertilized plot was significantly lesser than the non-fertilized plot. The average G_{max} for the fertilized plot was 82.0 mmol $m^{-2}s^{-1}$ and for the non-fertilized plot it was 107.9 mmol $m^{-2}s^{-1}$. Interactions such as I x CO2 and F x CO2 were significant (Table 4).

In the month of October 95, fertilization significantly affected the maximum stomatal conductance to water vapor. The maximum stomatal conductance to water vapor of the fertilized plots was significantly less than the non-fertilized plots. The

average G_{max} for the fertilized plots was 67.9 mmol $m^{-2}s^{-1}$ and for the non-fertilized plots it was 90.0 mmol $m^{-2}s^{-1}$. Interactions were not significant for carbon dioxide, irrigation and fertilization treatments during the study period (Table 4).

In the month of December 95, fertilization significantly affected the maximum stomatal conductance to water vapor. The maximum stomatal conductance to water vapor of the fertilized plots was significantly less than the non-fertilized plots. The average G_{max} for the fertilized plots was 28.8 mmol $m^{-2}s^{-1}$ and for the non-fertilized plots it was 44.7 mmol $m^{-2}s^{-1}$. This coincides very well with the decrease in P_{max} in the fertilized plots compared to the non-fertilized plots. Interactions were not significant for carbon dioxide, irrigation and fertilization treatments during the study period (Table 4).

The maximum stomatal conductance to water vapor was at its lowest in the month of January 96. During this month, when averaged across the main plot treatments, the maximum stomatal conductance to water vapor (G_{max}) was 35.1, 37.0 and 31.4 mmol $m^{-2}s^{-1}$ for the 350 µl l^{-1}, 525 µl l^{-1} and 700 µl l^{-1} treatments, respectively (Figure 8).

In the month of March 96, carbon dioxide, irrigation and fertilization significantly affected the maximum stomatal conductance to water vapor. The maximum stomatal conductance to water vapor decreased with an increase in carbon dioxide concentration. When averaged across the main plot treatments, the maximum stomatal conductance to water vapor was 40.1, 30.1 and 36.7 mmol $m^{-2}s^{-1}$. The maximum stomatal to water vapor did not differ significantly between the 350 and 700 µl l^{-1} treated needles but the G_{max} differed significantly between the 350 and 525 µl l^{-1} treated needles and also between the 525 and 700 µl l^{-1} treated needles. The maximum stomatal conductance to water vapor

of the irrigated plots was significantly greater than the non-irrigated plots. The average G_{max} for the irrigated plots was 39.6 mmol $m^{-2}s^{-1}$ and for the non-irrigated plots it was 31.5 mmol $m^{-2}s^{-1}$. The maximum stomatal conductance to water vapor of the fertilized plots was lesser than the non-fertilized plots. The average G_{max} for the fertilized plots was 33.7 mmol $m^{-2}s^{-1}$ and for the non-fertilized plots it was 37.4 mmol $m^{-2}s^{-1}$. Interactions such as I x F x CO2 were significant (Table 4).

Total chlorophyll content

One-year old needles

In general, the total chlorophyll content decreased with increasing carbon dioxide concentration. When averaged across the main plot treatments, the total chlorophyll content was 311.6, 297.5 and 290.5 mg/m^2 for the 350 $\mu l\ l^{-1}$, 525 $\mu l\ l^{-1}$ and 700 $\mu l\ l^{-1}$ treated needles, respectively.

The results from the split-plot analysis on a monthly basis indicated that the total chlorophyll content was significantly affected by either one of these treatments such as carbon dioxide, irrigation or fertilization in the months of July 94, August 94, April 95, May 95, June 95 and September 95 during the study period. In September 94, the total chlorophyll content was not affected by carbon dioxide, irrigation and fertilization treatments. During this month even interactions were not significant for carbon dioxide, irrigation and fertilization treatments (Table 5 and Figure 9).

In the month of August 94, elevated carbon dioxide concentration significantly affected the total chlorophyll content. The total chlorophyll content decreased with an

increase in carbon dioxide concentration. When averaged across the main plot treatments the total chlorophyll content was 358.5, 313.0 and 309.8 mg/m^{-2}. The total chlorophyll content did not differ significantly between the 525 and 700 $\mu l\ l^{-1}$ treated needles but the total chlorophyll content differed significantly between the 350 and 525 $\mu l\ l^{-1}$ treated needles and also between the 350 and 700 $\mu l\ l^{-1}$ treated needles.

In the month of April 95, fertilization significantly affected the total chlorophyll content (Table 5 and Figure 9). The total chlorophyll content of the fertilized plot was significantly greater than the non-fertilized plot. The average total chlorophyll content for the fertilized plot was 307.4 mg/m^{-2} and for the non-fertilized plot it was 276.1 mg/m^{-2}.

In the month of May 95, elevated carbon dioxide concentration significantly affected the total chlorophyll content. When averaged across the main plot treatments, the total chlorophyll content was 296.0, 283.2 and 322.9 mg/m^{-2}. The total chlorophyll content differed significantly between the 525 and 700 $\mu l\ l^{-1}$ treated needles but between the 350 and 525 $\mu l\ l^{-1}$ treated needles nor between the 350 and 700 $\mu l\ l^{-1}$ treated needles. In the months of July 94, June 95 and September 95 interactions such as I x CO2, F x CO2 and I x F x CO2 were significant (Table 5).

Current-year needles

When averaged across the main plot treatments, the total chlorophyll content was 200.7, 201.4 and 198.1 mg/m^2 for the 350 $\mu l\ l^{-1}$, 525 $\mu l\ l^{-1}$ and 700 $\mu l\ l^{-1}$ treated needles, respectively.

The results from the split-plot analysis on a monthly basis indicated that the total chlorophyll content was significantly affected by either one of these treatments such as carbon dioxide, irrigation or fertilization in the months of November 95, January 96 and March 96. During the months of June 95, September 95, October 95 and December 95 the total chlorophyll content was not affected by carbon dioxide, irrigation and fertilization treatments. During these months interactions were not significant for carbon dioxide, irrigation and fertilization treatments (Table 6 and Figure 10).

In the month of March 96, irrigation significantly affected the total chlorophyll content (Table 6 and Figure 10). The total chlorophyll content of the irrigated plot was significantly lesser than the non-irrigated plot. The average total chlorophyll content for the irrigated plot was 228.3 mg/m^{-2} and for the non-irrigated plot it was 274.4 mg/m^{-2}.

In the months of November 95, January 96 and March 96 interactions such as I x CO2 and F x CO2 were significant (Table 6).

Acclimation

July 1995

The light and CO_2-saturated rate of photosynthesis (A_{sat}), the rate of dark respiration at 0 ppm carbon dioxide concentration (R_d), the carbon dioxide compensation point for photosynthesis (Γ) and the net-photosynthetic rate at a given carbon dioxide concentration was determined from the individual A/C_i curves using equation 2. The relative measure of stomatal limitation (L_s) was calculated using equation 3.

In the control treatment (block ii) the needles treated with 700 μl l^{-1} carbon dioxide concentration showed evidence of acclimation. The net-photosynthetic rate of the needles grown at 700 μl l^{-1} carbon dioxide concentration tended to be lower than the net-photosynthetic rate of the needles grown at 350 μl l^{-1} carbon dioxide concentration when the net-photosynthetic rate was measured at the same carbon dioxide concentration. The A_{sat} and carboxylation efficiency of the needles grown at 350 μl l^{-1} carbon dioxide concentration was significantly different from the A_{sat} and carboxylation efficiency of the needles grown at 700 μl l^{-1} carbon dioxide concentration. R_d and Γ was not significantly different between the needles grown at 350 μl l^{-1} and the needles grown at 700 μl l^{-1} carbon dioxide concentration (Table 7 and Figure 11). The relative measure of stomatal limitation (L_s) was not significantly different between needles grown at 350 μl l^{-1} and the needles grown at 700 μl l^{-1} carbon dioxide concentration (Table 8).

In the irrigated treatment (blocks i, ii and iv) the needles treated with 700 μl l^{-1} carbon dioxide concentration showed evidence of acclimation. The net-photosynthetic rate of the needles grown at 700 μl l^{-1} carbon dioxide concentration tended to be lower than the net-photosynthetic rate of the needles grown at 350 μl l^{-1} carbon dioxide concentration when the net-photosynthetic rate was measured at the same carbon dioxide concentration. The A_{sat} and R_d of the needles grown at 350 μl l^{-1} carbon dioxide concentration was significantly different from the A_{sat} and R_d of the needles grown at 700 μl l^{-1} carbon dioxide concentration. Γ and carboxylation efficiency in the irrigated treatment (block i and iv) was not significantly different between the needles grown at 350 μl l^{-1} and the needles grown at 700 μl l^{-1} carbon dioxide concentration. In the

irrigated treatment (block ii) Γ was not significantly different between the needles grown at 350 μl l^{-1} and the needles grown at 700 μl l^{-1} carbon dioxide concentration but the carboxylation efficiency was significantly different between the needles grown at 350 μl l^{-1} and the needles grown at 700 μl l^{-1} carbon dioxide concentration (Table 7 and Figure 11). The relative measure of stomatal limitation (L_s) was not significantly different between needles grown at 350 μl l^{-1} and the needles grown at 700 μl l^{-1} carbon dioxide concentration (Table 8).

In the fertilized treatment (block ii) the needles treated with 700 μl l^{-1} carbon dioxide concentration showed evidence of acclimation. The net-photosynthetic rate of the needles grown at 700 μl l^{-1} carbon dioxide concentration tended to be lower than the net-photosynthetic rate of the needles grown at 350 μl l^{-1} carbon dioxide concentration when the net-photosynthetic rate was measured at the same carbon dioxide concentration. The A_{sat} and R_d of the needles grown at 350 μl l^{-1} carbon dioxide concentration was significantly different from the A_{sat} and R_d of the needles grown at 700 μl l^{-1} carbon dioxide concentration. Γ and carboxylation efficiency was not significantly different between the needles grown at 350 μl l^{-1} and the needles grown at 700 μl l^{-1} carbon dioxide concentration (Table 7 and Figure 11). The relative measure of stomatal limitation (L_s) was not significantly different between needles grown at 350 μl l^{-1} and the needles grown at 700 μl l^{-1} carbon dioxide concentration (Table 8).

In the irrigated and fertilized treatment (blocks ii and iv) the needles treated with 700 μl l^{-1} carbon dioxide concentration showed evidence of acclimation. The net-photosynthetic rate of the needles grown at 700 μl l^{-1} carbon dioxide concentration tended

to be lower than the net-photosynthetic rate of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration when the net-photosynthetic rate was measured at the same carbon dioxide concentration. In the irrigated and fertilized treatment (block ii) A_{sat} of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration was significantly different from the A_{sat} of the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration. R_d, Γ and carboxylation efficiency in the irrigated and fertilized treatment (block ii) was not significantly different between the needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration. In the irrigated and fertilized treatment (block iv) A_{sat}, R_d and carboxylation efficiency of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration was significantly different from the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration. Γ in the irrigated and fertilized (block iv) was not significantly different between the needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration (Table 7 and Figure 11). The relative measure of stomatal limitation (L_s) was not significantly different between needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration (Table 8).

October 1995

In the control treatment (blocks i, ii and iv) the needles treated with 700 $\mu l\ l^{-1}$ carbon dioxide concentration did not show any evidence of acclimation. The net-photosynthetic rate of the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration tended to be similar to the net-photosynthetic rate of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration when the net-photosynthetic rate was measured at the same carbon

dioxide concentration. A_{sat}, R_d, Γ and carboxylation efficiency did not differ significantly between the needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration (Table 9 and Figure 12). The relative measure of stomatal limitation (L_s) was not significantly different between needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration (Table 10).

In the irrigated treatment (blocks ii and iv) the needles treated with 700 $\mu l\ l^{-1}$ carbon dioxide concentration showed evidence of acclimation. The net-photosynthetic rate of the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration tended to be lower than the net-photosynthetic rate of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration when the net-photosynthetic rate was measured at the same carbon dioxide concentration. The A_{sat} and R_d of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration was significantly different from the A_{sat} and R_d of the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration. Γ and carboxylation efficiency in the irrigated treatment (block iv) was not significantly different between the needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration. In the irrigated treatment (block ii) Γ was not significantly different between the needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration but the carboxylation efficiency was significantly different between the needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration (Table 9 and Figure 12). The relative measure of stomatal limitation (L_s) was not significantly different between needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration (Table 10).

In the fertilized treatment (blocks ii and iv) the needles treated with 700 $\mu l\ l^{-1}$ carbon dioxide concentration showed evidence of acclimation. The net-photosynthetic rate of the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration tended to be lower than the net-photosynthetic rate of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration when the net-photosynthetic rate was measured at the same carbon dioxide concentration. The A_{sat}, R_d and carboxylation efficiency of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration was significantly different from the A_{sat}, R_d and carboxylation efficiency of the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration. Γ not significantly different between the needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration (Table 9 and Figure 12). The relative measure of stomatal limitation (L_s) was not significantly different between needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration (Table 10).

In the irrigated and fertilized treatment (blocks i, ii and iv) the needles treated with 700 $\mu l\ l^{-1}$ carbon dioxide concentration showed evidence of acclimation. The net-photosynthetic rate of the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration tended to be lower than the net-photosynthetic rate of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration when the net-photosynthetic rate was measured at the same carbon dioxide concentration. In the irrigated and fertilized treatment (block i, ii and iv) A_{sat} of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration was significantly different from the A_{sat} of the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration. R_d (block i and ii) of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration was significantly different from the R_d of the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration. R_d

(block iv) of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration was not significantly different from the R_d of the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration. Γ (block i, ii and iv) was not significantly different between the needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration. The carboxylation efficiency in the irrigated and fertilized treatment (block i and iv) was significantly different between the needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration. In the irrigated and fertilized treatment (block ii) the carboxylation efficiency of the needles grown at 350 $\mu l\ l^{-1}$ carbon dioxide concentration was not significantly different from the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration (Table 9 and Figure 12). The relative measure of stomatal limitation (L_s) was not significantly different between needles grown at 350 $\mu l\ l^{-1}$ and the needles grown at 700 $\mu l\ l^{-1}$ carbon dioxide concentration (Table 10).

CHAPTER IV

DISCUSSION

The light-saturated rate of photosynthesis was approximately 70 and 100% greater for the 525 $\mu l\ l^{-1}$ and 700 $\mu l\ l^{-1}$ treated needles, respectively compared to the 350 $\mu l\ l^{-1}$ treated needles for the whole study period for the one-year old needles. The light-saturated rate of photosynthesis was about 35 and 65% greater for the 525 $\mu l\ l^{-1}$ and 700 $\mu l\ l^{-1}$ treated needles, respectively compared to the 350 $\mu l\ l^{-1}$ treated needles for the whole study period for the current-year needles. The percentage increases in light-saturated rate of photosynthesis are within the range of values that have been obtained in other studies on loblolly pine (Murthy et al. 1996, Tissue et al. 1996, Groninger et al. 1996, Liu and Teskey 1995, Teskey 1995, Ellsworth et al. 1995, Fetcher et al. 1988). Studies on other tree species such as *Pinus sylvestris* (Wang et al. 1995), *Pinus eldarica* (Garcia et al. 1994), *Castanea sativa* (El Kohen and Mousseau 1994), three Australian tree species (Idso and Kimball 1993), *Castanea sativa* (Mousseau 1993), *Betula pendula* (Evans et al. 1993), *Populus grandidentata* (Curtis and Teeri 1992), *Abies fraseri* (Samuelson and Seiler 1992), *Pinus radiata* (Conroy et al. 1988), and *Picea glauca* (Higginbotham 1983) have reported similar types of responses. Kimball et al. (1993), Rogers and Dahlman (1993), Poorter (1993), and Drake (1992) have reported similar types of responses in crop and range species.

The values of light-saturated rate of photosynthesis obtained in this study were somewhat lower than those found for mature loblolly pine (Murthy et al. 1996, Liu and Teskey 1995, Teskey 1995) and for loblolly pine seedlings (Tissue et al. 1996, Groninger et al. 1995). However, their values were obtained from selected families of loblolly pine, whereas our values of light-saturated rate of photosynthesis were collected from a mixture of non-improved sources. Boltz et al. (1986) have shown seed source variation in light-saturated rate of photosynthesis among diverse sources of loblolly pine.

Irrigation and fertilization did not have any effect on the light-saturated rate of photosynthesis. Soil moisture content of the irrigated plots was not consistently different from non-irrigated plots because of the sandy soil which led to rapid infiltration of applied water. In addition needle xylem pressure potential obtained during gas exchange did not differ between trees growing on irrigated and non-irrigated plots. Gas exchange data obtained from trees growing on fertilized and non-fertilized plots did not differ. Although preliminary soil tests showed low levels of nitrogen and other nutrients, monthly sampling of foliage indicated growing season levels of nitrogen ranging from 1.20 % to 1.40 %. Because a value of 1.1 % N is considered to be adequate in loblolly pine (Allen 1987), it is not surprising that a main treatment effect was not found during the study. There have been a number of studies that report neither water nor nutrients affect light-saturated rate of photosynthesis under conditions of elevated carbon dioxide concentrations (Murthy et al. 1996, Groninger et al. 1995, Johnsen 1993, Conroy et al. 1990, Conroy et al. 1988, Conroy et al. 1986, Norby et al. 1986, Wray and Strain 1986). The results obtained in this study are in contrast to the results obtained in other studies

(Tissue et al. 1996, Wilkins et al. 1994, Thomas et al. 1994, Lewis et al. 1994, El Kohen and Mousseau 1994, Conroy 1992, Brown 1991, Conroy et al. 1990, Conroy et al. 1988, Cure et al. 1988, Conroy et al. 1986, Morrison and Gifford 1984, Goudriaan and Ruiter 1983) where nutrient availability was shown to increase light-saturated rate of photosynthesis under elevated carbon dioxide concentrations. Thiec and Dixon (1996), Kellomaki and Wang (1996), Stewart et al. (1995), Geuhl et al. (1994), Stoneman et al. (1994), Townend (1993), Brissette and Chambers (1992), Miao et al. (1992), Gimenez et al. (1992), and Tolley and Strain (1984) reported the availability of water affected the light-saturated rate of photosynthesis under elevated carbon dioxide concentrations.

In general, in our study the maximum stomatal conductance to water vapor (G_{max}) was not affected by elevated carbon dioxide concentration, irrigation or fertilization treatments. Murthy et al. (1996) have reported similar results in their study. Teskey (1995), Liu and Teskey (1995) and Ellsworth et al. (1995) have also reported that the maximum stomatal conductance to water vapor and stomatal sensitivity in loblolly pine were not affected by different levels of carbon dioxide concentration. Studies on other tree species such as *Picea sitchensis* (Lee et al. 1993), *Malus domestica, Quercus prinus,* and *Quercus robur* (Bunce 1992), and *Pinus contorta* (Higginbotham et al. 1985) have reported similar types of responses.

The above mentioned results differ from those obtained in other studies (Thiec and Dixon 1996, Tyree and Alexander 1993, Townend 1993, Kimball et al. 1993, Eamus et al. 1993, Evans et al. 1993, Samuelson and Seiler 1992, Eamus and Jarvis 1989, Fetcher et al. 1988, Hollinger 1987, Cure and Acock 1986 and Tolley and Strain 1985)

who have reported that the maximum stomatal conductance to water vapor decreased in response to increasing levels of carbon dioxide concentration, indicating that the stomates do respond to increasing levels of carbon dioxide concentration. In other studies it has also been reported that the maximum stomatal conductance to water vapor increased in response to elevated carbon dioxide concentration (Barton et al. 1993 and Norby and O'Neil 1991). According to Eamus and Jarvis (1989), the response of stomata to elevated carbon dioxide is not very clear and the stomatal sensitivity to elevated carbon dioxide may be influenced by a number of interacting factors such as temperature, light and plant water status.

In general, in our study the total chlorophyll content was not affected by elevated carbon dioxide concentration, irrigation or fertilization treatments. Tissue et al. (1996) and Eamus et al. (1993) reported that the chlorophyll content was not affected by elevated carbon dioxide concentration. These results are similar to the results obtained in our study. Drake (1992) reported total chlorophyll content increased in response to elevated carbon dioxide concentration. In other studies it has been reported that the total chlorophyll content decreased in response to elevated carbon dioxide concentration (Tissue et al. 1995, El Kohen and Mousseau 1994, Wilkins et al. 1994, Cui and Nobel 1994, Cui et al. 1993, Lee et al. 1993 and Evans et al. 1993). The decrease in chlorophyll content may be due to accumulation of carbohydrates and distortion of chloroplasts (Reining 1994, Wilkins et al. 1994) and also the decrease in chlorophyll content in response to elevated carbon dioxide concentration occurs under conditions of nutrient deficiency (El Kohen and Mousseau 1994). It has been reported in other studies that the

total chlorophyll content decreased in response to elevated carbon dioxide concentration when the light intensity was moderate to high (Wullschleger et al. 1992, Oberbauer et al.1985), and sometimes the total chlorophyll content increased in response to elevated carbon dioxide concentration when the light intensity was relatively low (Gaudillere and Mousseau 1989). Hence, the changes in total chlorophyll content in response to elevated carbon dioxide concentration depends upon the prevailing light intensities.

Acclimation, or downregulation, refers to the reallocation of resources to the processes that are most limited for optimal survival, growth and reproduction under the present environmental conditions. According to this hypothesis, the plants grown at elevated carbon dioxide concentration and measured at elevated carbon dioxide concentration are expected to show an increased performance compared to the plants grown at ambient carbon dioxide concentration, but when measured at low carbon dioxide concentration, the plants grown at ambient carbon dioxide concentration should perform better (Arp and Drake 1991).

An increased carbon dioxide concentration results in an increased rate of photosynthesis, reduced stomatal conductance and possibly an increase in the efficiency of nitrogen use by reallocation of nitrogen from the enzyme rubisco. Acclimation can occur due to a reduction in the activity of rubisco, to a decrease in the capacity for RuBP regeneration or to inorganic phosphate limitation. Sometimes the reduction in photosynthetic capacity is attributed to end product inhibition, due to the insufficient demand for the end product of photosynthesis such as starch and sucrose. This leads to an accumulation of starch in the leaf. A limitation in nitrogen nutrition may also lead to a

reduction in photosynthetic capacity. An other important factor that determines photosynthetic acclimation is the source-sink balance. A reduction in rooting volume also leads to the decrease in photosynthetic capacity (Sage 1994, Arp 1991). Elevated carbon dioxide concentration leads to a reduction in stomatal conductance hence decreasing the transport of carbon to the site of carboxylation (Reining 1994).

The photosynthesis of plants grown under elevated carbon dioxide concentration and ambient carbon dioxide concentration should be compared at the same C_i so that the effects of elevated carbon dioxide concentration on photosynthetic capacity can be distinguished from the effects on stomatal conductance. Hence, it is important to estimate C_i which allows us to draw conclusions about photosynthetic acclimation. According to von Caemmerer and Farquhar (1981), in an A/C_i curve the carboxylation efficiency is limited by the amount, activity and kinetic properties of rubisco at low intercellular $p(CO_2)$ and by the RuBP regeneration capacity or inorganic phosphate regeneration capacity at medium to high intercellular $p(CO_2)$.

In our study, A/C_i curves were used for testing acclimation to elevated carbon dioxide concentration and the mechanisms that contribute to acclimation. This is similar to the tests used in other studies (Thiec and Dixon 1996, Liu and Teskey 1995, Teskey 1995, Thomas et al. 1994, Cui and Nobel 1994, El Kohen and Mousseau 1994). In a number of studies, it has been reported that there has been a "positive acclimation or upward regulation" of photosynthesis to elevated carbon dioxide concentration. This means that the photosynthetic capacity actually increased in response to elevated carbon dioxide concentration (Liu and Teskey 1995, Teskey 1995, Garcia et al. 1994, Gunderson

et al. 1993, Barton et al. 1993, Curtis and Teeri 1992, Samuelson and Seiler 1992, Arp and Drake 1991, Sage 1989, Eamus and Jarvis 1989, Fetcher et al. 1988). However, in a number of other studies, it has been reported that there has been a "negative acclimation or downward regulation" of photosynthesis to elevated carbon dioxide concentration. This means that the photosynthetic capacity actually decreased in response to elevated carbon dioxide concentration. These negative responses may be due to deficiency of nutrients, decrease in sink capacity or reduction in rooting volume (Thiec and Dixon 1996, Cui and Nobel 1994, Thomas et al. 1994, El Kohen and Mousseau 1994, Lewis et al. 1994, Wilkins et al. 1994, Samuelson and Seiler 1992, Thomas and Strain 1991, Ziska et al. 1991, Eamus and Jarvis 1989).

It has been reported in a number of studies that in loblolly pine a "positive acclimation or upward regulation" of photosynthesis occurs in response to elevated carbon dioxide concentration (Liu and Teskey 1995, Teskey 1995, Ellsworth et al. 1995). The results obtained in this study are in contrast to results obtained in the latter studies. In this study, evidence was found to show a negative acclimation or downward regulation of photosynthesis. When acclimation was tested in July and October 1995, 7 of the 12 trees tested showed signs of acclimation (Table 7 and 9, Figure 11 and 12). Trees that showed evidence of acclimation were mostly limited by the RuBP regeneration capacity or inorganic phosphate regeneration capacity at medium to high carbon dioxide concentrations and also sometimes limited by the enzyme kinetics of rubisco at low carbon dioxide concentrations. The results obtained in our study are very similar to the results obtained in other studies (Thiec and Dixon 1996, Wilkins et al. 1994, Cui and

Noble 1994, Thomas et al. 1994, El Kohen and Mousseau 1994, Lewis et al. 1994, Thomas and Strain 1991, Ziska et al. 1991, Eamus and Jarvis 1989). In most of these studies a decline in photosynthetic capacity has been attributed to the limitation in nitrogen nutrition, a reduction in rooting volume or an imbalance in the source-sink relationship.

Thiec and Dixon (1996) concluded acclimation occurred in Norway spruce and red oak after exposure to elevated carbon dioxide concentration for three years and this could not be explained by leaf area differences, available soil for roots, nutrient limitation, or starch accumulation. Bunce (1992) stated that an eventual downregulation can occur even when nutrients were not limiting. Kerstiens and Hawes (1994) stated that downregulation can occur even without root volume problems . The results obtained in our study are very similar to the results obtained in the studies of Thiec and Dixon (1996), Bunce (1992) and Kerstiens and Hawes (1994). In this study, evidence of acclimation to elevated carbon dioxide concentration was found that could not be explained by either nutrient limitation or available soil volume for growth of roots. Tissue et al. (1996), in their long-term study on the effects of elevated carbon dioxide on loblolly pine, stated that during a certain portion of the study they noticed signs of photosynthetic adjustment to elevated carbon dioxide concentration because of the reductions in leaf N concentration and rubisco activity.

In summary, with increasing carbon dioxide concentration the light-saturated rate of photosynthesis increased and the response was persistent over the growing season and throughout the life of the needles. The maximum stomatal conductance to water vapor

and the total chlorophyll content was not affected by elevated carbon dioxide concentration, irrigation or fertilization treatments. The results from the A/C_i curves indicated a negative acclimation or downward regulation of photosynthesis due to the limitations imposed by RuBP regeneration capacity, inorganic phosphate capacity or the enzyme kinetics of rubisco. It is unlikely that the phenomenon of acclimation found in this study was based on either nutrient limitation or available soil volume for the growth of roots. This response was found in both July and October and therefore is not likely due to an artifact or experimental error.

In general, it can be concluded from this study that with global increases in atmospheric carbon dioxide concentration, the maximum potential for carbon assimilation will be enhanced, although needles may become acclimated to new conditions. Potentially large increases in pine growth rates, both in plantations and natural ecosystems, have several implications for forest management. These include lower planting densities, earlier thinning regimes, and shorter rotation lengths. However, future climate changes resulting in increased temperatures and decreased precipitation might limit the potential gain in forest productivity in response to elevated atmospheric carbon dioxide concentrations.

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APPENDIXES

APPENDIX A

TABLES

TABLE I

P-VALUES OBTAINED FROM THE SPLIT-PLOT ANALYSIS OF THE LIGHT-SATURATED RATE OF PHOTOSYNTHESIS (P_{max}) OF ONE-YEAR OLD NEEDLES

Source	df	July 94	Aug 94	Sep 94	Apr 95	May 95	Jun 95	Jul 95	Sep 95
Irri (I)	1	0.5672	0.2426	0.6121	0.6203	0.3698	0.2622	0.5158	0.9391
Fert (F)	1	0.2327	0.7689	0.1856	0.2546	0.5504	0.3486	0.8811	0.0956
I x F	1	0.9837	0.9545	0.4184	0.8844	0.3271	0.8997	0.2021	0.5447
CO2	2	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
I x CO2	2	0.7802	0.8942	0.3316	0.2811	0.3249	0.8067	0.4399	0.0308
F x CO2	2	0.8461	0.3965	0.3439	0.2111	0.7876	0.8996	0.7349	0.5983
I x F x CO2	2	0.6238	0.8896	0.5191	0.0832	0.4484	0.8247	0.0713	0.2837

TABLE II

P-VALUES OBTAINED FROM THE SPLIT-PLOT ANALYSIS OF THE LIGHT-SATURATED RATE OF PHOTOSYNTHESIS (P_{max}) OF CURRENT-YEAR NEEDLES

Source	df	June 95	July 95	Sep 95	Oct 95	Nov 95	Dec 95	Jan 96	Mar 96
Irri (I)	1	0.8286	0.6694	0.8008	0.4525	0.8956	0.8775	0.2383	0.7517
Fert (F)	1	0.6591	0.4463	0.4376	0.4404	0.5301	0.0015	0.2459	0.7894
I x F	1	0.3791	0.0750	0.6337	0.4026	0.8072	0.5292	0.9633	0.7922
CO2	2	0.0002	0.0001	0.0001	0.0001	0.0199	0.0001	0.0010	0.0001
I x CO2	2	0.8968	0.8036	0.9548	0.0561	0.2159	0.6851	0.6299	0.8104
F x CO2	2	0.8912	0.3648	0.8972	0.7448	0.6720	0.3521	0.9561	0.5992
I x F x CO2	2	0.6515	0.3373	0.6683	0.6633	0.8944	0.8355	0.5852	0.3789

TABLE III

P-VALUES OBTAINED FROM THE SPLIT-PLOT ANALYSIS OF THE MAXIMUM STOMATAL CONDUCTANCE TO WATER VAPOR (G_{max}) OF ONE-YEAR OLD NEEDLES

Source	df	July 94	Aug 94	Sep 94	Apr 95	May 95	Jun 95	Jul 95	Sep 95
Irri (I)	1	0.7402	0.2173	0.8239	0.7803	0.2352	0.0966	0.4788	0.2660
Fert (F)	1	0.4705	0.6251	0.3894	0.4763	0.0897	0.3303	0.8777	0.1727
I x F	1	0.9625	0.6017	0.3229	0.7184	0.4937	0.5915	0.1896	0.9639
CO2	2	0.0035	0.0018	0.2841	0.8520	0.7225	0.0729	0.1374	0.5816
I x CO2	2	0.7174	0.3972	0.3037	0.6268	0.4257	0.3057	0.6351	0.1935
F x CO2	2	0.8256	0.7859	0.7187	0.4482	0.7170	0.7338	0.7869	0.7187
I x F x CO2	2	0.5742	0.5778	0.6709	0.5902	0.0735	0.3806	0.6610	0.3921

TABLE IV

P-VALUES OBTAINED FROM THE SPLIT-PLOT ANALYSIS OF THE MAXIMUM STOMATAL CONDUCTANCE TO WATER VAPOR (G_{max}) OF CURRENT-YEAR NEEDLES

Source	df	June 95	July 95	Sep 95	Oct 95	Nov 95	Dec 95	Jan 96	Mar 96
Irri (I)	1	0.5400	0.8891	0.0383	0.8123	0.4154	0.0934	0.5394	0.0457
Fert (F)	1	0.5582	0.5812	0.0111	0.0354	0.3169	0.0001	0.1621	0.0481
I x F	1	0.9517	0.0969	0.5273	0.0874	0.4660	0.9845	0.5322	0.1775
CO2	2	0.4729	0.3708	0.2040	0.3366	0.1144	0.1838	0.2967	0.0002
I x CO2	2	0.5695	0.2445	0.0164	0.4221	0.6297	0.1511	0.3937	0.0930
F x CO2	2	0.6342	0.0458	0.0278	0.0537	0.8872	0.5630	0.6197	0.3443
I x F x CO2	2	0.3257	0.0642	0.6333	0.5361	0.4915	0.6979	0.9100	0.0230

TABLE V

P-VALUES OBTAINED FROM THE SPLIT-PLOT ANALYSIS OF THE TOTAL CHLOROPHYLL CONTENT OF ONE-YEAR OLD NEEDLES

Source	df	July 94	Aug 94	Sep 94	Apr 95	May 95	Jun 95	Sep 95
Irri (I)	1	0.9319	0.7808	0.8485	0.1710	0.0791	0.1767	0.3659
Fert (F)	1	0.1961	0.0638	0.2950	0.0457	0.7167	0.2087	0.6701
I x F	1	0.4256	0.9191	0.5150	0.5851	0.5537	0.4851	0.2727
CO2	2	0.0768	0.0082	0.1388	0.1034	0.0113	0.9045	0.1261
I x CO2	2	0.0390	0.6124	0.4862	0.6410	0.9483	0.0446	0.8036
F x CO2	2	0.0260	0.0527	0.6980	0.1243	0.6458	0.6438	0.4468
I x F x CO2	2	0.6485	0.0988	0.8134	0.9807	0.0509	0.6908	0.0068

TABLE VI

P-VALUES OBTAINED FROM THE SPLIT-PLOT ANALYSIS OF THE TOTAL CHLOROPHYLL CONTENT OF CURRENT-YEAR NEEDLES

Source	df	June 95	Sep 95	Oct 95	Nov 95	Dec 95	Jan 96	Mar 96
Irri (I)	1	0.4281	0.0639	0.8127	0.3424	0.5409	0.1115	0.0408
Fert (F)	1	0.2850	0.8492	0.5689	0.7810	0.6269	0.4935	0.4842
I x F	1	0.4420	0.6161	0.1351	0.9639	0.1082	0.8123	0.4003
CO2	2	0.8051	0.6517	0.0744	0.4553	0.7194	0.4943	0.2906
I x CO2	2	0.9866	0.8456	0.7188	0.0073	0.7383	0.6573	0.2222
F x CO2	2	0.3271	0.5385	0.4773	0.5539	0.9791	0.0496	0.0353
I x F x CO2	2	0.7440	0.6656	0.5353	0.5315	0.8631	0.1532	0.4255

TABLE VII

P-VALUES OBTAINED FROM THE ANALYSIS OF A/C_i CURVES (JULY 95)

Blk/Treatment	A_{sat}	R_d	Comp. Pt. (Γ)	Carb. Eff.
Block I (Control)	0.0200	0.0170	0.0300	0.0001
Block II (Control)	0.0200	0.2000	0.3800	0.0250
Block IV (Control)	0.0001	0.0400	0.0588	0.0006
Block I (Irrigated)	0.0001	0.0001	0.1700	0.2400
Block II (Irrigated)	0.0001	0.0001	0.0800	0.0001
Block IV (Irrigated)	0.0020	0.0052	0.3900	0.8800
Block I (Fertilized)	0.0020	0.0001	0.0001	0.3600
Block II (Fertilized)	0.0001	0.0001	0.4800	0.0600
Block IV (Fertilized)	0.0001	0.0700	0.0070	0.0100
Block I (Irrig. & Fert.)	0.0001	0.0001	0.0010	0.0512
Block II (Irrig. & Fert.)	0.0080	0.1000	0.1600	0.9500
Block IV (Irrig. & Fert.)	0.0001	0.0001	0.8700	0.0001

TABLE VIII

STOMATAL LIMITATION (L_s) VALUES IN % CALCULATED FROM A/C_i CURVES OBTAINED IN JULY 95 BY USING EQUATION 3. THE VALUES ARE MEANS ± SE FOR EACH TREATMENT (n = 3)

Treatment	350 $\mu l\ l^{-1}$	700 $\mu l\ l^{-1}$
Control	41.34±32.03 a	30.26±10.65 a
Irrigated	43.22±27.52 a	33.64±17.68 a
Fertilized	37.38±22.26 a	28.29±09.22 a
Irrigated & Fertilized	26.33±12.09 a	36.37±29.06 a

Values followed by the same letters in the same row are not significantly different from each other ($P < 0.005$).

TABLE IX

P-VALUES OBTAINED FROM THE ANALYSIS OF A/C_i CURVES (OCTOBER 95)

Blk/Treatment	A_{sat}	R_d	Comp. Pt. (Γ)	Carb. Eff.
Block I (Control)	0.1142	0.1300	0.9000	0.0200
Block II (Control)	0.6500	0.6200	0.1700	0.6200
Block IV (Control)	0.2000	0.3700	0.6200	0.7200
Block I (Irrigated)	0.0020	0.0012	0.0400	0.0001
Block II (Irrigated)	0.0001	0.0001	0.2600	0.0030
Block IV (Irrigated)	0.0200	0.0300	0.4400	0.5900
Block I (Fertilized)	0.0040	0.0030	0.0536	0.0001
Block II (Fertilized)	0.0001	0.0001	0.9000	0.0001
Block IV (Fertilized)	0.0006	0.0006	0.5000	0.0010
Block I (Irrig. & Fert.)	0.0200	0.0200	0.9600	0.0001
Block II (Irrig. & Fert.)	0.0001	0.0001	0.8300	0.0900
Block IV (Irrig. & Fert.)	0.0001	0.7700	0.6700	0.0006

TABLE X

STOMATAL LIMITATION (L_s) VALUES IN % CALCULATED FROM A/C_i CURVES OBTAINED IN OCTOBER 95 BY USING EQUATION 3. THE VALUES ARE MEANS ± SE FOR EACH TREATMENT (n = 3)

Treatment	350 µl l^{-1}	700 µl l^{-1}
Control	23.45±10.19 a	23.18±14.41 a
Irrigated	29.06±13.91 a	23.81±04.35 a
Fertilized	23.98±09.06 a	25.13±20.68 a
Irrigated & Fertilized	28.36±18.87 a	30.93±18.07 a

Values followed by the same letters in the same row are not significantly different from each other ($P < 0.005$).

APPENDIX B

FIGURES

Figure Captions

Figure 1: Monthly on-site precipitation in 1994, 1995 & 1996 and the thirty-year average monthly precipitation.

Figure 2: Mean weekly chamber temperature in 1994 & 1995 and mean weekly ambient temperature in 1994.

Figure 3: Mean weekly daytime photosynthetic photon flux density in 1994 & 1995 for the upper and lower part of the branch chamber.

Figure 4: Mean weekly chamber carbon dioxide concentration in 1994, 1995 & 1996.

Figure 5: Light-saturated rate of photosynthesis of the one-year old needles in the control (solid circle), irrigated (solid square), fertilized (solid upright triangle) and irrigated & fertilized (solid inverted triangle) treatments. Each point is an average of measurements obtained from four blocks.

Figure 6: Light-saturated rate of photosynthesis of the current-year needles in the control (solid circle), irrigated (solid square), fertilized (solid upright triangle) and irrigated & fertilized (solid inverted triangle) treatments. Each point is an average of measurements obtained from four blocks.

Figure 7: Maximum stomatal conductance to water vapor of the one-year old needles in the control (solid circle), irrigated (solid square), fertilized (solid upright triangle) and irrigated & fertilized (solid inverted triangle) treatments. Each point is an average of measurements obtained from four blocks.

Figure 8: Maximum stomatal conductance to water vapor of the current-year needles in the control (solid circle), irrigated (solid square), fertilized (solid upright triangle) and irrigated & fertilized (solid inverted triangle) treatments. Each point is an average of measurements obtained from four blocks.

Figure 9: Total chlorophyll content of the one-year old needles in the control (solid circle), irrigated (solid square), fertilized (solid upright triangle) and irrigated & fertilized (solid inverted triangle) treatments. Each point is an average of measurements obtained from four blocks.

Figure 10: Total chlorophyll content of the current-year needles in the control (solid circle), irrigated (solid square), fertilized (solid upright triangle) and irrigated & fertilized (solid inverted triangle) treatments. Each point is an average of measurements obtained from four blocks.

Figure 11: A/C_i curves obtained in July 95 for the one-year old needles in the control, irrigated, fertilized and irrigated & fertilized treatments. (•) represents the A/C_i curve for the 350 ppm treatment branches and (■) represents the A/C_i curve for the 700 ppm treatment branches. Each point is an average of four measurements.

Figure 12: A/C_i curves obtained in October 95 for the current-year needles in the control, irrigated, fertilized and irrigated & fertilized treatments. (•) represents the A/C_i curve for the 350 ppm treatment branches and (■) represents the A/C_i curve for the 700 ppm treatment branches. Each point is an average of four measurements.

Figure 13: Light-saturated rate of photosynthesis for July 94 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 14: Maximum stomatal conductance to water vapor for July 94 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 15: Total chlorophyll content for July 94 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 16: Light-saturated rate of photosynthesis for August 94 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 17: Maximum stomatal conductance to water vapor for August 94 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 18: Total chlorophyll content for August 94 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 19: Light-saturated rate of photosynthesis for September 94 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 20: Maximum stomatal conductance to water vapor for September 94 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 21: Total chlorophyll content for September 94 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 22: Light-saturated rate of photosynthesis for April 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 23: Maximum stomatal conductance to water vapor for April 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 24: Total chlorophyll content for April 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 25: Light-saturated rate of photosynthesis for May 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 26: Maximum stomatal conductance to water vapor for May 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 27: Total chlorophyll content for May 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 28: Light-saturated rate of photosynthesis for June 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 29: Maximum stomatal conductance to water vapor for June 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 30: Total chlorophyll content for June 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 31: Light-saturated rate of photosynthesis for July 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 32: Maximum stomatal conductance to water vapor for July 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 33: Light-saturated rate of photosynthesis for September 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 34: Maximum stomatal conductance to water vapor for September 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 35: Total chlorophyll content for September 95 (first flush of 1994) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 36: Light-saturated rate of photosynthesis for June 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 37: Maximum stomatal conductance to water vapor for June 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 38: Total chlorophyll content for June 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 39: Light-saturated rate of photosynthesis for July 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 40: Maximum stomatal conductance to water vapor for July 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 41: Light-saturated rate of photosynthesis for September 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 42: Maximum stomatal conductance to water vapor for September 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 43: Total chlorophyll content for September 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 44: Light-saturated rate of photosynthesis for October 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 45: Maximum stomatal conductance to water vapor for October 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 46: Total chlorophyll content for October 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 47: Light-saturated rate of photosynthesis for November 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 48: Maximum stomatal conductance to water vapor for November 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 49: Total chlorophyll content for November 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 50: Light-saturated rate of photosynthesis for December 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 51: Maximum stomatal conductance to water vapor for December 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 52: Total chlorophyll content for December 95 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 53: Light-saturated rate of photosynthesis for January 96 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 54: Maximum stomatal conductance to water vapor for January 96 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 55: Total chlorophyll content for January 96 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 56: Light-saturated rate of photosynthesis for March 96 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 57: Maximum stomatal conductance to water vapor for March 96 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 58: Total chlorophyll content for March 96 (first flush of 1995) in the control, irrigated, fertilized and irrigated & fertilized treatments. Each bar is an average of measurements obtained from four blocks.

Figure 59: A/C_i curves obtained in July 95 (1994 foliage) for the control plot (block i). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 60: A/C_i curves obtained in July 95 (1994 foliage) for the control plot (block ii). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 61: A/C_i curves obtained in July 95 (1994 foliage) for the control plot (block iv). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 62: A/C_i curves obtained in July 95 (1994 foliage) for the irrigated plot (block i). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 63: A/C_i curves obtained in July 95 (1994 foliage) for the irrigated plot (block ii). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 64: A/C_i curves obtained in July 95 (1994 foliage) for the irrigated plot (block iv). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 65: A/C_i curves obtained in July 95 (1994 foliage) for the fertilized plot (block i). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 66: A/C_i curves obtained in July 95 (1994 foliage) for the fertilized plot (block ii). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 67: A/C_i curves obtained in July 95 (1994 foliage) for the fertilized plot (block iv). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 68: A/C_i curves obtained in July 95 (1994 foliage) for the irrigated & fertilized plot (block i). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 69: A/C_i curves obtained in July 95 (1994 foliage) for the irrigated & fertilized plot (block ii). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 70: A/C_i curves obtained in July 95 (1994 foliage) for the irrigated & fertilized plot (block iv). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 71: A/C_i curves obtained in October 95 (1995 foliage) for the control plot (block i). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 72: A/C_i curves obtained in October 95 (1995 foliage) for the control plot (block ii). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 73: A/C_i curves obtained in October 95 (1995 foliage) for the control plot (block iv). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 74: A/C_i curves obtained in October 95 (1995 foliage) for the irrigated plot (block i). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 75: A/C_i curves obtained in October 95 (1995 foliage) for the irrigated plot (block ii). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 76: A/C_i curves obtained in October 95 (1995 foliage) for the irrigated plot (block iv). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 77: A/C_i curves obtained in October 95 (1995 foliage) for the fertilized plot (block i). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 78: A/C_i curves obtained in October 95 (1995 foliage) for the fertilized plot (block ii). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 79: A/C_i curves obtained in October 95 (1995 foliage) for the fertilized plot (block iv). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 80: A/C_i curves obtained in October 95 (1995 foliage) for the irrigated & fertilized plot (block i). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 81: A/C_i curves obtained in October 95 (1995 foliage) for the irrigated & fertilized plot (block ii). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 82: A/C_i curves obtained in October 95 (1995 foliage) for the irrigated & fertilized plot (block iv). (•) represents the A/C_i curve for the 350 ppm treatment branch and (■) represents the A/C_i curve for the 700 ppm treatment branch. Each point is an average of four measurements.

