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Response of Vegetation to Carbon Dioxide

**Effects of Elevated Atmospheric
CO₂ Concentrations and Water
Stress on Field-Grown Maize**

**Edited by:
K.A. Surano
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CO₂ Concentrations and Water
Stress On Field-Grown Maize**

MASTER

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Series: RESPONSE OF VEGETATION TO CARBON DIOXIDE

Number: 015

Report of Research:

**EFFECTS OF ELEVATED ATMOSPHERIC CO₂
CONCENTRATIONS AND WATER STRESS
ON FIELD-GROWN MAIZE**

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EXECUTIVE SUMMARY

Global atmospheric carbon dioxide (CO₂) concentrations are continuing to increase and will probably double during the next century. The effects of such an increase are of global concern. Carbon dioxide-induced climate changes may result in reduced precipitation in major agricultural areas. The potential therefore exists for severe CO₂-induced water-stress effects on agriculture.

Carbon dioxide may also directly affect the physiological processes of crops. The physiological mechanisms behind the phenotypic expression of combined direct and indirect CO₂ effects must be understood before an analysis of future effects is completed. Many crops respond to elevated CO₂ with increased biomass production and reduced water consumption because of CO₂-induced increases in photosynthesis and decreases in transpiration. The photosynthetic rate of maize (*Zea mays* L.), a C₄ species, will probably not increase because C₄ photosynthesis is not CO₂-limited. However, reduced transpiration for maize is likely to occur because CO₂ will cause stomatal closure. Additionally, water stress may impose limits on maize photosynthesis and transpiration. The quantification of the effects of CO₂ on maize under future conditions of combined elevated CO₂ and water stress is therefore of interest.

This set of studies determined the effects of long-term elevated atmospheric CO₂ concentrations and severe water stress on biomass production, evapotranspiration, water-use efficiency (WUE), water potential, photosynthesis, stomatal conductance, morphology and phenology of maize grown under field conditions. Plants were grown at one of four daytime mean CO₂ concentrations (348, 431, 506 or 656 μLL^{-1}) in open-top field exposure chambers and at one of two levels of available water (well-watered or 50% of well-watered).

Water stress caused reductions in biomass production that were partially compensated by CO₂ concentrations of 656 μLL^{-1} . Under well-watered conditions, all increases in atmospheric CO₂ concentration caused small increases in biomass production. Elevated CO₂ levels reduced evapotranspiration and increased WUE. Water-use efficiency was increased 31-33% at CO₂ concentrations of 656 μLL^{-1} , regardless of water treatment. Therefore, present yields may continue to be realized under doubled CO₂ concentrations by plants using 25% less water. As global CO₂ levels increase, maize may be able to expand its range into areas previously considered marginal with respect to available water. At a minimum, maize may be able to maintain its current range

without loss in biomass production, even if precipitation decreases and evaporative demand increases.

Severe water stress reduced the water potential of maize, indicative of sub-optimal internal plant water status. Elevated CO₂ did not compensate for the water stress effects on water potential. As expected for a C4 plant, gross and net photosynthetic rates were unaffected by elevated CO₂. Both elevated CO₂ and water stress reduced stomatal conductance, thereby reducing transpiration and ultimately, seasonal water consumption.

Water stress caused reductions in stem height, stem diameter and leaf area production. However, stem diameter was a poor indicator of morphological effects due to seasonal and diurnal variability in response to short-term water availability. Elevated CO₂ concentrations had no effect on the stem height or leaf area of maize, regardless of water treatment. Therefore, elevated CO₂ concentrations were unable to ameliorate water-stress induced reductions in stem height or leaf area.

Phenological development may have been delayed in water-stressed plants. The highest CO₂ treatment may have mitigated water stress-induced phenological effects. However, any phenological changes were minimal. Maize grown under future elevated CO₂ concentrations will probably continue to develop at rates similar to those presently seen, and its morphology will not be significantly altered unless water stress becomes severe.

Photosynthetic and respiratory activities were also assessed from elemental analyses of aboveground biomass. Elemental composition varied little with CO₂ or water treatment. The mean elemental composition of organic materials per 100 g biomass at a harvest during grain filling was C_{3.63} H_{6.04} N_{0.093} O_{2.87} S_{0.002}. (The balance of the mass, 3.08 g, was due to minerals.) That material had more C and H and less N and was more reduced chemically than preanthesis biomass. While crop growth rates were affected by CO₂ and water, the growth respiration factor (0.11 g C g⁻¹ biomass) and the fraction of estimated gross photosynthesis used in growth respiration were small and unaffected by treatment. It is estimated that net carbon storage amounted to 53% of gross photosynthesis while 14% went to growth respiration and 33% went to maintenance.

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INTRODUCTION

The effects of rising global atmospheric carbon dioxide (CO₂) are of global concern. The potential exists for significant CO₂-induced climatic changes. Such climatic changes, combined with direct CO₂ effects on plant physiological rates, may have great impacts on plants (Strain and Cure, 1985).

This report details the results from an experiment of the effects of elevated atmospheric carbon dioxide (CO₂) concentrations in combination with water stress on field-grown maize (*Zea mays* L.). The research was conducted as part of the U.S. Department of Energy Carbon Dioxide Research Division effort to determine the long-term effects of continuous elevated CO₂ enrichment on agriculture.

In the U.S. Department of Energy State-of-the Art Report on the direct effects of increasing CO₂ on vegetation, Strain and Cure (1985) gave research recommendations with respect to agricultural species. Although the experiment reported in this present document took place 2 years prior to the publication their report, many of their recommendations were followed *a priori*. Strain and Cure (1985) ranked species in decreasing order of priority for experimentation. Maize, the subject species of our study, was the #2 species they recommended. Strain and Cure (1985) stated that "experimentation in field and controlled environments is needed to elucidate the interactive mechanisms between the environmental factors of temperature, soil, water and nutrient availability.... and CO₂ concentration." Our experiment was conducted in the field and subjected the maize crop to both elevated CO₂ and variations in available water. Strain and Cure (1985) further stated that "plants should be grown in realistic field configurations...continuously exposed for their entire growth cycle to a CO₂-enriched atmosphere." In our study, the crop was grown using normal cultivation and production methods and it was exposed to elevated CO₂ concentrations from emergence to harvest, without interruption. Another recommendation by Strain and Cure (1985) was that "work should be initiated on the following areas: root growth, leaf net photosynthesis rates of plants grown from seed at various CO₂ concentrations, and carbon allocation relationships between photosynthetic leaves and nonphotosynthetic growing points." Our study explored all of these important research areas.

Preliminary results from this study were reported in an informal report (Surano and Shinn, 1984). The present document reflects more detailed and

thorough examination of the data. This report is organized into 4 chapters followed by appendices. The four chapters are independent papers regarding the various topics explored in the research. Each paper was written for submission to the open literature. The pages are numbered consecutively, but the figures and tables are numbered with a prefix, identifying the paper to which they belong.

Literature Cited

Strain, B.R., and Cure, J.D., (Editors), 1985. Direct Effects of Increasing Carbon Dioxide on Vegetation. DOE/ER-0238, U.S. Department of Energy, Office of Energy Research, Carbon Dioxide Research Division, Washington, DC.

Surano, K.A., And Shinn, J.H. 1984. CO₂ and Water Stress Effects on Yield, Water-Use Efficiency, and Photosynthate Partitioning in Field-Grown Corn. UCRL-90771, Lawrence Livermore National Laboratory, Livermore, CA, 94550.

**EFFECTS OF ELEVATED ATMOSPHERIC
CO₂ CONCENTRATIONS AND WATER STRESS
ON FIELD-GROWN MAIZE:
BIOMASS PRODUCTION AND WATER-USE EFFICIENCY**

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ABSTRACT

The effects of rising atmospheric carbon dioxide (CO₂) concentrations on agriculture are of global concern. Elevated levels of CO₂ can affect crops directly, through stomatal closure and increased photosynthetic rates, and indirectly, through climatic changes, such as increased air temperatures and reduced precipitation. This study determined the effects of long-term elevated atmospheric CO₂ concentrations and severe water stress on biomass production, evapotranspiration, and water-use efficiency (WUE) of maize (*Zea mays* L.) grown under field conditions. Plants were grown at one of four daytime mean CO₂ concentrations (348, 431, 506 or 656 μLL^{-1}) in open-top field exposure chambers and at one of two levels of available water (well-watered or 50% of well-watered). Water stress caused reductions in biomass production that were partially compensated by CO₂ concentrations of 656 μLL^{-1} . Under well-watered conditions, all increases in atmospheric CO₂ concentration caused small increases in biomass production. Elevated CO₂ levels reduced evapotranspiration and increased WUE. Water-use efficiency was increased 31-33% at CO₂ concentrations of 656 μLL^{-1} , regardless of water treatment. Therefore, present yields can continue to be realized under doubled CO₂ concentrations by plants using 25% less water. As global CO₂ levels increase, maize may be able to expand its range into areas previously considered marginal with respect to available water. At a minimum, maize may be able to maintain its current range without loss in biomass production, even if precipitation decreases and evaporative demand increases.

INTRODUCTION

The postulated effects on agriculture of the well-documented and inevitable future increase in global atmospheric carbon dioxide (CO₂) concentrations (Clark, 1982) range from catastrophic to extremely encouraging. These effects are summarized in numerous publications (Blasing and Soloman, 1983; Lemon, 1983; Wittwer, 1970, 1980, 1981, 1983; Kramer, 1981; Kimball, 1983a, 1983b; Strain and Cure, 1985). Some forecasts depict reduced precipitation and increased mean annual temperatures in the North American maize (*Zea mays* L.) belt as the result of a doubling of atmospheric CO₂ concentrations (Blasing and Soloman, 1983; Rosenberg, 1982; Manabe et al., 1981). These changes, which represent indirect effects of future atmospheric CO₂ levels, could lead to shifts in the agricultural ranges of many crops (Wittwer,

1983) and of maize in particular (Blasing and Soloman, 1983; Newman, 1980). If maize cannot be adapted to future CO₂-induced meteorological conditions, the potential exists for its replacement as a preeminent grain in the United States (Wittwer, 1983). Maize is one of the world's most important field crops and 47% of global maize production occurs in North America (Terjung et al., 1984). The effects of elevated CO₂ on maize in North America alone are therefore of global concern.

Because maize utilizes the C4 photosynthetic pathway, which is not CO₂-limited, direct benefits to maize from increased photosynthesis are unlikely. However, maize may directly benefit from elevated CO₂ levels in another manner. Elevated CO₂ levels may result in increased water-use efficiency (WUE), where WUE is defined as the ratio of biomass produced to water transpired. While biomass production may not increase, maize will probably conserve water due to CO₂-induced stomatal closure that results in decreased transpiration (Lemon, 1983; Carlson and Bazzaz, 1980; Rosenberg, 1982). Maize may then be able to persist in areas where CO₂-induced changes in temperature and precipitation would otherwise cause maize to be excluded.

The need exists to understand and adequately quantify the long-term effects of elevated CO₂ on field-grown crops so that future impacts of elevated CO₂ can be predicted (Dahlman, 1984) and energy policies can be shaped (Riches, 1983; Kramer, 1981). But despite all that has been written about the potential effects of elevated CO₂ levels on agriculture, there is very little information that describes how crops will respond in the field (Strain and Cure, 1985). Field studies of the effects of elevated CO₂ and water stress are necessary because plants grown under artificial conditions do not necessarily respond the same as plants in natural field environments (Tanner and Sinclair, 1983; Newman, 1980). While field studies are often logistically difficult and can be prohibitively expensive, they are necessary to validate previous laboratory and greenhouse studies. In addition, given that future carbon dioxide concentrations will have both direct and indirect effects on maize, investigators cannot realistically examine the future fate of maize production without incorporating both direct and indirect CO₂ effects into their studies (Wittwer, 1983).

Previous studies on maize have been conducted on WUE without elevated CO₂ (Green and Read, 1983; Mtui et al., 1981; Gardner et al., 1981; Wenda and Hanks, 1981); on well-watered potted plants subjected to elevated CO₂ in greenhouses or controlled-environment chambers (Goudriaan and de

Ruiter, 1983; Patterson and Flint, 1980; Carlson and Bazzaz, 1980; Wong, 1979; Akita and Moss, 1972; Ford and Thorne, 1967; Pallas, 1965); and on potted plants exposed in open-top field chambers (Rogers et al., 1983a, 1983c). Only one study specifically examined the effects of combined elevated CO₂ levels and water stress on maize (King and Greer, 1986). However, that study was conducted on potted plants in controlled-environment chambers.

In general, these previous studies have indicated that maize biomass production does not increase, or increases slightly, under elevated CO₂. These studies have shown that maize transpiration rates decrease due to CO₂-induced stomatal closure. Reduced transpiration rates result in seasonal water use declines and WUE increases under elevated CO₂.

Our study documents the effects of long-term elevated atmospheric CO₂ concentrations and reduced available water on maize grown in open-top exposure chambers under otherwise normal field conditions. This paper details the results of the exposures on biomass production and WUE. Other documents relate the effects of long-term elevated CO₂ exposures on maize morphology, phenology, and physiology (Surano and Shinn, 1988; Surano and Houppis, 1988; Surano et al., 1988).

MATERIALS AND METHODS

Each experimental treatment consisted of one of 4 CO₂ concentrations and one of 2 levels of applied water in complete factorial design with 2 replications, for a total of 16 chambers. The CO₂ exposures were designed to track ambient concentrations throughout the season. The setpoint concentrations were ambient+0 μLL^{-1} (control; 350 μLL^{-1}), ambient+75 μLL^{-1} , ambient+150 μLL^{-1} , and ambient+300 μLL^{-1} . The water treatments were well-watered (WW; normal irrigation frequency) and water-stressed (ws; 50% of normal irrigation frequency).

A hybrid maize cultivar (*Zea mays* L., cv. Funk G4040) of class-I maturity rate (105-120 days) was chosen for the experiment. This cultivar is a single-line cross, and therefore had less genetic variability than other cultivars under consideration. In addition, this cultivar was chosen because at maturity it reaches 2 to 2.5 m in height and would therefore still be contained in the exposure chambers.

Sixteen experimental areas, each 7.6 by 9.8 m, were established on a well-drained Rincon soil (Typic Palexeralf) (Welch et al., 1966) at Livermore,

California. Each experimental area contained a randomly placed exposure chamber and an associated non-chambered control plot, termed a companion plot. Data from the companion plots were used to assess and correct for field position variability and chamber effects.

The 0.2-ha study site was fertilized with 327 kg N, 78 kg P, and 149 kg K ha⁻¹, ridged into 76-cm wide rows and pre-irrigated to bring the soil to field capacity. The crop was sown 13 June 1983 at a density of 5.4 seeds m⁻¹ (71,000 plants ha⁻¹). This planting scheme provided that 3 full rows of 16 to 20 plants each were contained within each exposure chamber.