Figure 83: Study design and layout of the experiment.

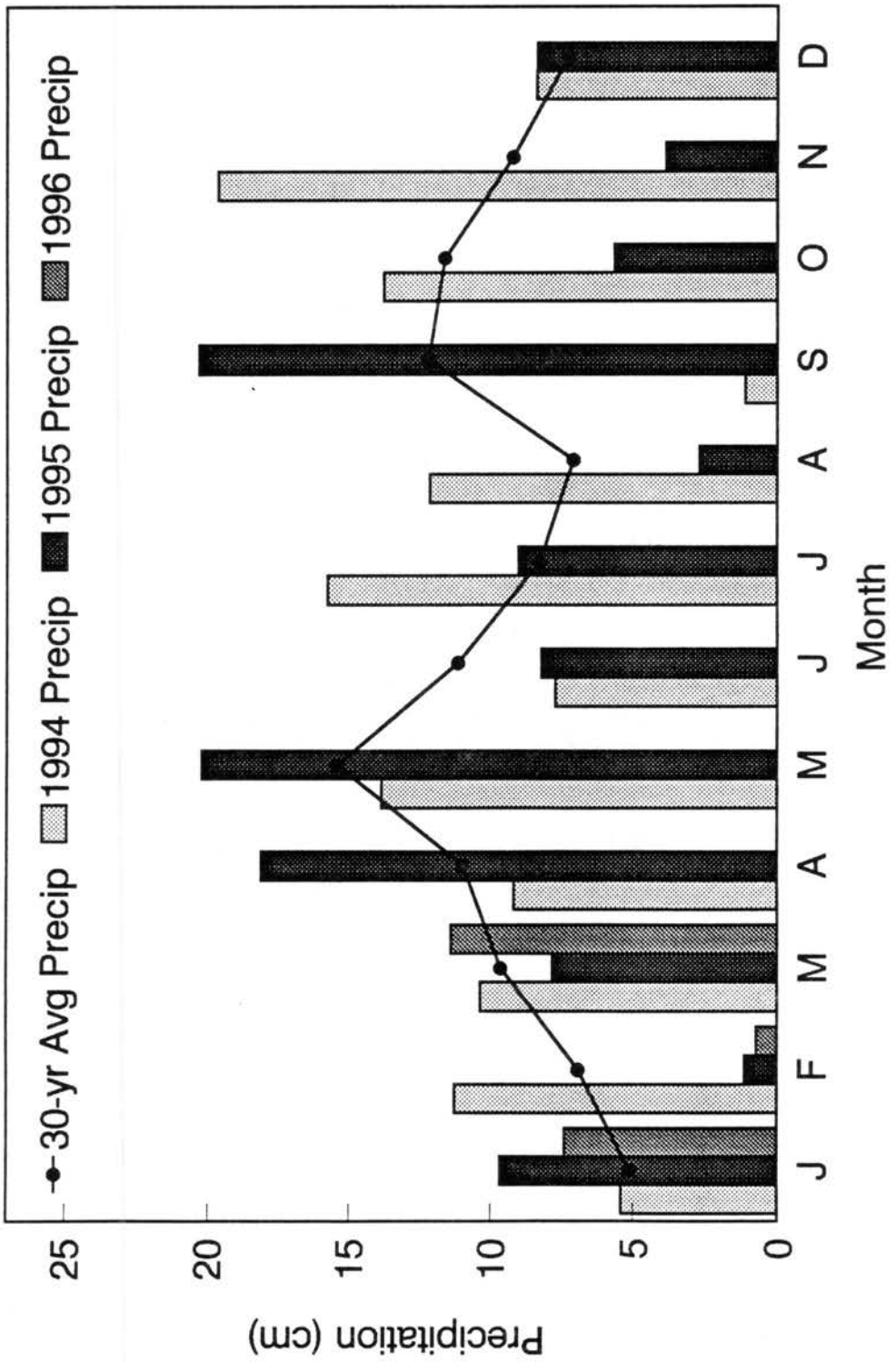
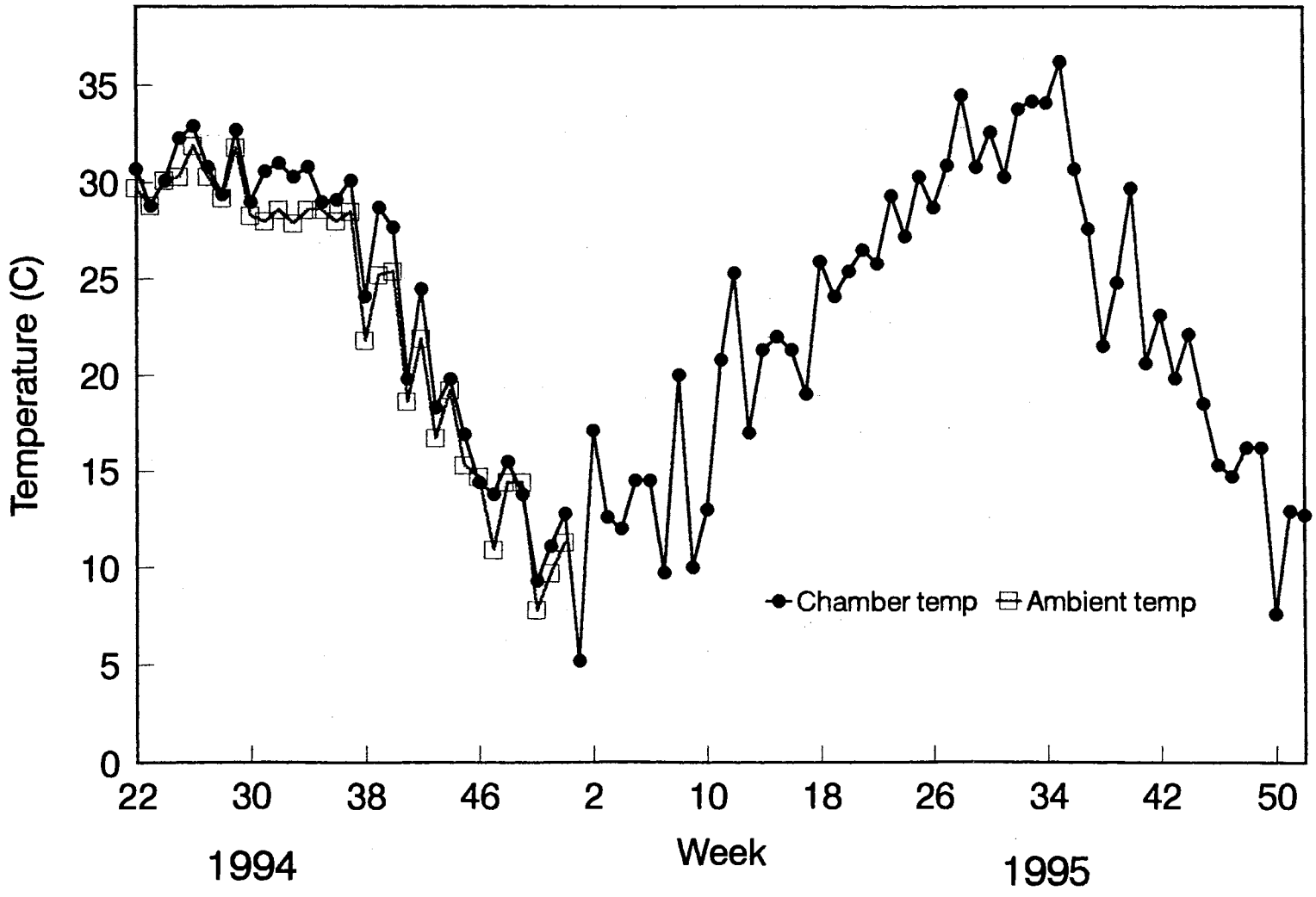

30-yr Avg Precip
1994 Precip
1995 Precip
1996 Precip
Precipitation (cm)
0
5
10
15
20
25
J
F
M
A
M
J
J
A
S
O
N
D
Month

Figure 1

Figure 2


Temperature (C)
35
30
25
20
15
10
5
0
22
30
38
46
2
10
18
26
34
42
50
1994
Week
1995
Chamber temp
Ambient temp

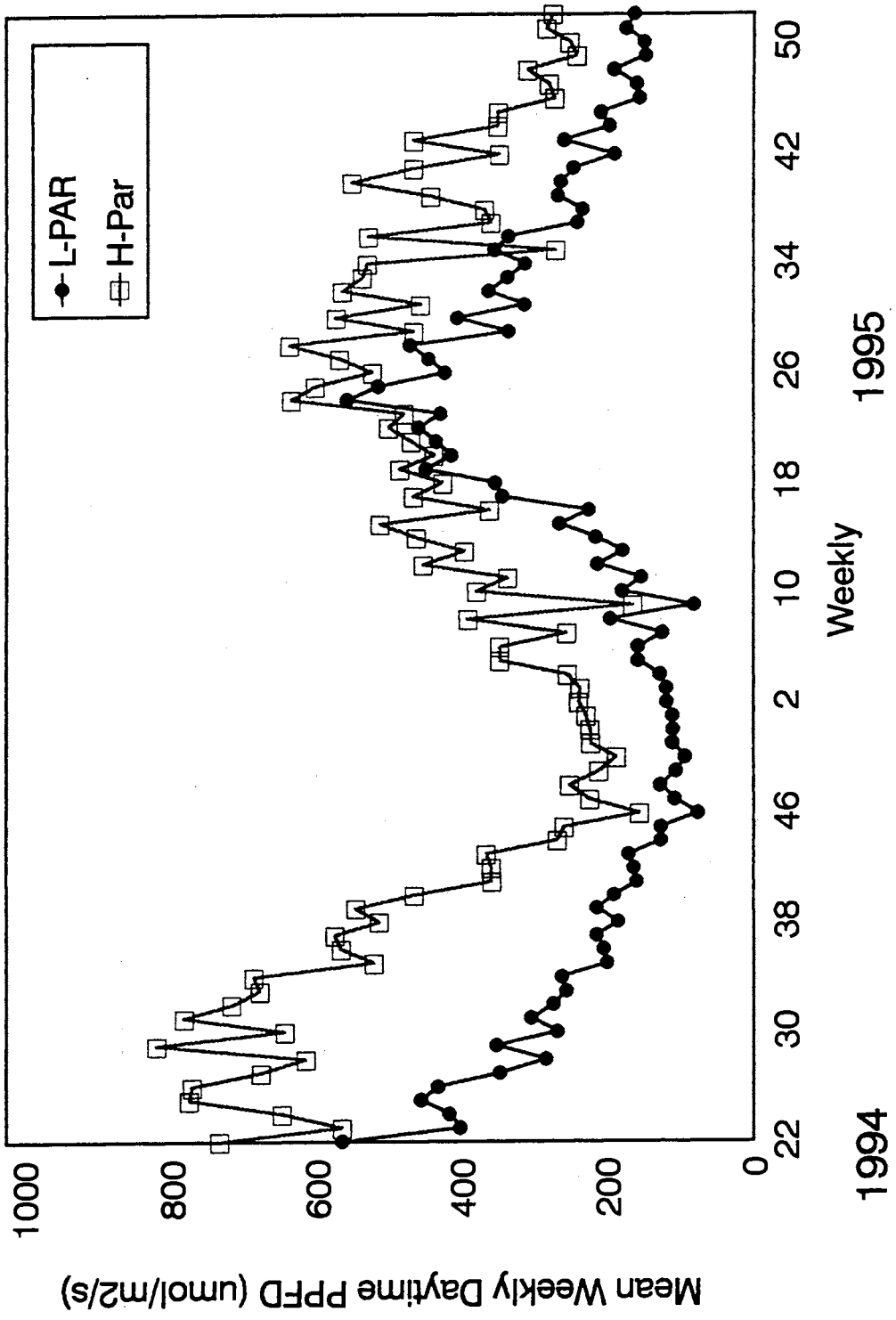

L-PAR
H-Par
Mean Weekly Daytime PPFD (umol/m2/s)
1000
800
600
400
200
0
22
30
38
46
2
10
18
26
34
42
50
1994
Weekly
1995

Figure 3

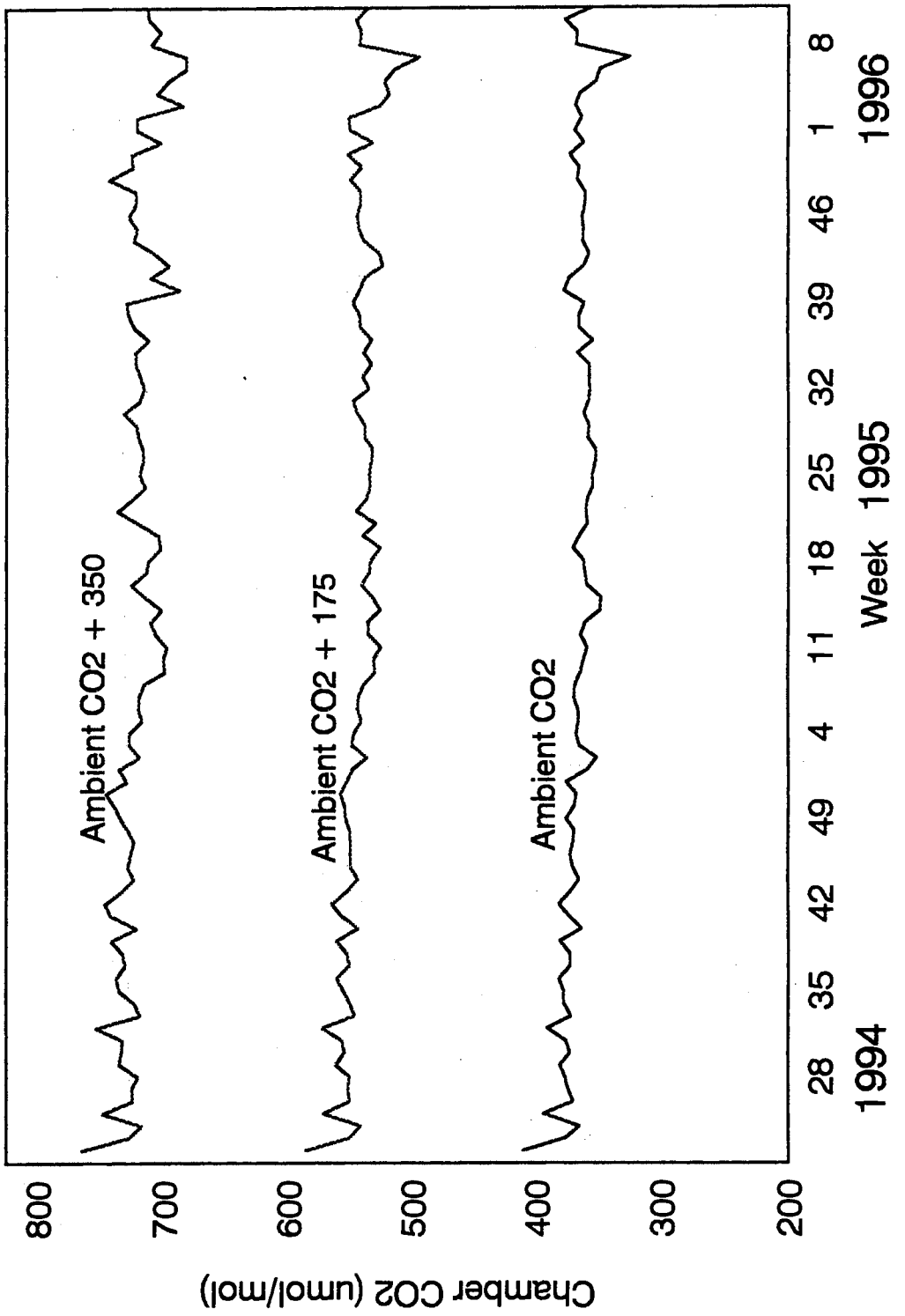

Chamber CO2 (umol/mol)
800
700
600
500
400
300
200
Ambient CO2 + 350
Ambient CO2 + 175
Ambient CO2
28 35 42 49 4 11 18 25 32 39 46 1 8
1994
1995
1996
Week

Figure 4

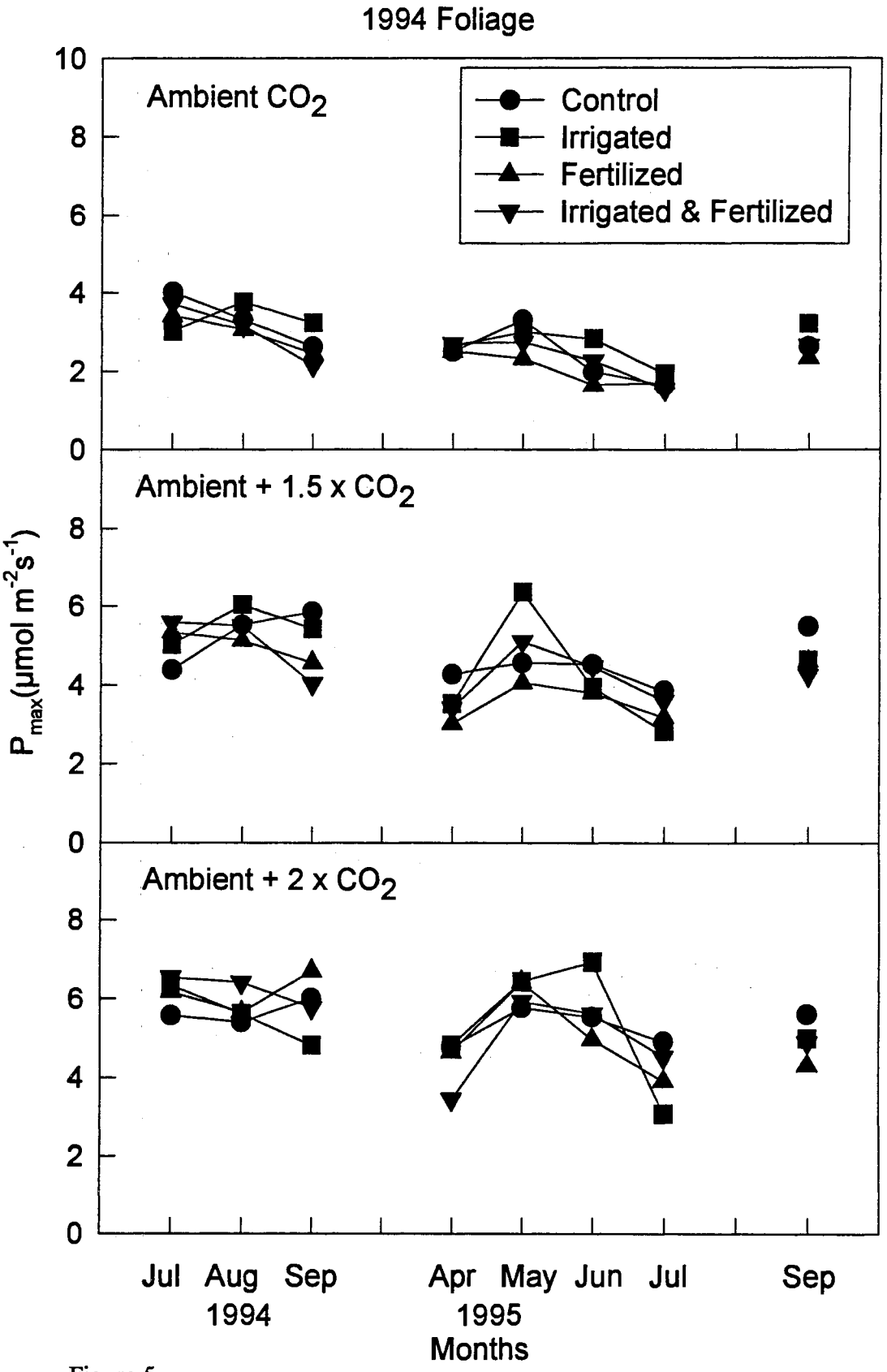

1994 Foliage
Ambient CO_2
Ambient + 1.5 x CO_2
Ambient + 2 x CO_2
Control
Irrigated
Fertilized
Irrigated & Fertilized
P_{max} (μmol $m^{-2}s^{-1}$)
0
2
4
6
8
10
Jul
Aug
Sep
1994
Apr
May
Jun
Jul
Sep
1995
Months

Figure 5

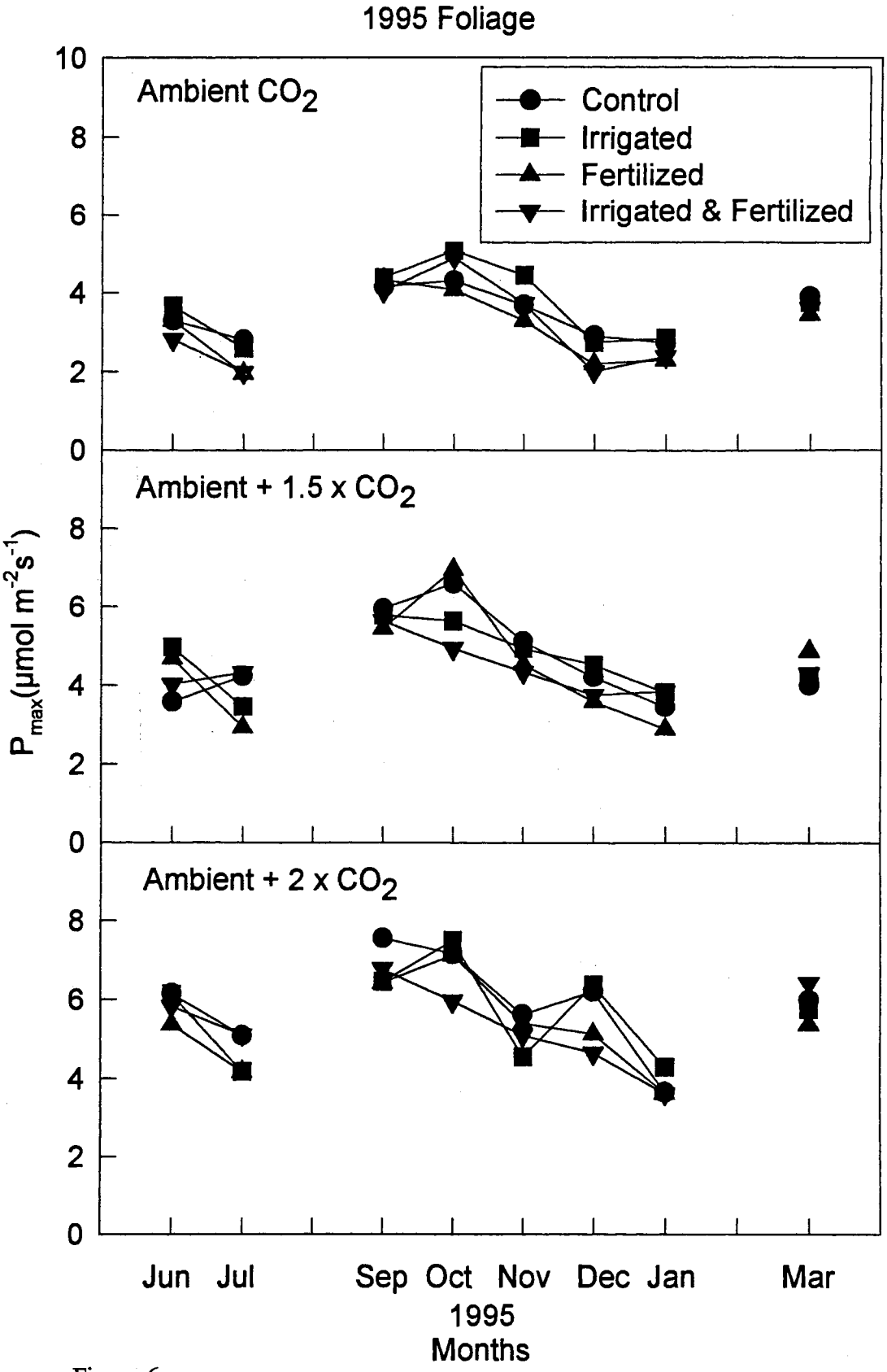

1995 Foliage
Ambient CO_2
Ambient + 1.5 x CO_2
Ambient + 2 x CO_2
Control
Irrigated
Fertilized
Irrigated & Fertilized
P_{max}(μmol $m^{-2}s^{-1}$)
0
2
4
6
8
10
Jun
Jul
Sep
Oct
Nov
Dec
Jan
Mar
1995
Months

Figure 6

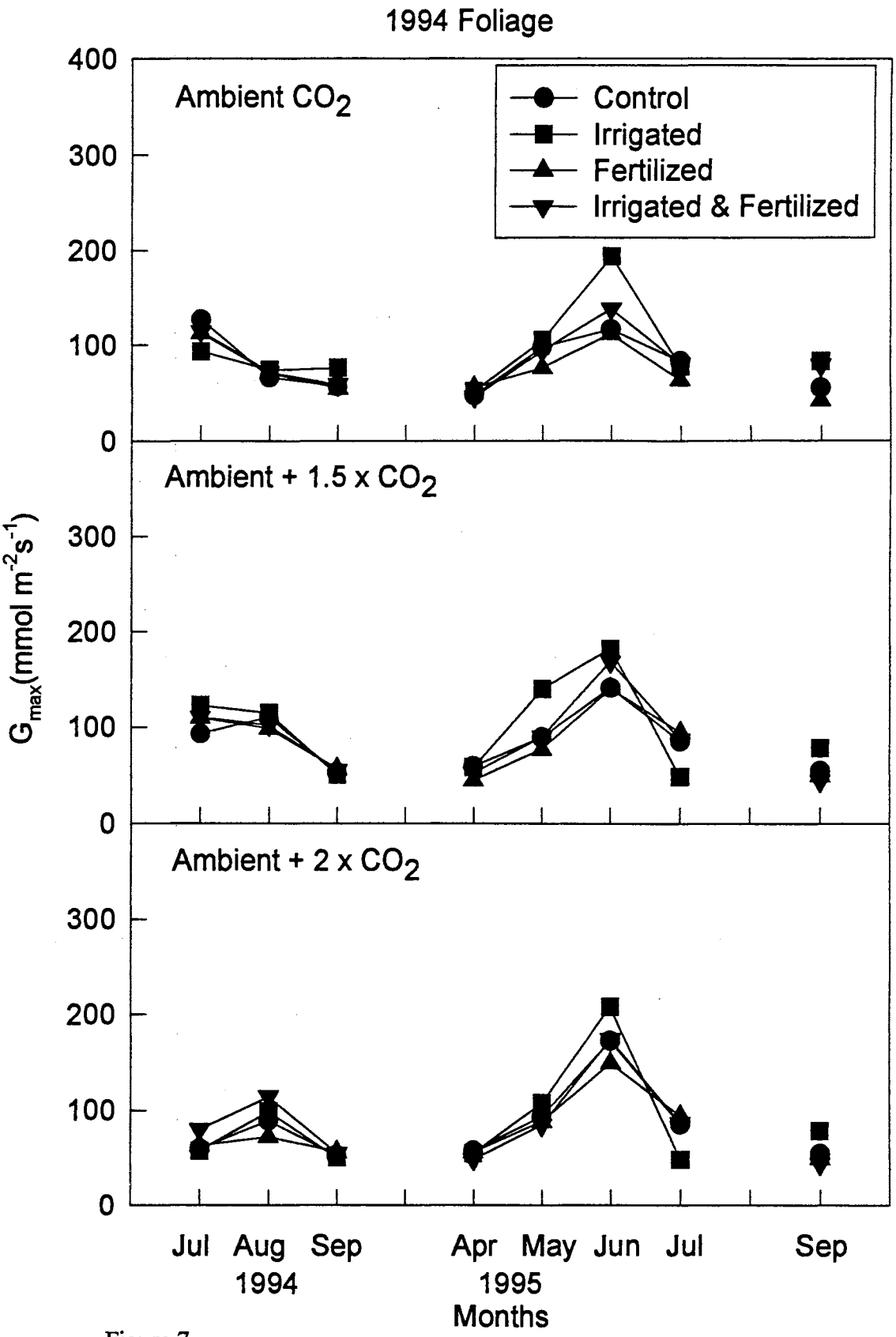

1994 Foliage
Ambient CO_2
Ambient + 1.5 x CO_2
Ambient + 2 x CO_2
Control
Irrigated
Fertilized
Irrigated & Fertilized
G_{max}(mmol $m^{-2}s^{-1}$)
0
100
200
300
400
Jul
Aug
Sep
Apr
May
Jun
Jul
Sep
1994
1995
Months

Figure 7

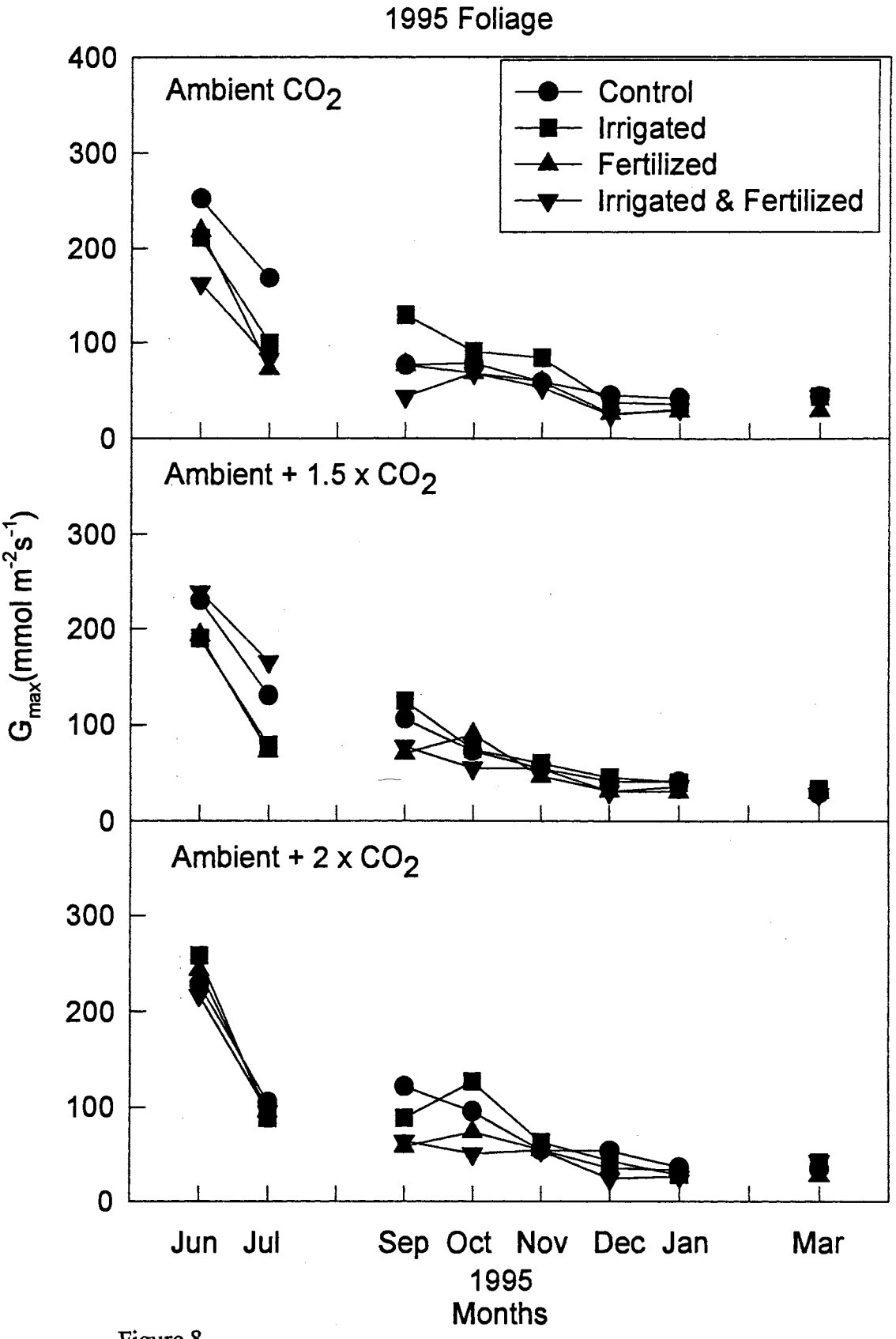

1995 Foliage
Ambient CO_2
Ambient + 1.5 x CO_2
Ambient + 2 x CO_2
Control
Irrigated
Fertilized
Irrigated & Fertilized
G_{max}(mmol $m^{-2}s^{-1}$)
400
300
200
100
0
Jun
Jul
Sep
Oct
Nov
Dec
Jan
Mar
1995
Months

Figure 8

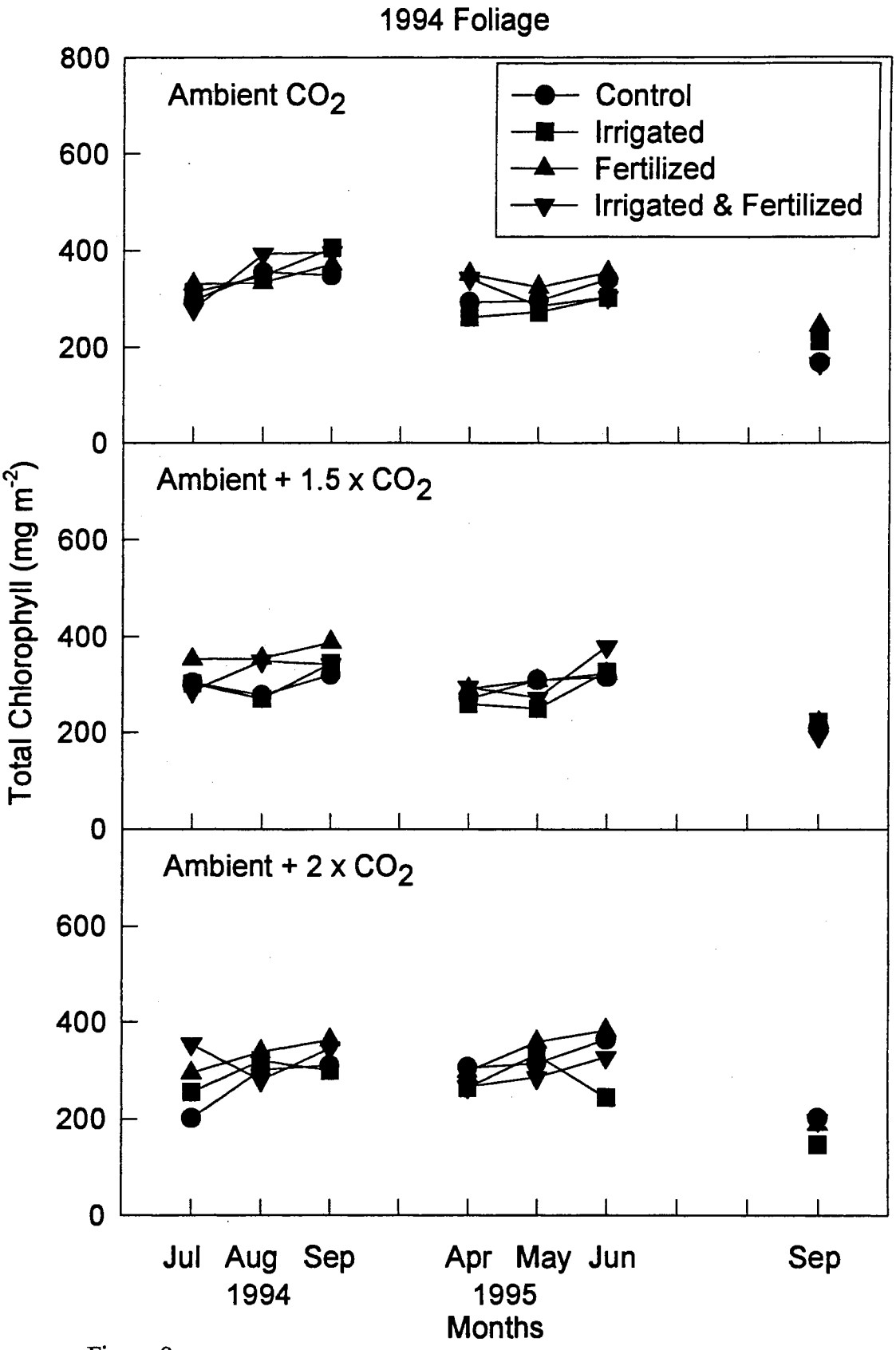

1994 Foliage
Ambient CO_2
Ambient + 1.5 x CO_2
Ambient + 2 x CO_2
Control
Irrigated
Fertilized
Irrigated & Fertilized
Total Chlorophyll (mg m^{-2})
800
600
400
200
0
Jul
Aug
Sep
1994
Apr
May
Jun
1995
Sep
Months

Figure 9

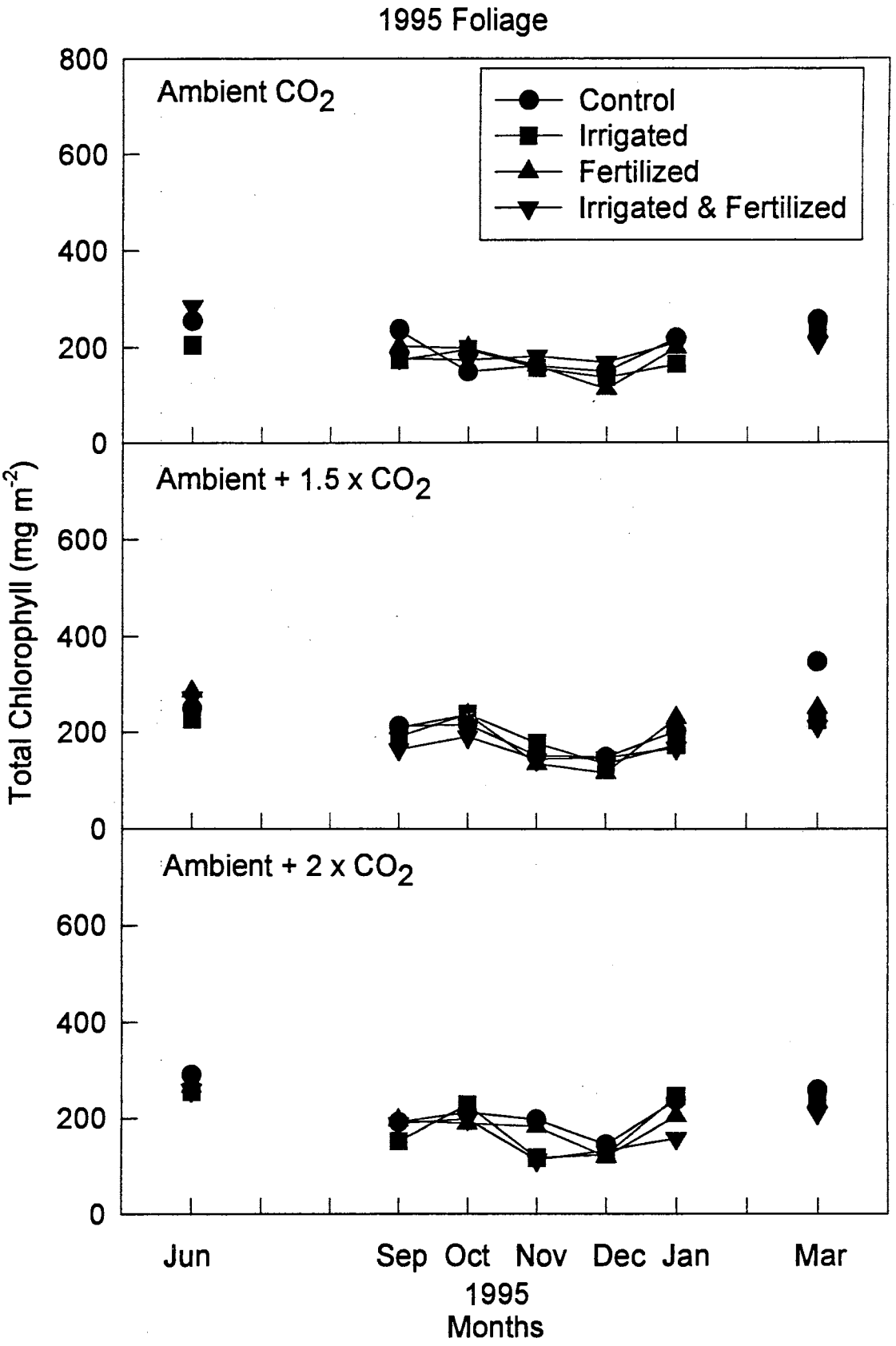

1995 Foliage
Ambient CO_2
Ambient + 1.5 x CO_2
Ambient + 2 x CO_2
Control
Irrigated
Fertilized
Irrigated & Fertilized
Total Chlorophyll (mg m^{-2})
800
600
400
200
0
Jun
Sep
Oct
Nov
Dec
Jan
Mar
1995
Months

Figure 10

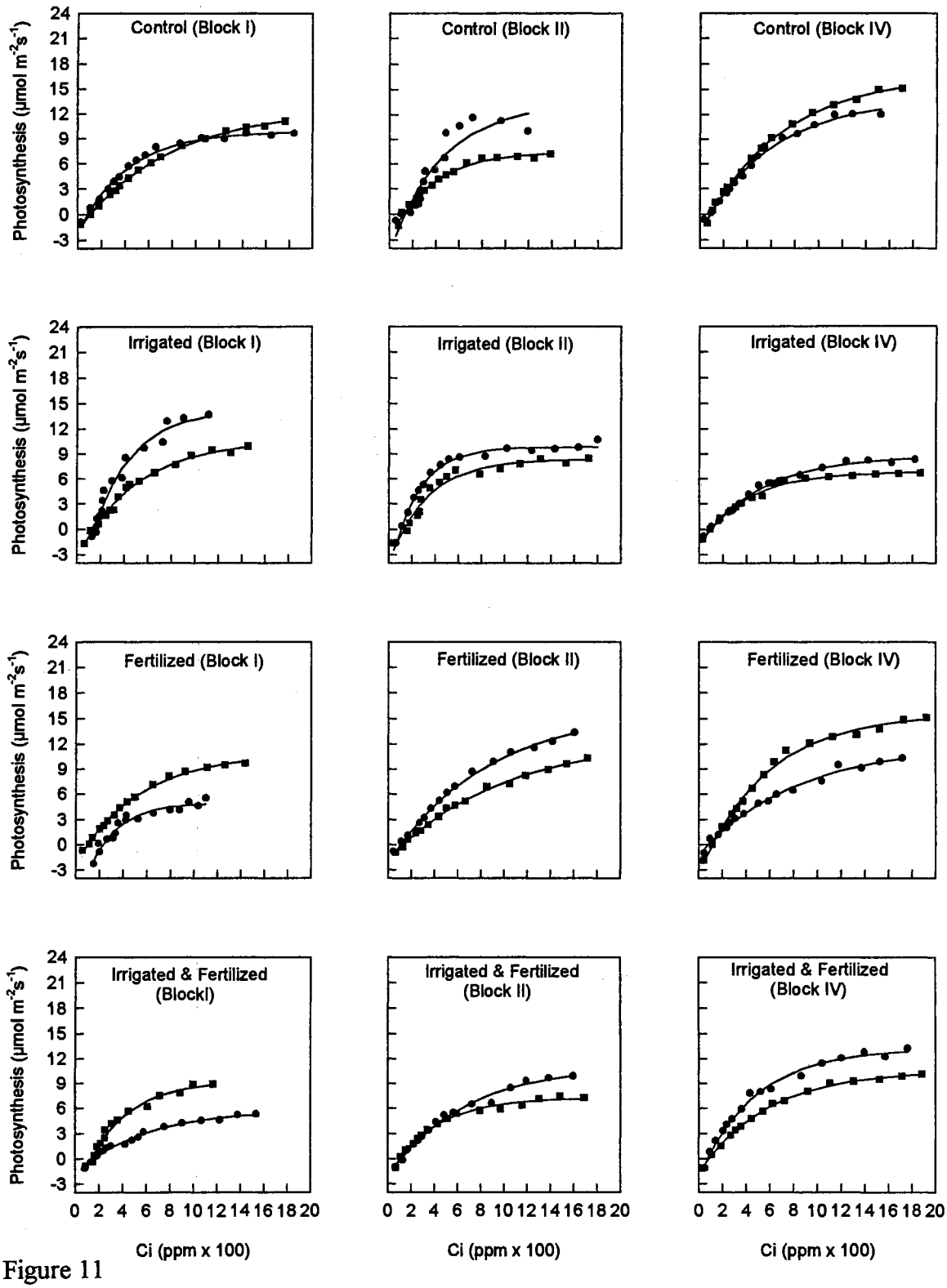

July 1995 (1994 Foliage)
Control (Block I)
Control (Block II)
Control (Block IV)
Irrigated (Block I)
Irrigated (Block II)
Irrigated (Block IV)
Fertilized (Block I)
Fertilized (Block II)
Fertilized (Block IV)
Irrigated & Fertilized (BlockI)
Irrigated & Fertilized (Block II)
Irrigated & Fertilized (Block IV)
Photosynthesis (µmol m-2s-1)
Ci (ppm x 100)
24
21
18
15
12
9
6
3
0
-3
0 2 4 6 8 10 12 14 16 18 20