The crop was exposed to CO₂ in open-top field exposure chambers as described by Heagle et al. (1973), and Rogers et al. (1983a, 1983b). The chambers were constructed of cylindrical aluminum frames, 3 m in diameter and 2.4 m in height, covered on the sides by clear polyvinyl chloride (PVC) film. Cone-top baffles (frustra) placed on the tops of the chambers reduced turbulent air exchange and thus facilitated control of CO₂ concentrations (Davis et al., 1983). The bottom half of the chamber film cover was double-walled with the inner surface perforated by 2.5-cm holes through which air and additional CO₂ were introduced. Ambient air was drawn through particle filters by 560-W axial fans and was delivered to the perforated portions of the chambers through plenums. Air speeds of approximately 1.0 m s⁻¹ (four chamber air changes min⁻¹; Heagle et al., 1973, 1979) were designed to provide adequate mixing and uniform distribution of CO₂ concentrations throughout the chamber.

Pure CO₂ from a 12.7 Mg liquid CO₂ receiver was vaporized and delivered to the chambers through a custom-made high-volume dispensing manifold consisting of heated regulators, a flowmeter for each chamber and Teflon tubing. Mixing of the pure CO₂ with the fan-driven ambient air stream took place in the fan housings, chamber plenums and perforated chamber covers prior to injection into the chamber interior. Concentrations of CO₂ were controlled manually in each chamber by altering the flow of pure CO₂ to the chamber through adjustments of the chamber's flowmeter. Exposure of the crop to elevated CO₂ began at emergence (20 June 1983) and continued without interruption through harvest (25 September 1983).

A drip irrigation system was installed in each experimental area. The system had pressure-compensating and line-position insensitive emitters (Model TF-1, Irridelco, Fresno, CA) to provide even distribution of water. Well-watered treatments (WW) received a total of 340 to 360 mm of water in six irrigations.

Water-stressed treatments (ws) received a total of 150 to 180 mm of water in three irrigations.

Samples of ambient air and chamber atmospheres were drawn continuously at 0.05 L s^{-1} through Teflon tubing capped with $0.5\text{-}\mu\text{m}$ Teflon particle filters (Nuclepore, Pleasanton, CA) located 1 m above the ground. The sampling intakes were placed inside inverted 500-mL Erlenmeyer flasks to buffer short-term CO_2 concentration fluctuations. Chamber CO_2 concentrations were sampled for a 1-min period every 20 min. Mean concentrations were computed for each sampling period. A multiple valve system (Samplivalve, Scanivalve Corp., San Diego, CA) made one sample available for analysis while others were purged. The CO_2 concentrations were analyzed with an infrared gas analyzer (Model PIR-2000, Horiba Instruments, Inc., Santa Ana, CA). Data acquisition was provided by a desk-top calculator/data-acquisition system (Models 9830A and 3497A, respectively, Hewlett-Packard, Palo Alto, CA). Ambient CO_2 was monitored continuously and data were averaged in 10-min intervals. Zero and span checks were performed hourly to correct for analyzer drift, and multipoint calibrations over the entire sampling range were conducted daily to assess analyzer linearity and general performance. All calibration gases were referenced to standards analyzed by the Scripps Institution of Oceanography (La Jolla, CA).

Soil-surface temperature, air temperature at 1 m, and photosynthetically-active radiation (PAR) were measured inside and outside of a designated chamber with calibrated, shielded precision thermistors and a PAR sensor (LI-COR, Inc., Lincoln, Nebraska), respectively. All temperature and light parameters were continuously measured and were recorded as 8-min means. Growing degree-days were calculated following Newman (1980) for all plants.

Soil-water depletion was measured biweekly by neutron moderation technique (Long and French, 1967; Gardner and Kirkham, 1952). A neutron probe (Model 503, CPN Corp., Concord, CA) was placed down an aluminum field-access tube located in the center of each chamber. The tubes were 1.5 m long and readings were taken at 15, 30, 46, 61, 91, and 122 cm to characterize the profile. Total seasonal evapotranspiration (ET) was calculated using the water-balance approach (Hanks, 1974). Water-use efficiency was calculated as the ratio of total above ground biomass (AGB) at harvest to total seasonal ET (Hanks, 1974, 1982; Tanner and Sinclair, 1983; Sinclair et al., 1984).

At final harvest, every plant in each chamber and companion plot row was harvested at ground level. Plants from each row were counted, dissected and then separated into tissue types. The tissue types were leaf, stem, mature and immature ears. Mature ears were defined as those having 50% or more filled grains. Fresh weights of each tissue type were determined. Subsamples of each tissue type were taken from each chamber and companion plot. Freshweights of the subsamples were recorded. The subsamples were oven dried at 70°C for approximately 48 h. Dry weight of the subsamples were determined and the resulting subsample fresh-to-dry weight ratios were used to calculate the dryweights of the various tissue types from the appropriate chamber or companion plot harvest. Additionally, grain was removed from mature ears and weighed following drying of the subsamples. The grain/ear ratios were used to calculate grain biomass production values from the total harvest.

It was not feasible to excavate entire root systems. However, the majority of maize roots are typically found in the 0-15 cm depth range directly under planted rows (Robertson et al., 1979). Therefore, following the above-ground harvest, three 20- by 20- by 15-cm deep soil samples were excavated from directly beneath randomly chosen plant stumps in each chamber. The roots in these soil samples were washed, collected, dried and weighed.

Biomass data from each chamber row were corrected for number of plants and were then scaled to hectare proportions. The scaling was necessary because water-use data was expressed on an area basis (ET as related to equivalent precipitation), thus necessitating that biomass be expressed on an equal area basis as well for the computation of WUE.

All chamber data were normalized with data from the companion plots. The normalization allowed correction for both field position and chamber effects. To normalize data from any chamber rows for any given biomass or water-use variable, a normalization factor, N, was computed according to the following equation:

$$N = \frac{M_t}{M_c}$$

where M_t = the mean value for the variable from all the companion rows across the field and M_c = the mean value for the variable from the companion rows associated with the chamber in question. Raw data from the chamber rows was multiplied by N to attain normalized values for the given variable. Separate

normalization was necessary for the two water treatments because companion plots in the two water treatments were grown under different water conditions.

Three-factor analyses of variance were initially conducted on all harvest and water-use variables (Sokal and Rohlf, 1969). The 3-factor analyses used CO₂ concentration (+0, +75, +150 and +300 μLL^{-1}), water treatment (ws or WW), and row (east, middle, west) as factors. Because row was never a significant factor in any of the 3-factor analyses, it was dropped as a factor and 2-factor analyses of variance were used.

Fischer's Least Significant Difference Multiple Range Test was used to test for significant differences among the means of variables that showed a significant CO₂ or CO₂ x water treatment interaction in the analyses of variance (Snedecor and Cochran, 1967). A multiple range test was not necessary for variables that showed a water-treatment effect because there were only two water treatments.

RESULTS

Conditions of Growth

Table 1 shows the conditions of growth for the crop both inside and outside the open-top chambers. Soil temperatures were very similar during the day, but were reduced inside the chamber at night. This was due to convective cooling effects of the chamber air flow.

Growing degree days were increased in the chamber when compared to the environment outside. While nighttime air temperatures were similar inside and outside of the chambers, daytime air temperatures were elevated in the chambers. Daytime chamber air temperatures increased because the chamber panels were not transparent to reradiated infrared radiation, therefore causing a "greenhouse" effect. We feel that the increased air temperatures are not of great concern for three reasons. First, the elevated temperatures are not out of the temperature range for optimal maize production, and all chamber treatments experienced similar increases in temperature. Second, the increases in air temperatures are within the range of many scenarios regarding future climatic conditions where air temperatures increase under elevated CO₂ concentrations. Finally, all data from the chambers were corrected using adjacent companion plot data. The normalization of the data corrected for all chamber effects which included both air temperature and field position effects.

Table 1. Conditions of growth (seasonal means) for maize in exposure chambers and open field, Livermore, California, 1983.

	Chamber	Open Field
Surface Soil Temperature (°C)		
day	28 ± 3	29 ± 4
night	20 ± 3	24 ± 3
Air Temperature (°C)		
day	27 ± 3	23 ± 4
night	18 ± 3	17 ± 4
Growing Degree-Days	1150	998
PAR (μmol (quanta)/m ² /s)	1670	1820
Ambient CO ₂ Concentration (μL/L)		
day	348	353
night	373	367

Photosynthetically active radiation (PAR) transmission efficiency was 92% inside the chambers through the course of the experiment. These light levels agree well with data reported from other open-top chamber studies (Heagle et al., 1973, 1979; Rogers et al., 1983b). However, because of a lack of summer rainfall, dust accumulation on the chambers had to be removed weekly for maintenance of these light levels. The small decrease from ambient light levels probably did not affect maize production to any significant degree. In addition, any chamber-induced light effects were corrected by normalization of the data using the companion plot data.

Figure 1 shows the daily mean concentrations for all CO₂ treatments throughout the growing season. Seasonal mean daytime (0500 to 1900 PST) concentrations were 348, 431, 506 and 656 μLL⁻¹. Seasonal mean nighttime (1900 to 0500 PST) concentrations were 373, 457, 535 and 686 μLL⁻¹. Control of fumigation concentrations was maintained and adequate separation existed between CO₂ treatments. Carbon dioxide levels in the ambient+0 CO₂ treatments generally tracked ambient CO₂ concentrations, but daytime CO₂ concentrations in those chambers were somewhat decreased. The decrease can be attributed to photosynthetic drawdown. Nighttime CO₂ concentrations were

Figure 1. Daily mean CO₂ concentrations for maize grown in open-top exposure chambers at Livermore, CA, 1983.

somewhat elevated in the chambers. This was attributed to the chamber air flow, which brought CO₂ from soil respiration from near the ground upward towards the sampling intakes.

Biomass Production, ET and WUE

Results from the 2-factor ANOVAs on various biomass and water-use variables are given in Table 2. The biomass production of leaves and immature ears was unaffected by any treatment or the interaction of treatments. Significant effects of the remaining variables are shown in greater detail in Tables 3 to 5.

Carbon dioxide concentrations significantly affected grain and root sample biomass production. The mean values for root and grain biomass under the various CO₂ treatments and the multiple range test results are given in Table 3. Essentially, the table indicates that plants in the ambient+300 CO₂ treatments produced more grain and root biomass than did plants in the ambient+0 CO₂ treatments.

Table 2. p values for 2-factor analyses of variance on various biomass, water-use, and ear production variables of maize subjected to elevated CO₂ and water stress. Values ≤ 0.05 are statistically significant.

Variable	Source of variation		
	CO ₂	Water Stress	CO ₂ x Water Stress
Stem Biomass	0.1218	0.7038	0.0257
Leaf Biomass	0.3506	0.9565	0.9311
Mature Ear Biomass	0.1288	0.0001	0.0500
Immature Ear Biomass	0.7810	0.6191	0.6383
Total Ear Biomass	0.1288	0.0001	0.0500
Grain Biomass	0.0157	0.0001	0.0028
Above-Ground Biomass	0.1500	0.0001	0.0091
Evapotranspiration	0.0554	0.0001	0.0257
Water-Use Efficiency	0.1110	0.0084	0.0365
Root Sample Biomass	0.0059	0.0145	0.3396
Number of Mature Ears	0.1173	0.0001	0.0404
Number of Immature Ears	0.9752	0.0001	0.3325
Total Number of Ears	0.9174	0.0043	0.2389

Water treatment significantly affected the biomass production of mature ears, total ears, grain, and total above ground biomass (Table 4). The number of mature, immature and total ears produced were also significantly affected by water treatment. Evapotranspiration and WUE were also significantly affected by water treatment. In general, the ws treatment severely reduced production of mature ear, grain, and total above ground biomass. Water stress resulted in the reduction of numbers of mature ears and an increase in numbers of immature ears. However, immature ear biomass production was unaffected. The increase in total numbers of ears produced by plants in the ws treatment was due to the increased numbers of immature ears, although total ear biomass production was dominated by the biomass of mature ears. Evapotranspiration was significantly decreased for plants in the ws treatment. Water-use efficiency was increased for plants in the ws treatment. This indicates that plants in the ws treatment,

Table 3. Resultant mean values for variables that were significantly affected ($p < 0.05$) by CO₂ treatment alone. For each variable, values followed by the same letter are not significantly different (Fisher Protected Least Significant Difference Test. See also Materials and Methods).

CO ₂ Concentration μL/L above ambient (A)	DW Root Sample Mg/ha		DW Grain Mg/ha	
A+300	2.15	a	5.94	a
A+75	1.88	ab	4.68	ab
A+150	1.46	bc	5.25	ab
A+0	1.37	c	3.49	b

although producing less biomass, produced a unit of biomass with less evapotranspired water than did plants in the WW treatment.

The carbon dioxide x water treatment interaction was significant for the production of stem, mature ear, total ear, grain and above ground biomass. Also, there was a significant interaction for numbers of mature ears, ET and WUE. The means and multiple range test results for production and water-use variables that showed a significant CO₂ x water treatment interaction are given in Table 5. Two general interaction trends are apparent in the data from the biomass variables. Within the WW treatment, maize grown under any elevated CO₂ treatment generally produced significantly more biomass than maize grown under ambient CO₂ concentrations. Furthermore, there was no difference in biomass production between plants in any of the elevated CO₂ treatments in the WW treatment. Within the ws treatment, plants in the ambient+300 CO₂ treatment produced more biomass than did plants in all the other CO₂ treatments. Additionally, the biomass production values for plants grown in the ws ambient+300 treatment approached, and in some cases exceeded, the biomass values for plants grown in the WW ambient+0 CO₂ treatment.

With respect to ET for plants in the WW treatment, plants in the ambient+0 CO₂ treatment had the highest values, and plants in the ambient+300 CO₂ treatment the lowest values. In the ws treatment, there was no statistical difference between the ET of plants in the CO₂ treatments. This may have been because evaporation, on which CO₂ had no direct effect, was the major component of ET.

Table 4. Resultant mean values for variables that were significantly affected ($p < 0.05$) by water treatment alone. For all variables, mean values for the water-stressed treatment were significantly different from those for the well-watered treatment.

Variable	Well-Watered (WW)	Water-stressed (ws)
DW Mature Ears (Mg/ha)	8.88	3.59
DW Total Ears (Mg/ha)	8.88	3.59
DW Grain (Mg/ha)	6.68	3.01
DW Above Ground Biomass (AGB; Mg/ha)	16.10	10.80
Evapotranspiration (ET; Mg/ha)	5.96E+03	3.28E+03
Water-Use Efficiency (AGB/ET)	2.70E-03	3.29E-03
Number of Mature Ears/ha	6.26E+04	3.37E+04
Number of Immature Ears/ha	5.43E+04	1.24E+05
Total Number of Ears/ha	1.17E+05	1.58E+05

The CO_2 x water treatment interaction effects with respect to WUE are somewhat difficult to interpret. The analysis is confounded because the WUE of plants in ws treatments is inherently higher than that of plants in the WW treatments, even though total biomass production may be lower. However, within the WW treatment, plants in the two highest CO_2 treatments had higher WUE than plants in the two lower CO_2 treatments. In the ws treatment, the only statistical difference was that plants in the ambient+300 CO_2 treatment had higher WUE than plants in the ambient+75 and ambient+150 CO_2 treatments. Once again, similar generalizations about interaction trends can be made. Plants in the higher CO_2 treatments under well-watered conditions had higher WUE values than those in the ambient+0 CO_2 treatment. Under water-stressed conditions, plants in the ambient+300 CO_2 treatment had higher WUE than those in the other CO_2 treatments.