Figure 11

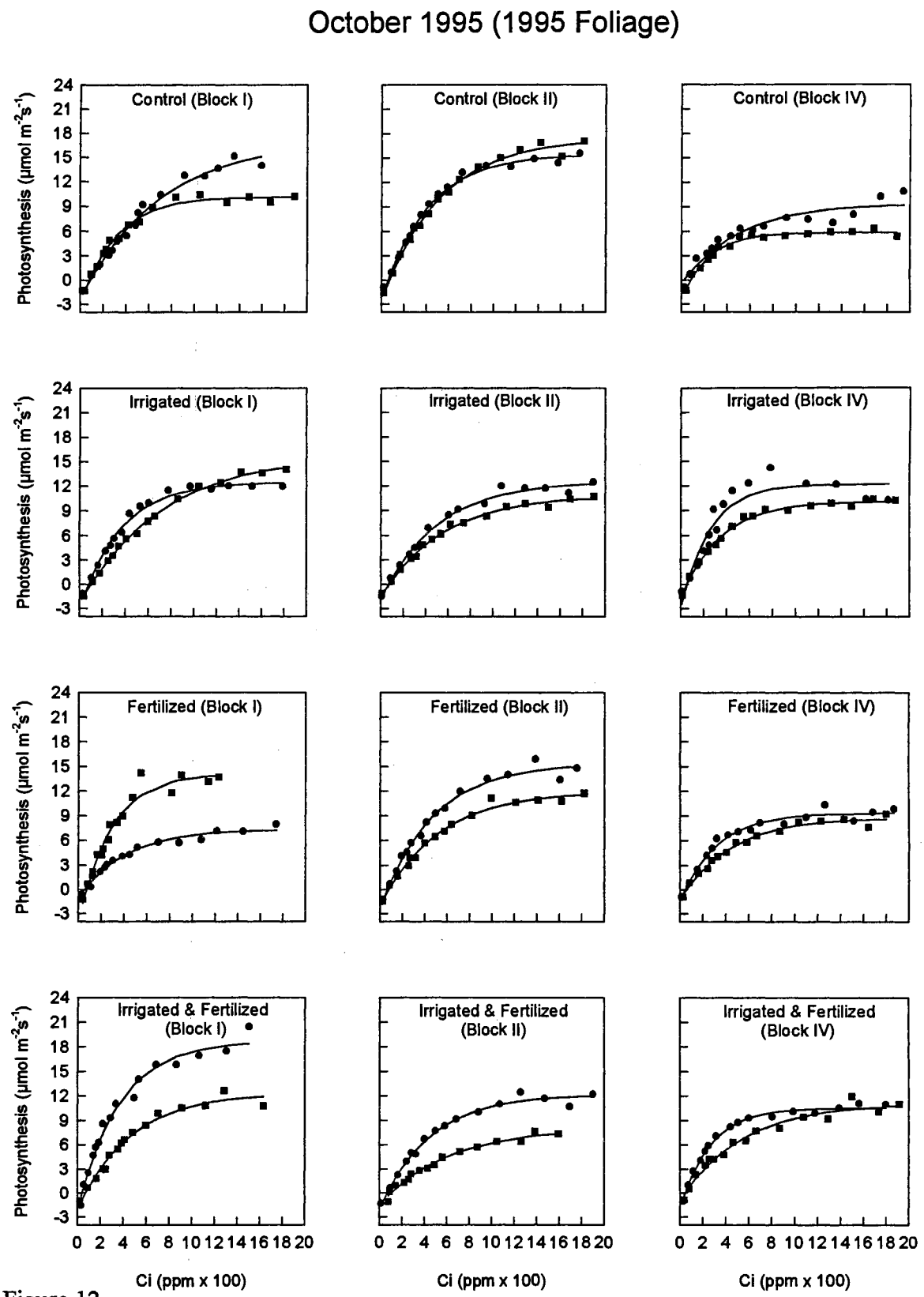

October 1995 (1995 Foliage)
Control (Block I)
Control (Block II)
Control (Block IV)
Irrigated (Block I)
Irrigated (Block II)
Irrigated (Block IV)
Fertilized (Block I)
Fertilized (Block II)
Fertilized (Block IV)
Irrigated & Fertilized (Block I)
Irrigated & Fertilized (Block II)
Irrigated & Fertilized (Block IV)
Photosynthesis (µmol m-2s-1)
Ci (ppm x 100)
24
21
18
15
12
9
6
3
0
-3
0 2 4 6 8 10 12 14 16 18 20

Figure 12

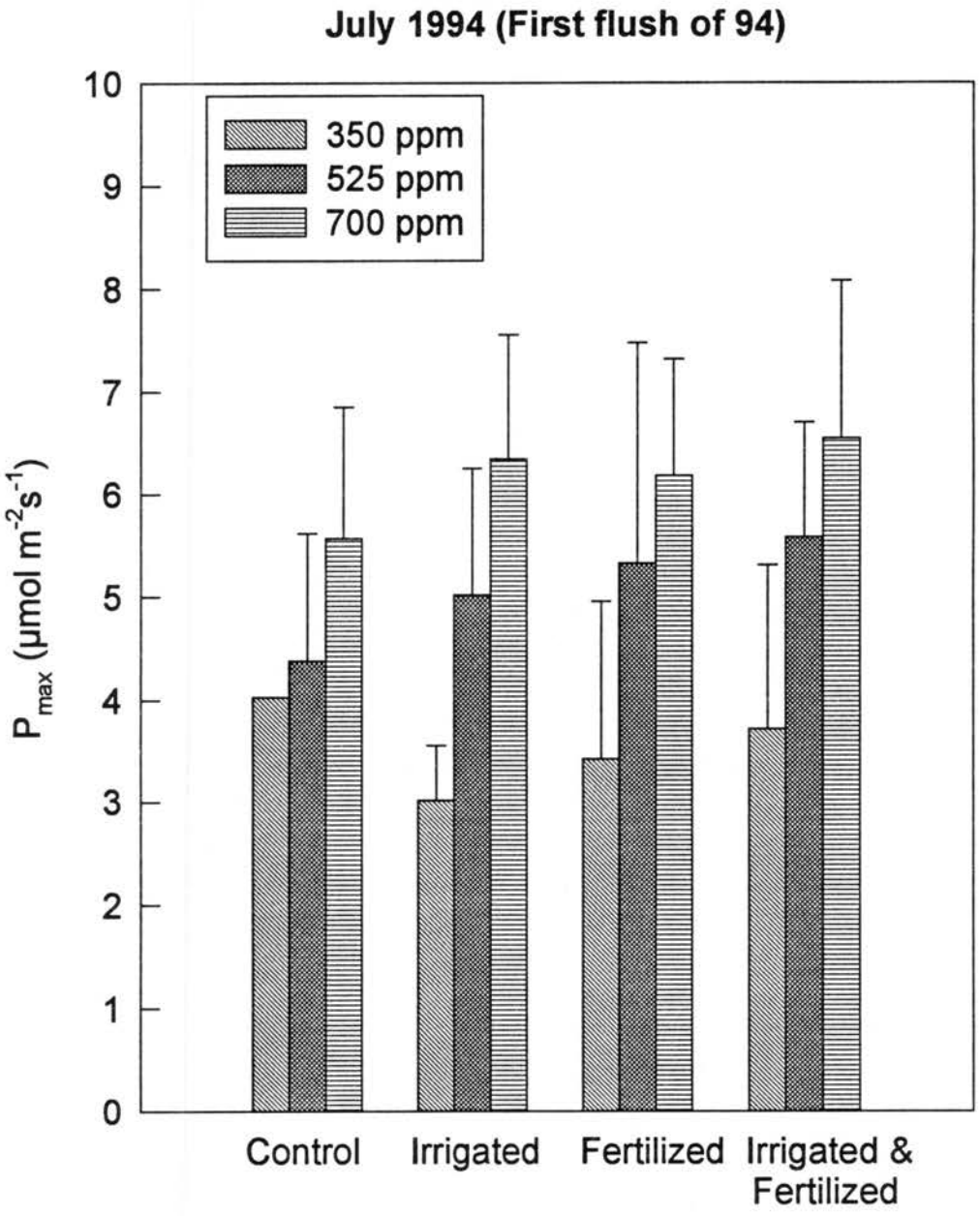

July 1994 (First flush of 94)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 13

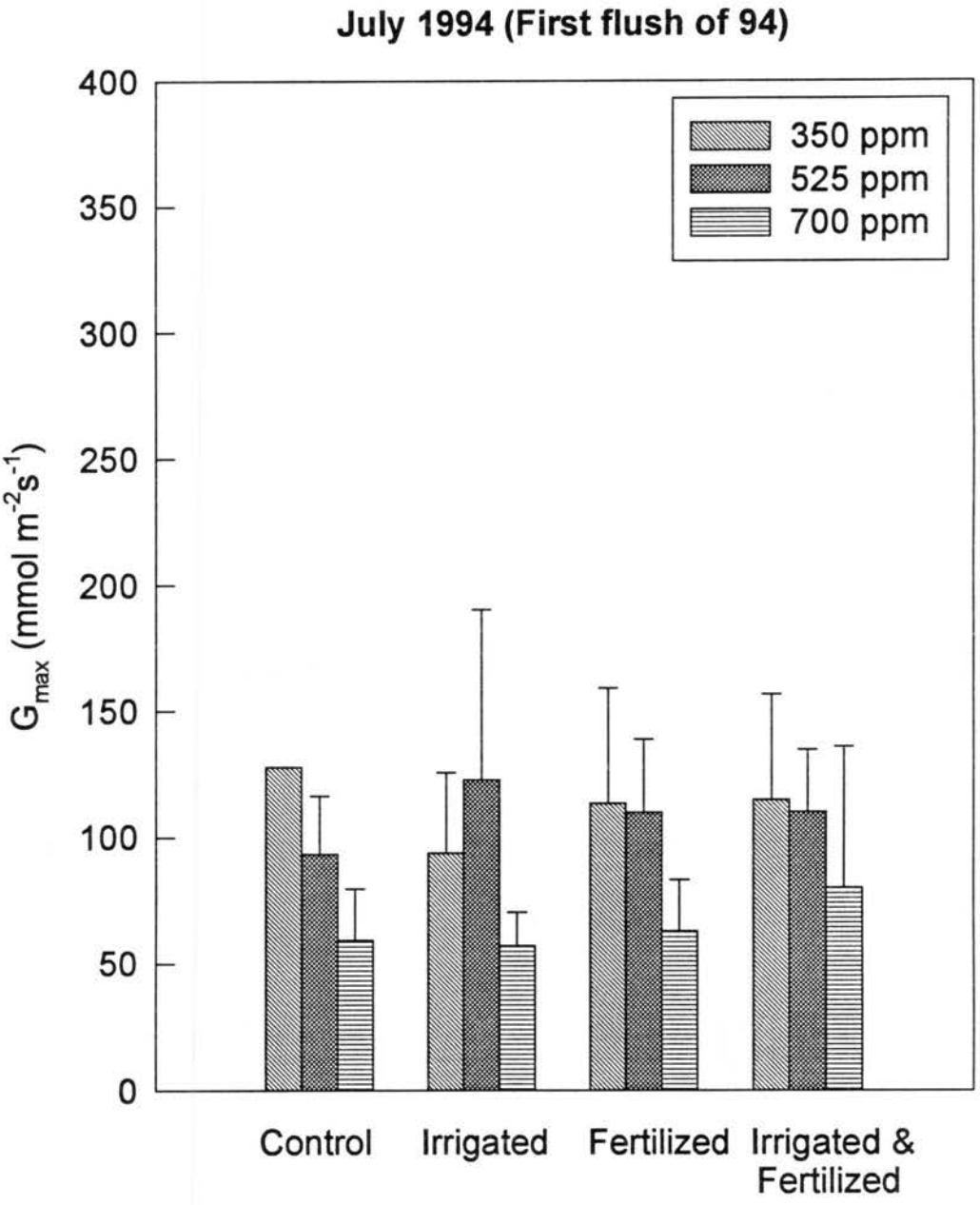

July 1994 (First flush of 94)
350 ppm
525 ppm
700 ppm
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 14

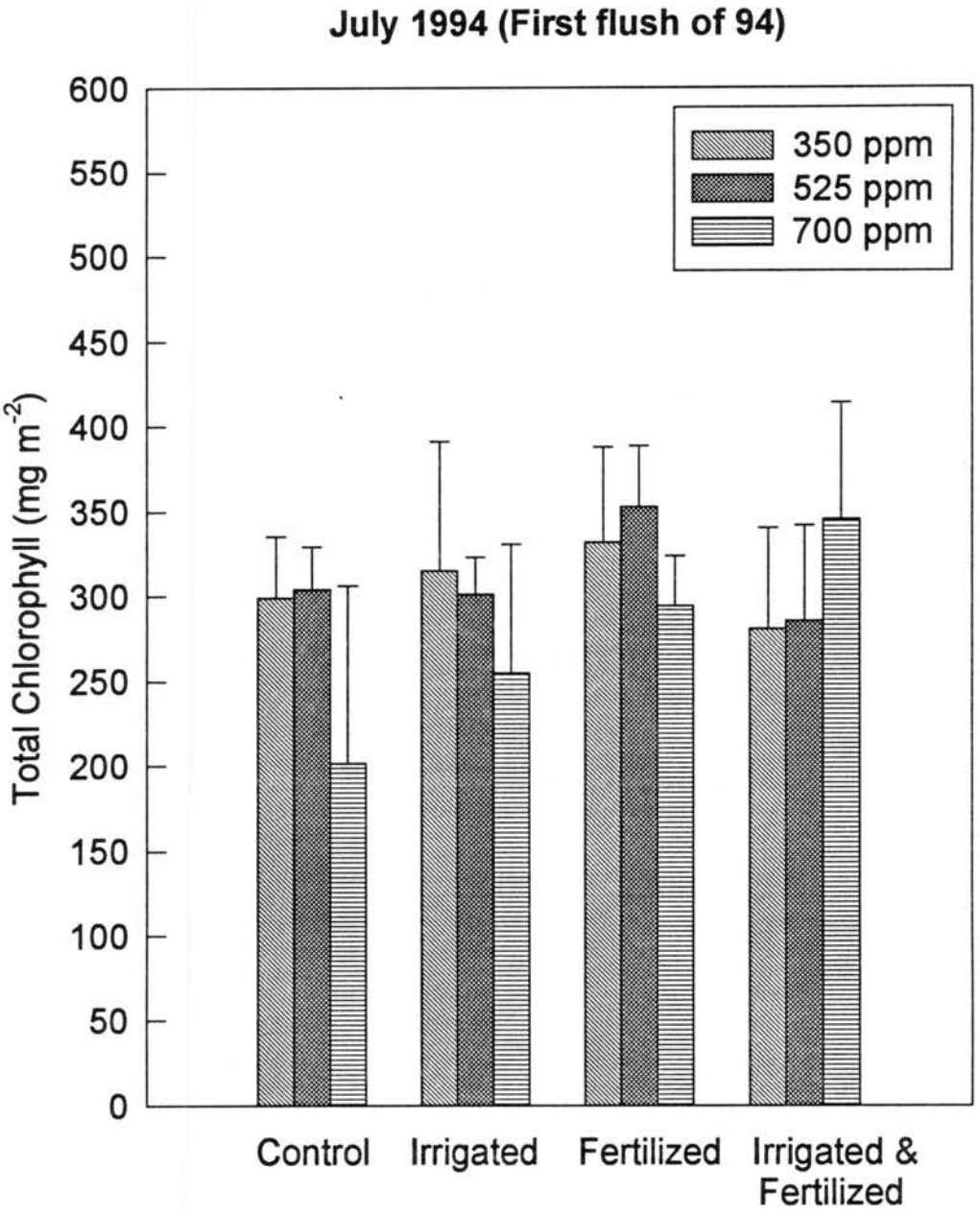

July 1994 (First flush of 94)
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 15

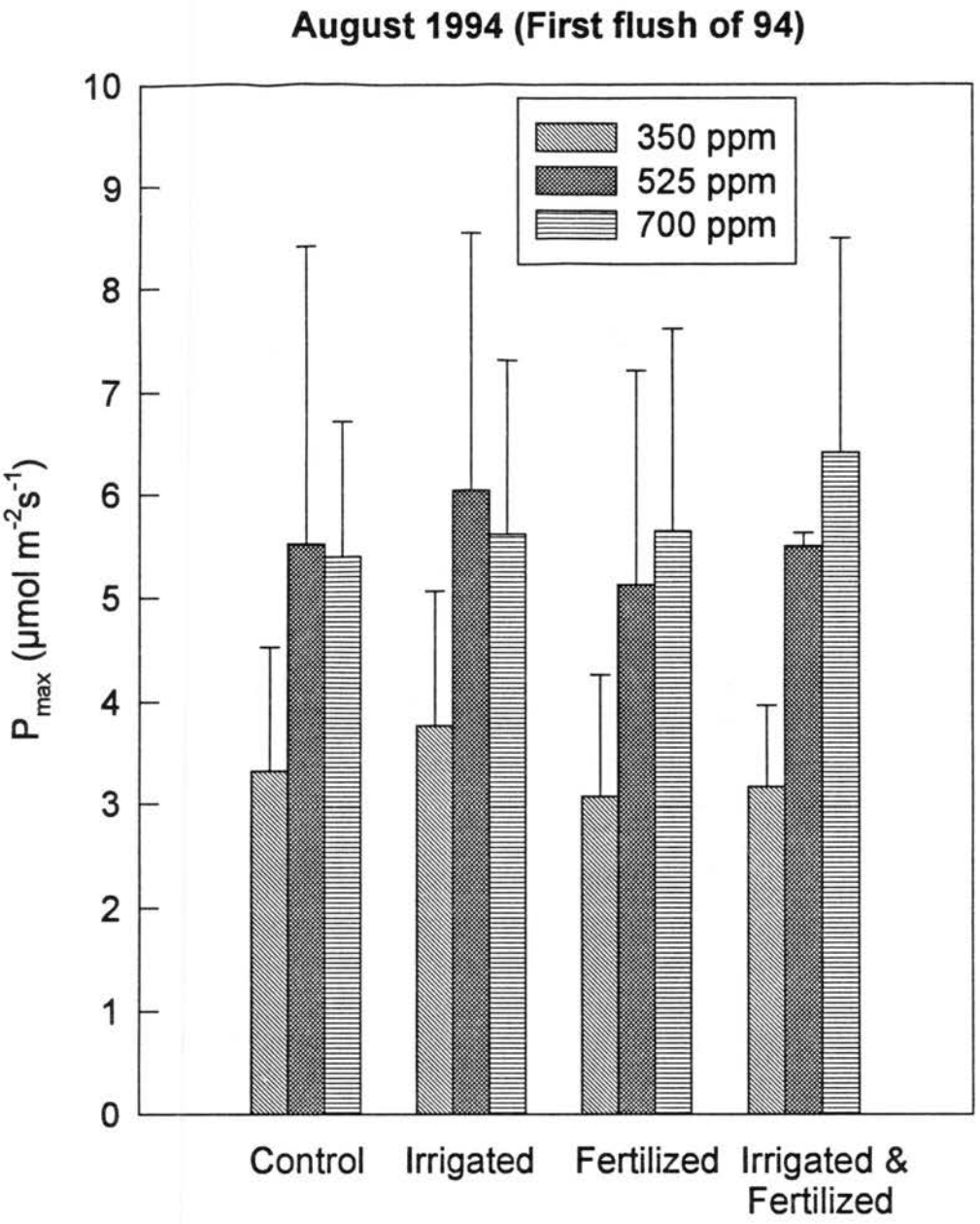

August 1994 (First flush of 94)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 16

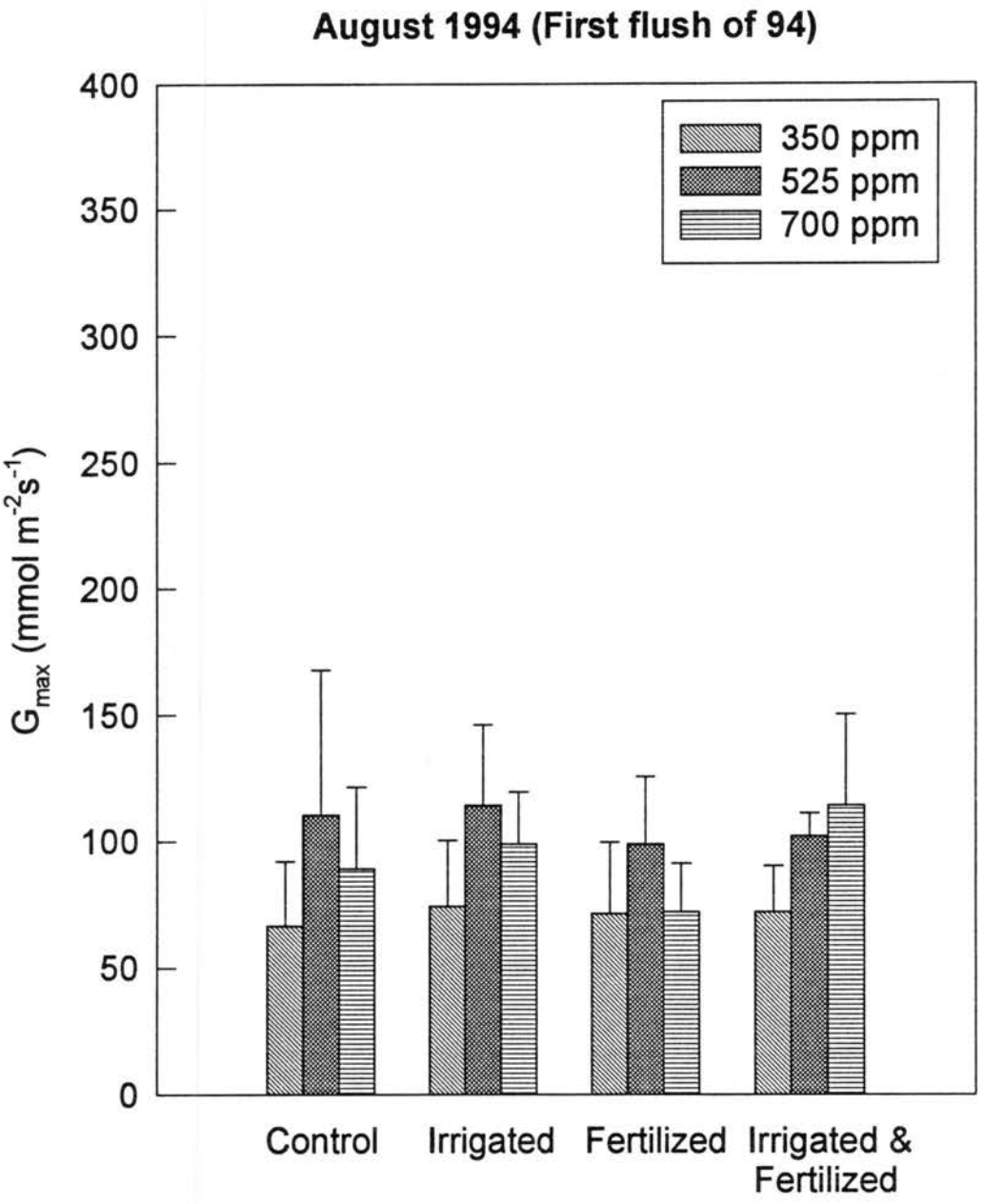

August 1994 (First flush of 94)
350 ppm
525 ppm
700 ppm
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 17

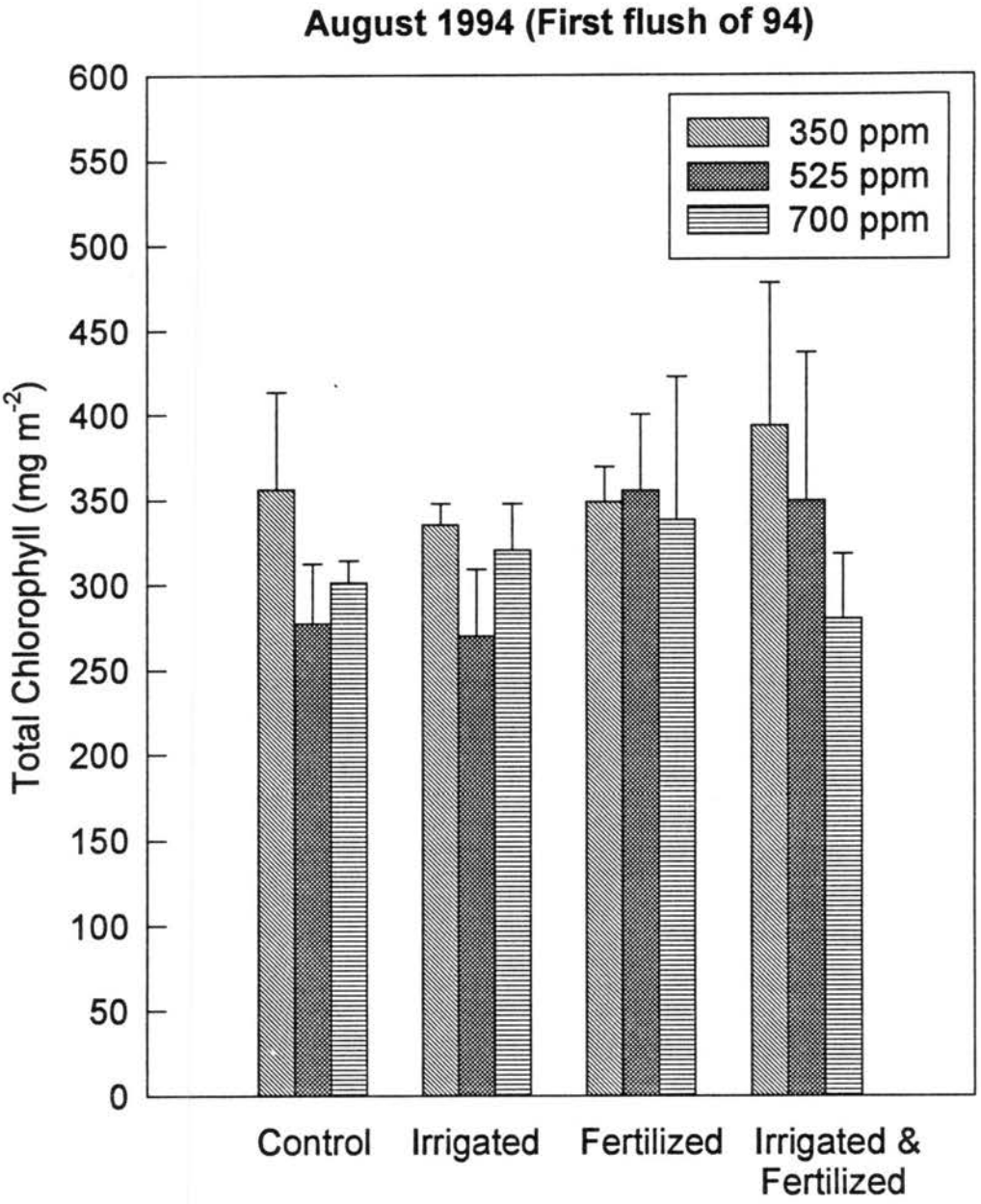

August 1994 (First flush of 94)
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 18

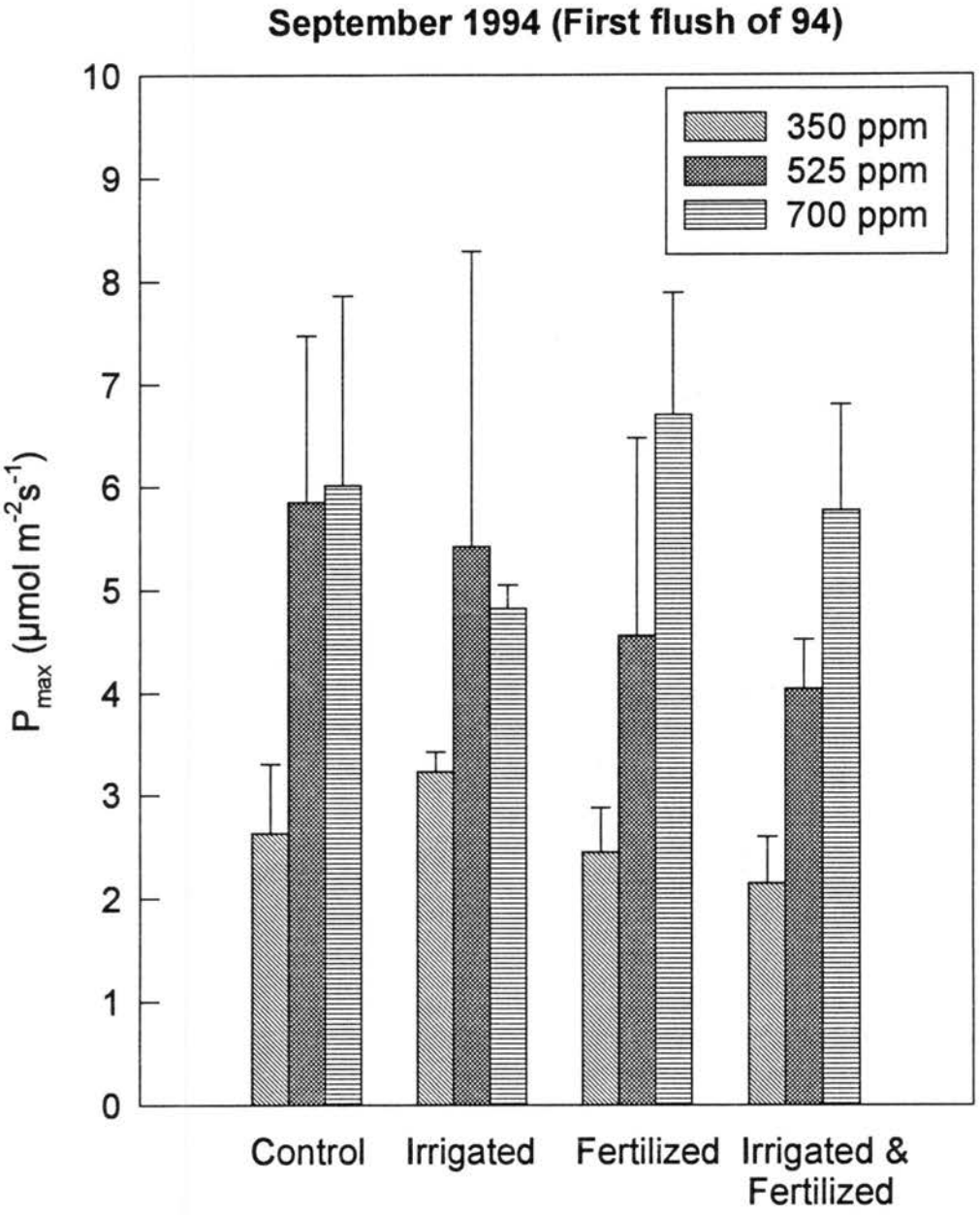

September 1994 (First flush of 94)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 19

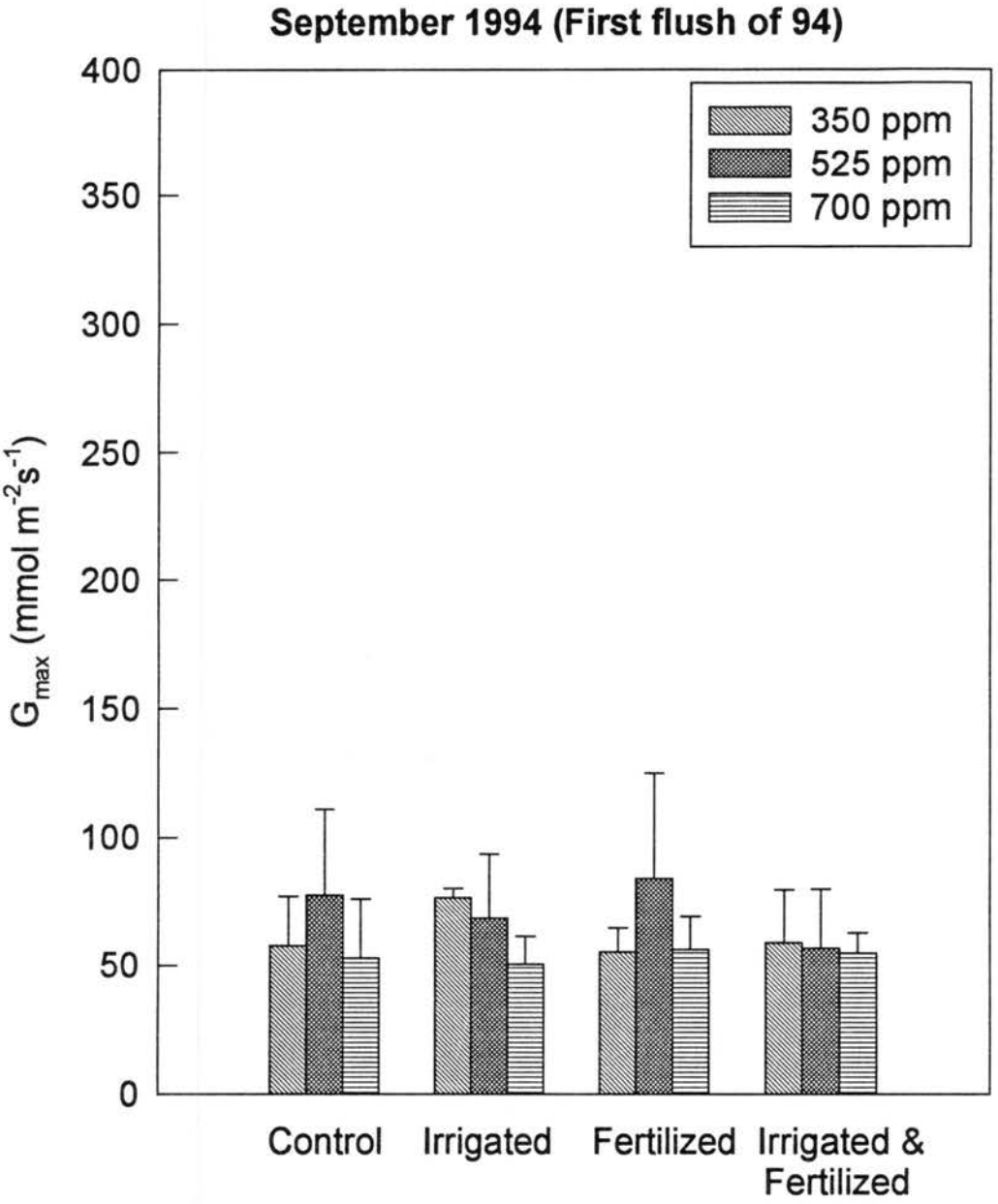

September 1994 (First flush of 94)
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 20

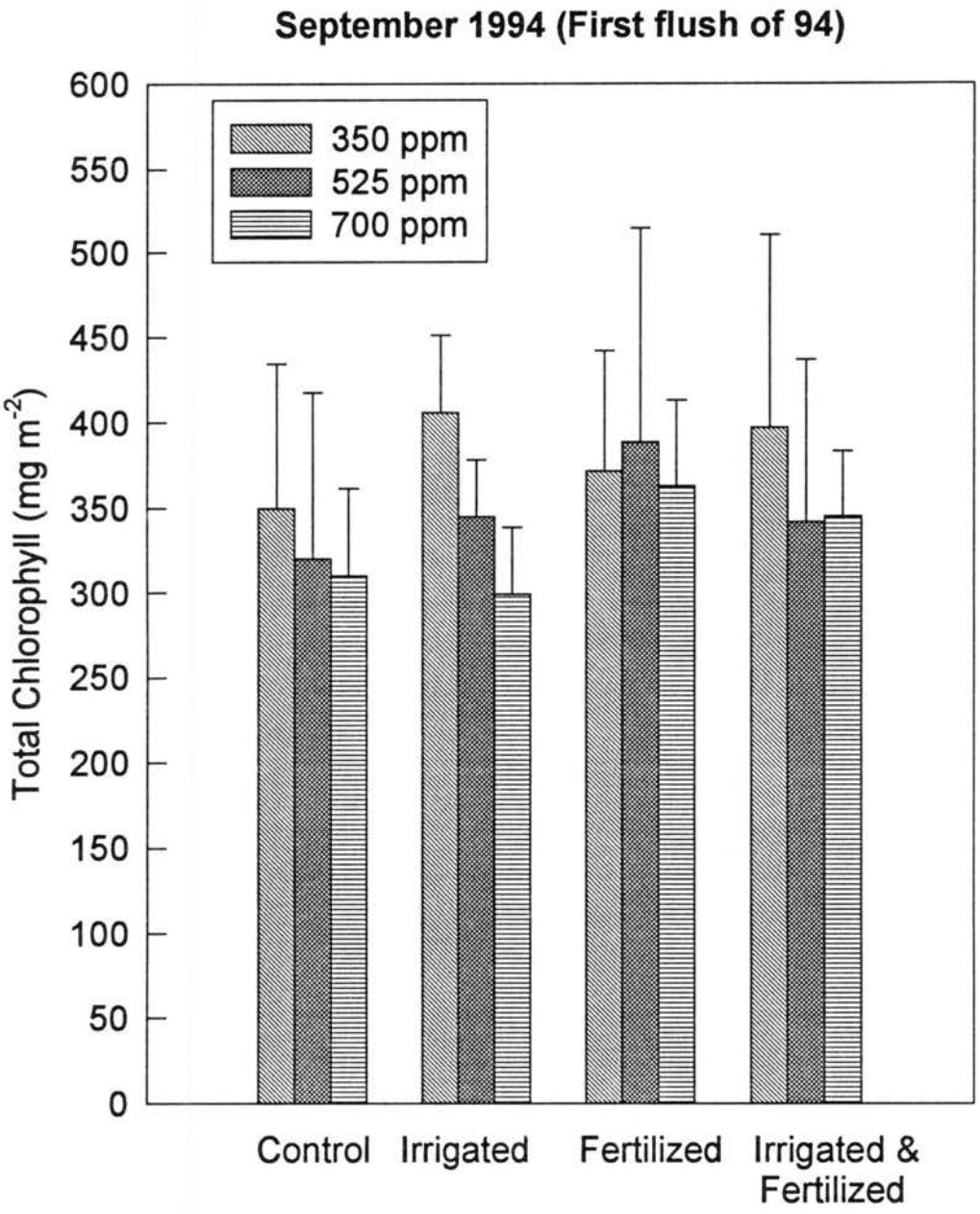

September 1994 (First flush of 94)
350 ppm
525 ppm
700 ppm
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 21

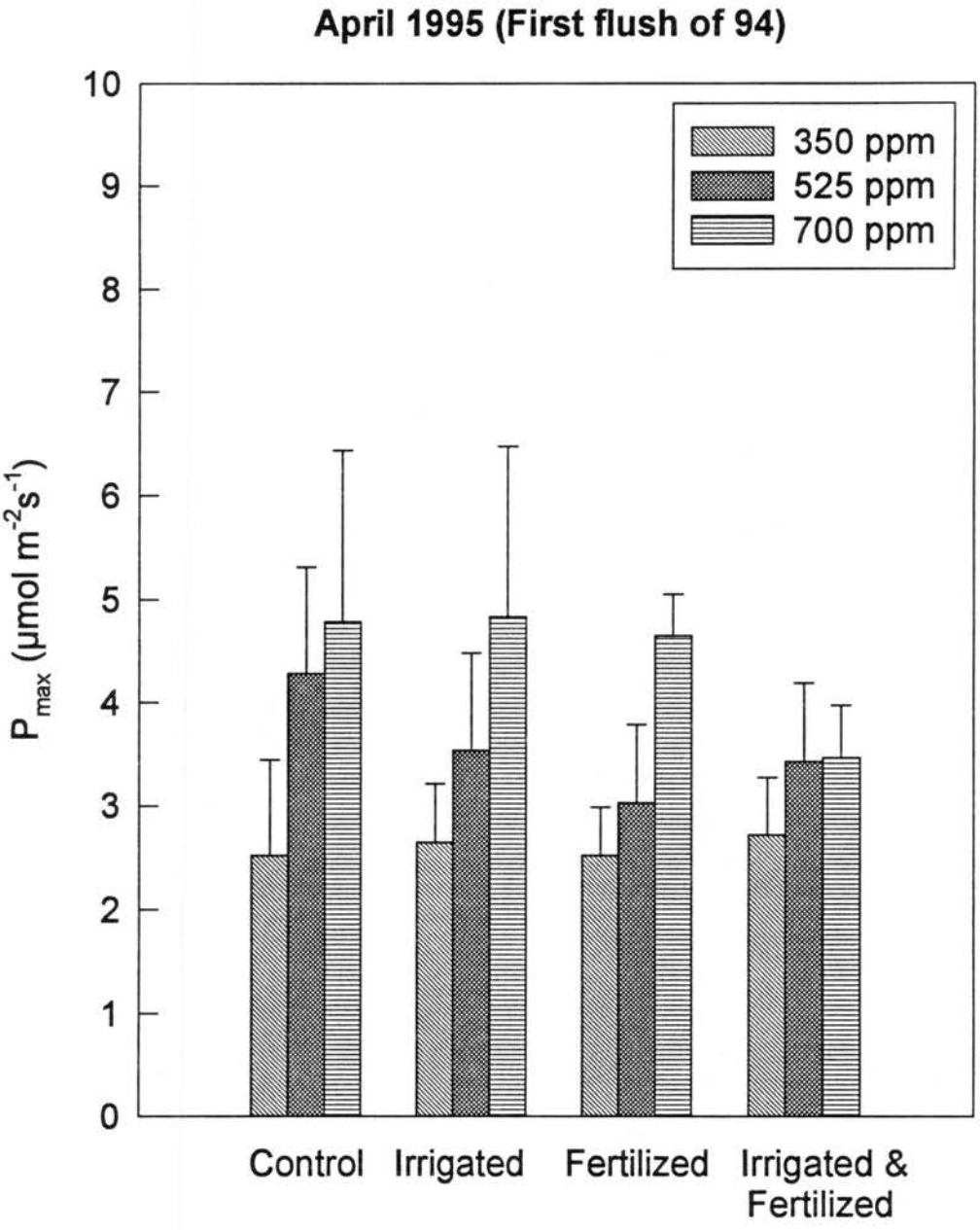

April 1995 (First flush of 94)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 22

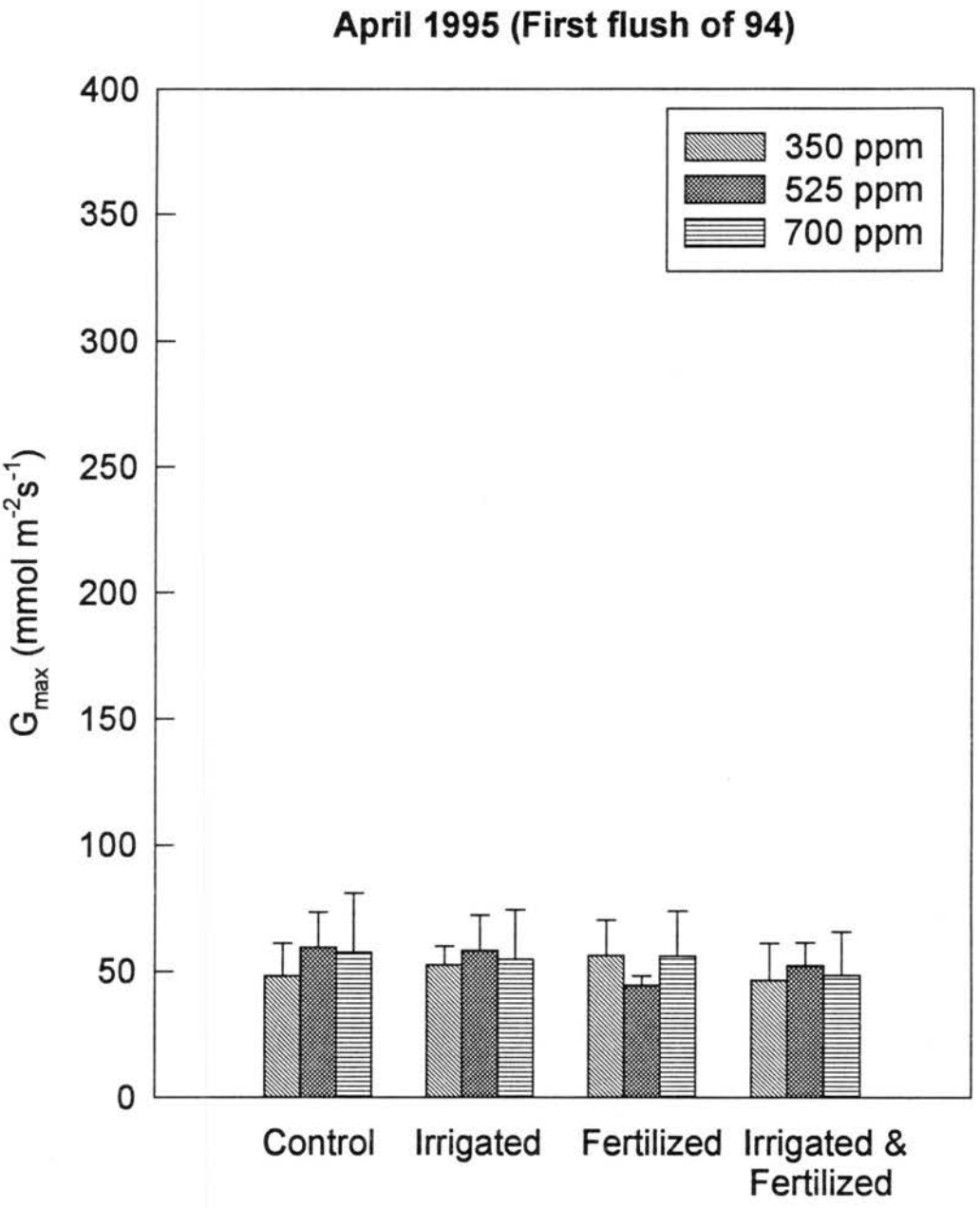

April 1995 (First flush of 94)
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 23