DISCUSSION

The degree of water stress in this experiment was extreme. It is not surprising that biomass production of maize grown under these water stress

Table 5. Resultant mean values for biomass, water use and ear production variables significantly affected ($p < 0.05$) by the CO₂ x water interaction. CO₂ treatment is expressed as $\mu\text{L/L}$ above ambient (A). Water treatments are expressed as ws (water-stressed) and WW (well-watered), respectively. Within each component, values followed by the same letter are not significantly different (Fisher Protected Least Significant Difference Test. See also Materials and Methods).

Stem Biomass (Mg/ha)			Mature Ear Biomass (Mg/ha)		
Treatments			Treatments		
A+300 ws	7.98	a	A+150 WW	10.50	a
A+0 ws	7.89	a	A+300 WW	9.71	a
A+150 WW	7.80	ab	A+75 WW	8.80	ab
A+300 WW	7.58	abc	A+0 WW	6.55	bc
A+75 WW	6.84	abcd	A+300 ws	5.01	cd
A+0 WW	6.20	bcd	A+0 ws	3.87	d
A+150 ws	6.06	cd	A+75 ws	2.90	d
A+75 ws	5.87	d	A+150 ws	2.59	d

Total Ear Biomass (Mg/ha)			Grain Biomass (Mg/ha)		
Treatments			Treatments		
A+150 WW	10.50	a	A+150 WW	8.37	a
A+300 WW	9.71	a	A+300 WW	7.68	a
A+75 WW	8.80	ab	A+75 WW	6.97	a
A+0 WW	6.55	bc	A+300 ws	4.19	b
A+300 ws	5.01	cd	A+0 WW	3.69	b
A+0 ws	3.87	d	A+0 ws	3.30	b
A+75 ws	2.90	d	A+75 ws	2.40	b
A+150 ws	2.59	d	A+150 ws	2.14	b

# Mature Ears/ha			Above-Ground Biomass (AGB) (Mg/ha)		
Treatments			Treatments		
A+150 WW	6.93E+04	a	A+150 WW	18.30	a
A+300 WW	6.80E+04	a	A+300 WW	16.90	a
A+75 WW	6.23E+04	ab	A+75 WW	16.10	ab
A+0 WW	5.07E+04	bc	A+300 ws	13.20	bc
A+300 ws	4.20E+04	cd	A+0 WW	13.10	bc
A+0 ws	3.65E+04	de	A+0 ws	12.00	cd
A+75 ws	2.95E+04	de	A+75 ws	9.06	d
A+150 ws	2.68E+04	e	A+150 ws	9.00	d

Evapotranspiration (ET) (Mg/ha)			Water-Use Efficiency (AGB/ET)		
Treatments			Treatments		
A+0 WW	6.30E+03	a	A+300 ws	3.83E-03	a
A+75 WW	6.15E+03	ab	A+0 ws	3.57E-03	ab
A+150 WW	5.85E+03	bc	A+150 WW	3.14E-03	abc
A+300 WW	5.55E+03	c	A+300 WW	3.03E-03	abc
A+300 ws	3.45E+03	d	A+150 ws	2.90E-03	bcd
A+0 ws	3.40E+03	d	A+75 ws	2.88E-03	bcd
A+75 ws	3.15E+03	d	A+75 WW	2.61E-03	cd
A+150 ws	3.10E+03	d	A+0 WW	2.09E-03	d

conditions was reduced. Effects of water stress on maize production have been shown previously (King and Greer, 1986). In addition, numbers of mature ears

and total grain production was severely impacted. The water-stressed plants attempted to produce many more ears, but most were aborted. This resulted in the large numbers of immature ears for those plants. A possible mechanism for the biomass reductions may be the inhibition of photosynthesis at low water potentials (Westgate and Boyer, 1985). A more detailed look at the physiology of plants from the current experiment is presented in Surano and Houpis (1988).

It is important, however, to realize that the effects of water stress did not completely cause the absence of CO₂ effects. Within the ws treatment, the ambient +300 CO₂ treatment ameliorated some of the water-stress effects. Biomass production of plants grown under water stress at this CO₂ concentration was able to approach levels attained by well-watered plants grown in ambient CO₂ concentrations. This demonstrates the beneficial effects of elevated CO₂ concentrations for water-stressed plants. While the benefits to water-stressed plants in this experiment were only seen in the ambient+300 CO₂ treatment, it should be noted this was probably due to the severity of the ws treatment. It is probable that lower CO₂ concentrations could ameliorate the effects of lesser degrees of water stress.

Under well-watered conditions there were small increases in biomass production at all levels of elevated CO₂ concentrations. This is in agreement with previous investigators (Rogers et al., 1983a, 1983c; King and Greer, 1986; Sionit et al., 1982; Goudriaan and de Ruiter, 1983). However other investigators showed no increases in maize production under elevated CO₂ concentrations (Wong, 1979; Patterson and Flint, 1980; Morison and Gifford, 1984). With respect to individual biomass variables, this study agrees with previous work that showed leaf biomass production was unaffected by CO₂ and that root biomass production increased (Rogers et al., 1983a). It is important to note, however, that plants grown in all elevated CO₂ concentrations in the WW treatment exhibited beneficial effects, and that increases in CO₂ concentrations past ambient+75 $\mu\text{L L}^{-1}$ did not provide additional benefits.

Water-use efficiency was increased regardless of water treatment. Under well-watered conditions, WUE increased 31% for plants in the two highest CO₂ treatments over that of plants at the two lower CO₂ treatments. Under water-stressed conditions, WUE was increased 33% in plants grown in the ambient+300 CO₂ treatment over that of plants in lower treatments. The increase in WUE agrees with other studies that have shown WUE increases as the result of CO₂ exposures (Rogers et al., 1983a, 1983c; Wong, 1979; Green and Read,

1983; Morison and Gifford, 1984). The WUE data are corroborated in concept and magnitude with data reported by King and Greer (1986). They reported a 34% increase in WUE for plants grown at CO₂ concentrations similar to our ambient+300 CO₂ treatment.

The mechanism by which WUE is increased appears to be stomatal closure (Surano and Houpis, 1988; Akita and Moss, 1972; Pallas, 1965; Wong, 1979; Goudriaan and de Ruiter, 1983). As is expected for a C4 plant, the photosynthetic rate of maize approaches its maximum under ambient conditions and does not increase as more CO₂ becomes available (Patterson and Flint, 1980; Rogers et al., 1983a; Surano and Houpis, 1988). With a steeper gradient from external elevated CO₂ to nearly constant internal CO₂ concentration (Carlson and Bazzaz, 1982; Wittwer, 1983), the photosynthetic rate is similar to that at ambient CO₂ concentrations through reduced stomatal openings. Maize is therefore able to maintain production while reducing the rate of transpiration, thereby saving water.

Wittwer (1983) stated that water was the most constraining resource limiting global agricultural production and that it would be the most crucial resource in the future. A prime concern with regard to maize production has been the availability of water (Sinclair et al., 1984). If precipitation in major maize producing areas decreases in the future, production may be impacted. Therefore, the finding that elevated CO₂ increases WUE and that the detrimental effects of water stress can be compensated by elevated CO₂ concentrations is significant.

Maize ET and biomass production have been shown to be strongly linearly correlated (Wenda and Hanks, 1981; Hanks, 1983; Isfan, 1984). The result of the doubling of atmospheric CO₂ and its subsequent increasing of WUE will affect the linear ET-production response in two ways. The slope of the relationship will increase 33% (WUE is actually defined as the slope of the relationship: biomass production/ET) and the x-intercept, or point where a given ET produces no biomass, will decrease 25%, thereby causing a shift in the relationship. This implies that current biomass production can be produced under doubled CO₂ concentrations by plants using 25% less water.

Because WUE will increase as CO₂ concentrations increase, maize may be able to expand its range into areas previously marginal for maize biomass production with respect to available water. Or maize may at least be able to maintain its current range with no loss in biomass production even if precipitation

decreases and evaporative demand increases. The degree of water stress imposed by available water will determine to what extent CO₂-induced increased WUE will moderate changes in the range of maize and how biomass production will be affected.

CONCLUSIONS

As stated by Wong (1979), the responses of maize to elevated CO₂ concentrations depend on a complex of partially compensatory processes that are not readily predictable. Carbon dioxide concentrations and plant water status both contribute to stomatal control and therefore have interacting effects.

Some generalizations can be made from this study regarding the effects of elevated atmospheric CO₂ concentrations and water stress on maize biomass production, water use, and WUE. Severe water stress caused reductions in production that were partially compensated by CO₂ concentrations elevated to ambient+300 μLL^{-1} . Under well-watered conditions, any increase in atmospheric CO₂ concentration caused small increases in production. Elevated CO₂ concentrations reduced evapotranspiration and increased WUE.

It should be remembered that maize is an annual crop species constantly being adapted to new conditions by breeding and deliberate selection. Cultivars in use today may be obsolete by the time the atmospheric CO₂ concentration doubles. Through genetic engineering and breeding programs that will inherently account for gradually increasing atmospheric CO₂ concentrations, maize production may continue at present or greater levels, even if available water should become reduced. The range of maize has already been expanded northward over 800 km in the last 50 years (Wittwer, 1980), and continued attention to possible future climatic effects should ensure a program that can meet the challenge of future environments.

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**EFFECTS OF ELEVATED ATMOSPHERIC
CO₂ CONCENTRATIONS AND WATER STRESS
ON FIELD-GROWN MAIZE:
GAS EXCHANGE AND WATER POTENTIAL**

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ABSTRACT

Global atmospheric carbon dioxide (CO₂) concentrations are continuing to increase and will double during the next century. Carbon dioxide-induced climate changes may result in reduced precipitation in major agricultural areas. The potential therefore exists for severe CO₂-induced water-stress effects on agriculture.

Carbon dioxide may also directly affect the physiological processes of crops. The physiological mechanisms behind the phenotypic expression of the combined direct and indirect CO₂ effects must be understood before an analysis of future effects is completed. Many crops respond to elevated CO₂ with increased biomass production and reduced water consumption because of CO₂-induced increases in photosynthesis and decreases in transpiration. The photosynthetic rate of maize (*Zea mays* L.), a C₄ species, will probably not increase because C₄ photosynthesis is not CO₂-limited. However, reduced transpiration for maize is likely to occur because CO₂ will cause stomatal closure. Additionally, water stress may impose limits on maize photosynthesis and transpiration. The quantification of the effects of CO₂ on maize physiology under future conditions of combined elevated CO₂ and water stress is therefore of interest.

This study examined the physiological effects of field-grown maize exposed to elevated CO₂ and water stress in open-top exposure chambers under otherwise normal conditions. Severe water stress reduced the water potential of maize, indicative of sub-optimal internal plant water status. Elevated CO₂ did not compensate for the water stress effects on water potential. As expected for a C₄ plant, gross and net photosynthetic rates were unaffected by elevated CO₂. Both elevated CO₂ and water stress reduced stomatal conductance, thereby reducing transpiration and ultimately, seasonal water consumption.

INTRODUCTION

Global atmospheric carbon dioxide (CO₂) concentrations have steadily increased in this century and are currently increasing at rates related to global fossil fuel emissions. Carbon dioxide concentrations will continue to increase until they double sometime during the next century. The increases may cause changes in global climate (Strain and Cure, 1985). Most scenarios predict the earth will be warmer and wetter under doubled CO₂ concentrations. Agricultural production will undoubtedly be affected (Wittwer, 1970, 1980, 1983). Some

areas, including the North American maize belt (*Zea mays* L.), may experience reduced precipitation (Rosenberg, 1982; Newman, 1980). This may cause water stress for crops grown in those areas.

Indirect CO₂-induced climatic changes are not the only way that crop plants may be affected. Carbon dioxide may also affect plants directly, through effects on the physiological processes of photosynthesis and transpiration. These processes are linked, because CO₂ uptake for photosynthesis and water loss in transpiration take place through common openings, the stomata. Stomatal apertures, and therefore rates of gas exchange, are affected by both external CO₂ concentrations and internal water status. When water is not abundant, plant growth is a compromise between maximum photosynthesis and minimal water loss through transpiration (Pearcy and Bjorkman, 1983). Therefore, the combination of indirect CO₂ effects, such as water stress from CO₂-induced climatic change, and direct CO₂ effects, such as those on physiological rates, may be of critical importance.

It is important to understand the effects of CO₂ on physiological mechanisms as well as the physical expressions of CO₂-induced effects such as yield and morphology. By understanding basic physiological mechanisms, assessment of the effects of future elevated CO₂ levels can be made with greater certainty (Pearcy and Bjorkman, 1983). Additionally, if the biochemical and physiological characteristics that result in better adaptations to increased CO₂ concentrations can be identified, plants can then be bred to take full advantage of positive CO₂ effects and reduce the impact of any negative effects (Surano et al, 1988; Kimball, 1985).

In general, plants exhibit increased photosynthetic rates under elevated CO₂ concentrations (Moss et al., 1961; Lemon, 1983; Acock and Allen, 1985; Kramer, 1981). An increased CO₂ gradient from the atmosphere to the site of carboxylation can result in increased photosynthesis. Coincidentally, although the actual mechanism remains unknown, elevated CO₂ concentrations cause stomatal closure, thereby reducing rates of transpiration (Bingham et al., 1981; Acock and Allen, 1985; Lemon, 1983). This combination of effects may result in increased availability of internal water and CO₂ (Pearcy and Bjorkman, 1983).

Not all plants will be similarly affected. For non-CO₂-limited C₄ species such as maize, increases in photosynthesis are unlikely (Rogers et al., 1983a,c; Chaudhuri, 1986; Ford and Thorne, 1967; Patterson and Flint, 1980; Wong, 1979; Tolbert and Zelitch, 1983). However, the stomata of C₄ plants may be

more responsive to elevated CO_2 than those of C_3 plants, resulting in a greater potential for reduced transpiration and water use (Pallas, 1965; Akita and Moss, 1972). Leaf transpiration will likely decrease in maize under elevated CO_2 , resulting in reduced water use (Surano et al., 1988; King and Greer, 1986) and increased water-use efficiency (WUE; Rogers et al., 1983 a,c; Bingham et al., 1981; Moss et al, 1961).

Leaf water potential is an important measure of internal plant water status. Growth and photosynthesis may be reduced at low water potentials (Shinn and Lemon, 1968; Boyer 1970), and if water potential drops are large, complete inhibition of photosynthesis may result. If photosynthesis is inhibited, carbohydrate reserves diminish the plant may be prohibited from sustaining anthesis and grain fill (Westgate and Boyer, 1985). There can also be diurnal effects of water potential on photosynthesis (Acevedo et al., 1979). Carbon dioxide-induced water stress from climatic changes could cause reduced water potential, thereby affecting photosynthesis and stomatal behavior (Wong et al, 1985). Paez et al. (1983) indicated that for pea (*Pisum sativum* L.), there was no effect of elevated CO_2 on water potential under well-watered conditions, but that an increase in water potential was observed under elevated CO_2 in water-stressed plants. Therefore, elevated CO_2 concentrations may cause mediation of water stress effects on internal plant water status (Kimball, 1985, Pearcy and Bjorkman, 1983). This has been shown in soybean (Rogers et al, 1984) and in C_4 grasses (Sionit and Patterson, 1985.)