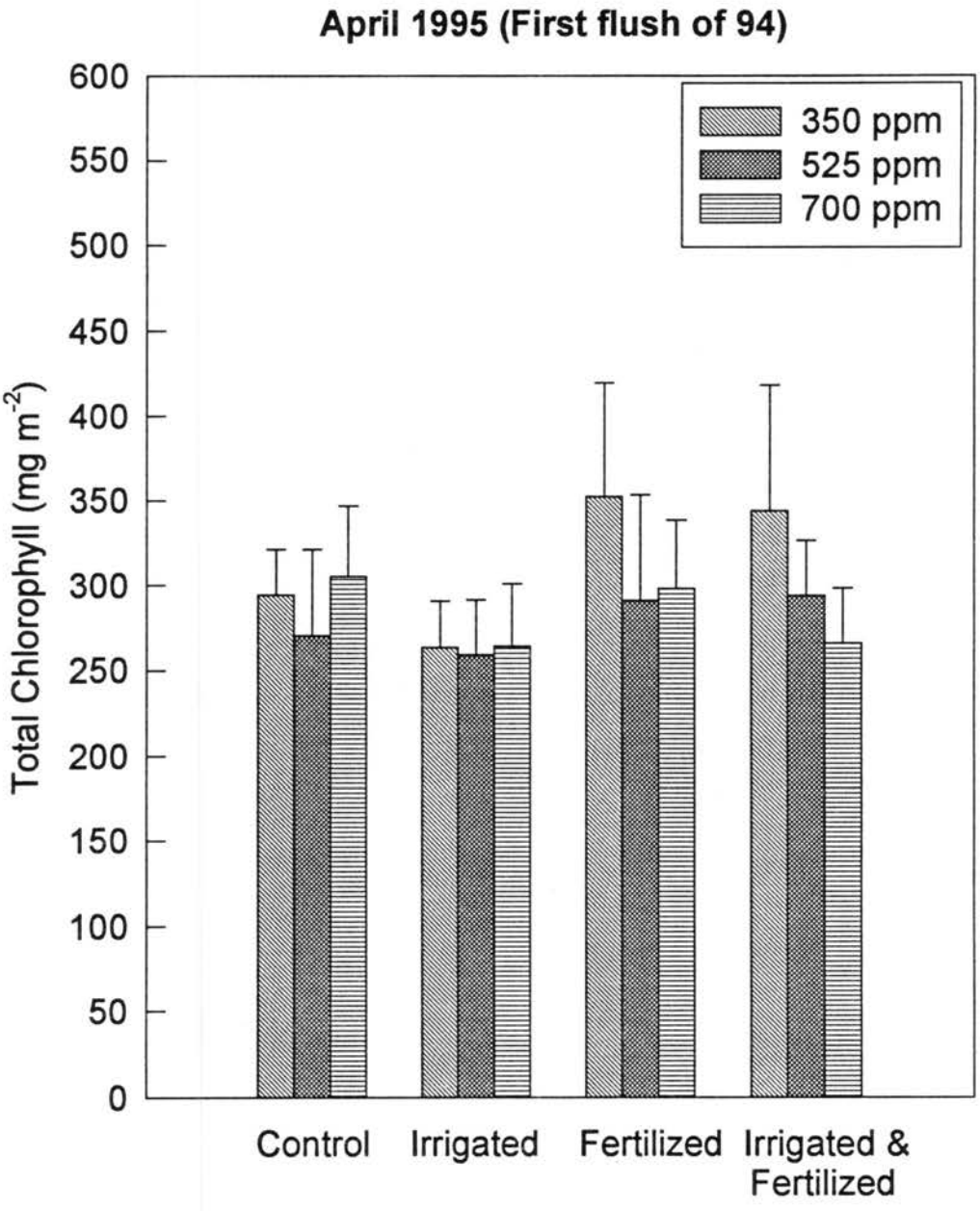

April 1995 (First flush of 94)
350 ppm
525 ppm
700 ppm
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 24

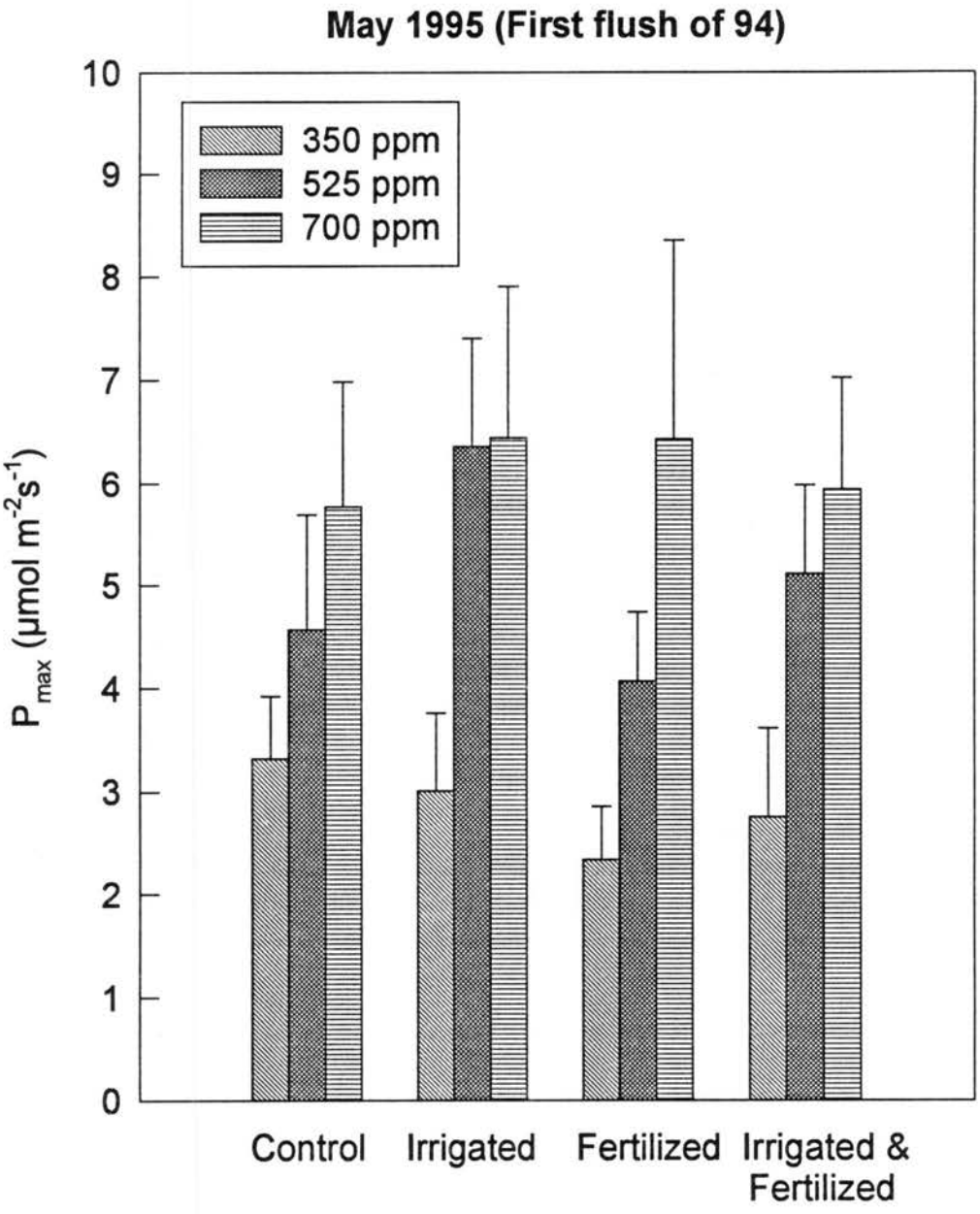

May 1995 (First flush of 94)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 25

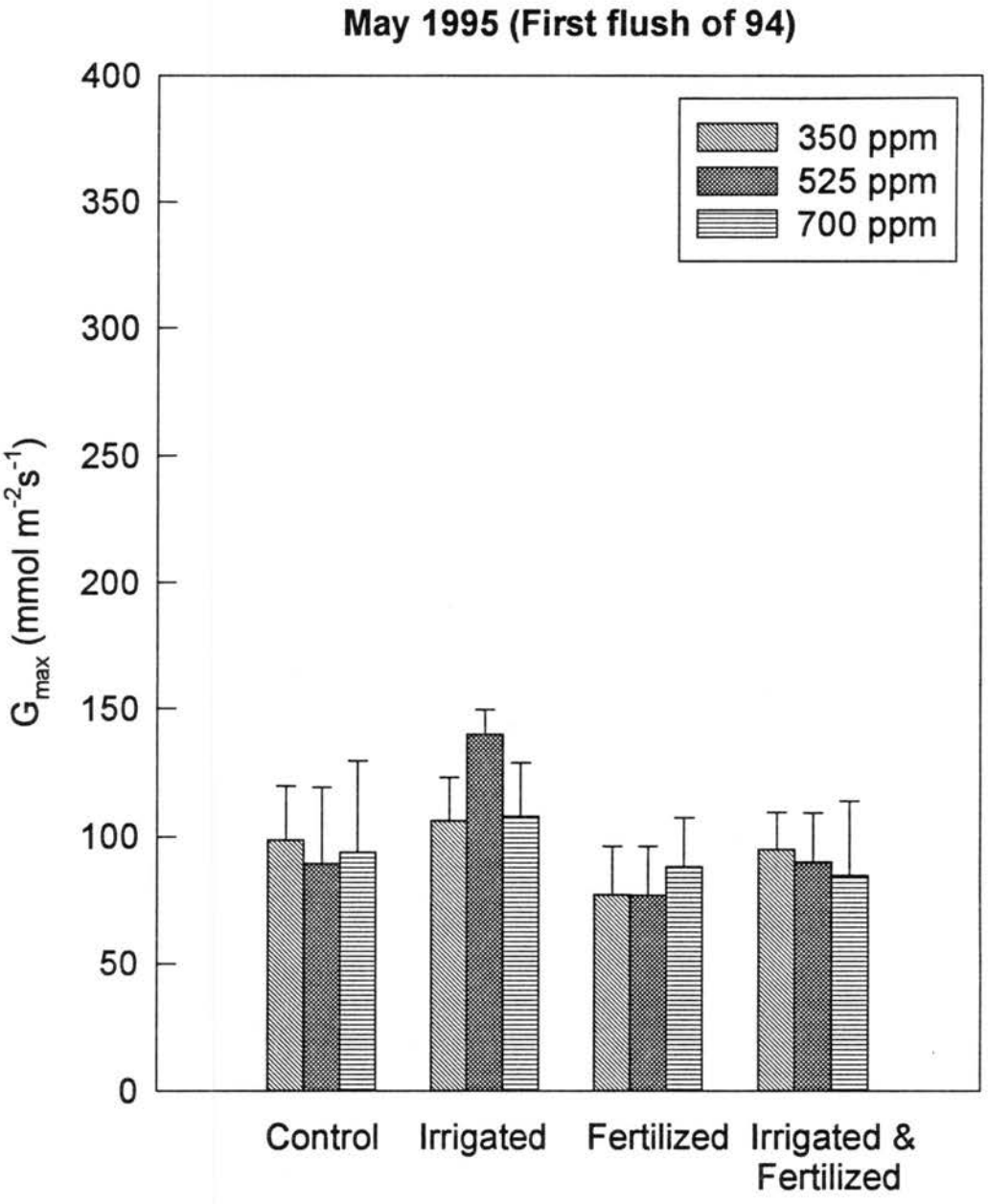

May 1995 (First flush of 94)
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 26

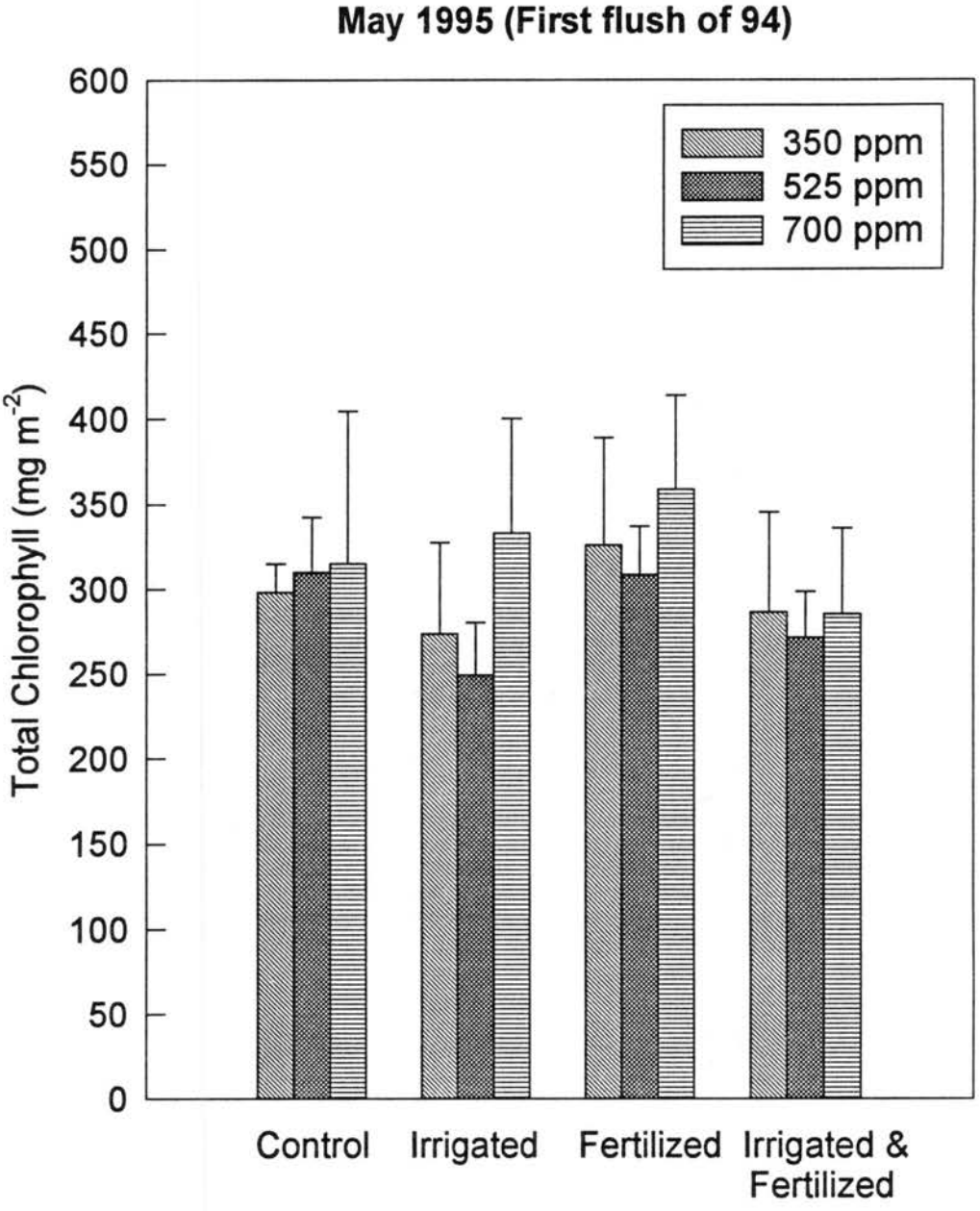

May 1995 (First flush of 94)
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 27

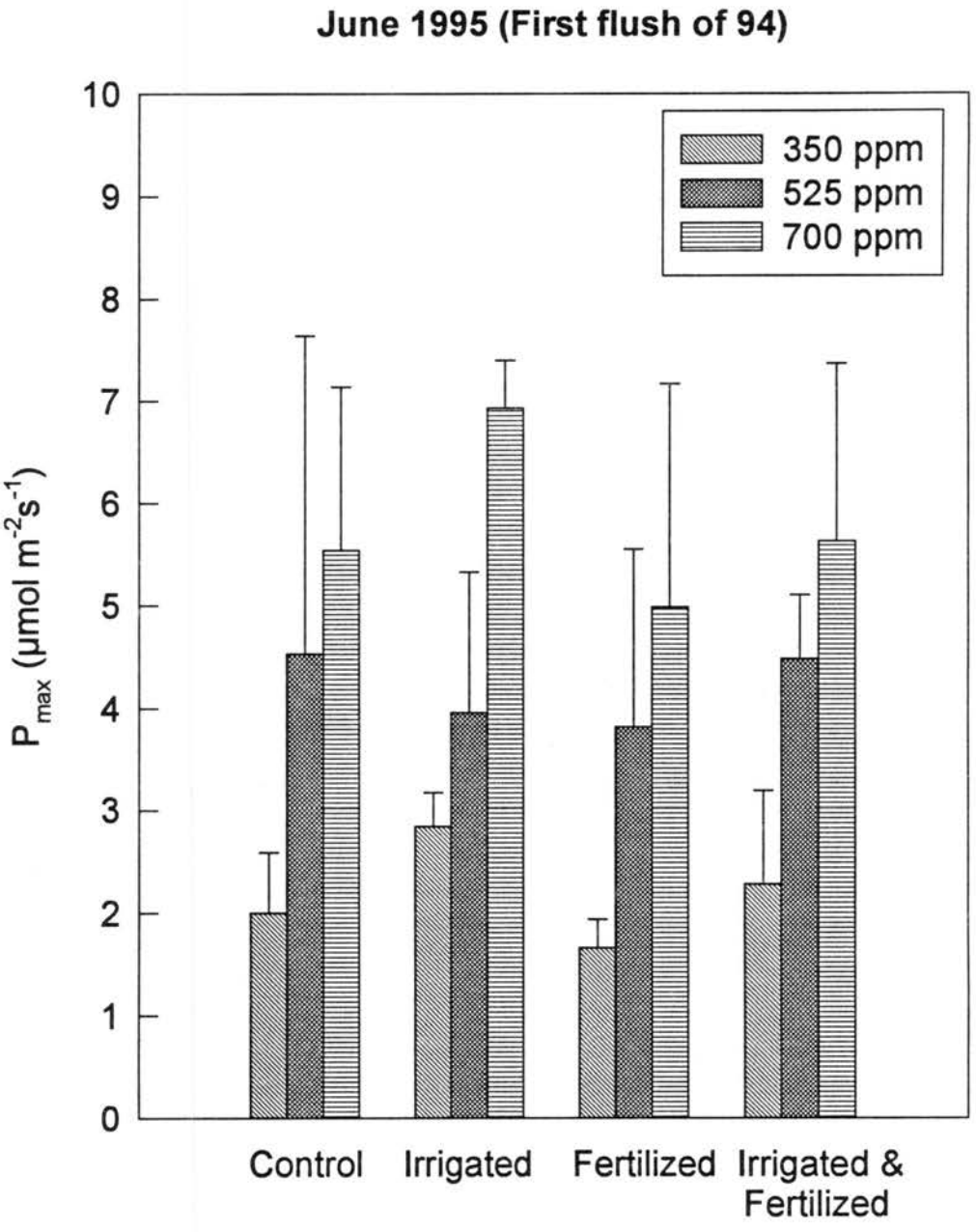

June 1995 (First flush of 94)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 28

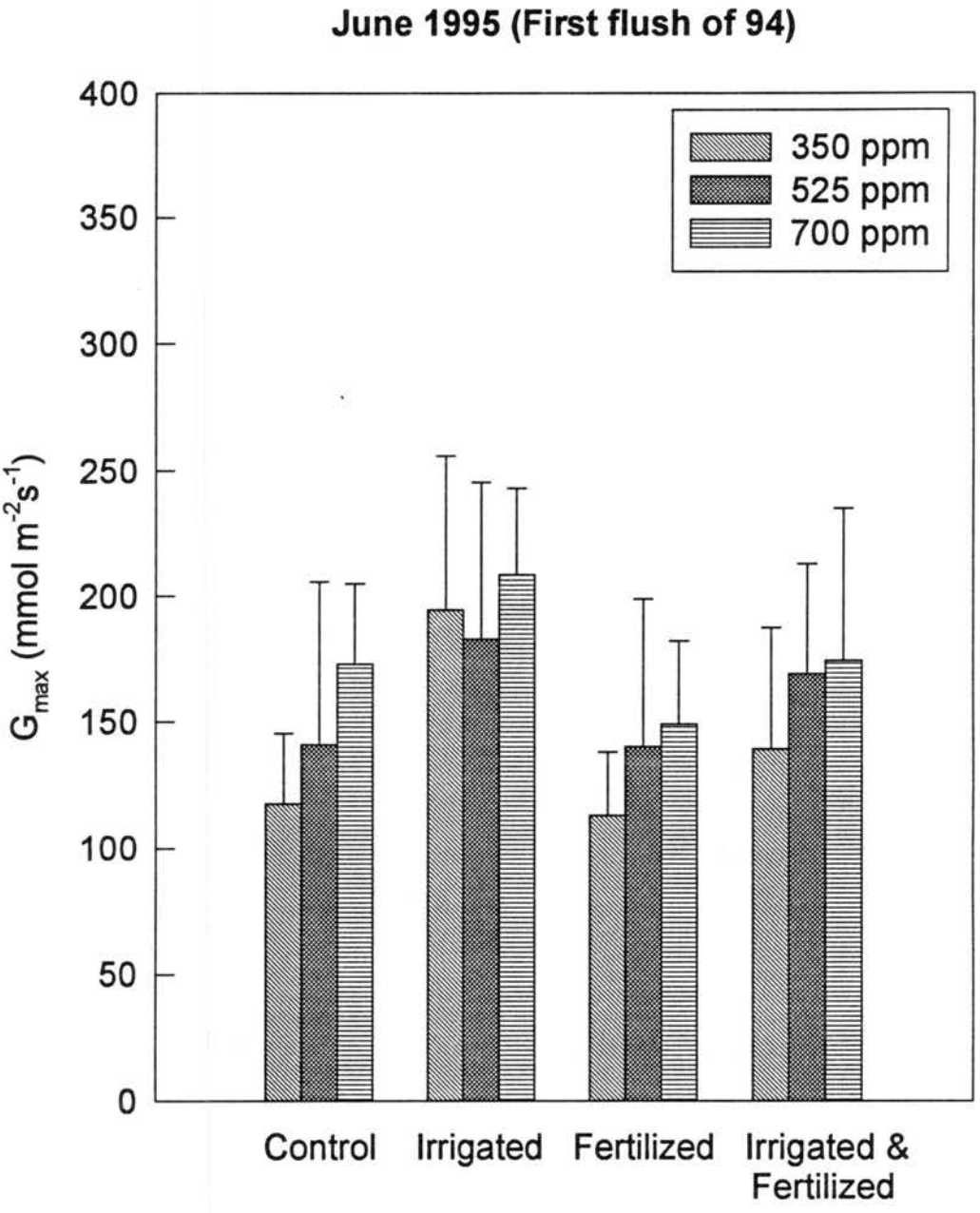

June 1995 (First flush of 94)
350 ppm
525 ppm
700 ppm
G_{max} (mmol $m^{-2}s^{-1}$)
400
350
300
250
200
150
100
50
0
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 29

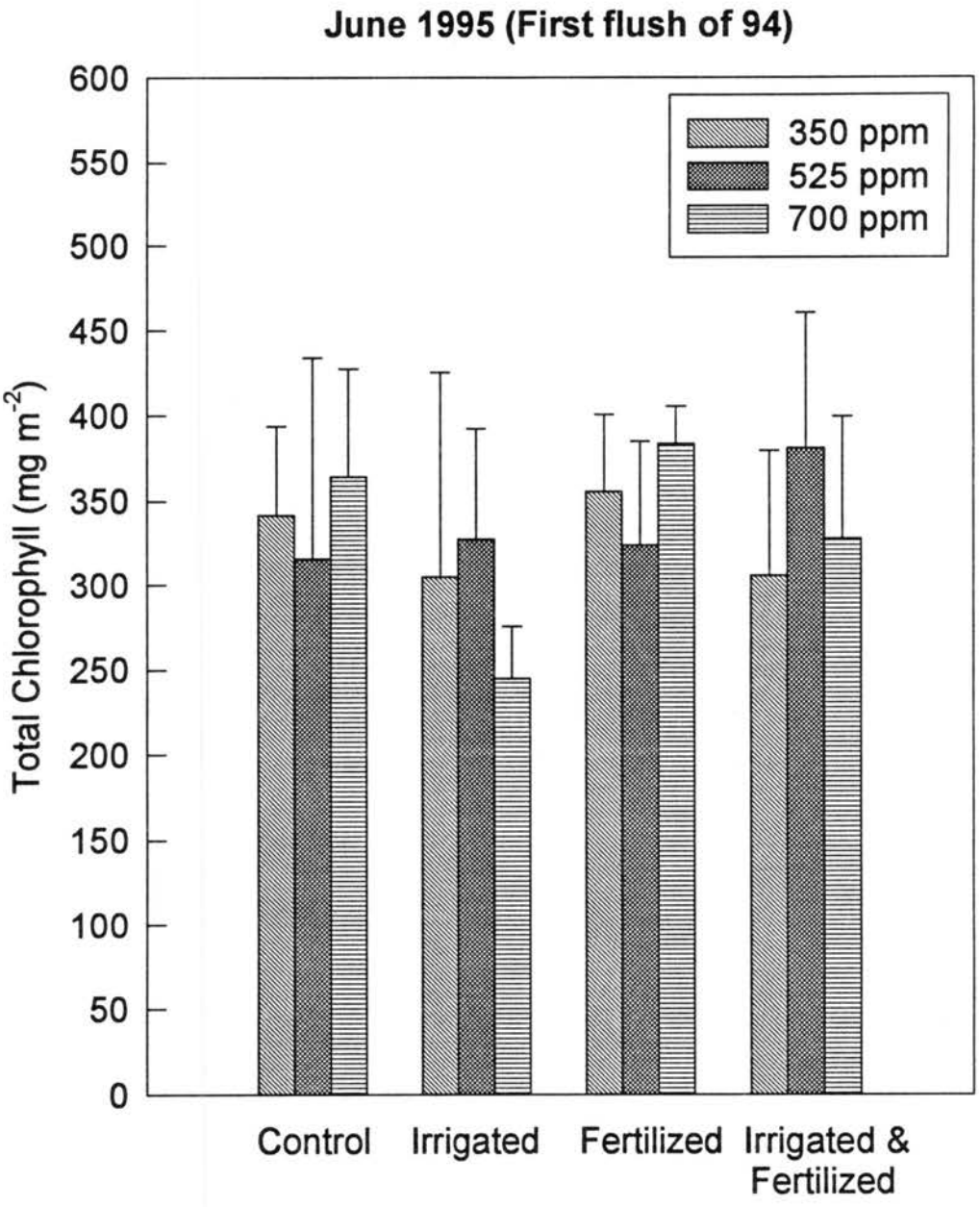

June 1995 (First flush of 94)
350 ppm
525 ppm
700 ppm
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 30

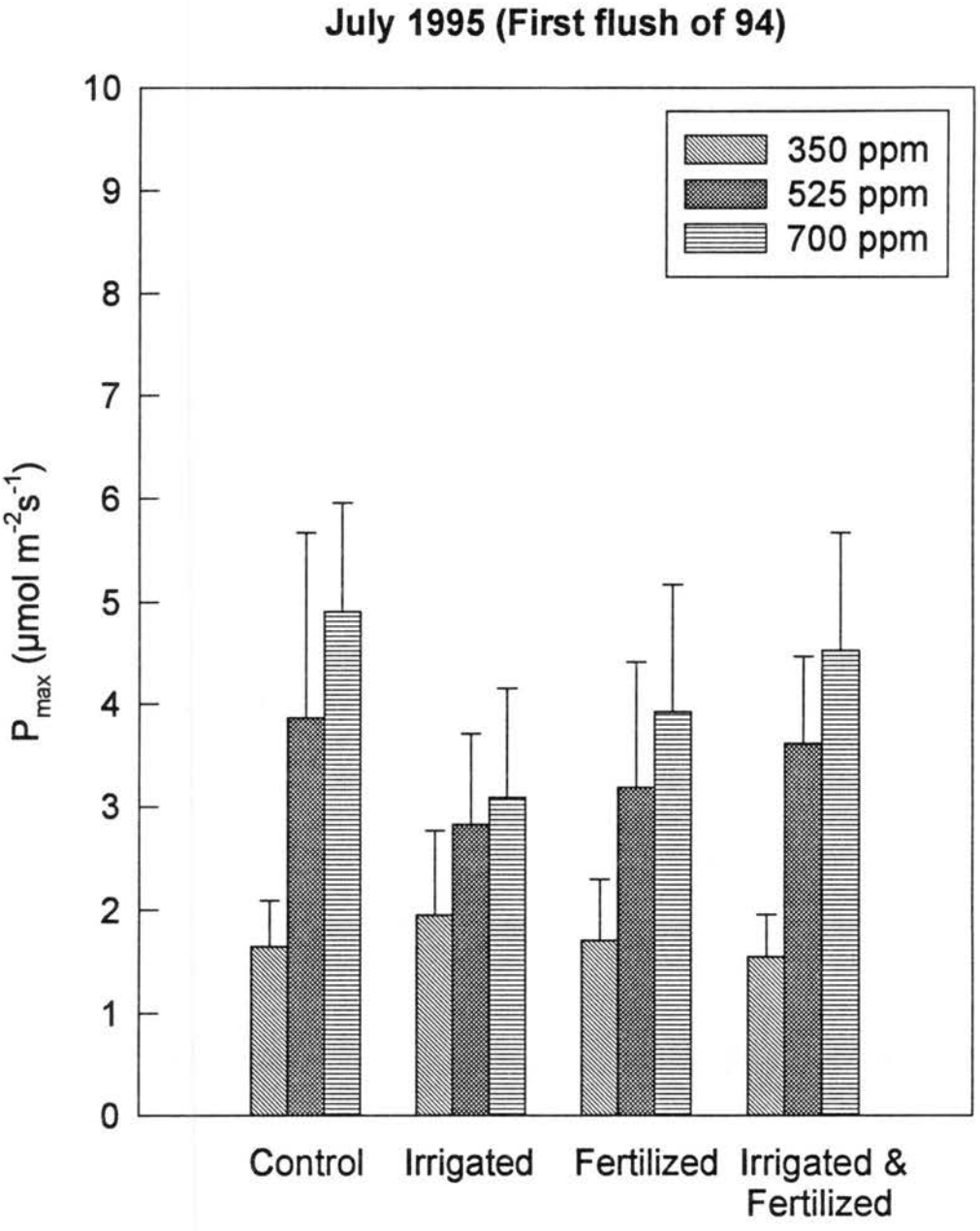

July 1995 (First flush of 94)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 31

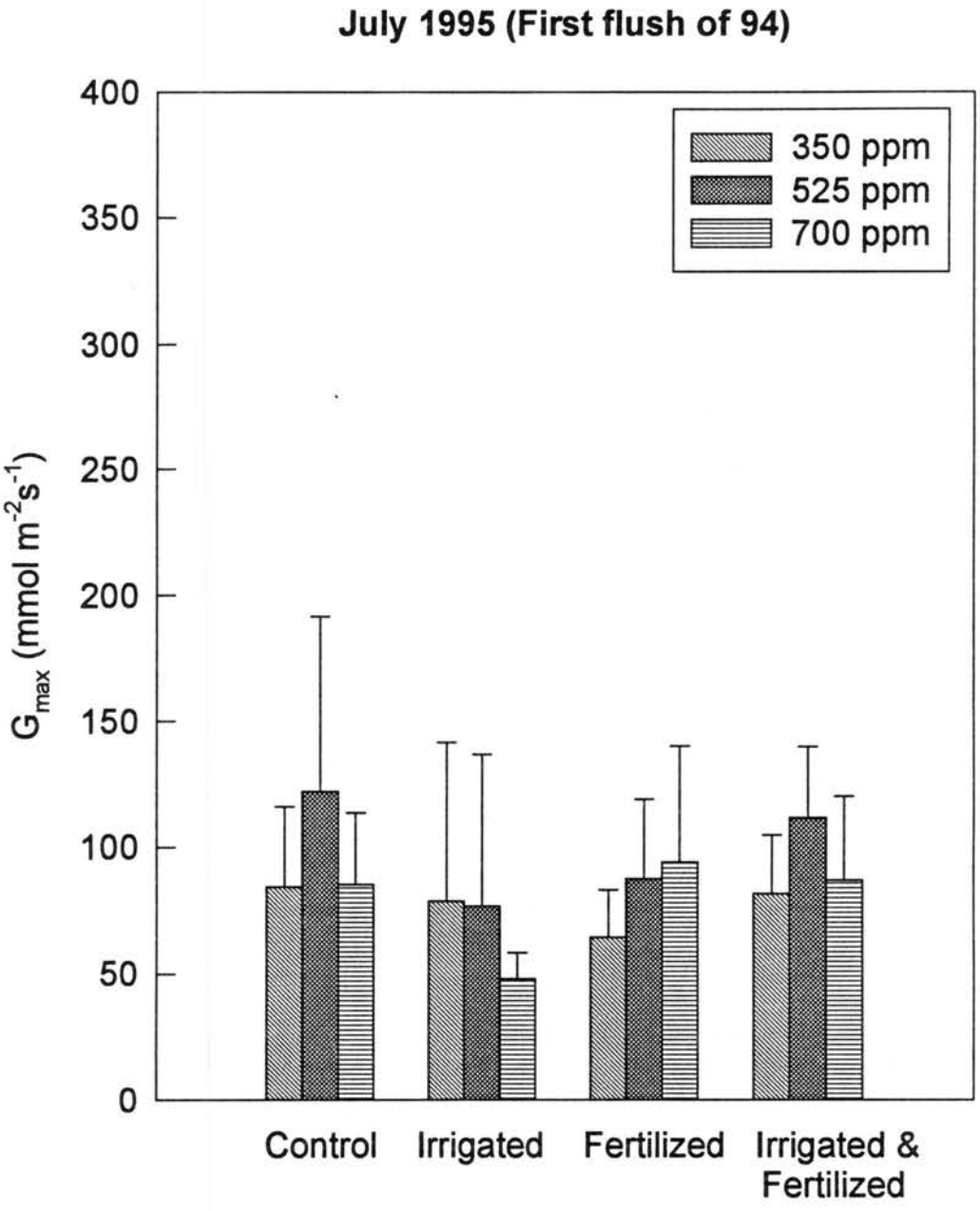

July 1995 (First flush of 94)
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 32

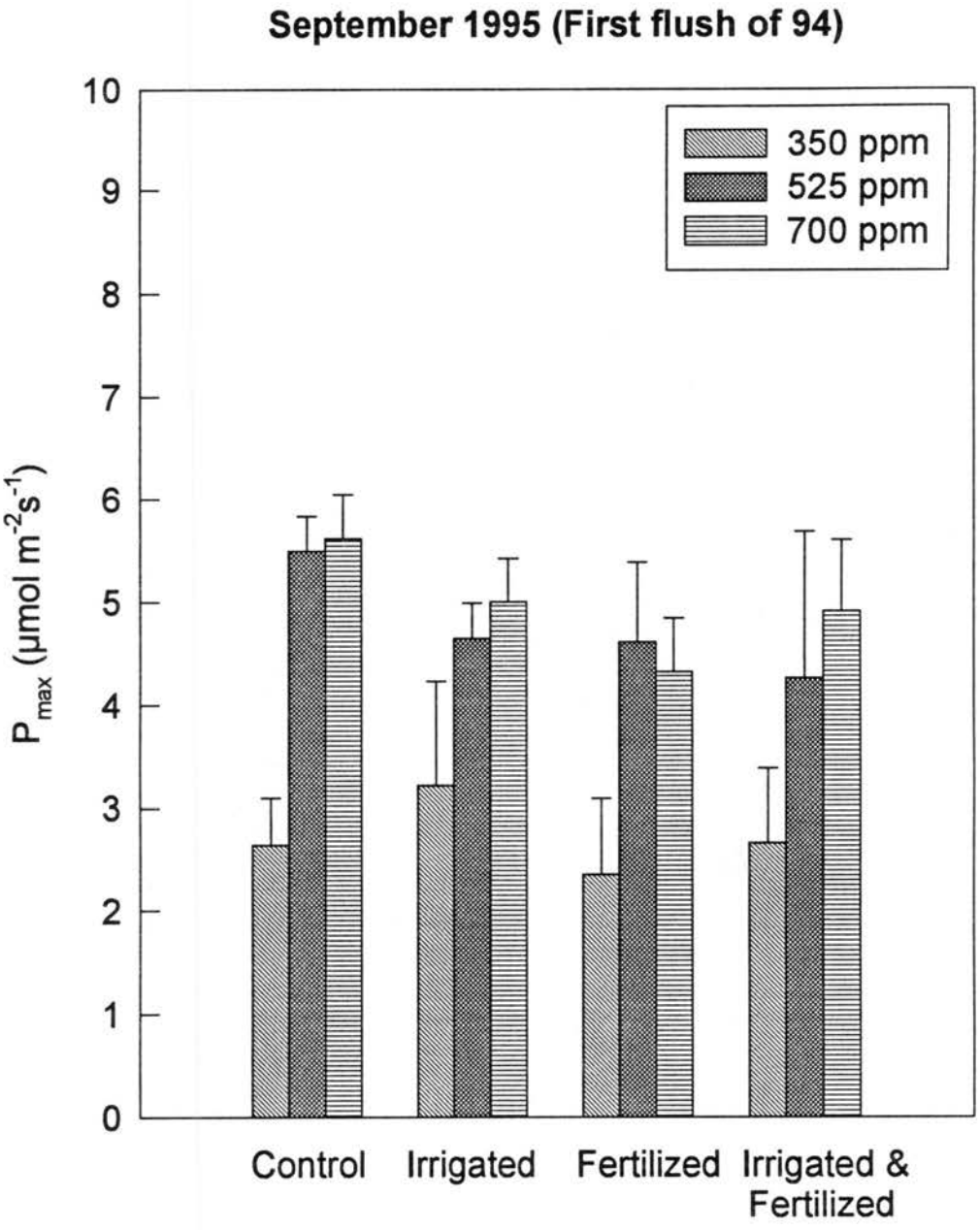

September 1995 (First flush of 94)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 33

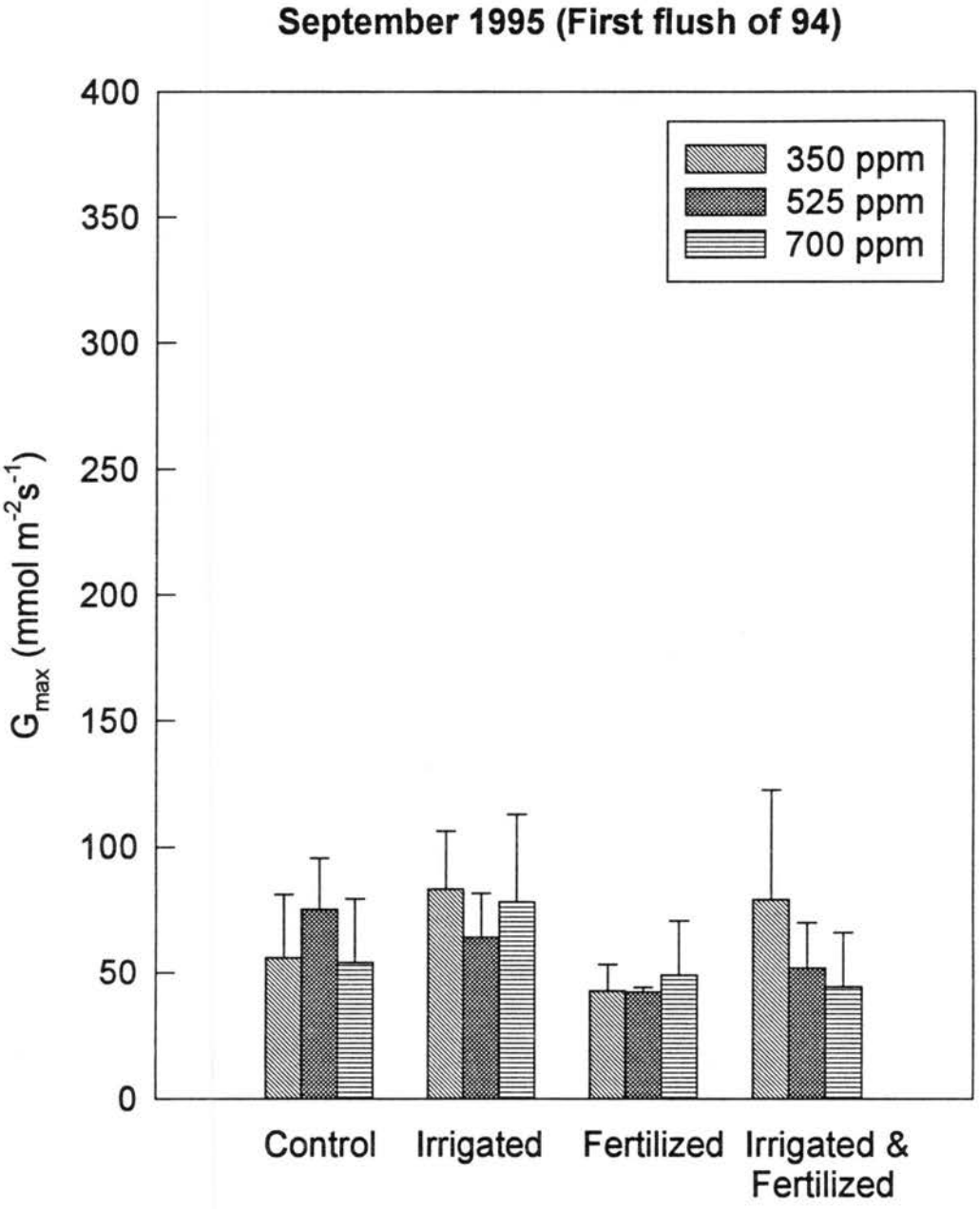

September 1995 (First flush of 94)
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 34

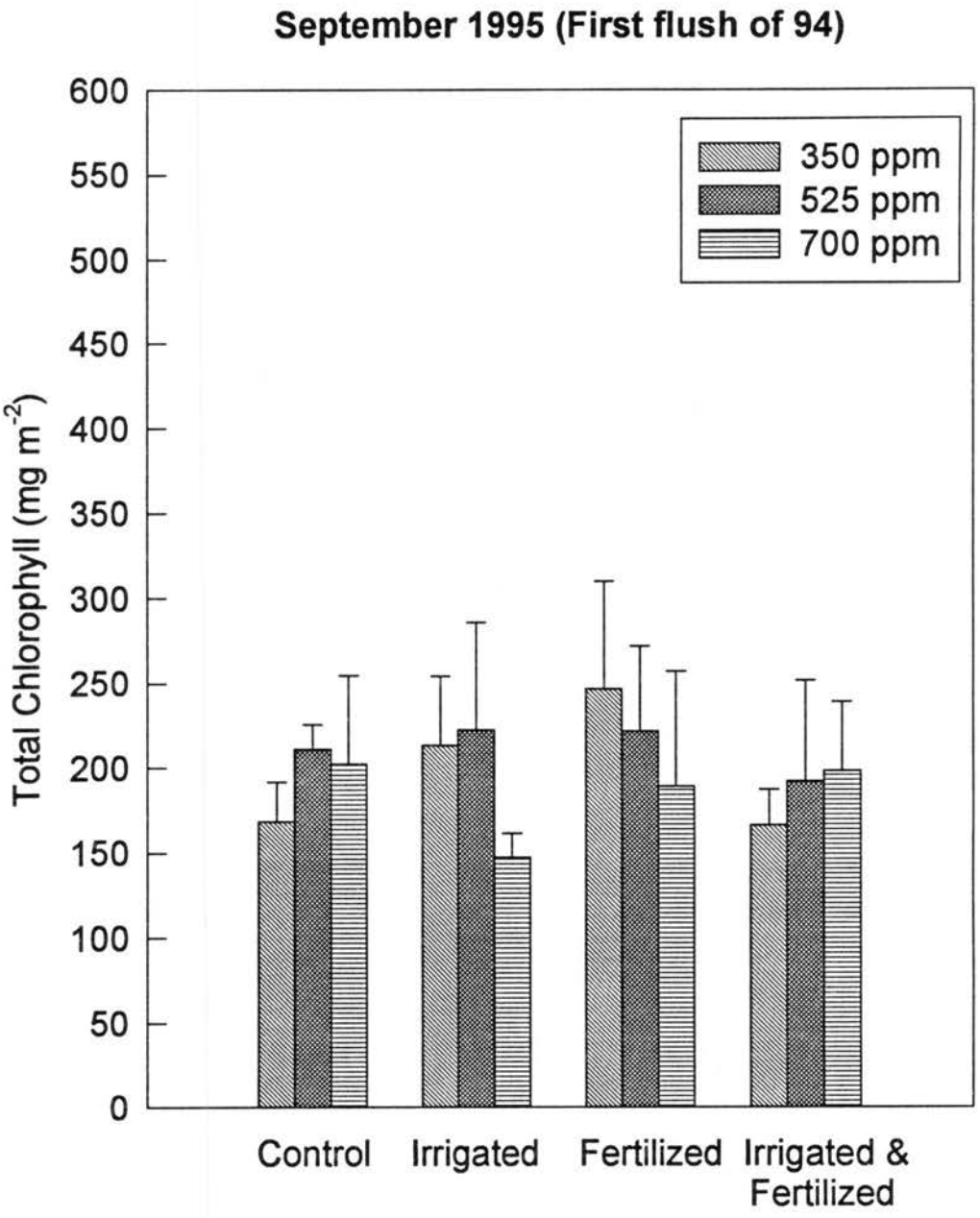

September 1995 (First flush of 94)
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 35

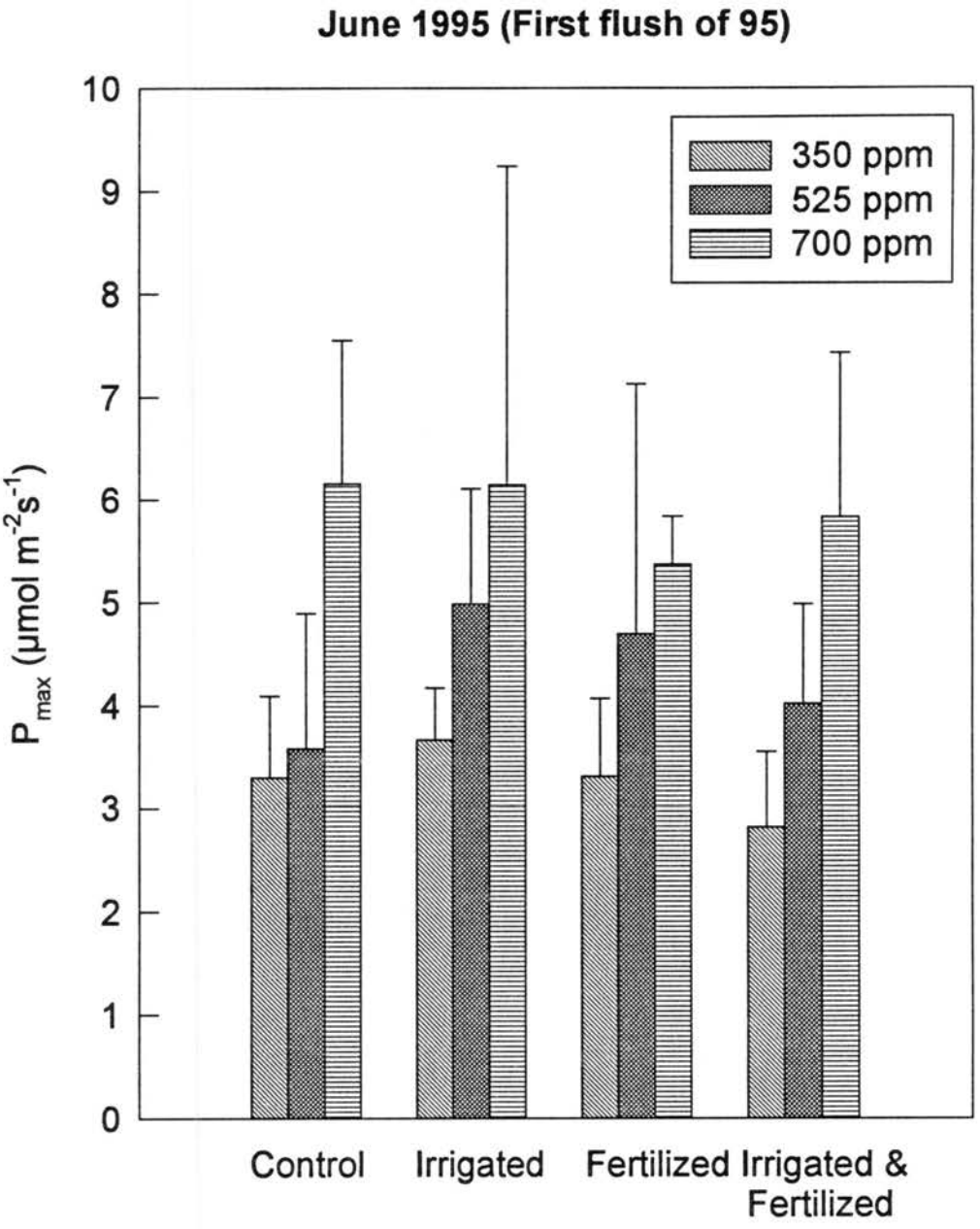

June 1995 (First flush of 95)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 36

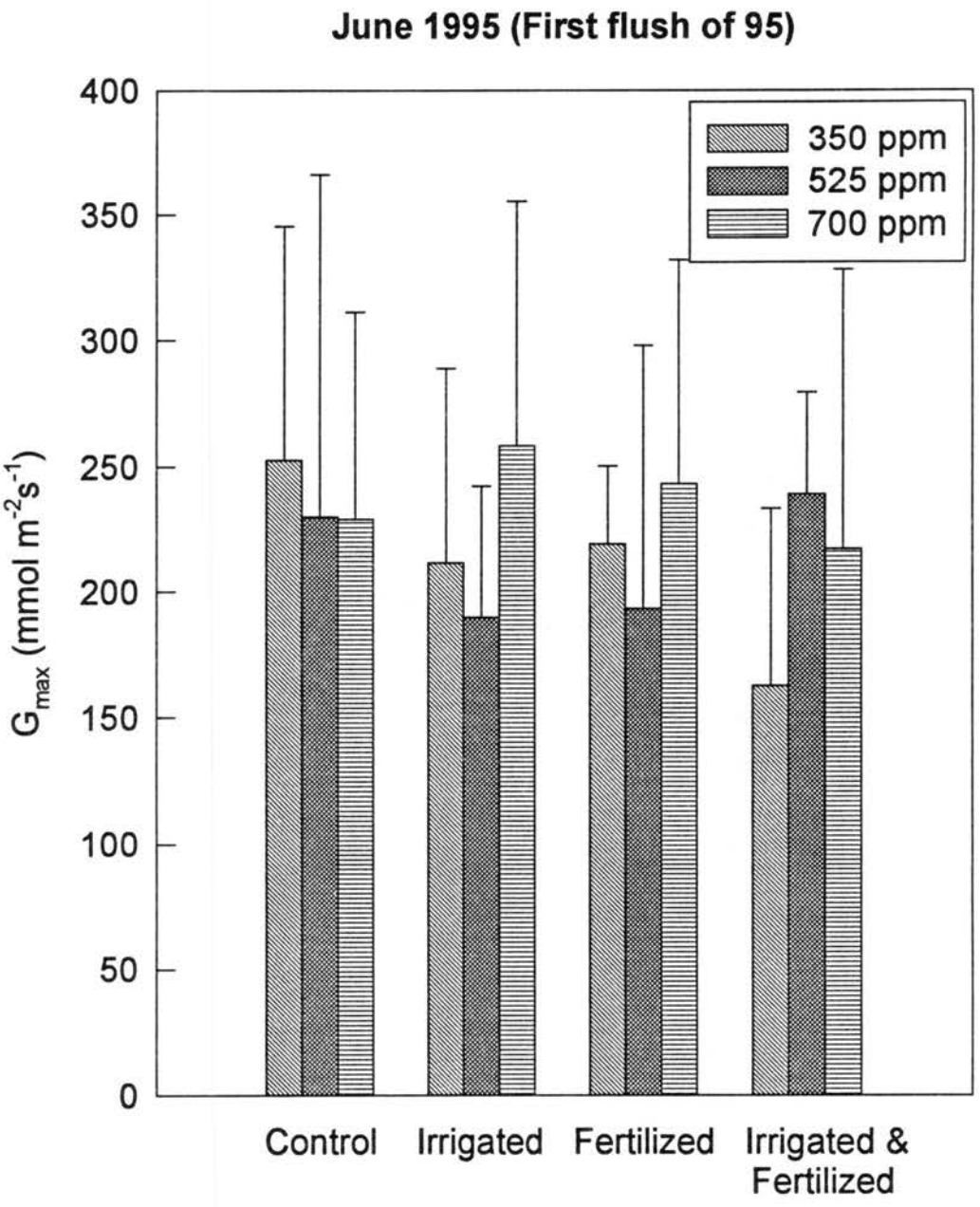

June 1995 (First flush of 95)
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 37

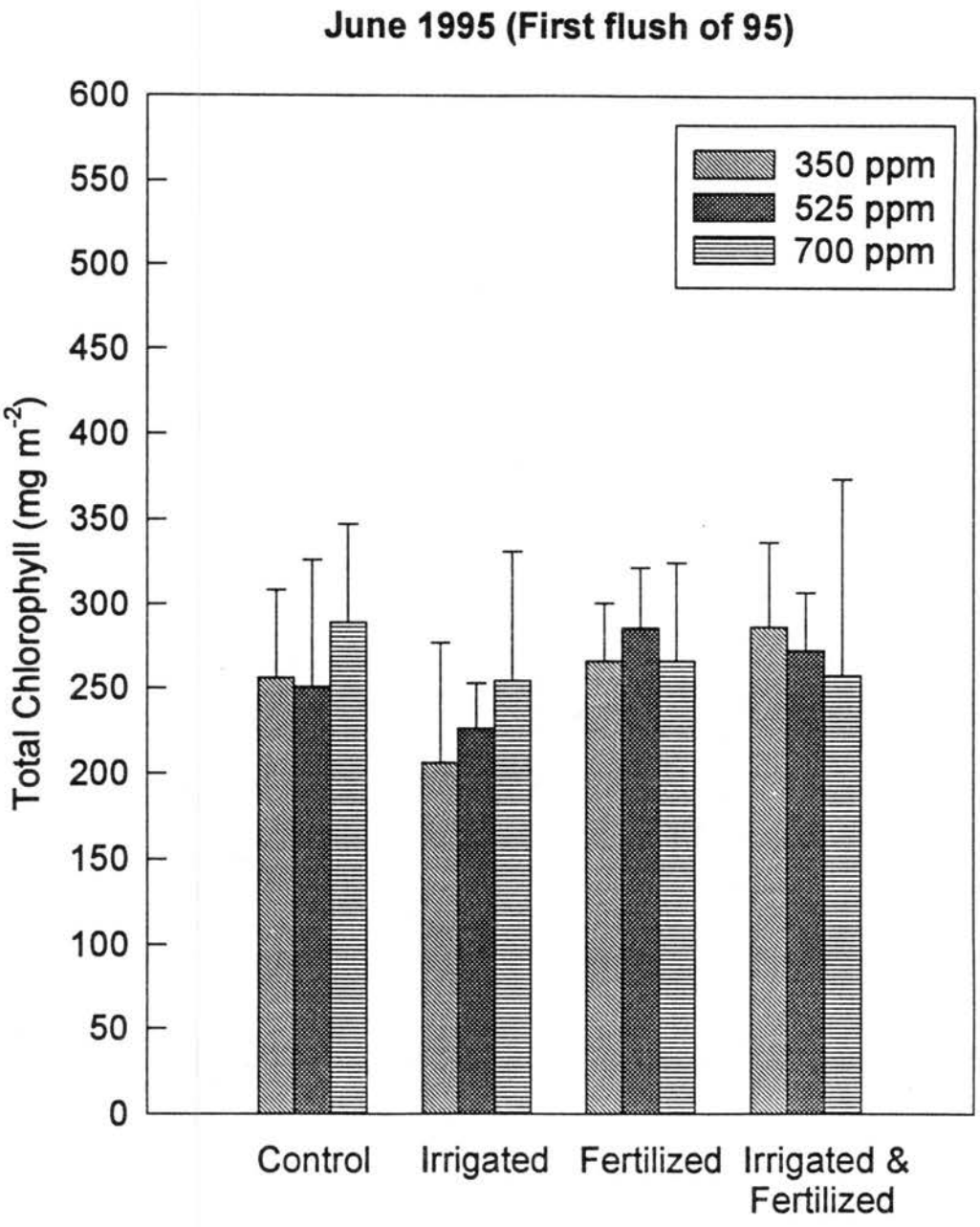

June 1995 (First flush of 95)
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 38

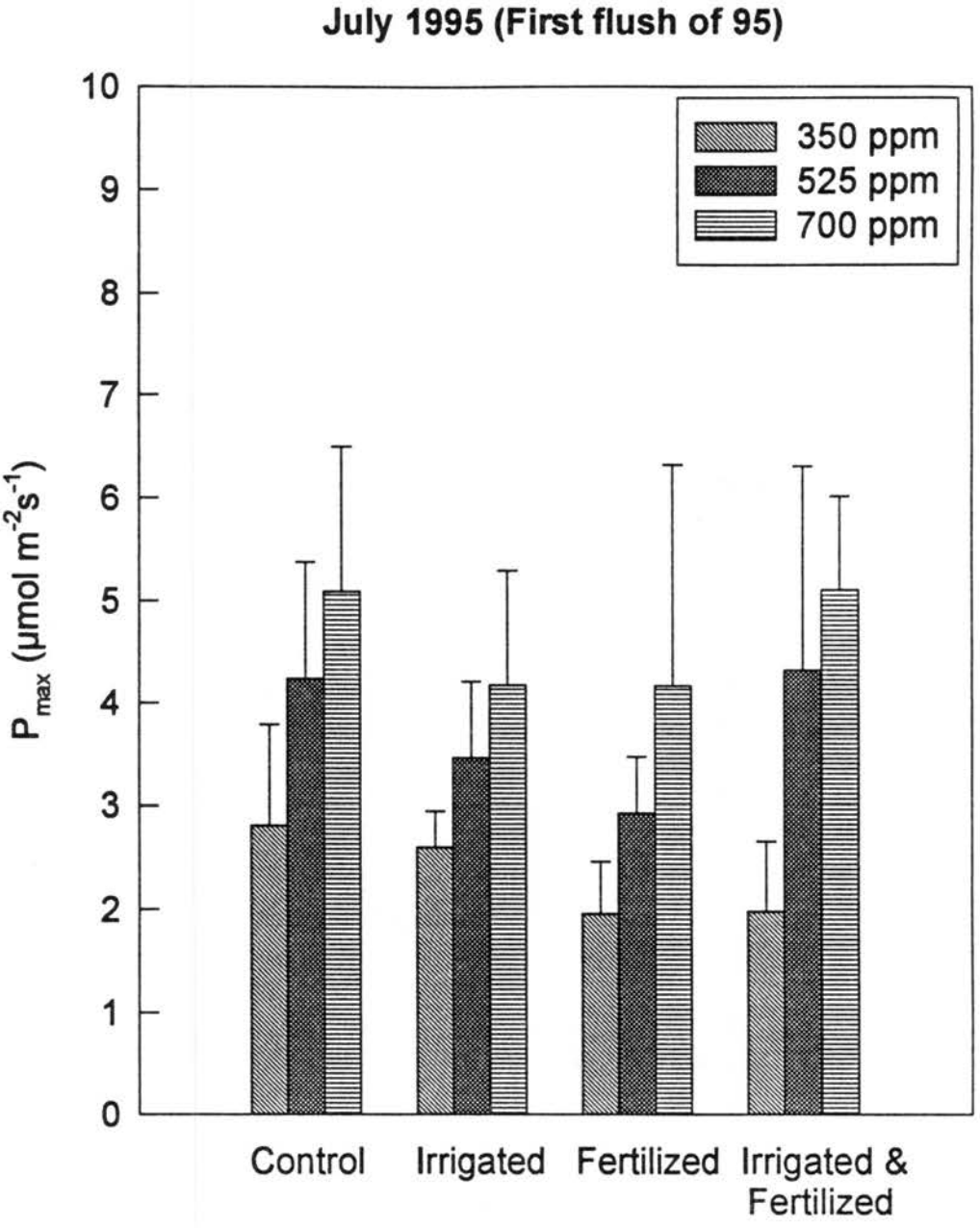

July 1995 (First flush of 95)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 39

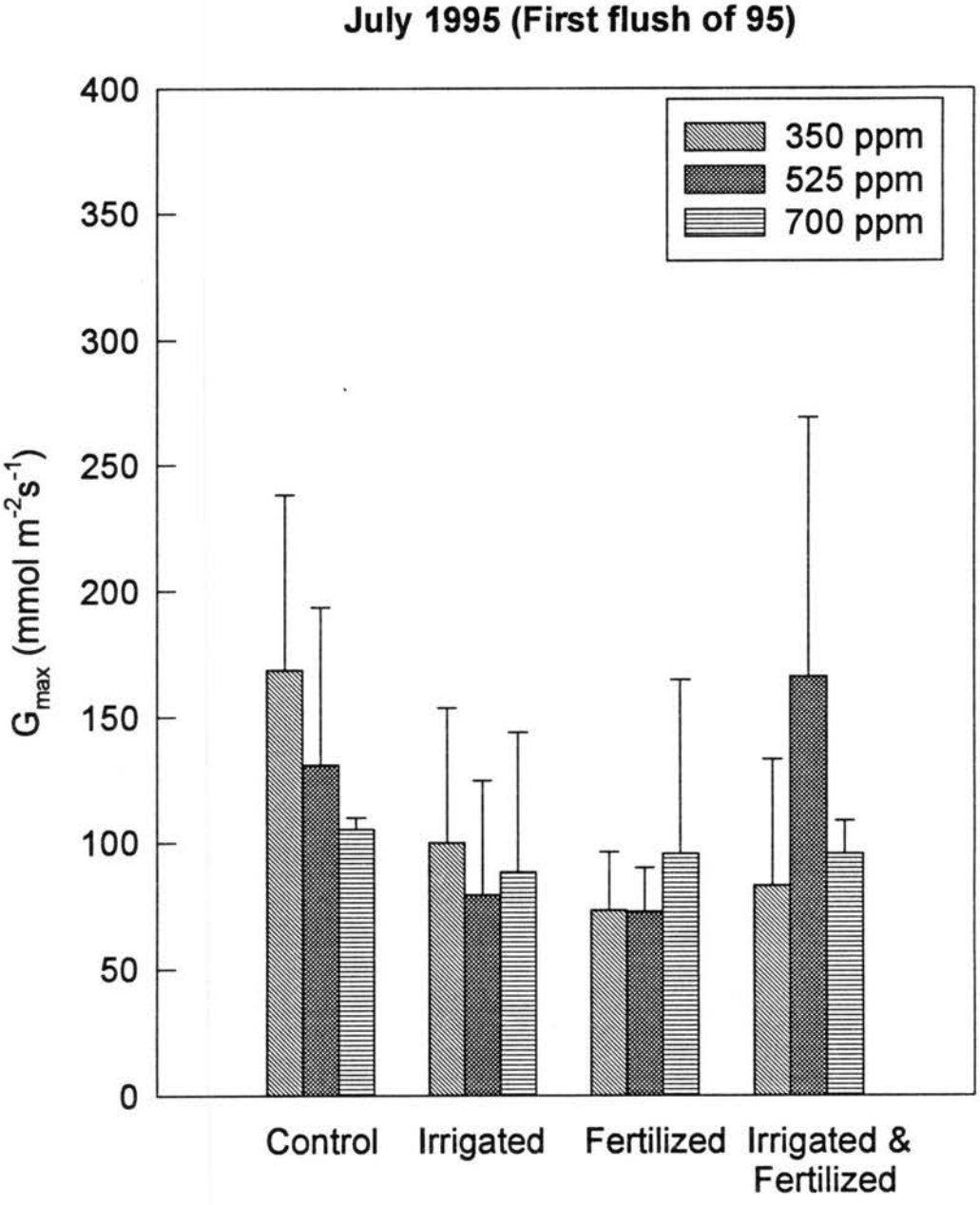

July 1995 (First flush of 95)
350 ppm
525 ppm
700 ppm
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 40

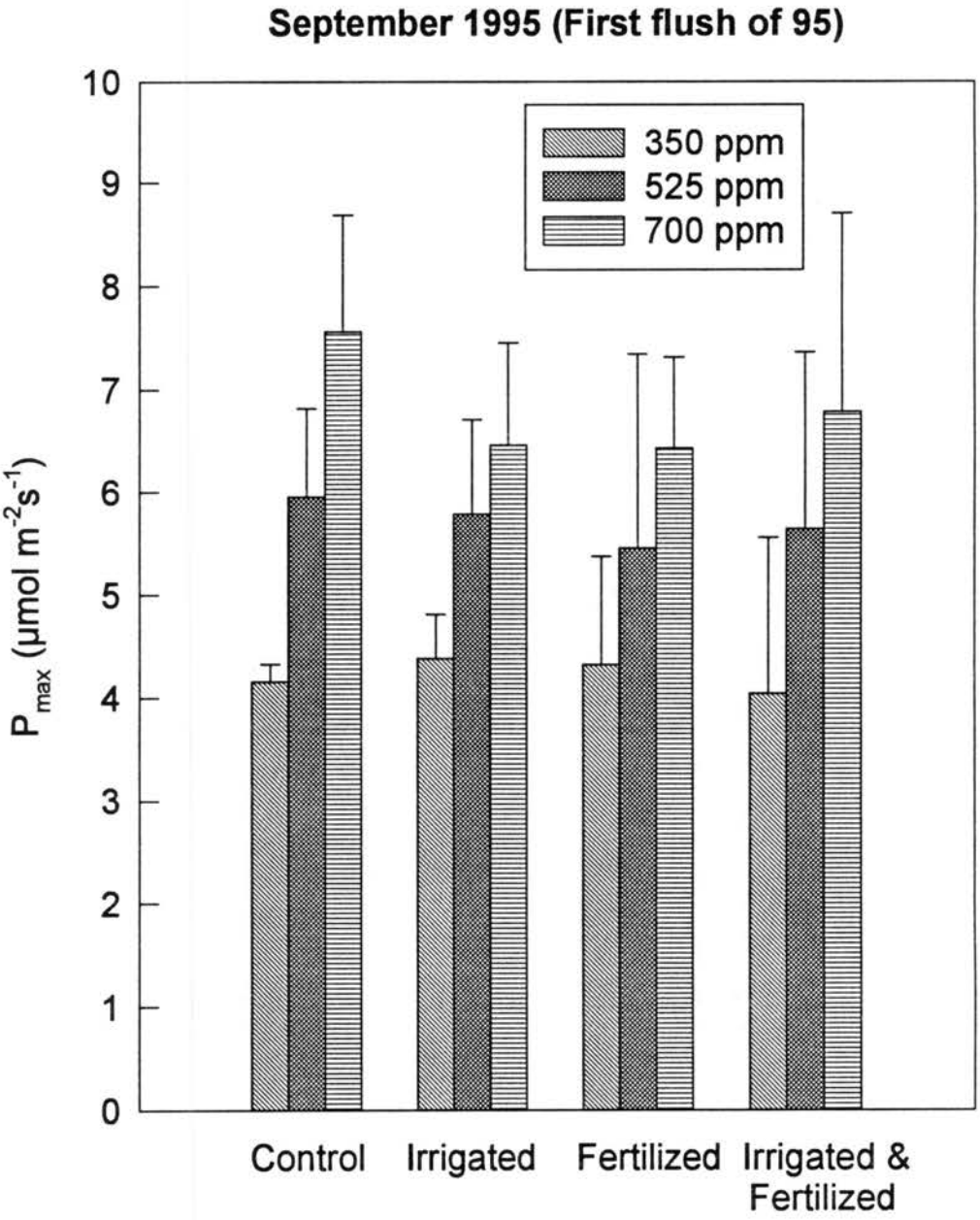

September 1995 (First flush of 95)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 41

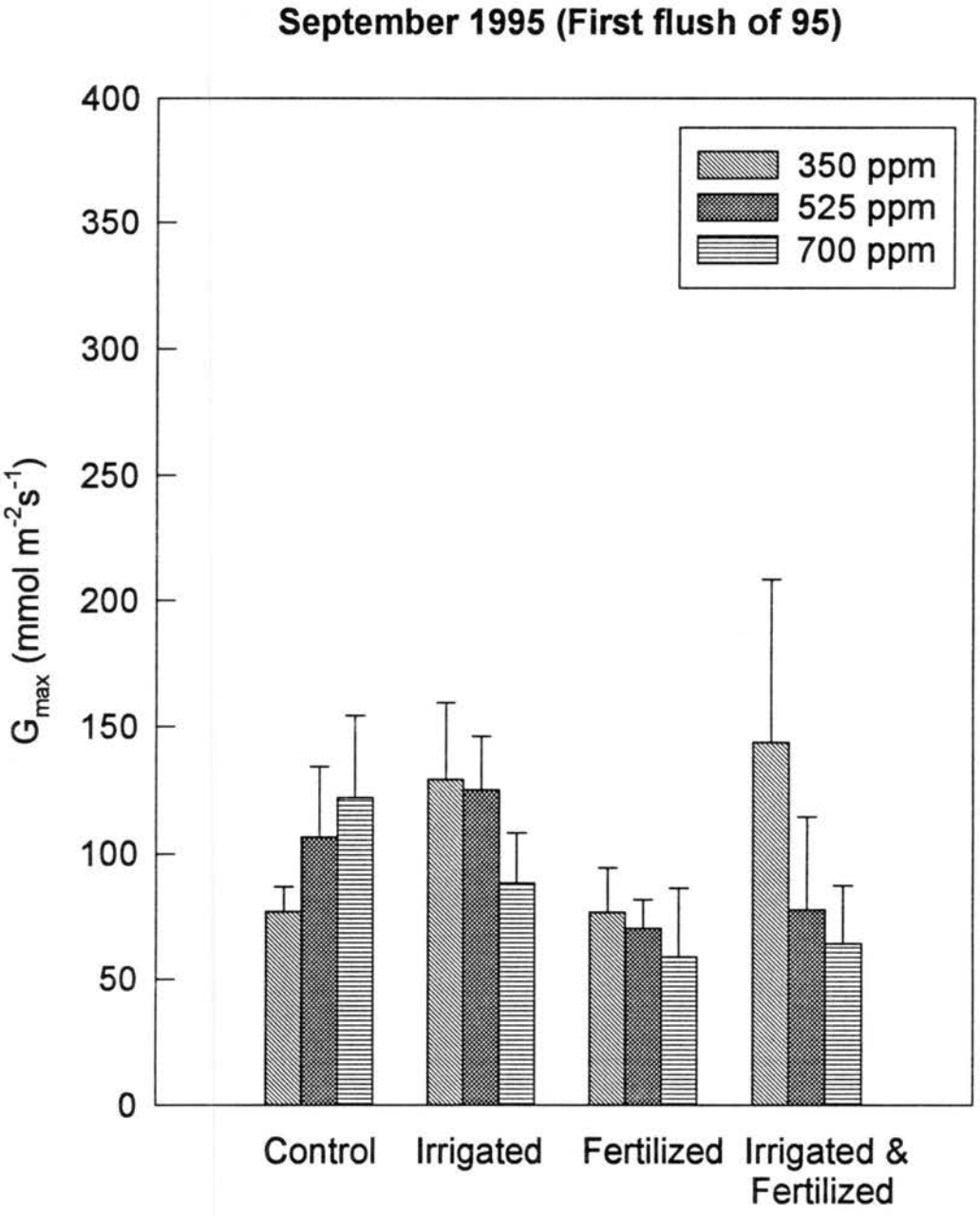

September 1995 (First flush of 95)
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 42

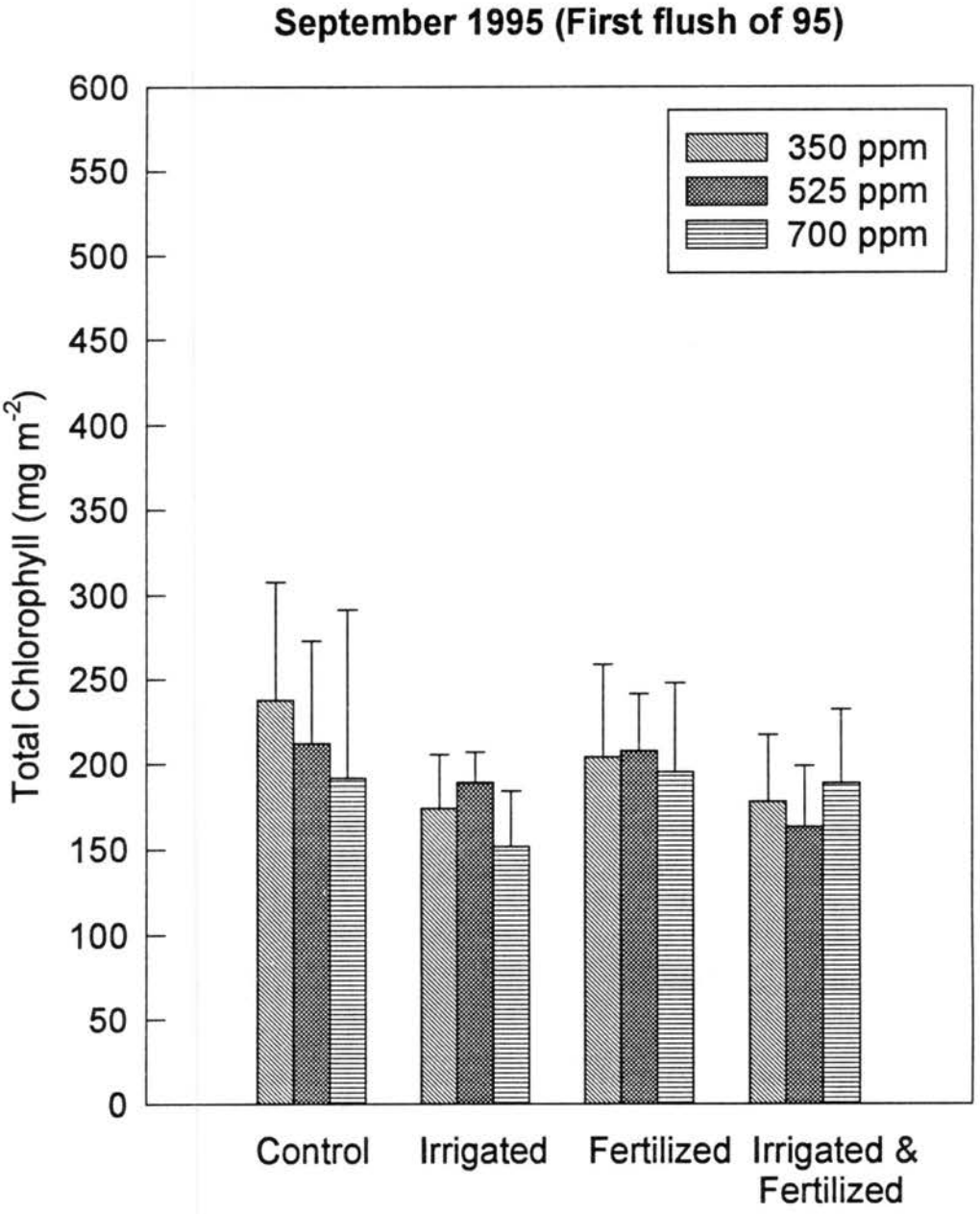

September 1995 (First flush of 95)
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 43

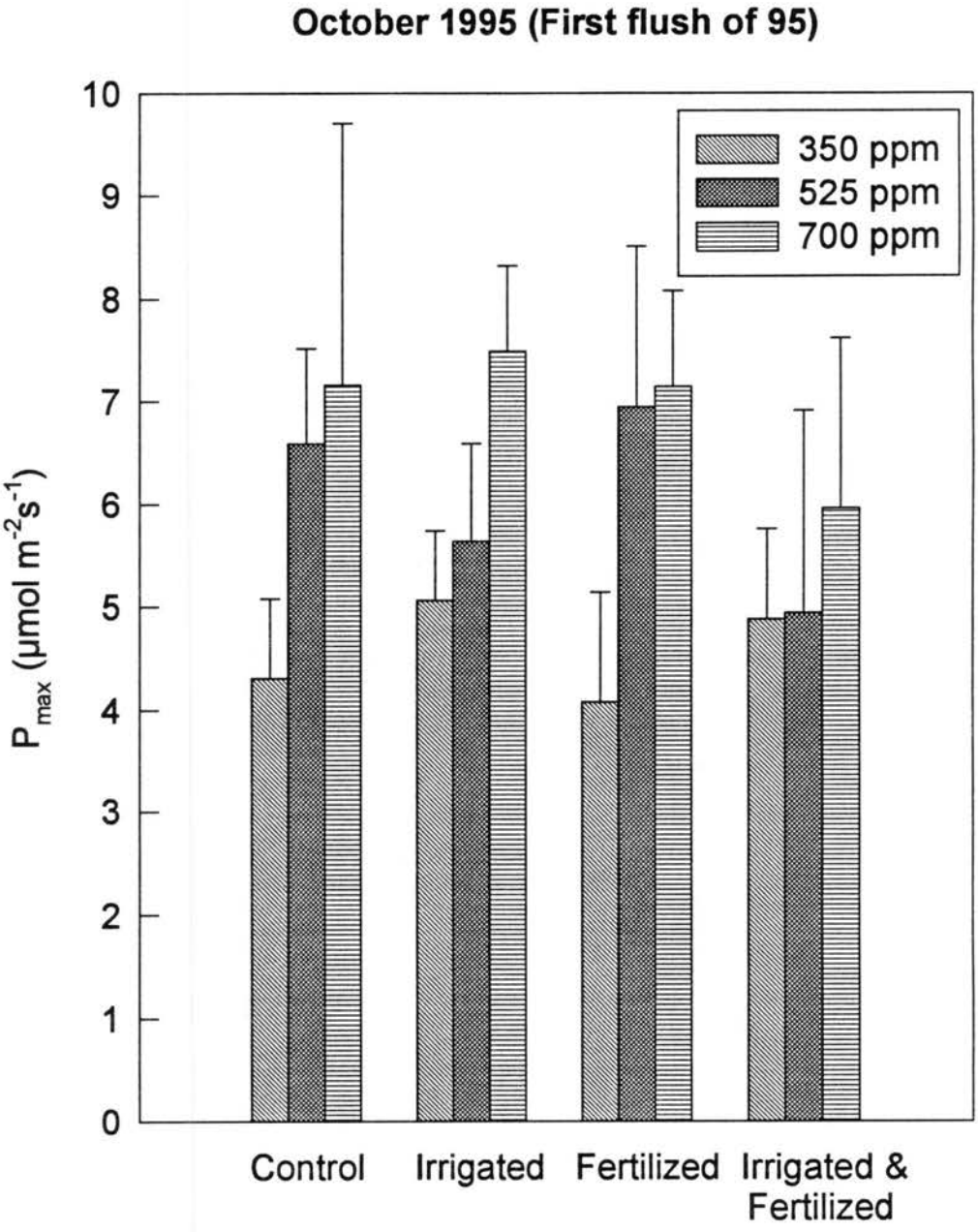

October 1995 (First flush of 95)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 44

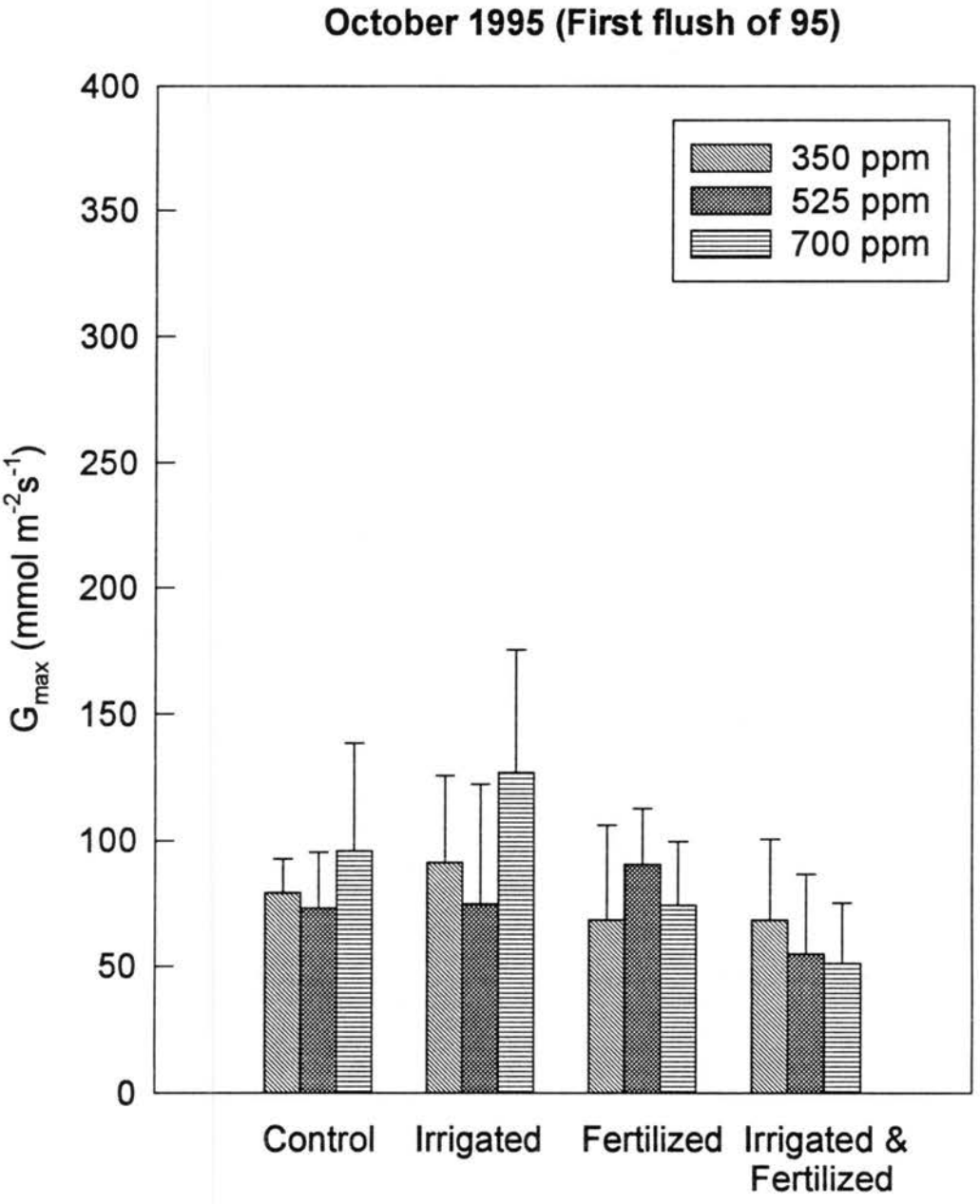

October 1995 (First flush of 95)
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 45

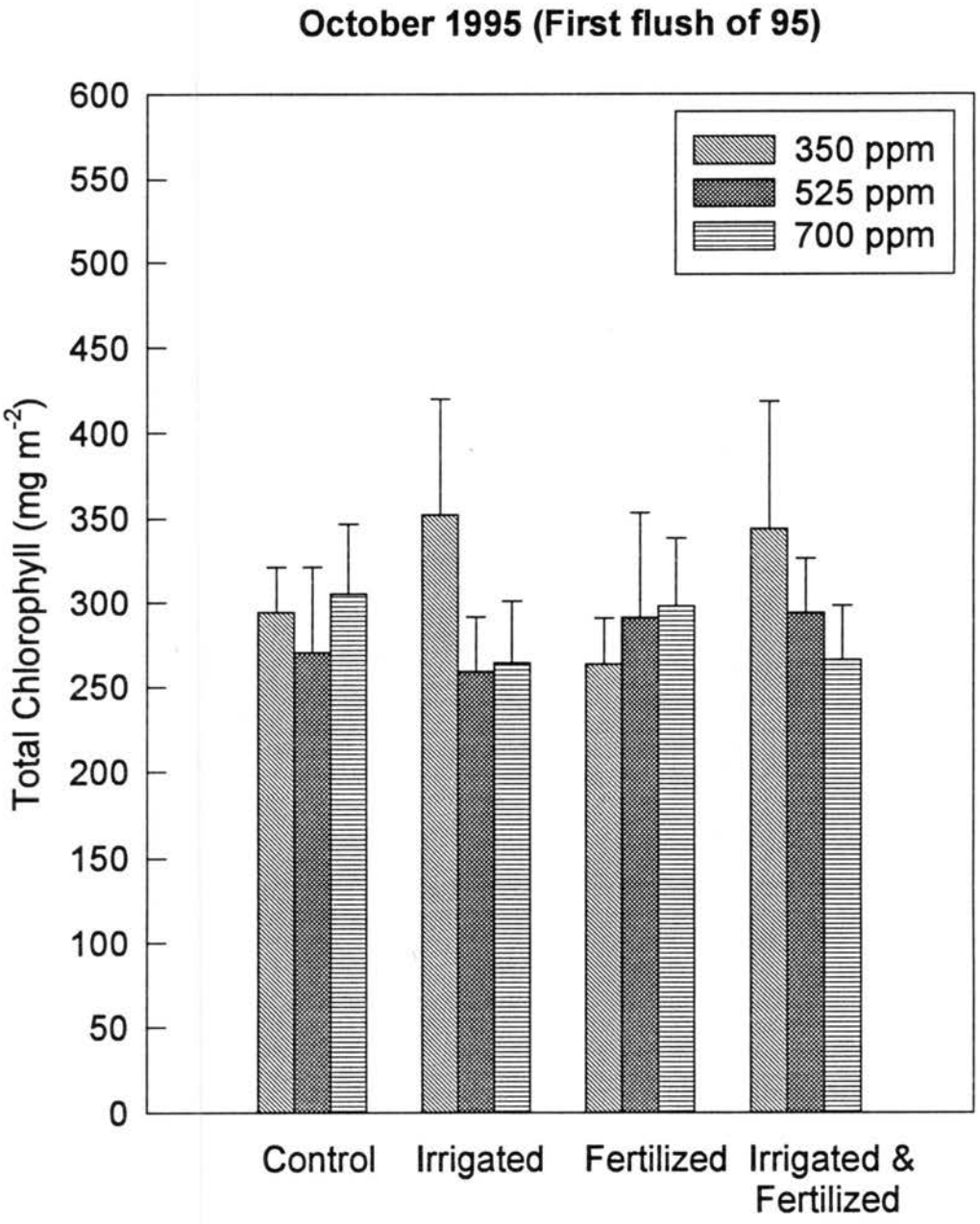

October 1995 (First flush of 95)
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 46

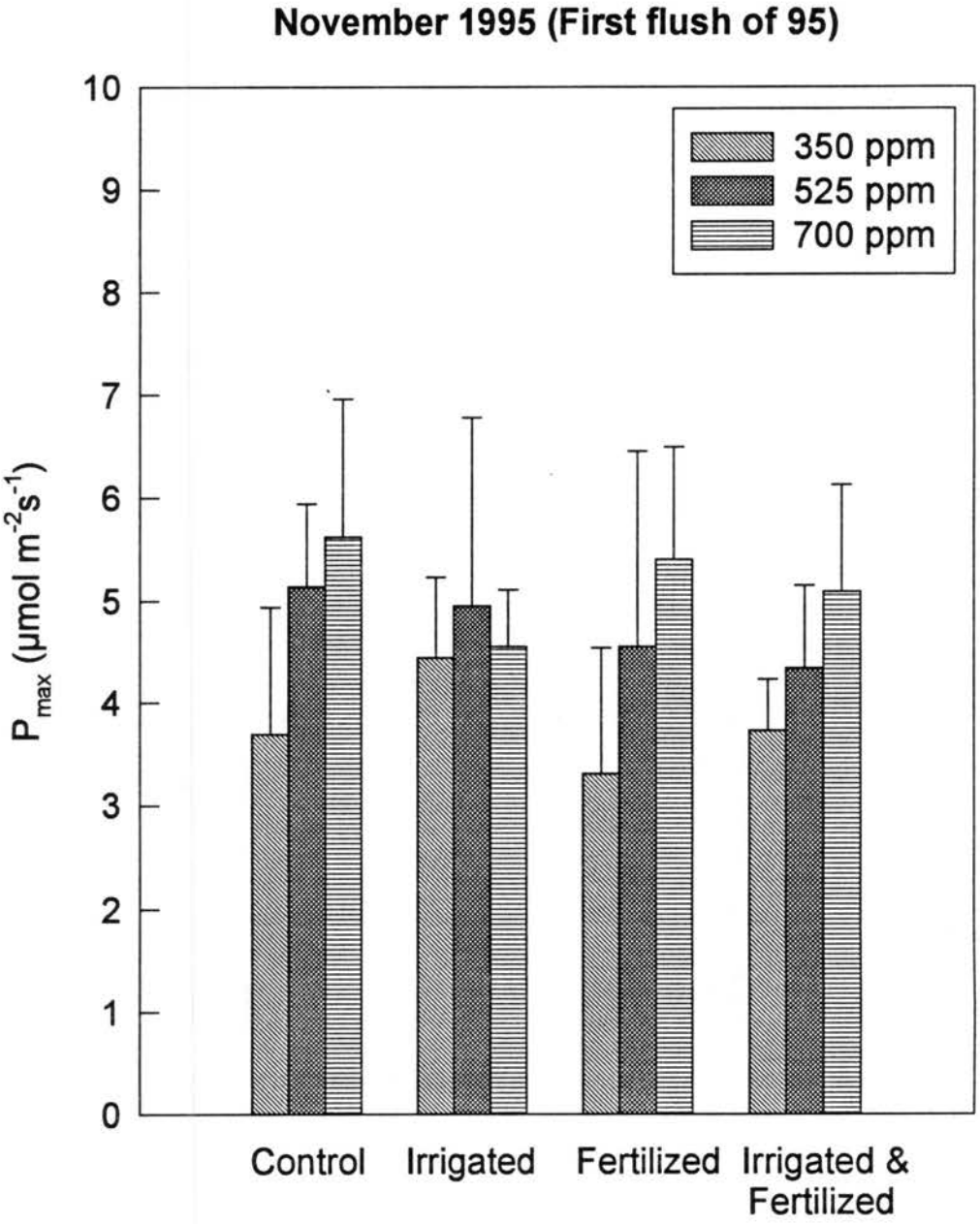

November 1995 (First flush of 95)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 47