Photosynthesis of field-grown plants is most likely limited to a greater degree by water availability than by CO_2 (Kramer, 1981), especially for C_4 species such as maize. Additionally, results from field experiments of elevated CO_2 may be less than those reported from controlled environment experiments due to the buffering action of other abiotic and biotic influences (Acock and Allen, 1985; Kramer, 1981; Gates, 1983). There may therefore be a tendency for investigators to overestimate CO_2 effects if conclusions are based solely on short-term laboratory and greenhouse experiments (Kramer, 1981). There have been few field studies investigating the effects of long-term elevated CO_2 concentrations on the physiology of plants, let alone experiments using both CO_2 and water-stress treatments (Lemon, 1983; Strain and Cure, 1985).

This paper details the results of physiological measurements made on a maize crop subjected to elevated CO_2 concentrations and water stress in open-top chambers under otherwise normal field conditions. Results from other

aspects of the experiment are reported elsewhere (Surano et al., 1988; Surano and Shinn, 1988).

MATERIALS AND METHODS

A detailed accounting of materials and methods from this experiment can be found in Surano et al. (1988). That document contains descriptions of the maize cultivar, cultural practices, field chambers, CO₂ exposure procedures and atmospheric sampling protocols. These topics are summarized below and are followed by a detailed accounting of physiological measurements.

Maize was exposed to elevated CO₂ in standard open-top field exposure chambers (Heagle et al., 1973, 1979; Rogers et al., 1983b) at Livermore, California. Each experimental treatment consisted of one of 4 levels of CO₂ and one of 2 levels of applied water. The study used a complete factorial design with two replications, for a total of 16 chambers. The treatment exposures were designed to track and supplement ambient CO₂ concentrations. The setpoint concentrations for the study were ambient+0, ambient+75, ambient+150 and ambient+300 μLL^{-1} CO₂. The exposures began at emergence (20 June 1983) and were continuous through harvest (25 September 1983). The seasonal daytime mean ambient CO₂ concentration was 350 μLL^{-1} . The seasonal mean daytime CO₂ treatment concentrations were 348, 431, 506 and 656 μLL^{-1} , respectively.

Water was applied uniformly in all experimental plots with individual drip-irrigation systems. The well-watered treatments (WW) received 340-360 mm water in 6 irrigations. The water-stressed treatments (ws) received 150-180 mm water in 3 irrigations.

A hybrid maize cultivar (*Zea mays* L., cv. Funk G4040) was planted on a well-drained Rincon soil (Typic Palexeralf) at a density of 71,000 plants ha⁻¹. Sixteen experimental plots were established within the 0.2 ha experimental site. Each plot contained a randomly placed exposure chamber. Each chamber contained 3 rows of 16-20 plants each.

Pure CO₂ was injected continuously into the fan inlet air streams to increase the atmospheric concentrations of CO₂ in the treatment chambers. Concentrations were controlled manually by adjustment of the CO₂ flow to each chamber. Atmospheric samples were drawn continuously from mid-chamber at a height of 1-m and were analyzed for CO₂ concentration with an infrared gas analyzer. Chamber atmospheres were sampled every 20 min. Ambient CO₂

concentrations were analyzed continuously with mean concentrations calculated every 10 min.

Predawn and midday (1300 PST) measurements of mid-canopy leaf water potential were made weekly with a Scholander-type pressure-chamber (Squire et al., 1981). The excised leaf samples were enclosed in plastic envelopes before and during measurements to avoid problems of sample dessication (Turner and Long, 1980; Leach et al. 1982).

Stomatal conductance was measured throughout the growing season with a steady-state, leaf-diffusion porometer (Model LI-1600, LI-COR Corp., Lincoln, NE). Measurements were made on adaxial surfaces of two upper canopy leaves on each of 5 plants from each chamber every two hours throughout the day (0530-1730 PST). The sampled leaf tissue was well illuminated before and during measurements. Plots of diurnal seasonal mean values were made. The seasonal mean of the sampling date maximum values was computed.

Gross leaf photosynthetic rates were measured once during the season with an isotope porometer using carbon-14 (^{14}C) labelling techniques (Karlsson and Sveinbjörnsson, 1981; Jackson et al., 1987). The measurements were taken in late season, when the plants had reached physiological maturity. Three midcanopy leaves were exposed to $^{14}\text{C O}_2$ for thirty seconds at CO_2 concentrations approximating the treatments during midmorning (approximately 1030 PST). Leaf tissue was immediately killed and fixed carbon secured with the use of liquid nitrogen. Samples were stored on dry ice until laboratory analysis was performed. Following determination of leaf area, leaf samples were combusted with a Packard Tri-Carb sample oxidizer. Disintegrations per minute (DPM) were determined with liquid scintillation counter (Jones and Mansfield, 1982). Calculations converting the data from DPM to $\mu\text{mol m}^{-2} \text{s}^{-1}$ allowed the expression of the ^{14}C fixed in photosynthesis in standard SI units.

Leaf net photosynthetic rates were measured with the Lawrence Livermore National Laboratory steady-state minicuvette system (Bingham et al., 1980). Because of lengthy response times that are inherent with this type of system, net photosynthesis measurements were made in the WW treatments only. Net photosynthesis measurements were made at midseason, when the plants were in the grain-fill stage of growth. Leaves near the top of the canopy were placed in the cuvette at midday. Conditions were balanced at $30 \pm 1^\circ\text{C}$, $40 \pm 2\%$ relative humidity, and a photosynthetic photon flux density of 1900 ± 100 micromol (quanta) $\text{m}^{-2} \text{s}^{-1}$. Carbon dioxide concentrations in the cuvette were

maintained at the treatment level of the chamber in which the measurements were being taken.

Two-factor analyses of variance were performed on the physiology data (Sokal and Rohlf, 1969). The factors used in the ANOVAs were CO₂ concentration and water treatment.

RESULTS

The results of the ANOVAs on water potential, photosynthesis and stomatal conductance, together with mean values from each of the treatments, are presented in Table 1. Water treatment was a significant factor for water potential. Plants in the ws treatment had significantly lower water potentials at both predawn and midday than did plants in the WW treatment. There were no significant CO₂ or CO₂ x water treatment interaction effects on water potential.

There were no significant factors in either of the photosynthesis ANOVAs. Photosynthetic rates in this experiment were unaffected by CO₂ and water stress. It should be noted, however, that the measured rates of gross photosynthesis were an order of magnitude lower than those measured for net photosynthesis. Gross and net photosynthetic rates for C₄ plants should be of similar magnitude, since C₄ plants exhibit minimal photorespiration. The apparent discrepancy in the magnitude of the photosynthesis data is resolved when the measurement dates are considered. The gross photosynthesis measurements were made in late season, when the crop was at physiological maturity. The net photosynthesis measurements were made in mid-season, when the plants were in the grain-filling stages. Maize photosynthetic rates have been shown to decline an order of magnitude from early and mid-season highs of approximately 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to late season rates of approximately 3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Dwyer and Stewart, 1986).

Carbon dioxide concentration was a significant factor for daily maximum stomatal conductance. Water treatment was also a significant factor. However, the CO₂ x water treatment interaction factor was insignificant for stomatal conductance. Reductions in maximum stomatal conductance due to CO₂ were roughly linear, with a 33% reduction occurring in the +300 CO₂ treatment over that at ambient concentrations.

Diurnal plots of stomatal conductance from representative treatments are shown in Figure 1. The plots show bimodal peaks, with the conductance of plants in all treatments returning to approximately 80% of late morning peak

Table 1. p values from 2-factor analyses of variance and mean values of various physiological variables of maize subjected to elevated CO₂ and water stress. Values ≤ 0.05 are statistically significant.