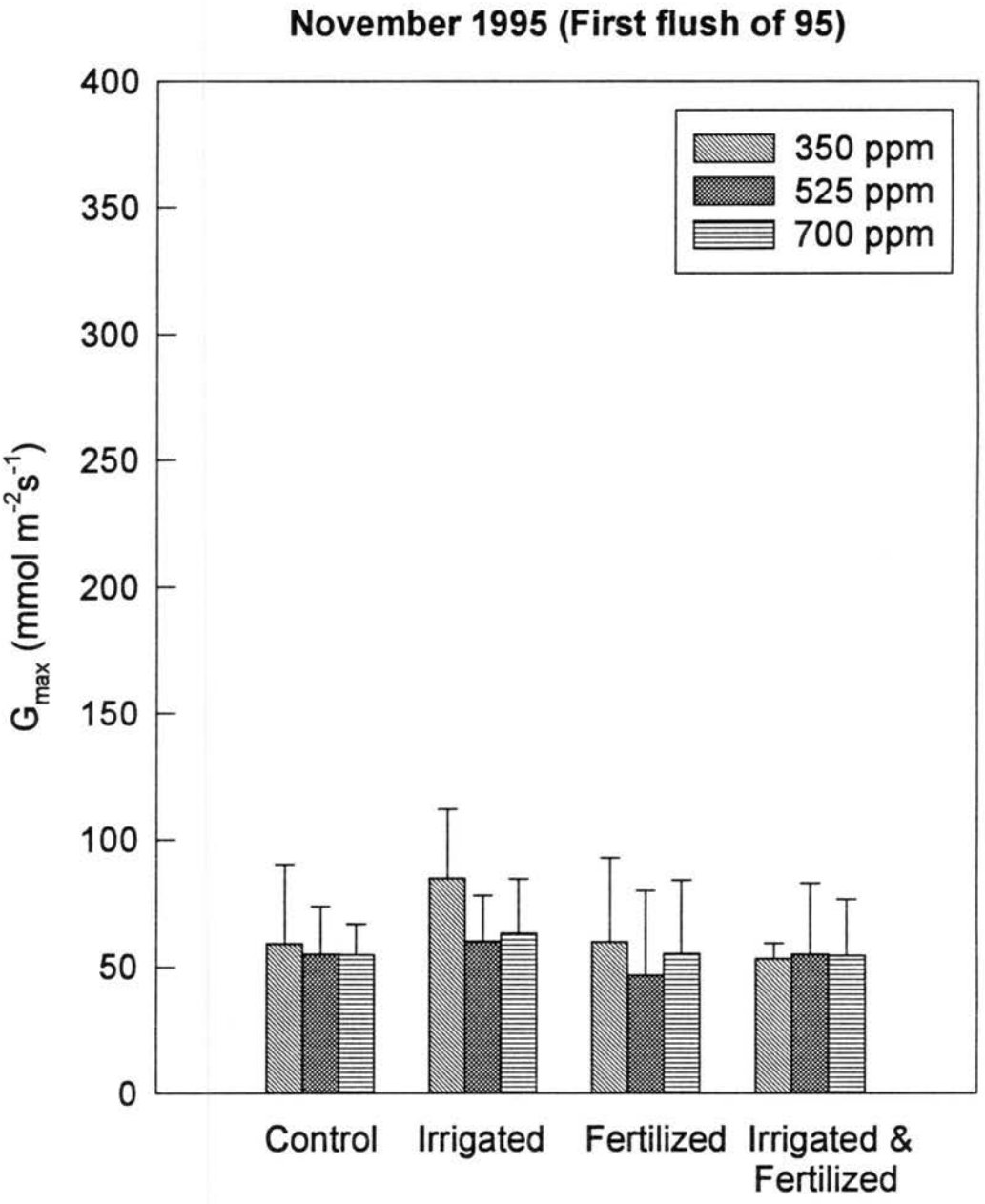

November 1995 (First flush of 95)
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 48

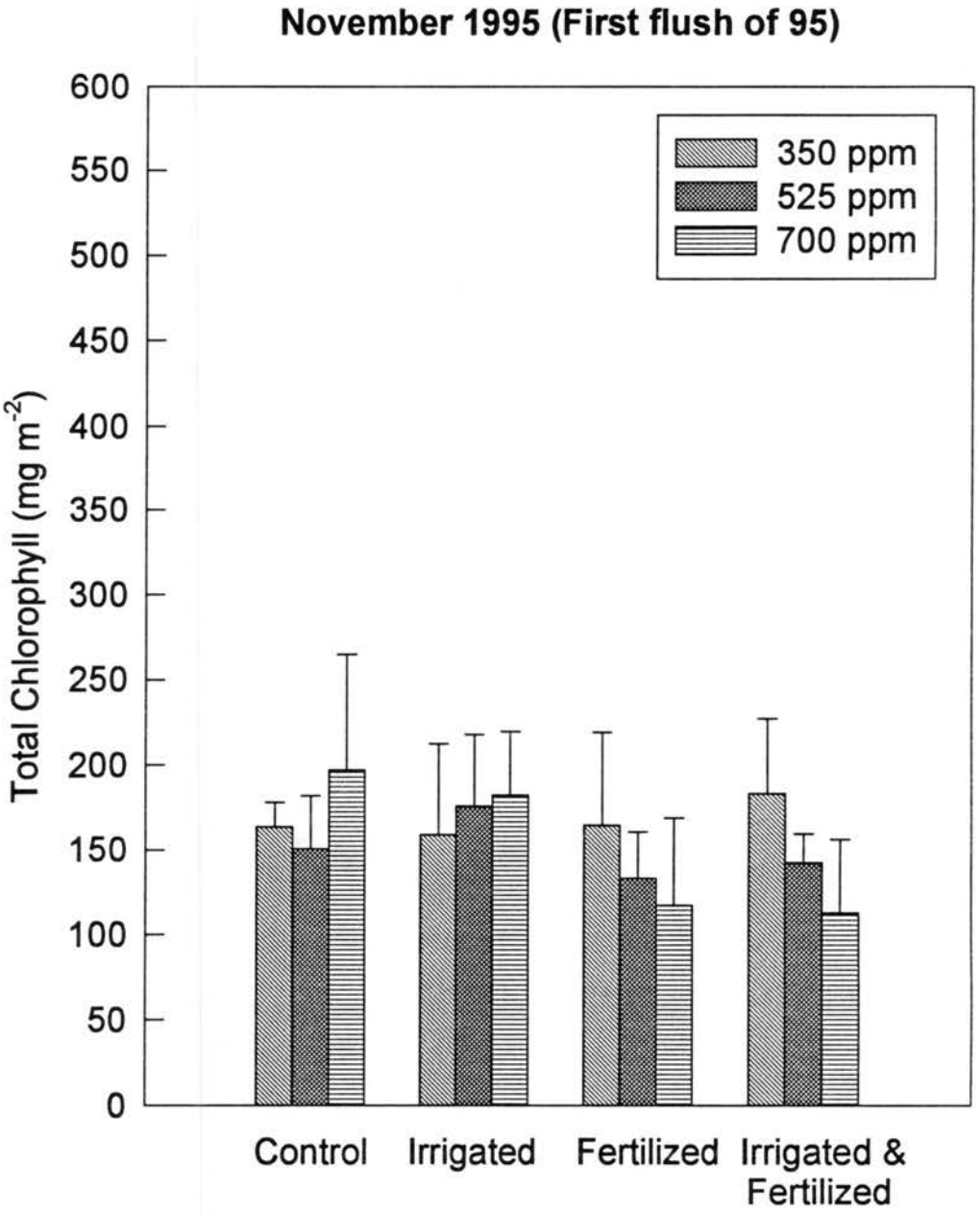

November 1995 (First flush of 95)
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 49

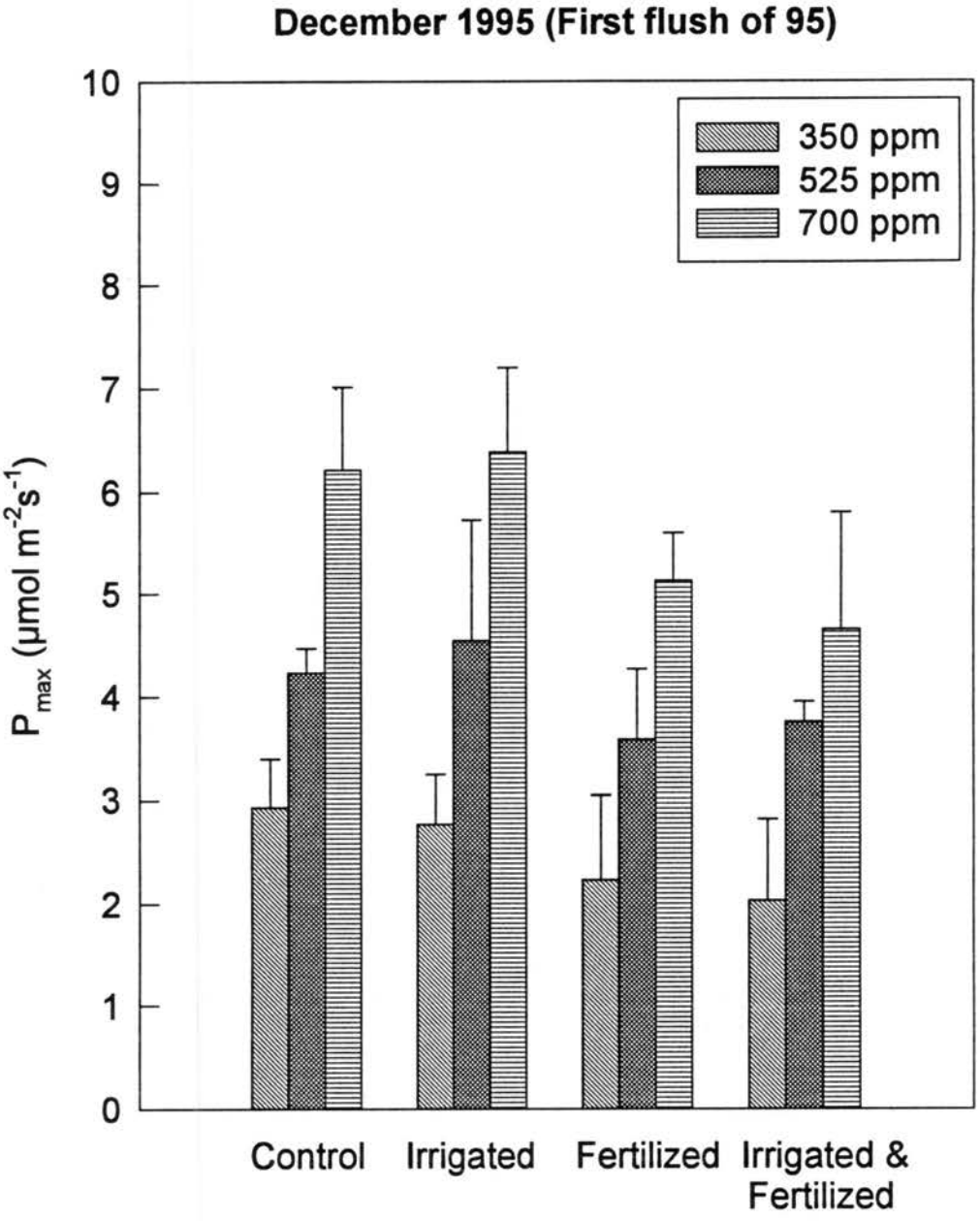

December 1995 (First flush of 95)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 50

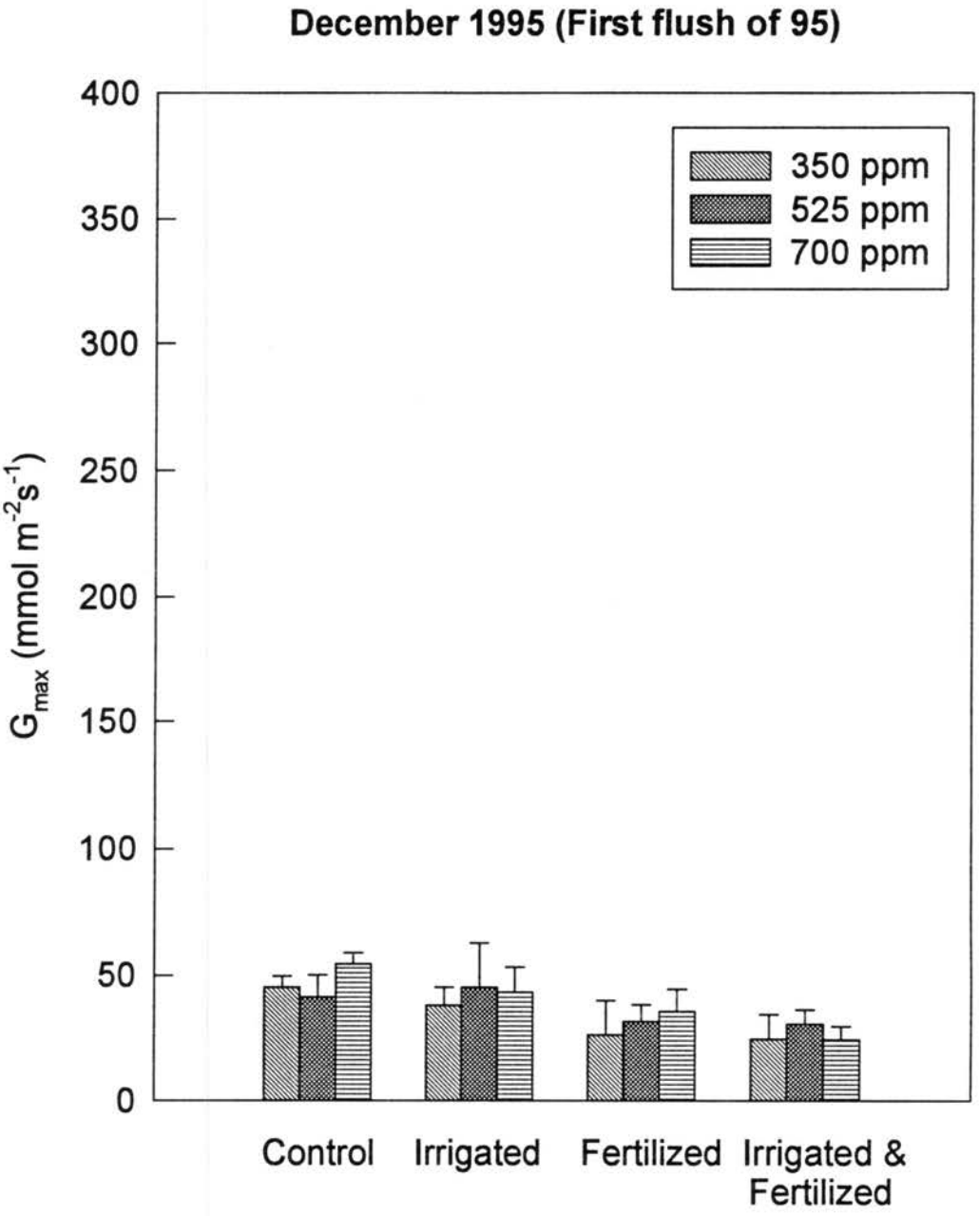

December 1995 (First flush of 95)
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 51

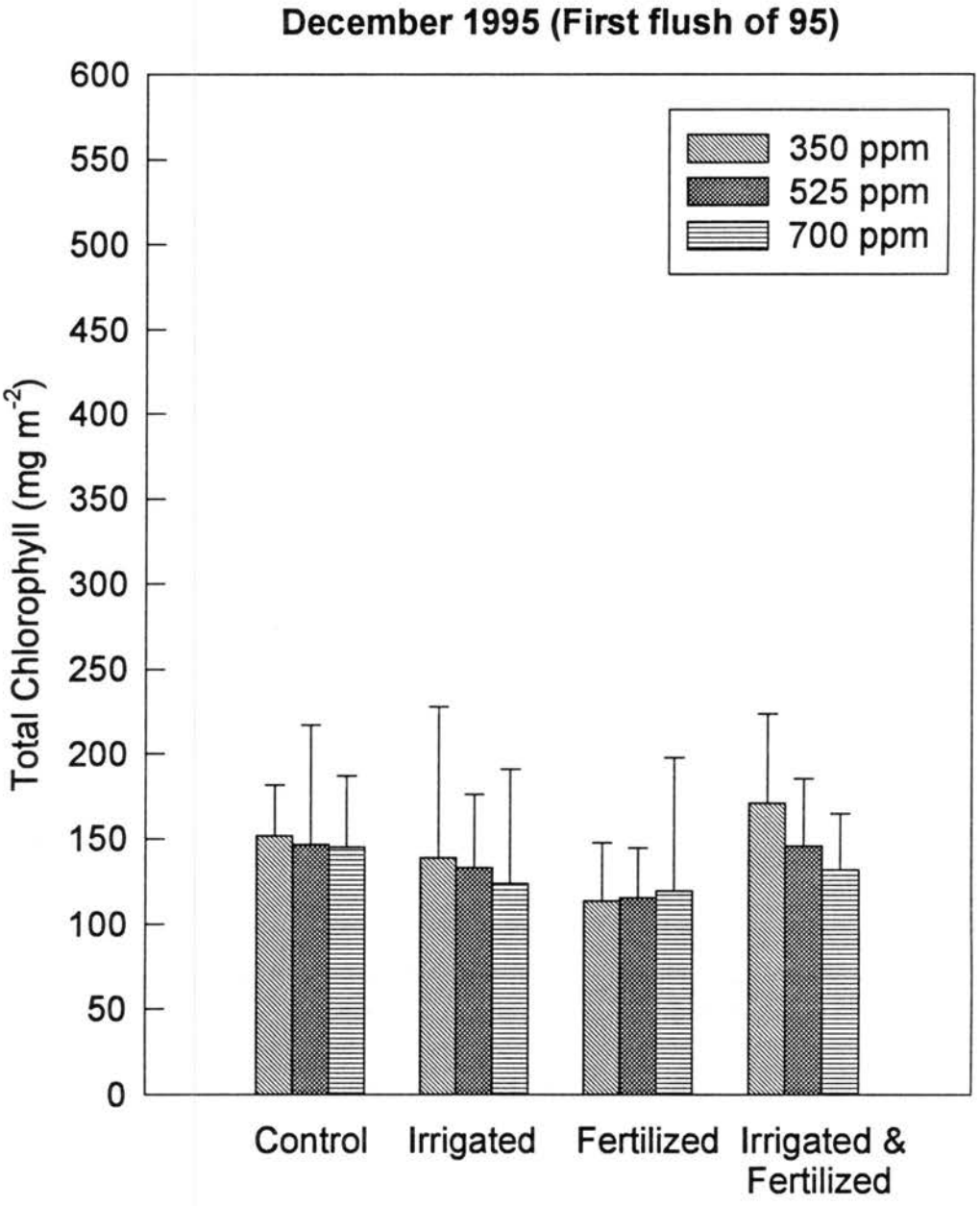

December 1995 (First flush of 95)
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 52

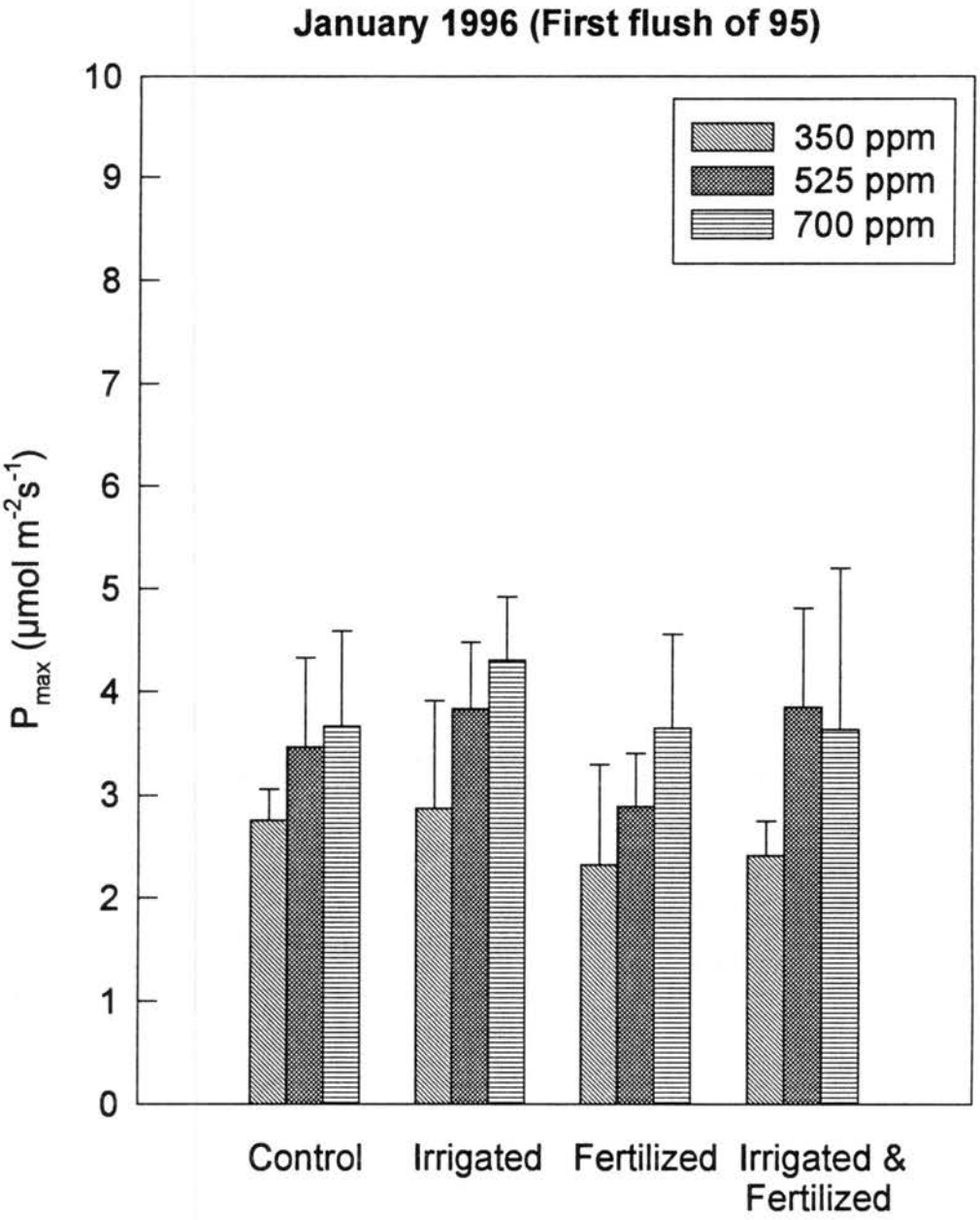

January 1996 (First flush of 95)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 53

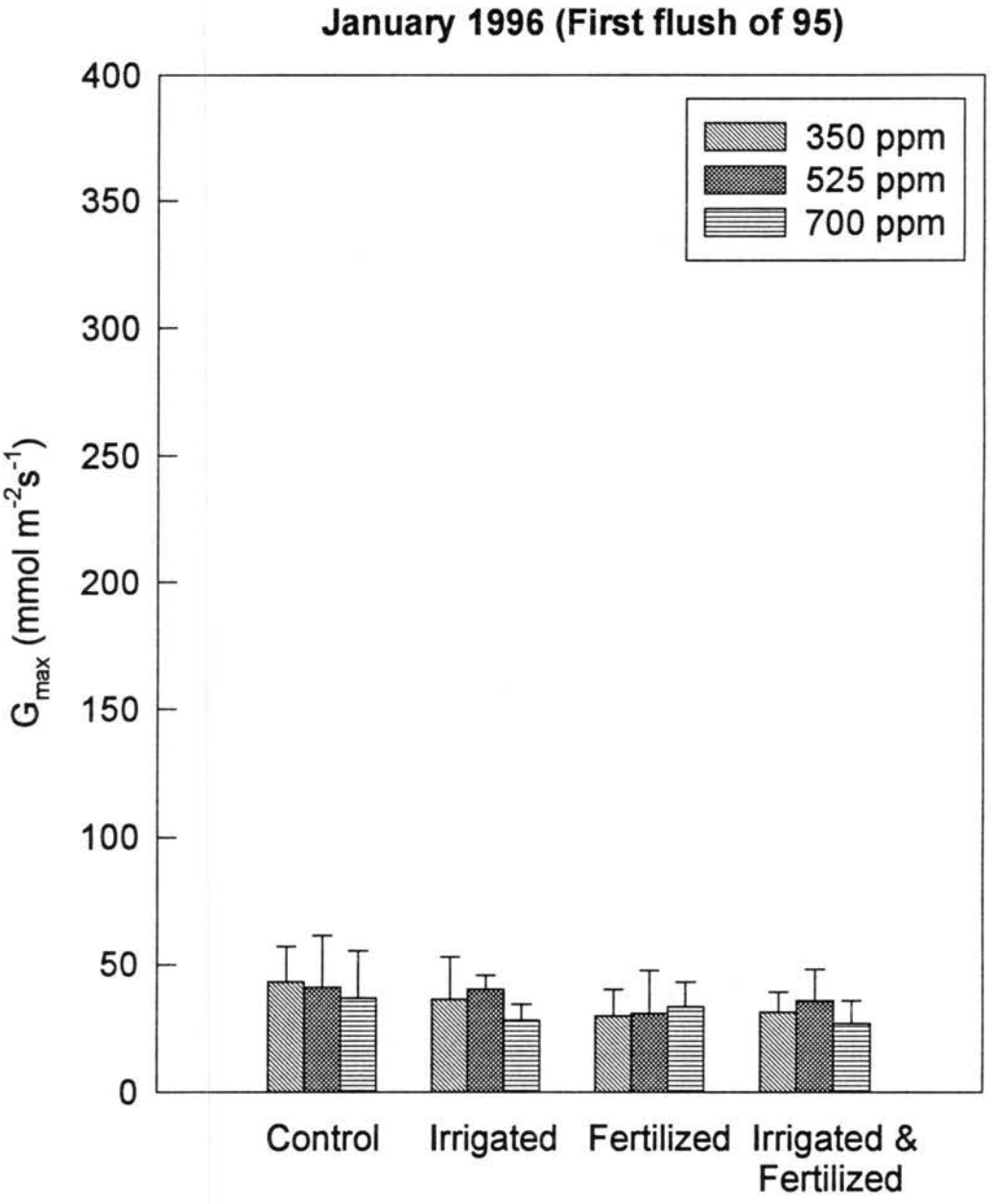

January 1996 (First flush of 95)
350 ppm
525 ppm
700 ppm
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 54

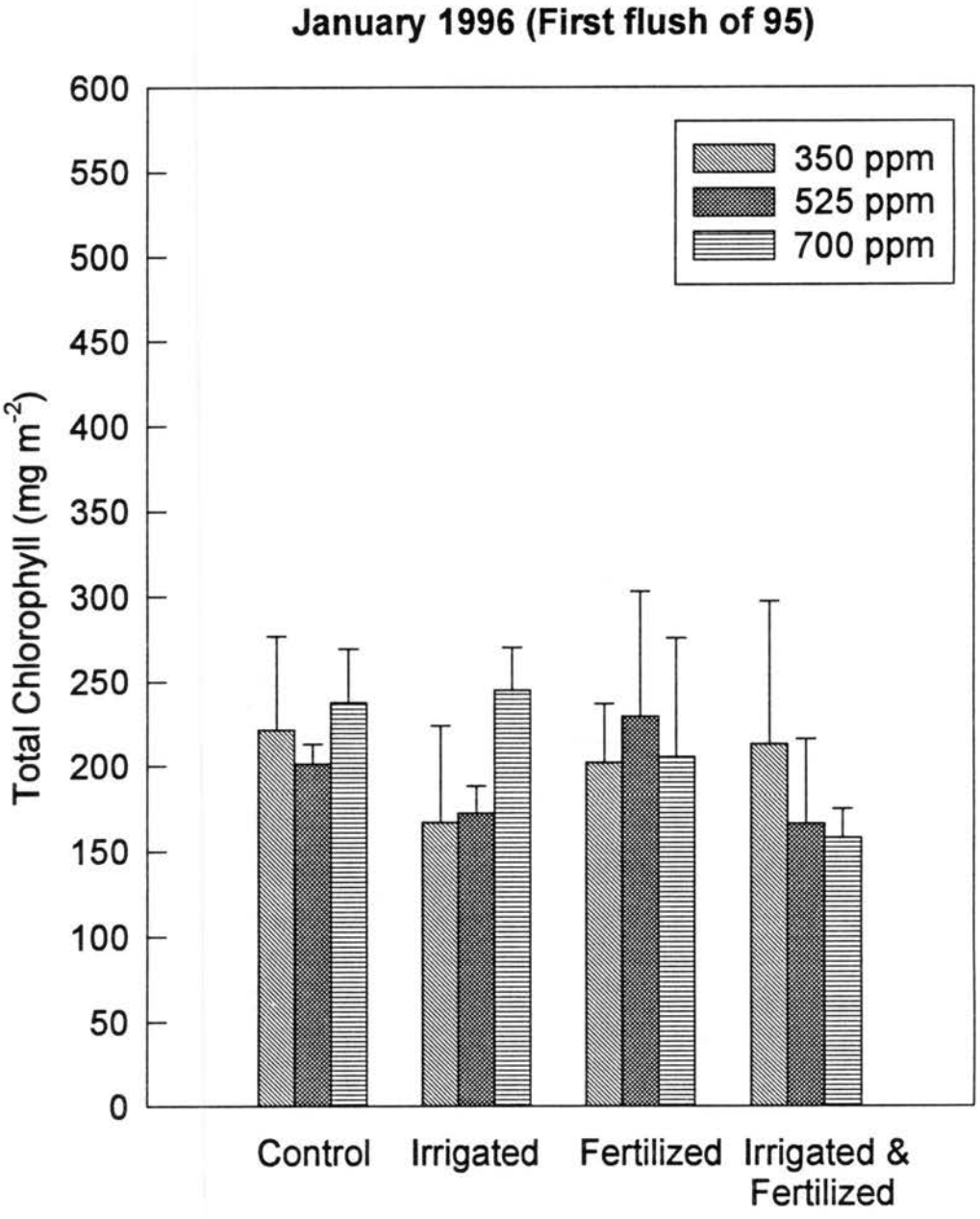

January 1996 (First flush of 95)
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 55

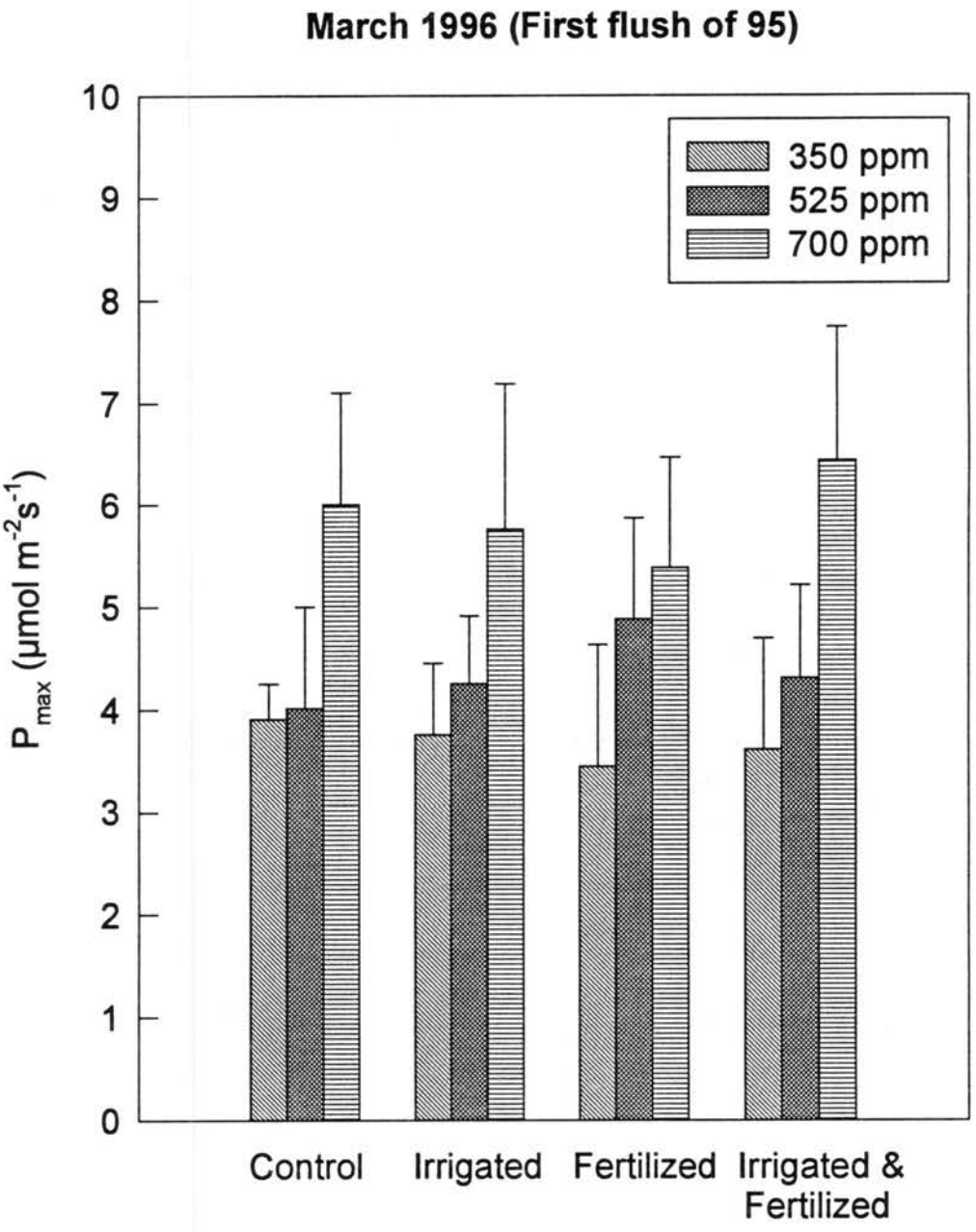

March 1996 (First flush of 95)
350 ppm
525 ppm
700 ppm
P_{max} (µmol $m^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 56

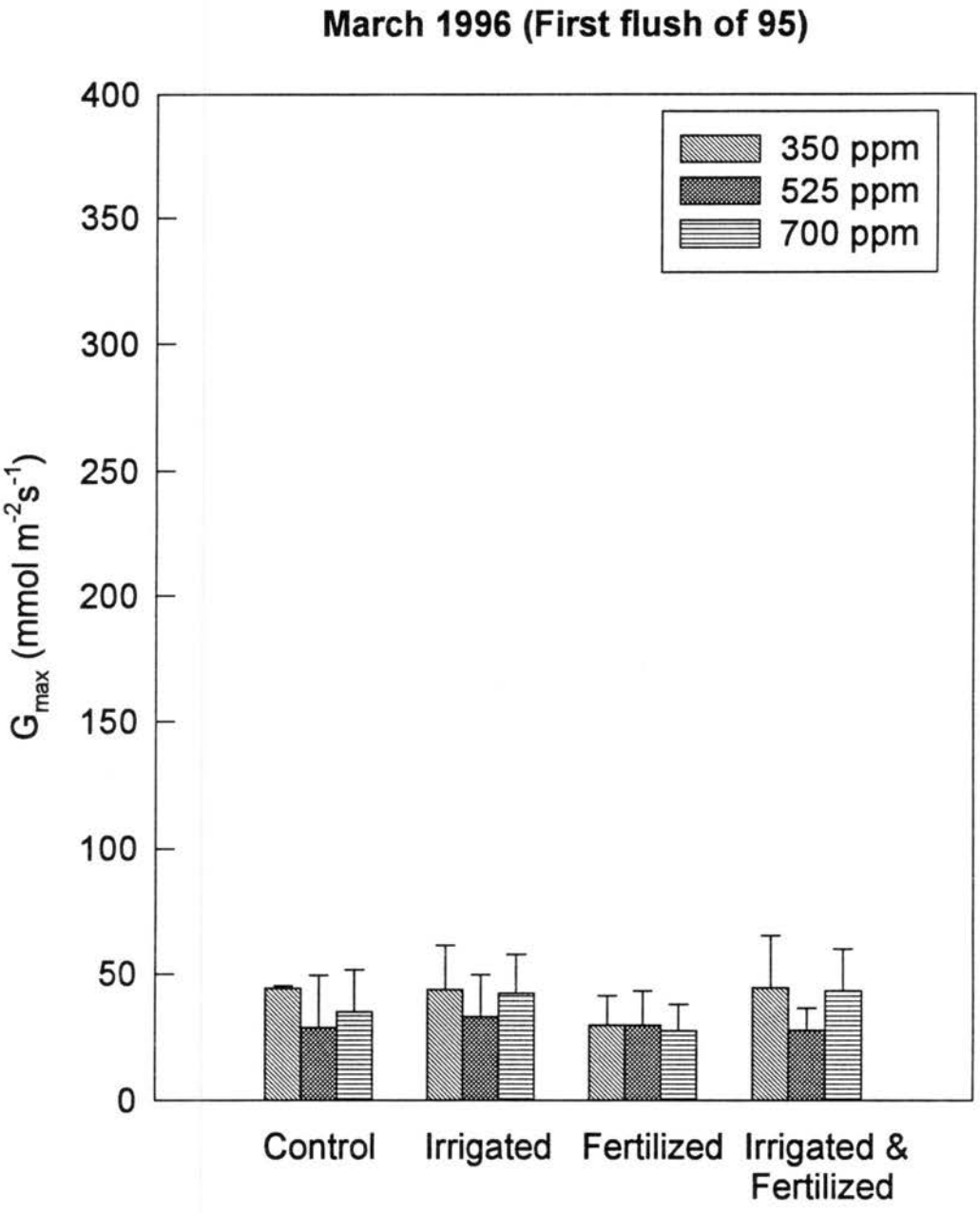

March 1996 (First flush of 95)
400
350
300
250
200
150
100
50
0
G_{max} (mmol $m^{-2}s^{-1}$)
350 ppm
525 ppm
700 ppm
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 57

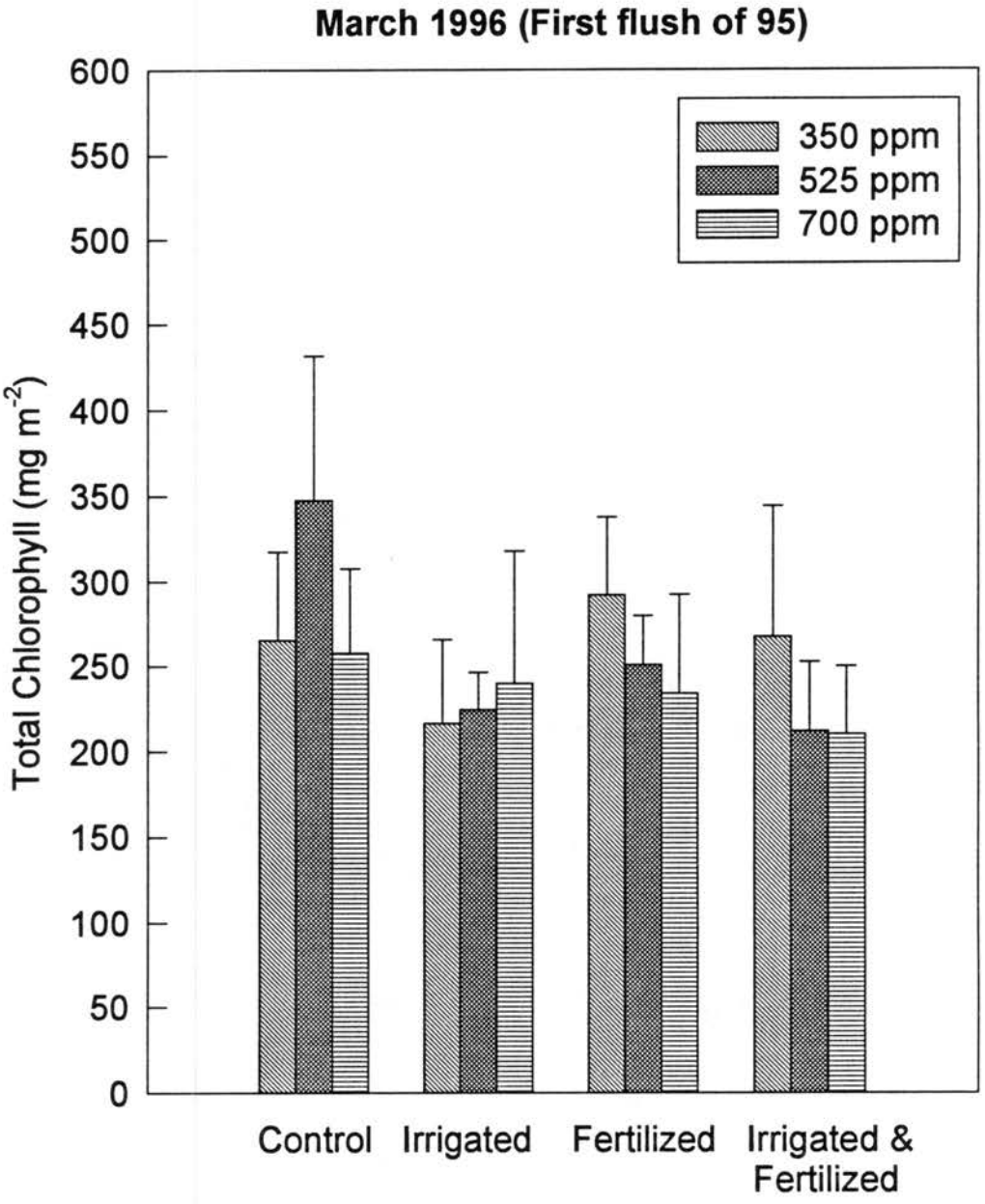

March 1996 (First flush of 95)
350 ppm
525 ppm
700 ppm
Total Chlorophyll (mg m-2)
600
550
500
450
400
350
300
250
200
150
100
50
0
Control
Irrigated
Fertilized
Irrigated & Fertilized

Figure 58

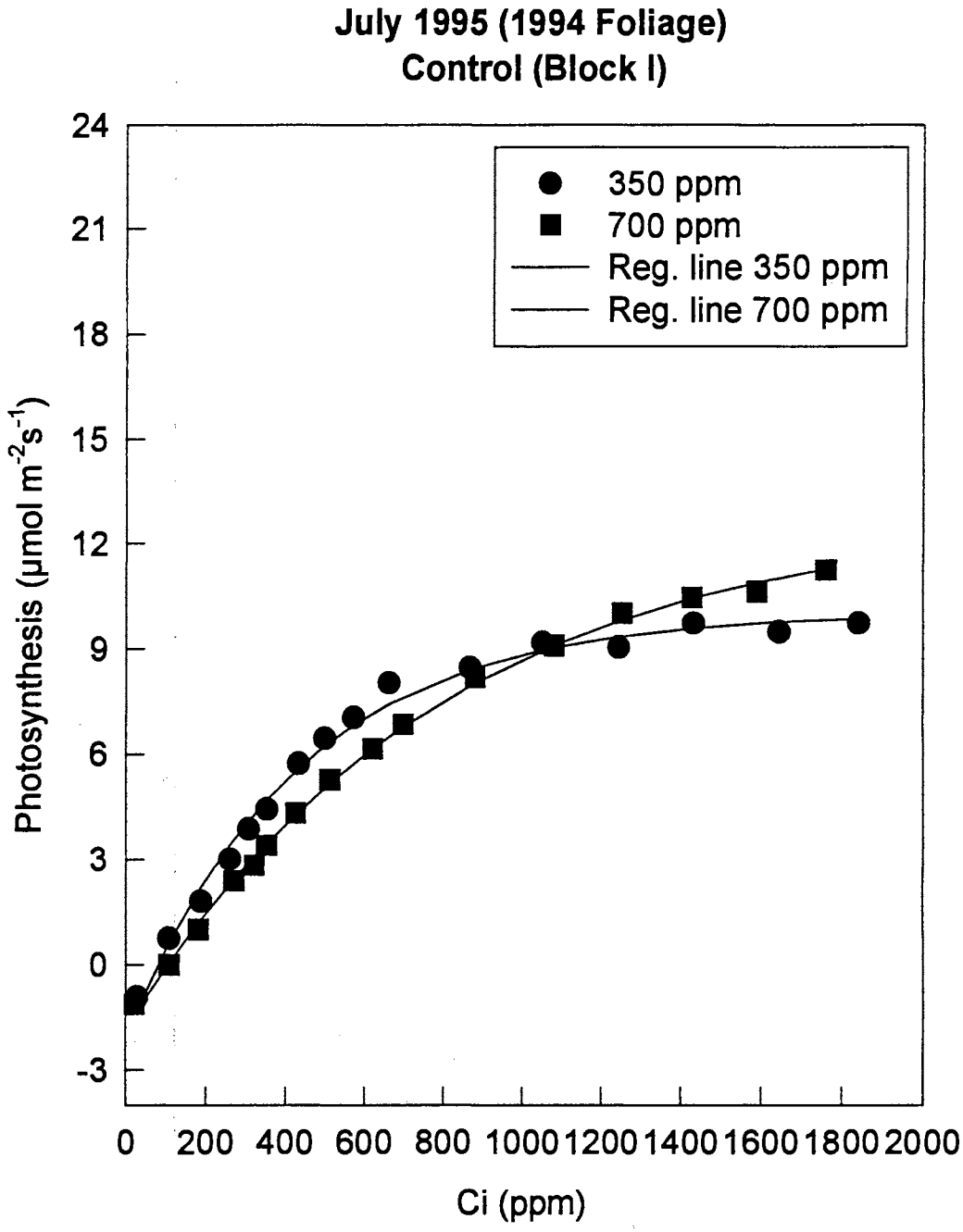

July 1995 (1994 Foliage)
Control (Block I)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 59

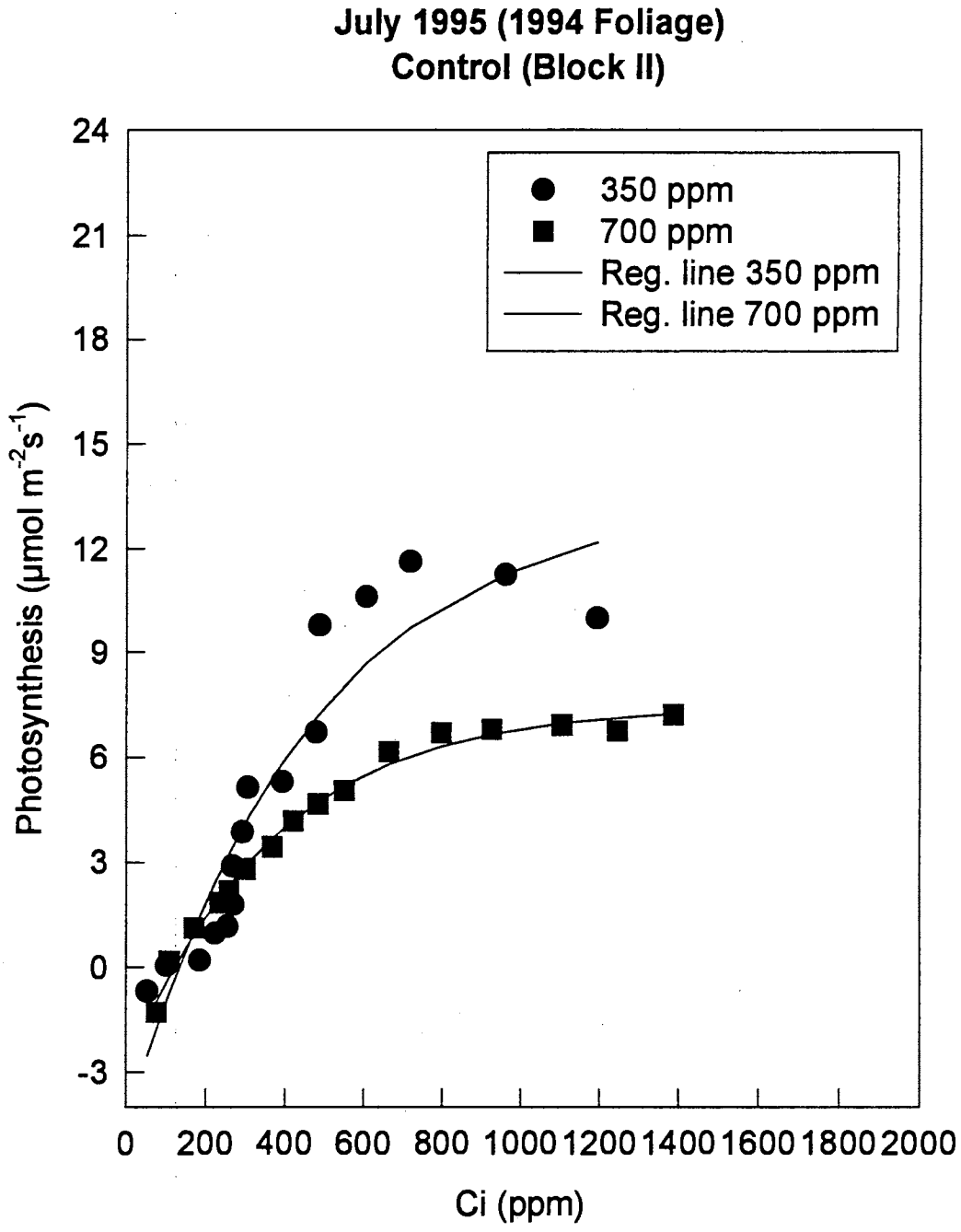

July 1995 (1994 Foliage)
Control (Block II)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 60

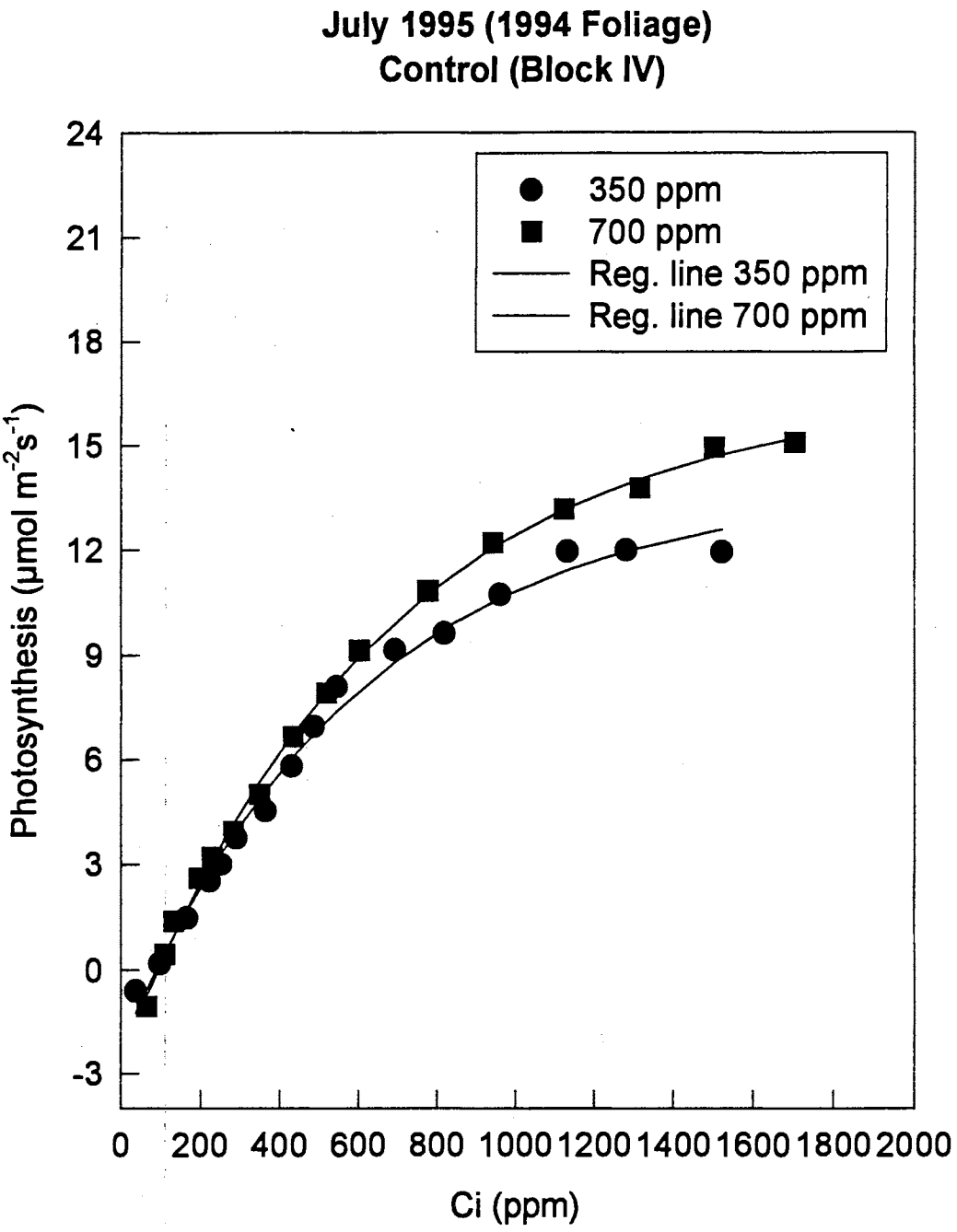

July 1995 (1994 Foliage)
Control (Block IV)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 61

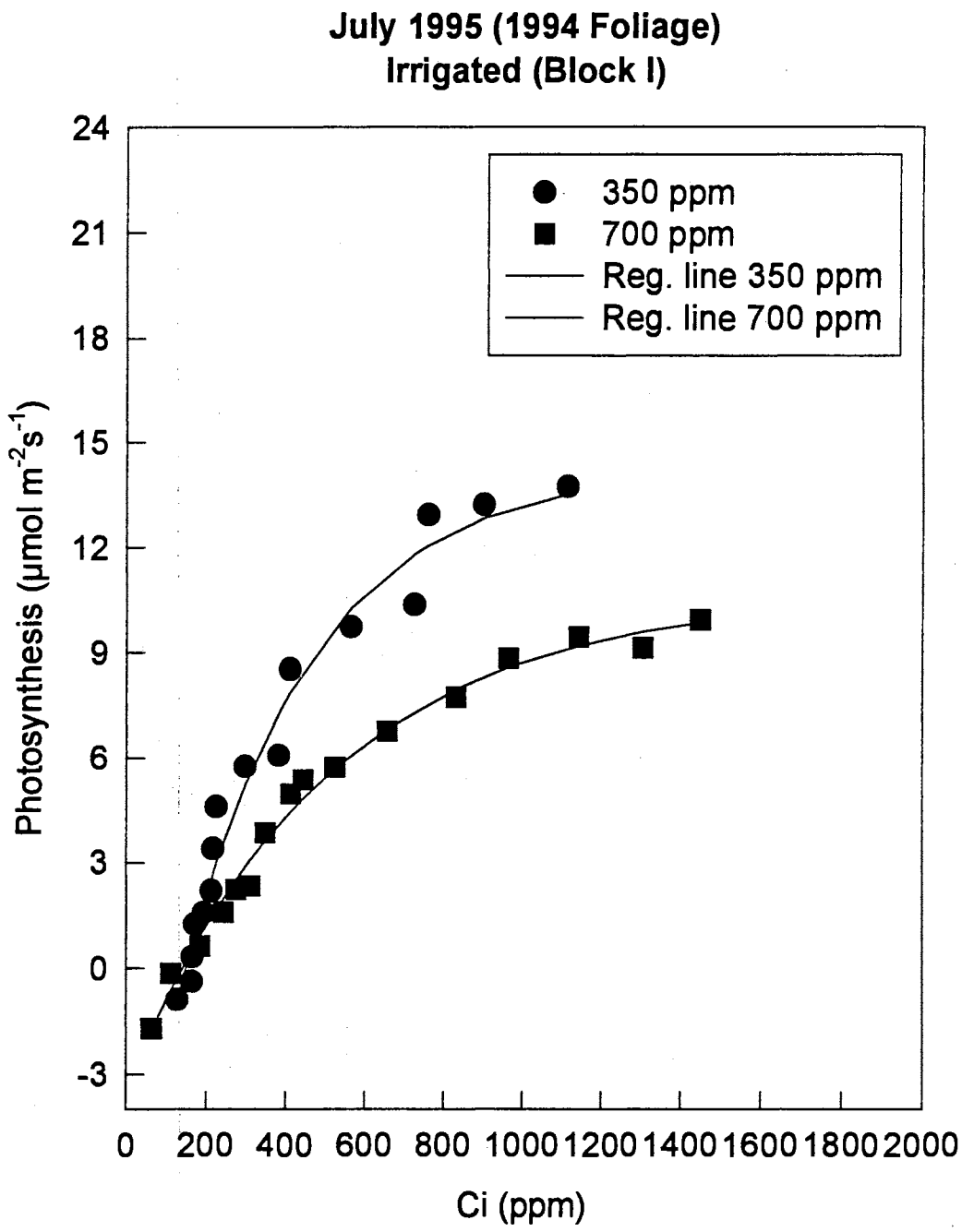

July 1995 (1994 Foliage)
Irrigated (Block I)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 62

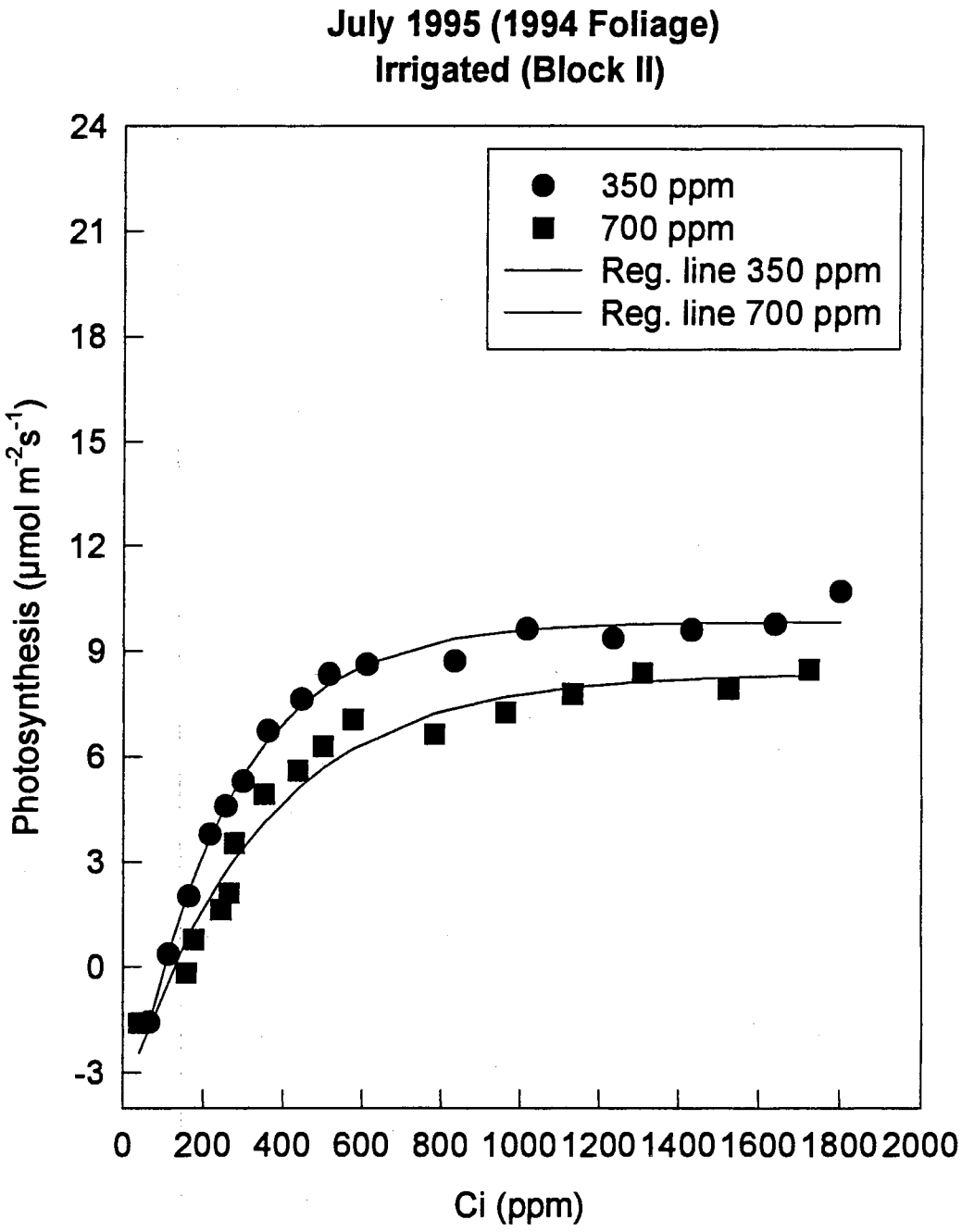

July 1995 (1994 Foliage)
Irrigated (Block II)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 63

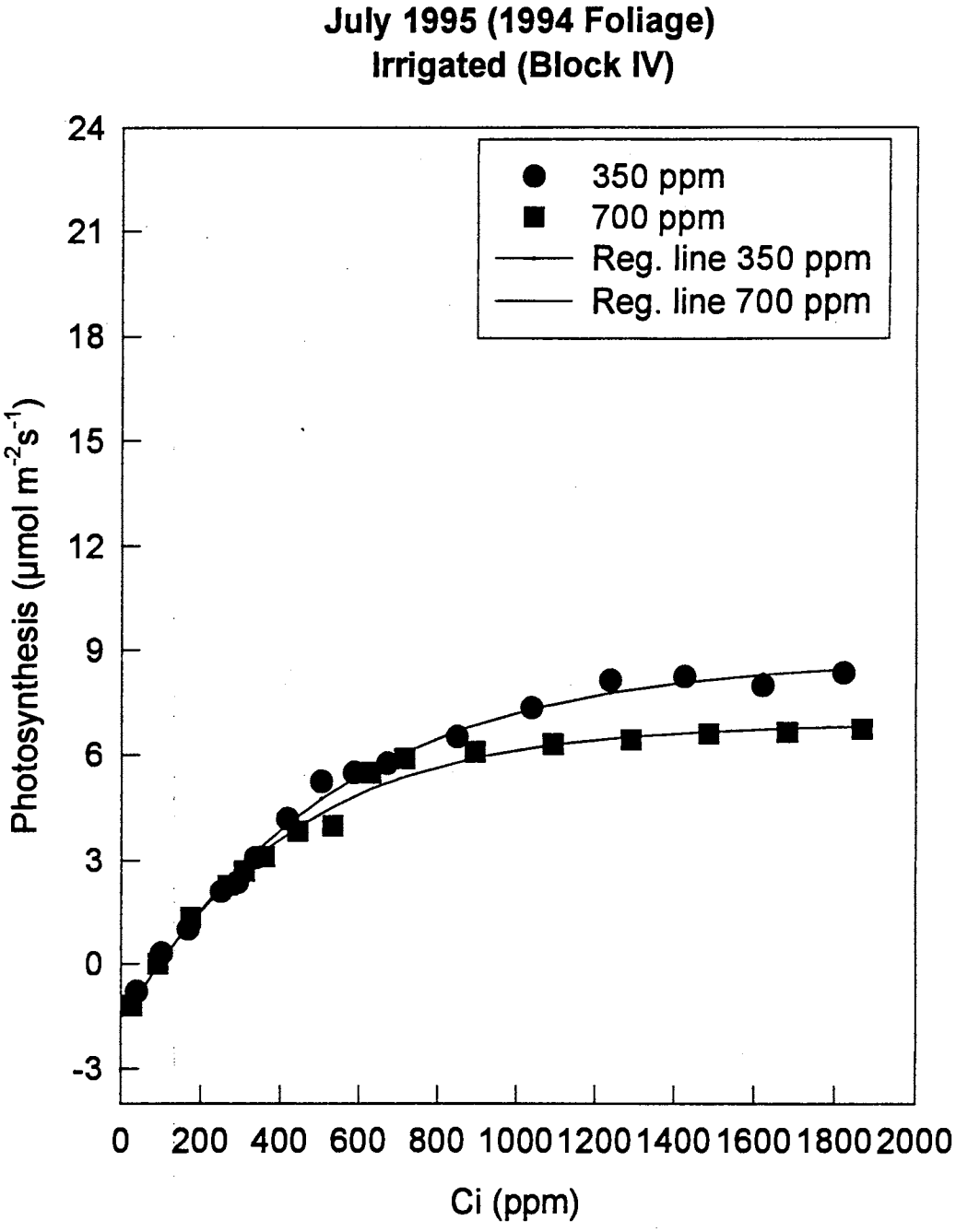

July 1995 (1994 Foliage)
Irrigated (Block IV)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 64

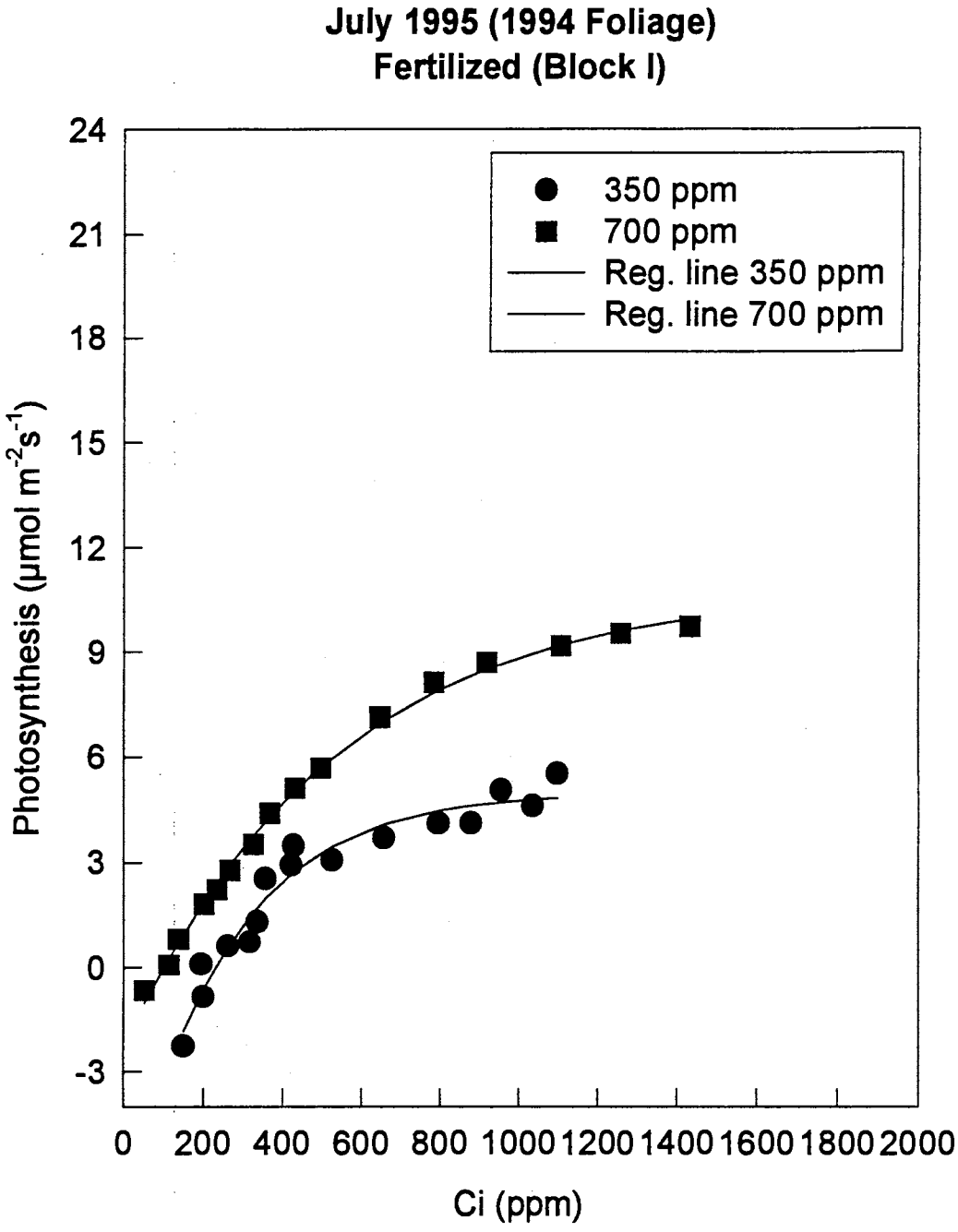

July 1995 (1994 Foliage)
Fertilized (Block I)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 65

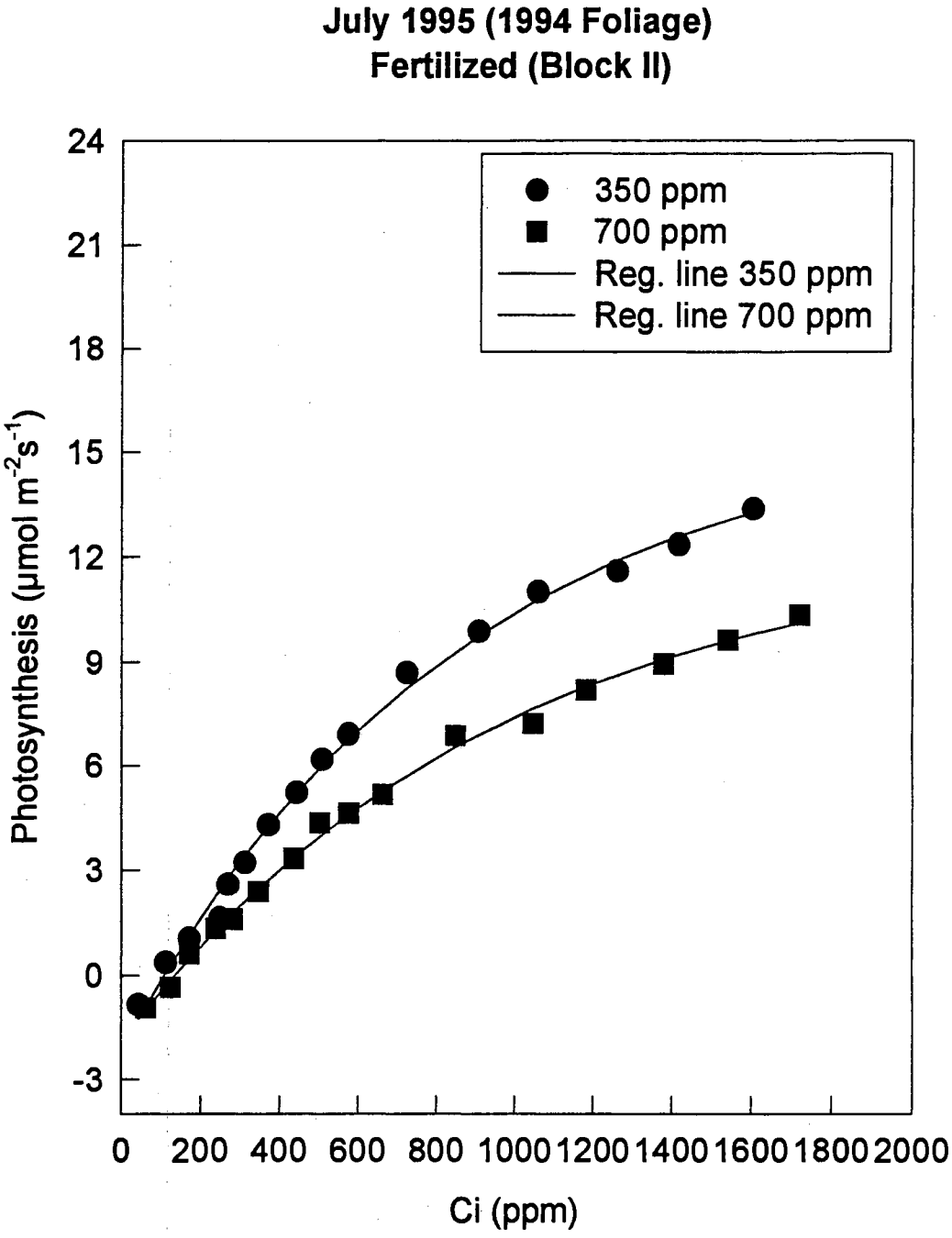

July 1995 (1994 Foliage)
Fertilized (Block II)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 66

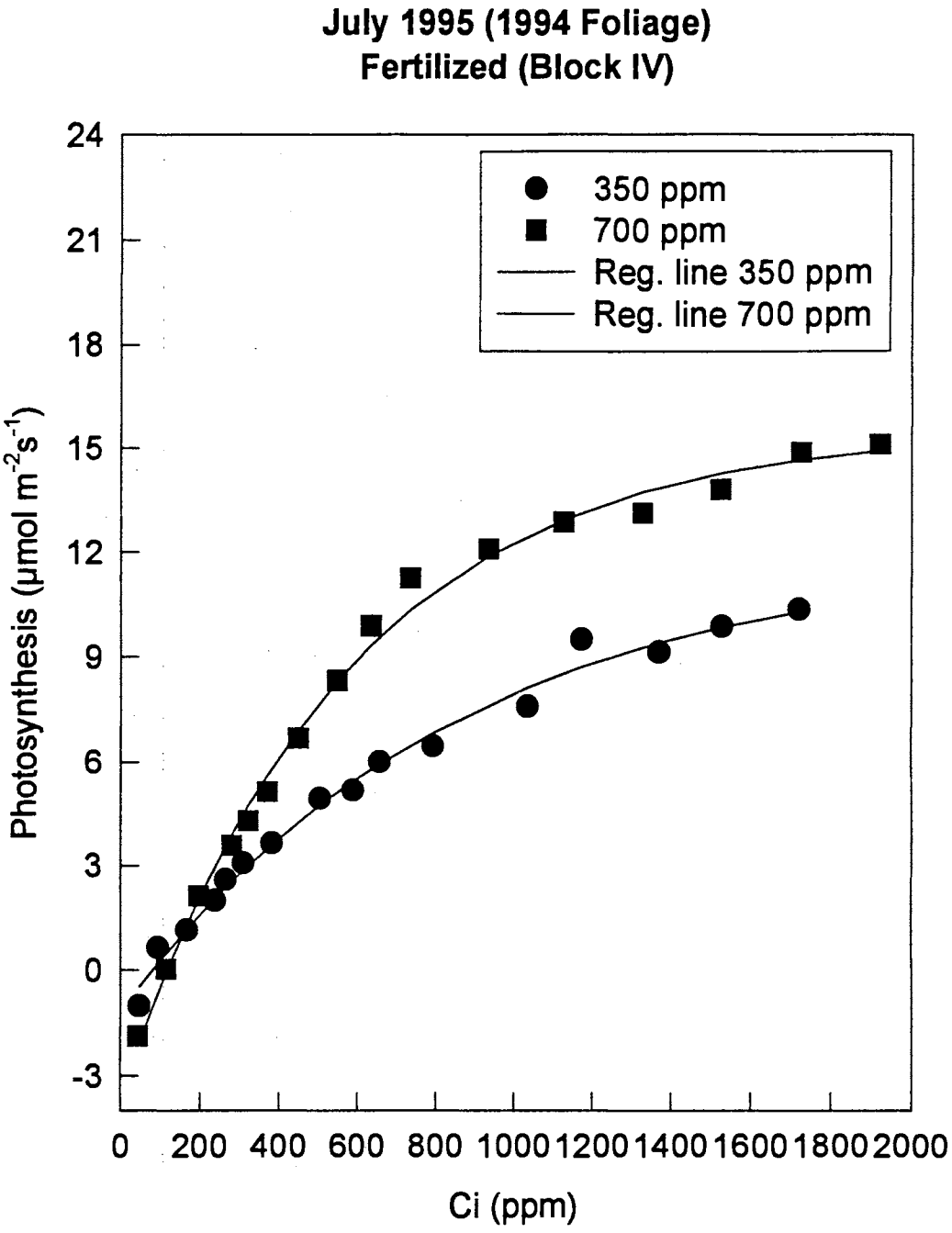

July 1995 (1994 Foliage)
Fertilized (Block IV)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 67

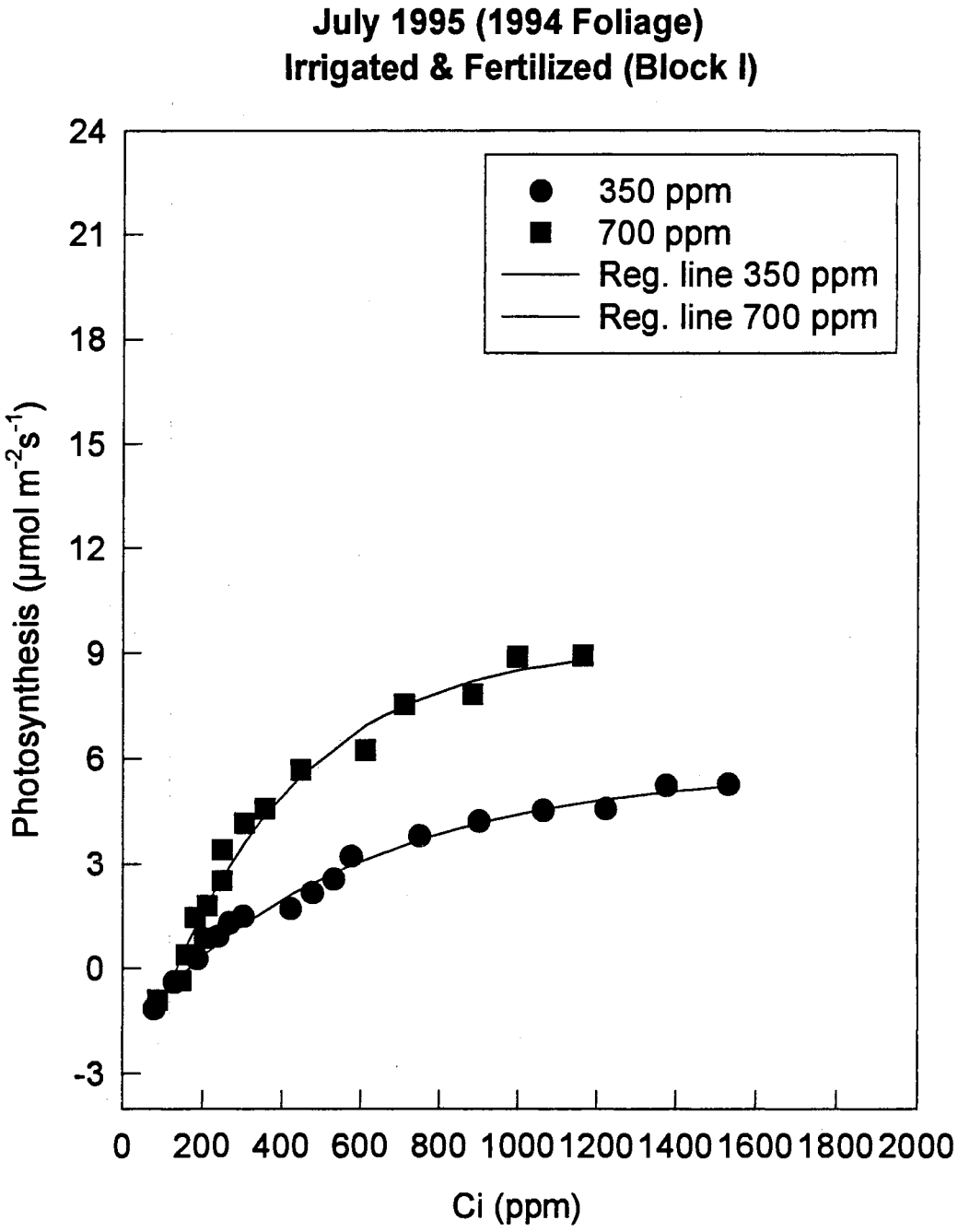

July 1995 (1994 Foliage)
Irrigated & Fertilized (Block I)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 68

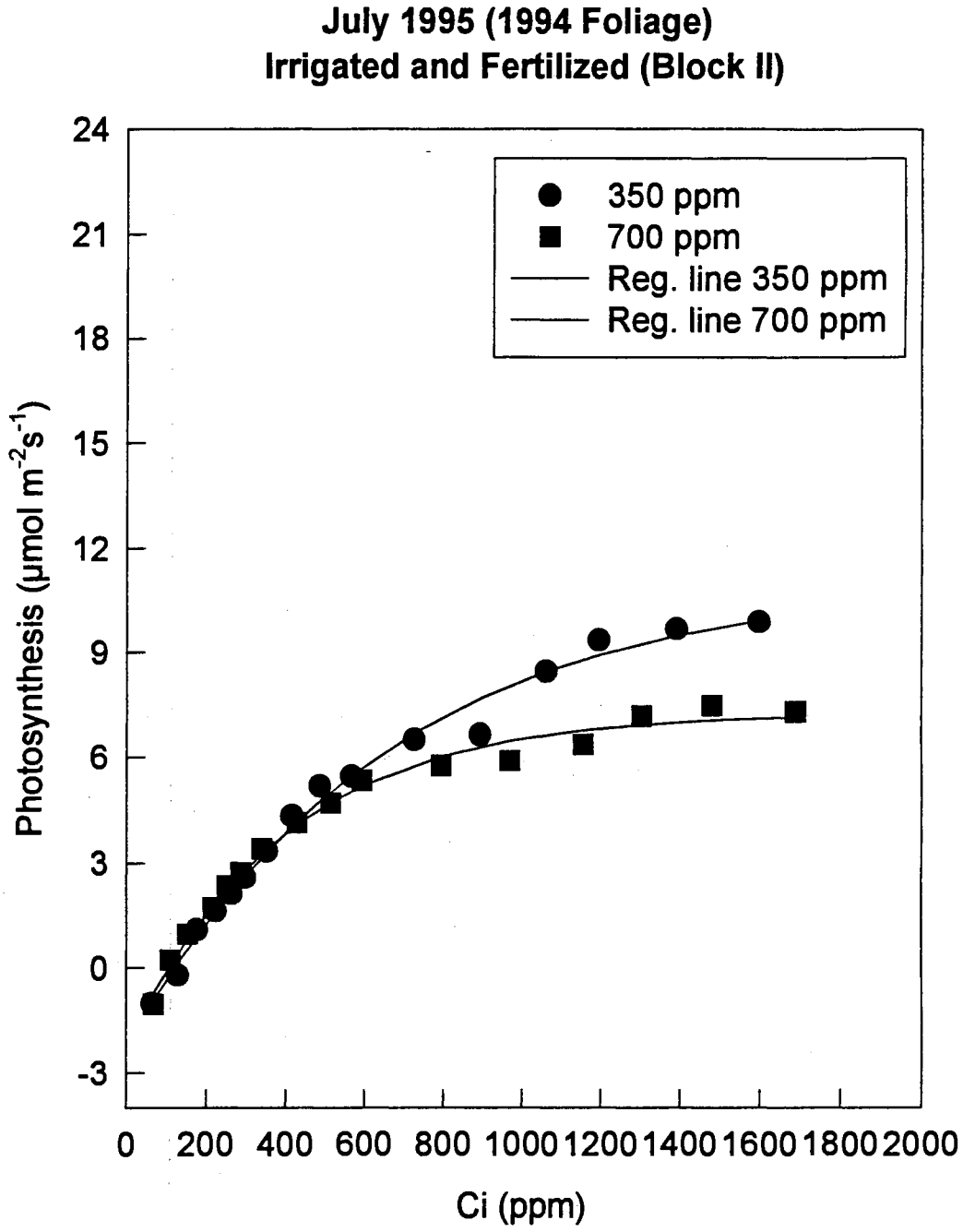

July 1995 (1994 Foliage)
Irrigated and Fertilized (Block II)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 69

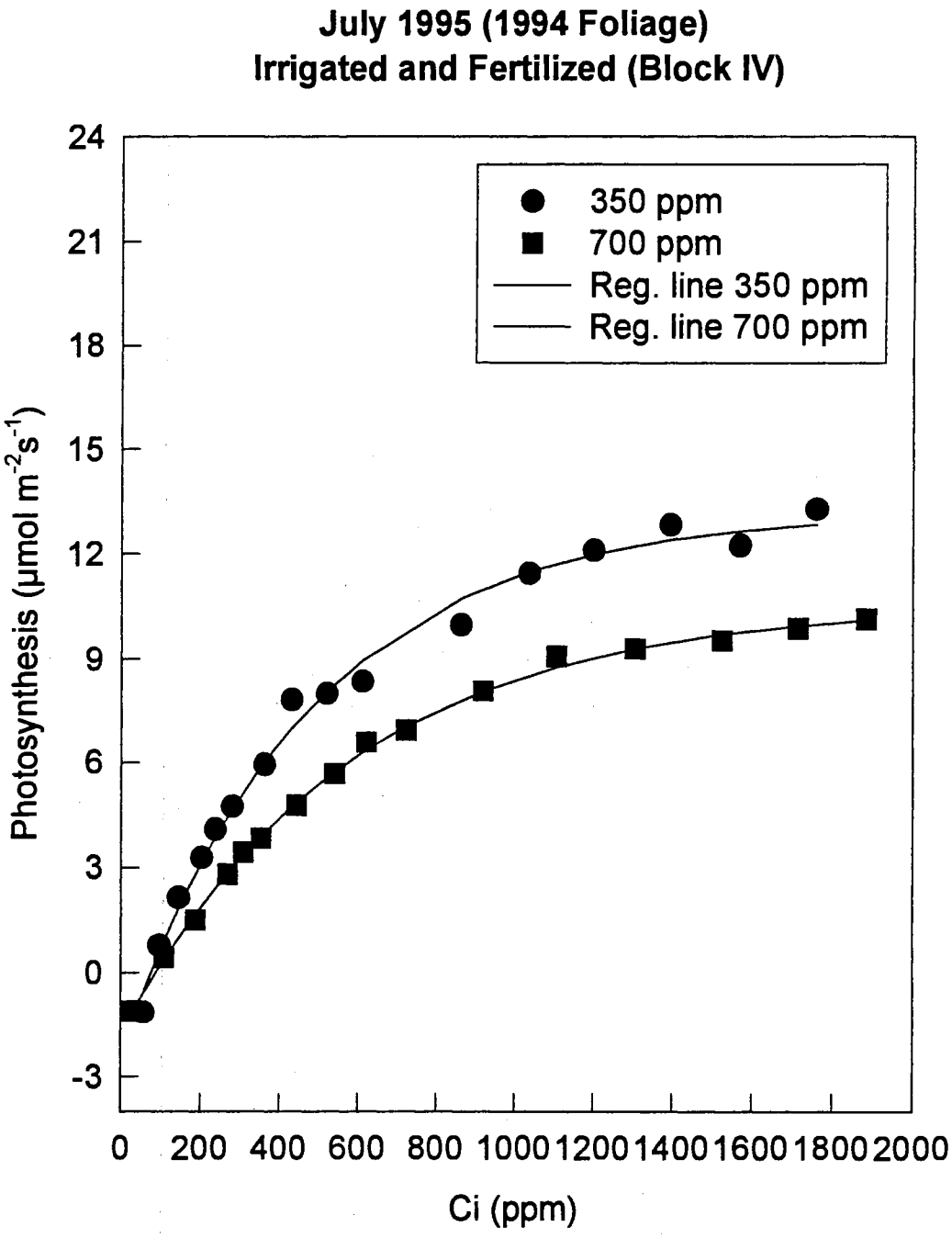

July 1995 (1994 Foliage)
Irrigated and Fertilized (Block IV)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 70

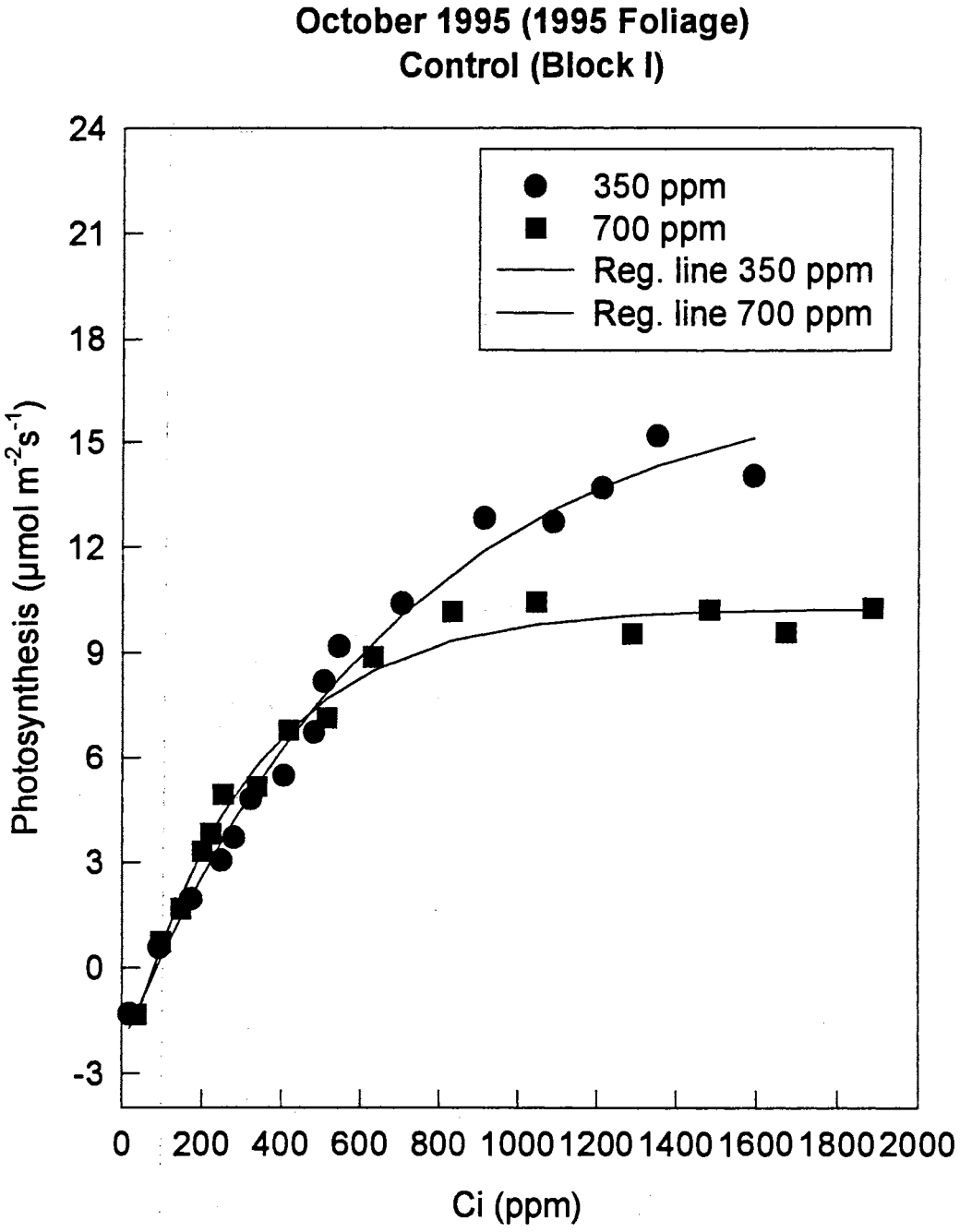

October 1995 (1995 Foliage)
Control (Block I)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 71

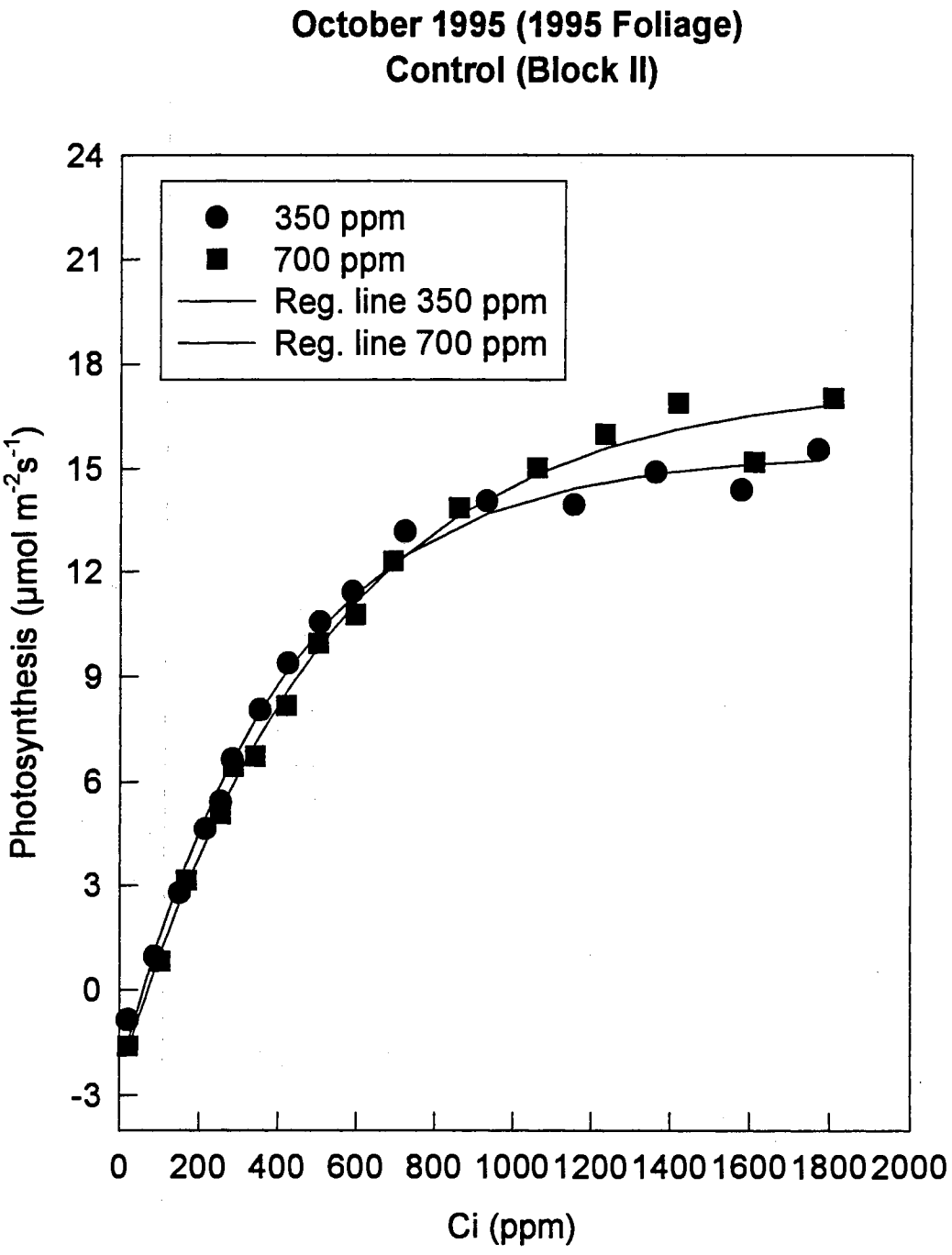

October 1995 (1995 Foliage)
Control (Block II)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 72

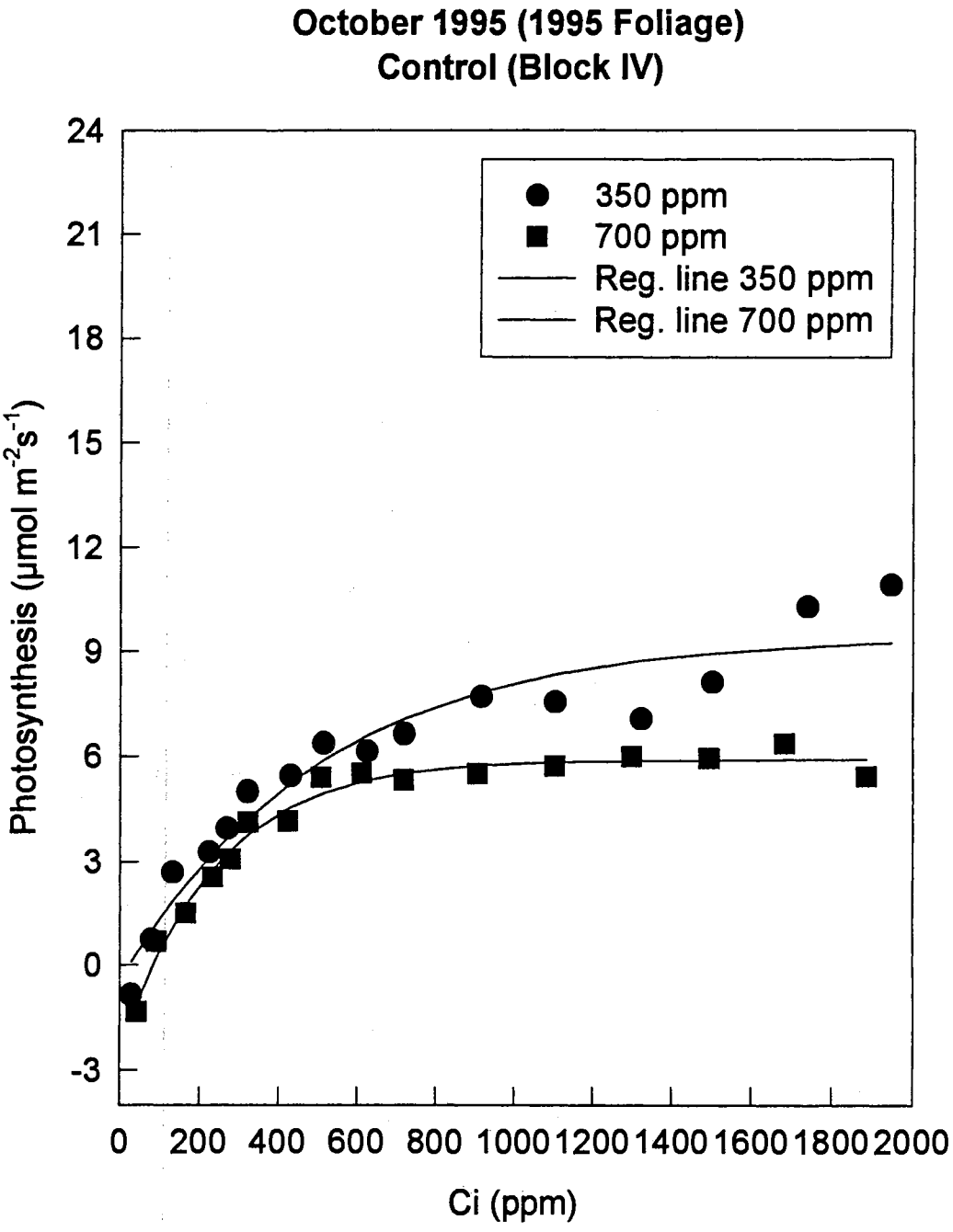

October 1995 (1995 Foliage)
Control (Block IV)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 73

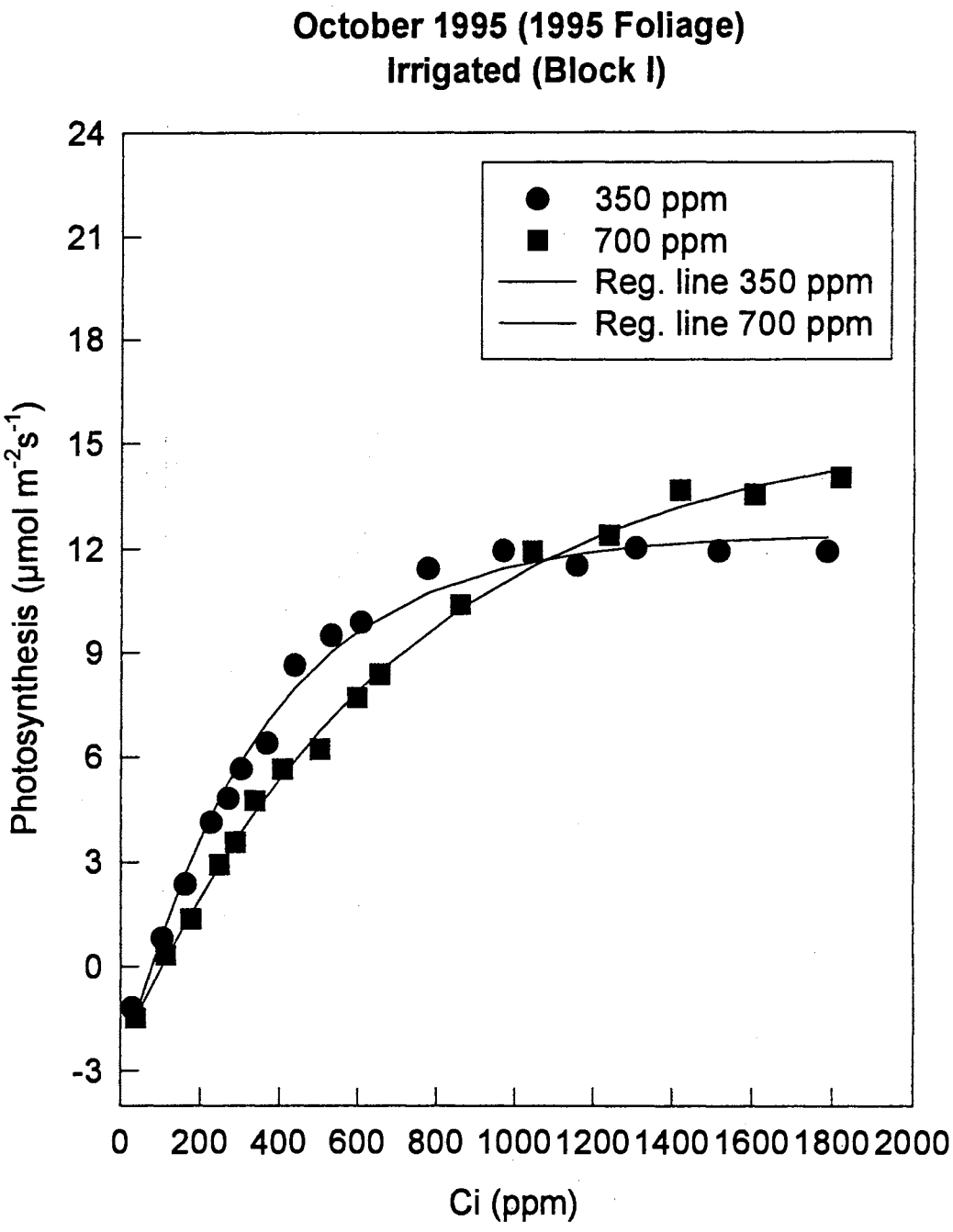

October 1995 (1995 Foliage)
Irrigated (Block I)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 74

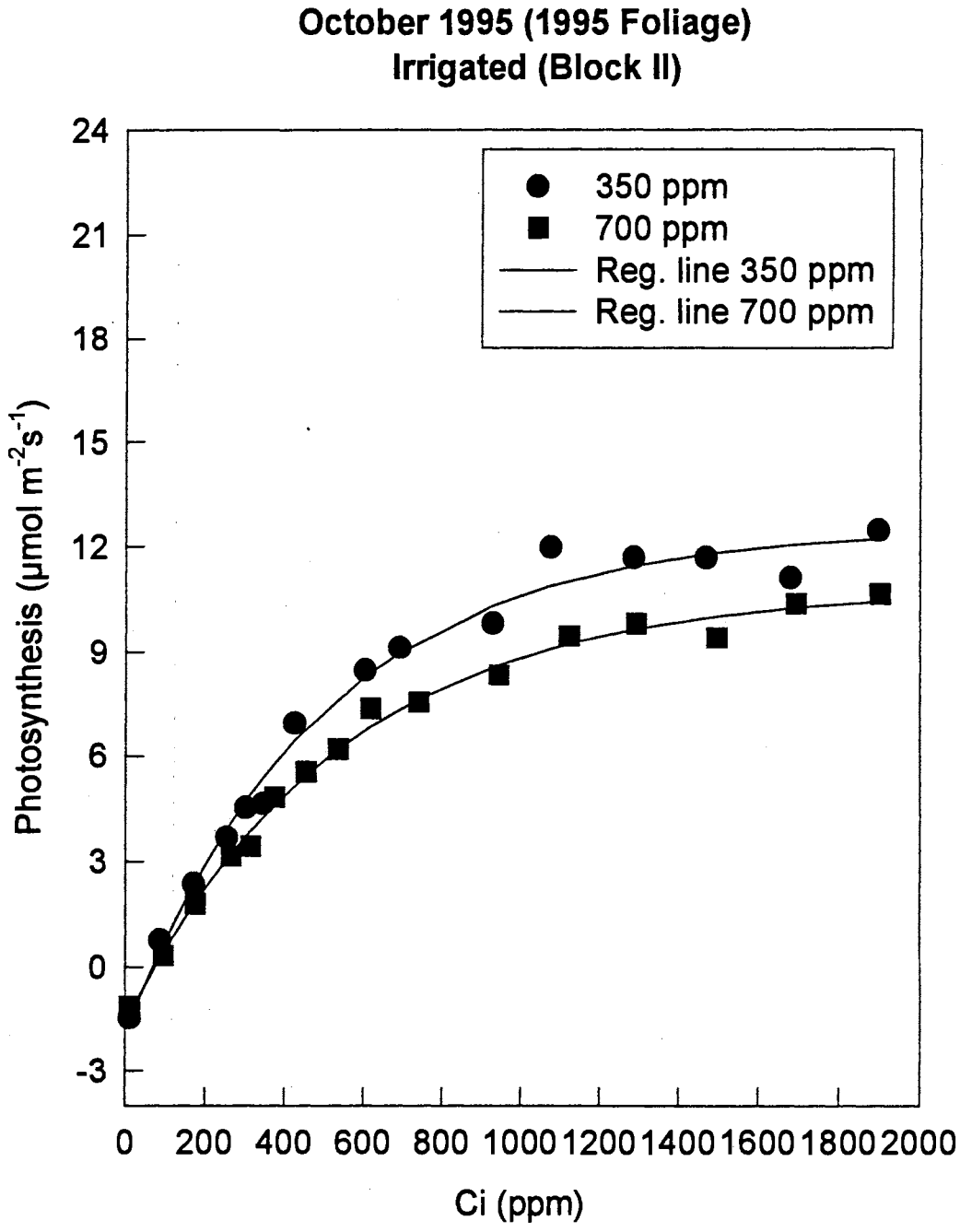

October 1995 (1995 Foliage)
Irrigated (Block II)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 75

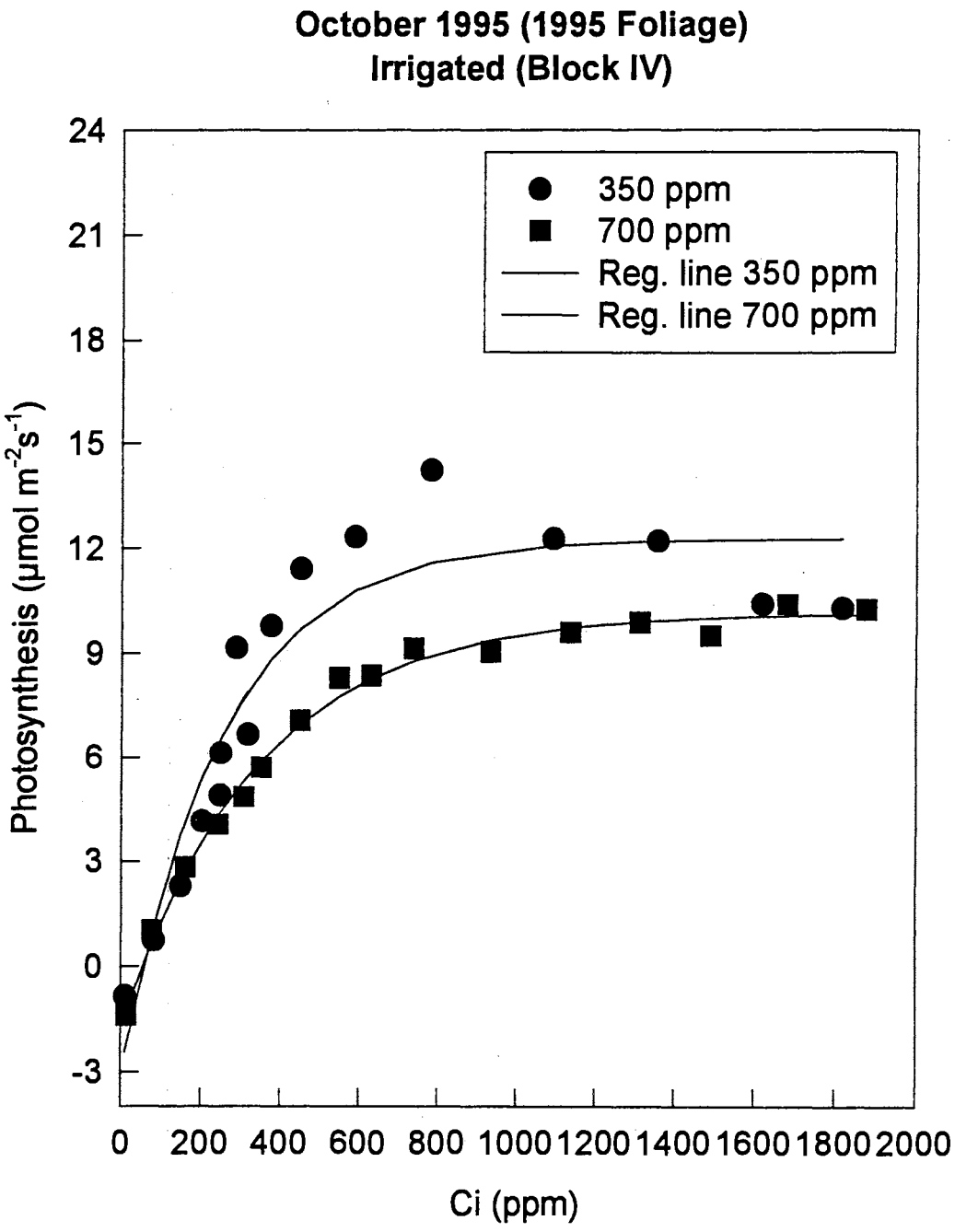

October 1995 (1995 Foliage)
Irrigated (Block IV)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 76

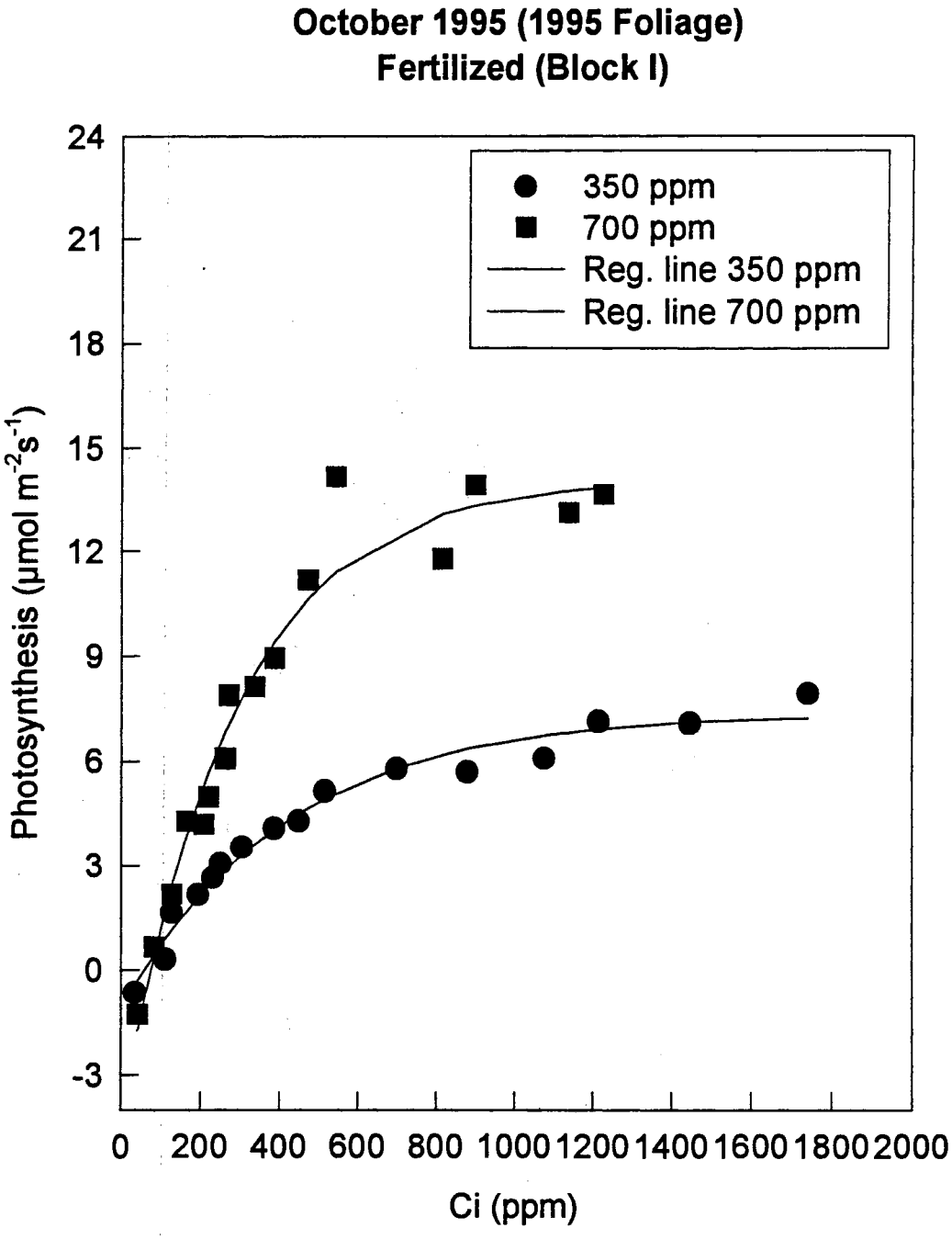

October 1995 (1995 Foliage)
Fertilized (Block I)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 77

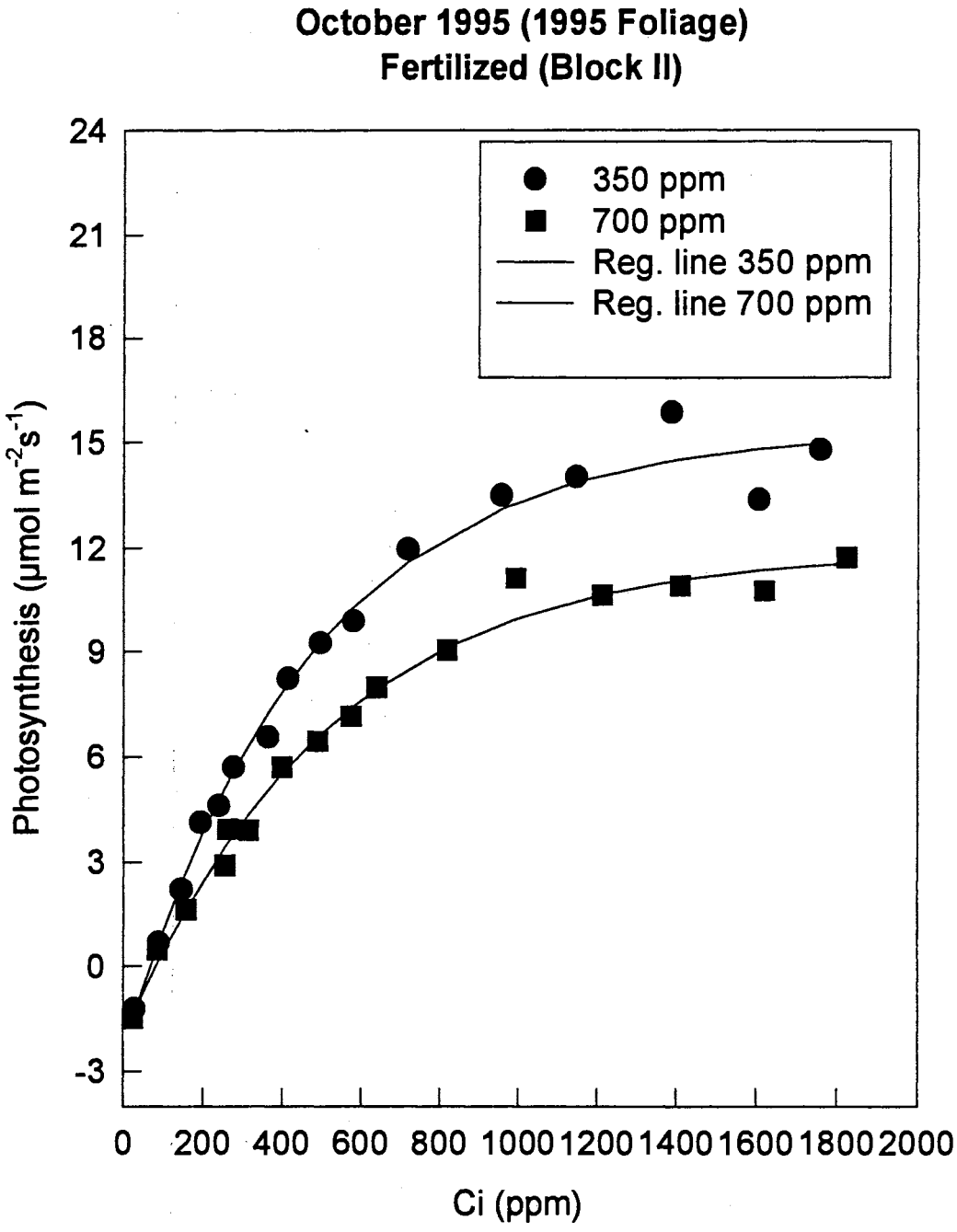

October 1995 (1995 Foliage)
Fertilized (Block II)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 78

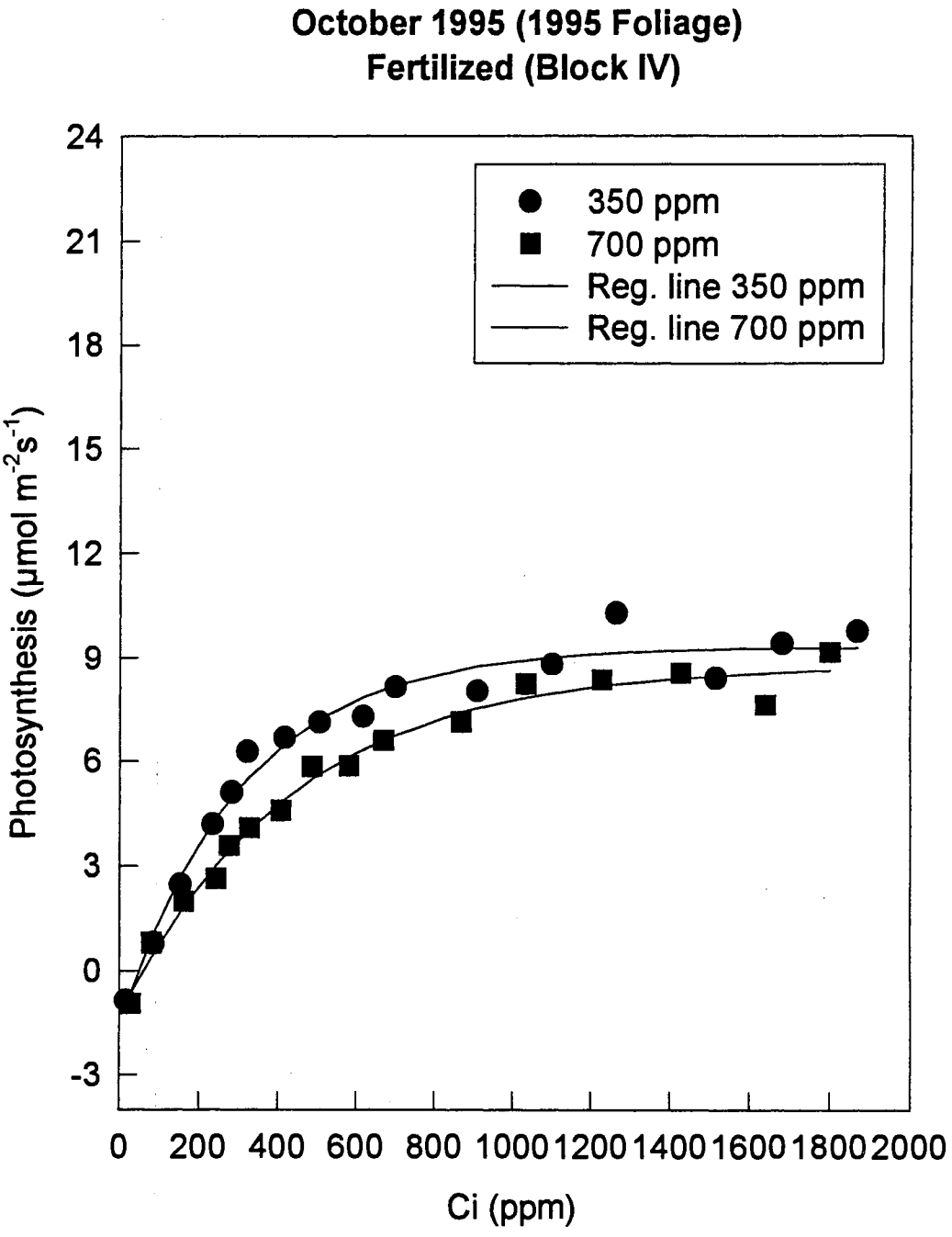

October 1995 (1995 Foliage)
Fertilized (Block IV)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 79

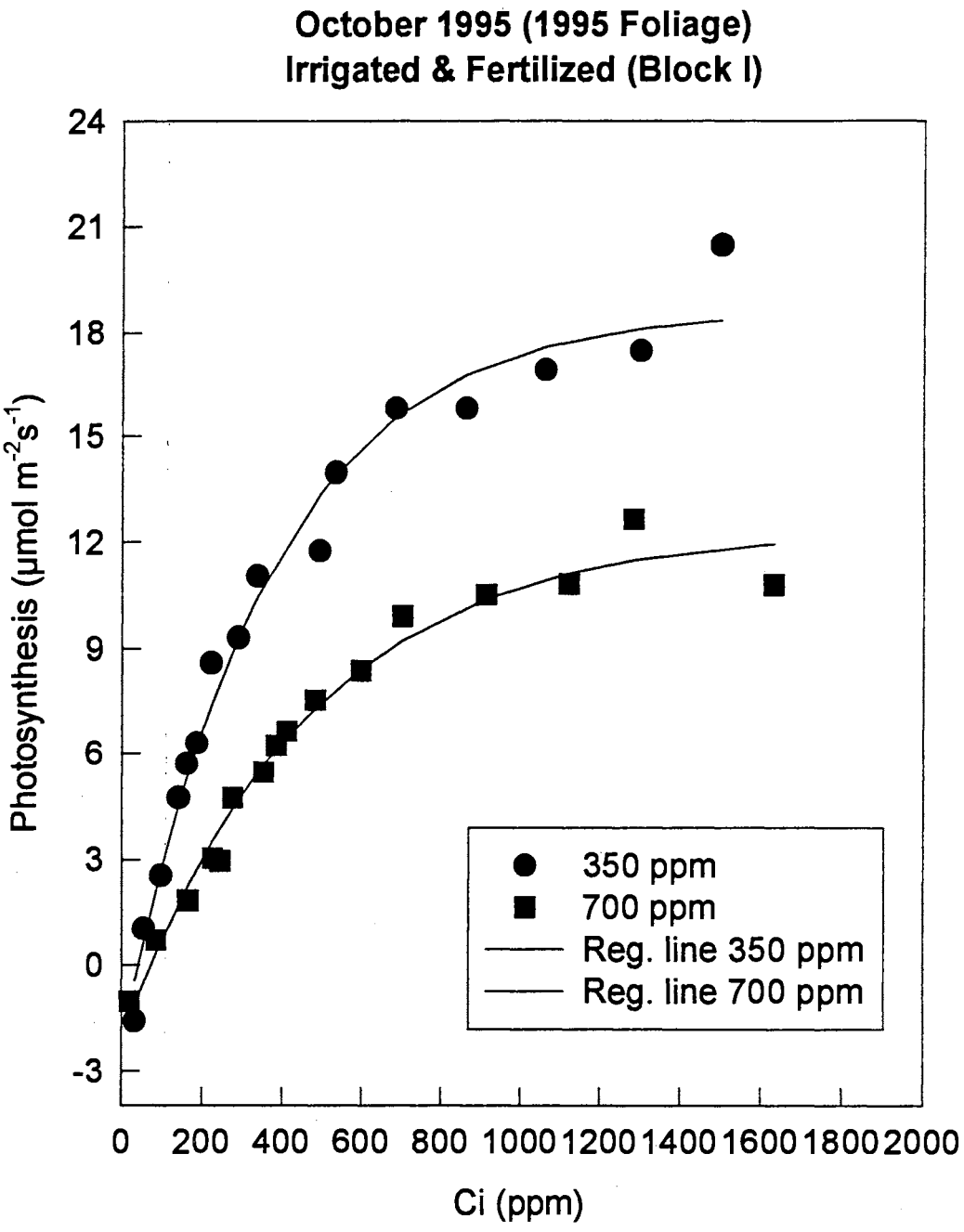

October 1995 (1995 Foliage)
Irrigated & Fertilized (Block I)
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm

Figure 80

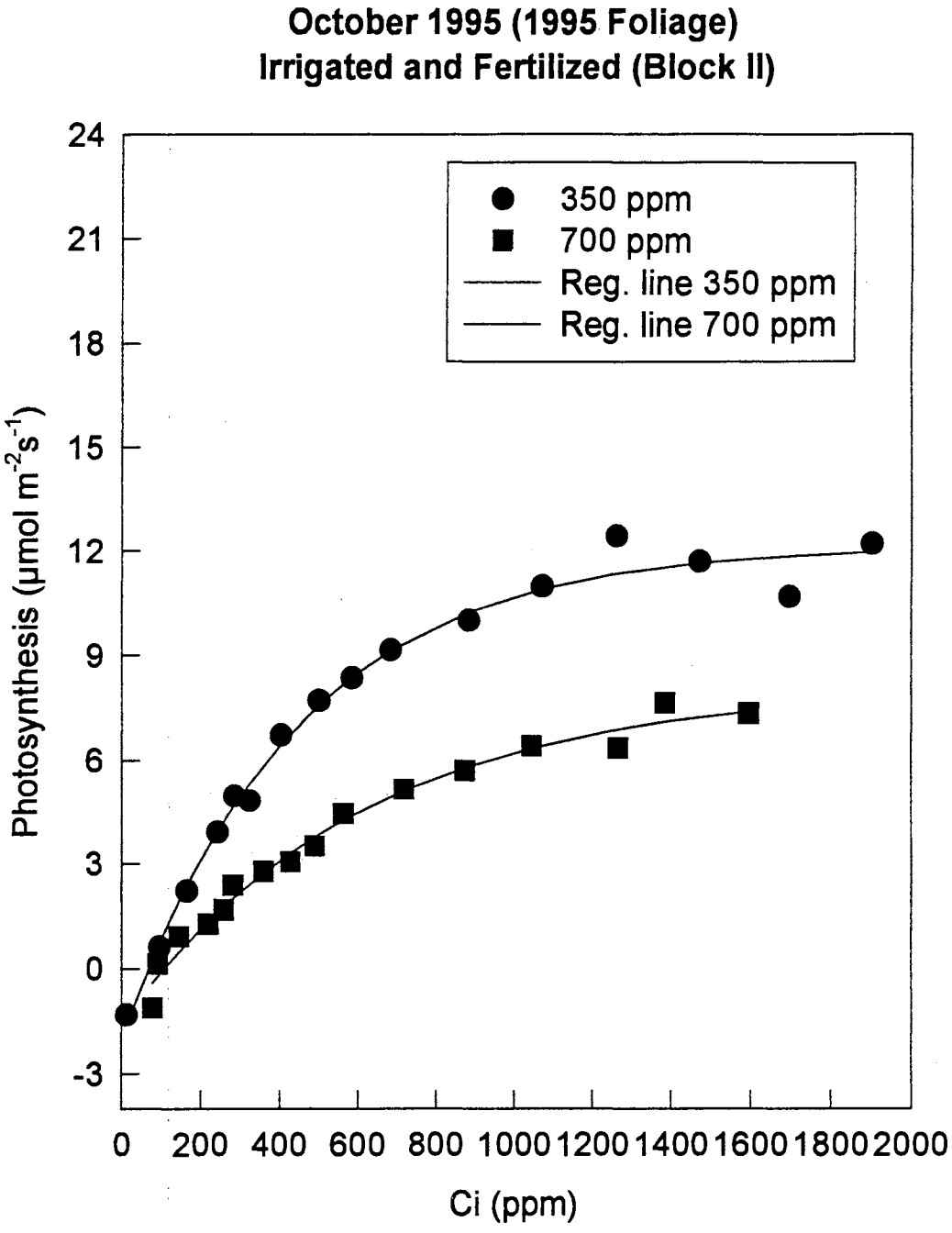

October 1995 (1995 Foliage)
Irrigated and Fertilized (Block II)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 81

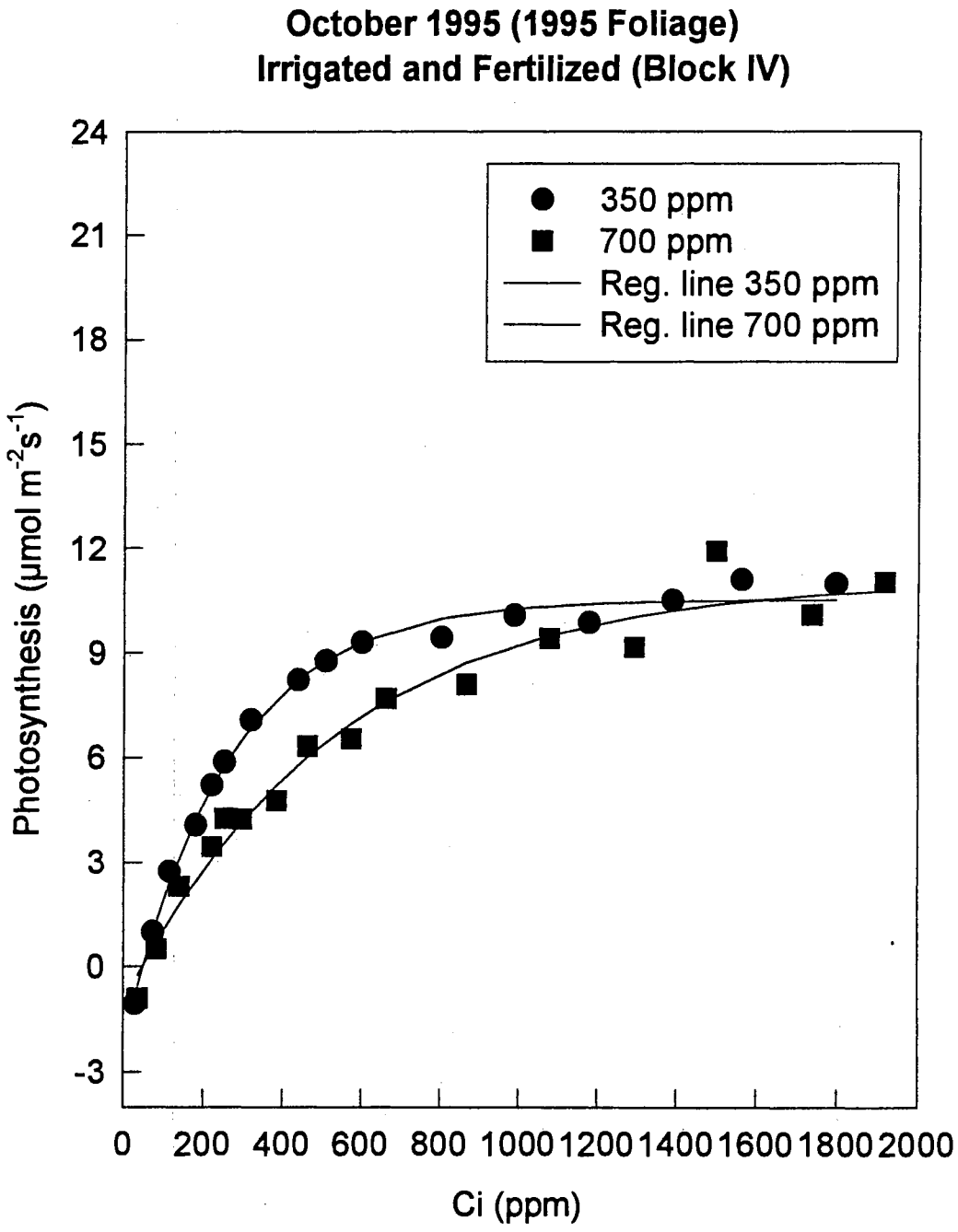

October 1995 (1995 Foliage)
Irrigated and Fertilized (Block IV)
350 ppm
700 ppm
Reg. line 350 ppm
Reg. line 700 ppm
Photosynthesis (µmol m-2s-1)
24
21
18
15
12
9
6
3
0
-3
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Ci (ppm)

Figure 82

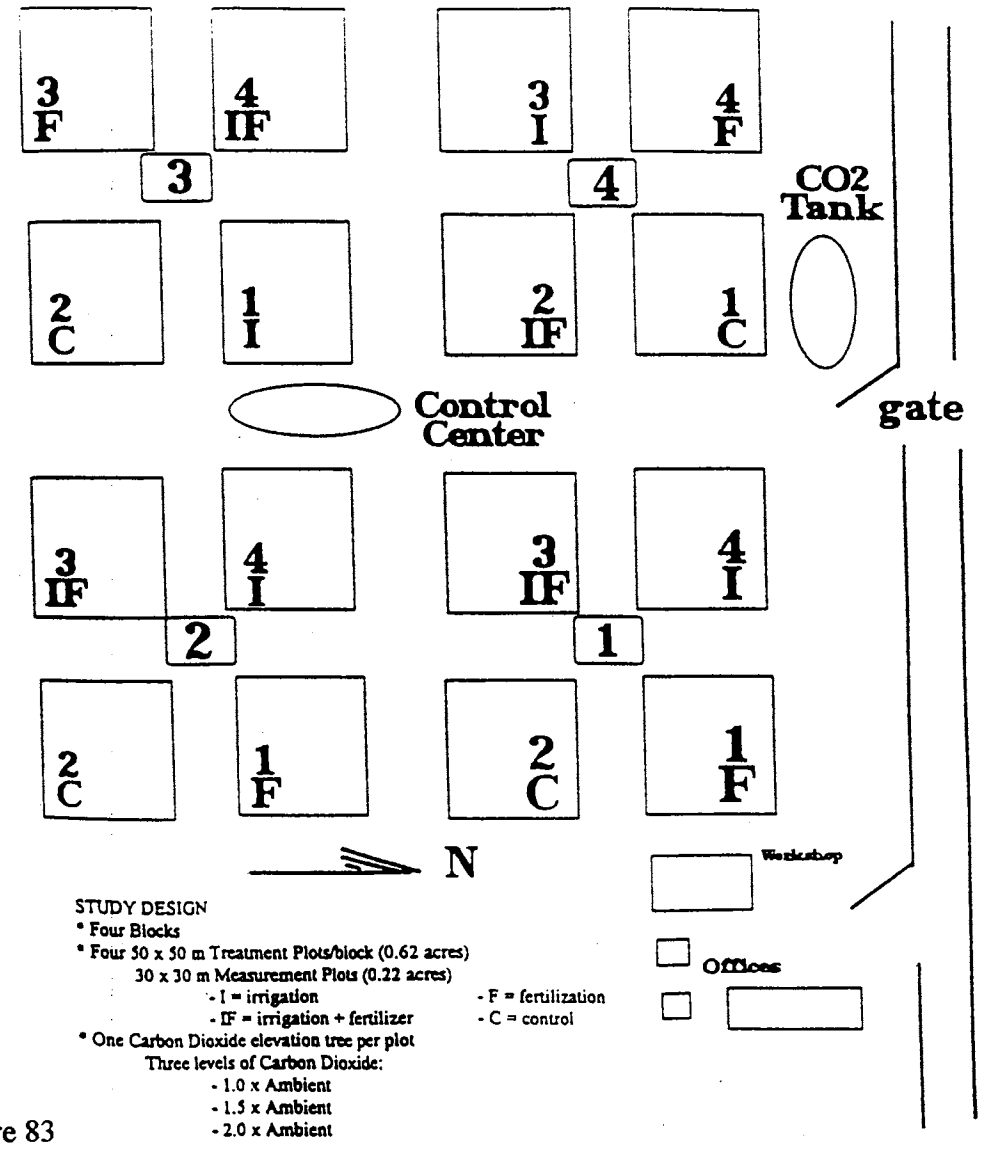

3 F
4 IF
3 I
4 F
3
4
CO2 Tank
2 C
1 I
2 IF
1 C
Control Center
gate
3 IF
4 I
3 IF
4 I
2
1
2 C
1 F
2 C
1 F
N
Workshop
Offices
STUDY DESIGN
* Four Blocks
* Four 50 x 50 m Treatment Plots/block (0.62 acres)
30 x 30 m Measurement Plots (0.22 acres)
- I = irrigation
- IF = irrigation + fertilizer
- F = fertilization
- C = control
* One Carbon Dioxide elevation tree per plot
Three levels of Carbon Dioxide:
- 1.0 x Ambient
- 1.5 x Ambient
- 2.0 x Ambient

Figure 83

VITA

Venkatesh Kumar Harinath

Candidate for the Degree of

Doctor of Philosophy

Thesis: EFFECTS OF CARBON DIOXIDE, WATER AND NUTRIENT FLUXES ON LOBLOLLY PINE (*Pinus taeda* L.)

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