Component	p value (source of variation)			Water Treatment Means		CO ₂ Treatment Means (μL/L)			
	CO ₂	water	CO ₂ x water	ws	WW	+0	+75	+150	+300
Predawn Water Potential (MPa)	0.1878	0.0001	0.2752	-0.40	-0.21	0.28	0.35	0.33	0.27
Midday Water Potential (MPa)	0.8771	0.0001	0.3276	-1.74	-1.28	1.54	1.52	1.48	1.49
Net Photosynthesis (μmol/m ² /s)	0.6093	-	-	-	31.31	28.73	34.02	32.57	29.99
Gross Photosynthesis (μmol/m ² /s)	0.3894	0.8932	0.0759	3.15	3.15	3.21	3.09	3.21	3.09
Daily Maximum Stomatal Conductance (cm/s)	0.0001	0.0510	0.8872	0.72	0.78	0.89	0.81	0.70	0.59

values following early afternoon closure. Elevated CO₂ caused reduced stomatal conductance in the morning and an earlier and more rapid recovery after early afternoon closure for plants in the WW treatment. Water-stressed plants at ambient CO₂ concentrations had higher stomatal conductance throughout the day than plants grown under water stress at +300 μLL⁻¹ CO₂. Plants in the WW treatment had higher stomatal conductance in general, although water-stressed plants at ambient CO₂ had similar values in the morning to plants grown in the WW ambient +300 CO₂ treatment.

The peak stomatal conductance values shown in Figure 1 are less than those reported for daily maximum stomatal conductances in Table 1. This is because the values reported in Table 1 are means generated from the maximum

Figure 1. The diurnal course of stomatal conductance for field-grown maize subjected to elevated CO_2 concentrations and water stress. Each point is a seasonal mean for the shown time period, with standard error bars. Well-watered (WW) and water-stressed (ws) treatments are shown separately. The +0 and +300 refer to CO_2 treatment concentrations of ambient +0 μLL^{-1} and ambient +300 μLL^{-1} , respectively.

values from each measurement day. The maximum values were not always attained at the same time of day. Therefore, the peak in the diurnal plots is the mean of some daily maximum values, and some values less than the maximum.

DISCUSSION

The degree of water stress in this experiment was severe. It is not surprising, then, that lower water potentials were observed in water-stressed plants. It should be noted, however, that the data presented in Table 1 are seasonal means. There were periods of time during the growing season when the differences in water potential between plants in the two water treatments was greater. Conversely, there were also periods, following irrigations of the ws treatment, when the water potential of all plants was very similar. Unlike the results reported by Paez (1983), CO_2 was unable to compensate significantly for water-stressed imposed decreases in water potential at the levels of water stress in this experiment.

Gross and net photosynthesis values compared well with values reported by previous investigators (Dwyer and Stewart, 1986; Rogers et al., 1983a,c). Unfortunately, the gross and net photosynthesis values cannot be compared within this experiment, due to the timing of the measurements, as was previously discussed. However, there is ample evidence that rates of net and gross photosynthesis in C4 plants are equal. We have verified that for maize, neither gross or net photosynthetic rates increase under elevated CO_2 . This finding is once again in agreement with previously reported studies (Louwerse, 1980; Rogers et al., 1983a; Wong, 1979; Ford and Thorne, 1967; Patterson and Flint, 1980).

There were no water stress effects on photosynthesis. This is in apparent disagreement with previous investigators (Boyer, 1970; Shinn and Lemon, 1968). It is probably due to the fact that measurements were taken during seasonal and diurnal periods when the water-stressed plants were not under severe stress. The measurements were taken at midmorning in weeks following irrigations of the water-stressed treatment, when water stress was least severe. Future studies should incorporate measurements of photosynthesis under many degrees of actual water stress.

Stomatal conductance was significantly reduced by both elevated CO_2 levels and water stress. The measured conductance values were lower than those reported by Rogers et al. (1983a). This was probably due to larger vapor

pressure deficits that are found in Livermore, California. Nearly all plants in this area undergo diurnal water stress in the summer months, causing reduced stomatal conductance.

Because the crop did not exhibit increased leaf area (Surano and Shinn, 1988), canopy transpiration was reduced as a function of reduced stomatal conductance. Reductions in seasonal water use (Surano et al., 1988) support this conclusion.

Increases in maize water-use efficiency (WUE) from this experiment were reported in another publication (Surano et al., 1988). The increases were due to both reduced seasonal water use and small increases in production under elevated CO_2 . Rogers et al. (1983c) hypothesized that increased production was possible without increases in photosynthetic rates because CO_2 -induced increases in WUE allowed plants to photosynthesize at normal rates for longer periods of time, both seasonally and diurnally. There is evidence to support this idea from this experiment, as seen in the plots of seasonal diurnal conductance values (Figure 1). During peak water-stress periods, increased WUE may have allowed plants to maintain satisfactory internal plant water status for longer periods. Plants may have been able to delay water-stress induced stomatal closure and termination of photosynthesis.

CONCLUSIONS

Severe water stress caused reductions in internal plant water status, as determined through measurements of plant leaf water potential. Elevated levels of CO_2 did not compensate for water stress effects on water potential. Gross and net photosynthesis were unaffected by elevated CO_2 concentrations.

Reductions in transpiration are the most important element in CO_2 -induced increases in the WUE of maize. Elevated CO_2 caused reduced stomatal conductance, reduced transpiration, and ultimately, reduced consumptive water use. The WUE increases can not only result in the savings of water and the persistence of maize in areas with reduced precipitation, but can possibly increase production as well. Many investigators have shown that decreases in maize stomatal conductance and transpiration result from elevated CO_2 in controlled environments and greenhouses. We have verified the physiological basis for increases in maize WUE in a field setting.

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**EFFECTS OF ELEVATED ATMOSPHERIC
CO₂ CONCENTRATIONS AND WATER STRESS
ON FIELD-GROWN MAIZE:
MORPHOLOGY AND PHENOLOGY**

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ABSTRACT

Most previous studies of CO₂ effects on maize have focused on biomass production because of the socioeconomic importance of crop yield. Few studies have examined more subtle CO₂ effects, which may also be important. This study examined the morphological and phenological effects of elevated CO₂ and water stress on field-grown maize.

Maize was grown at one of 4 seasonal daytime mean CO₂ concentrations (348, 431, 506, or 656 μLL^{-1}) in open-top field exposure chambers and at one of 2 levels of available water (well-watered or 50% of well-watered).

Water stress caused reductions in stem height, stem diameter and leaf area production. However, stem diameter was a poor indicator of morphological effects due to seasonal and diurnal variability in response to short-term water availability. Elevated CO₂ concentrations had no effect on the stem height or leaf area of maize, regardless of water treatment. Therefore, elevated CO₂ concentrations were unable to ameliorate water-stress induced reductions in stem height or leaf area.

Phenological development may have been delayed in water-stressed plants. The highest CO₂ treatment may have mitigated water stress-induced phenological effects. However, any phenological changes were minimal.

Maize grown under future elevated CO₂ concentrations will probably continue to develop at rates similar to those presently seen, and its morphology will not be significantly altered unless water stress becomes severe.

INTRODUCTION

Global atmospheric carbon dioxide (CO₂) concentrations have increased significantly during this century and will continue to increase in the future (Newman, 1980; Rosenberg, 1982). Elevated CO₂ levels may affect plants directly through effects on physiological rates, or indirectly through CO₂-induced climatic change (Lemon, 1983; Strain and Cure, 1985; Kramer, 1981). Plants use atmospheric CO₂ in photosynthesis and thereby provide the basis for all biological activity (Tolbert and Zelitch, 1983). Any CO₂ effects on plants may therefore have important implications for the entire biosphere.

Agriculture is likely to be impacted both directly and indirectly by future increases in atmospheric CO₂ levels (Tolbert and Zelitch, 1983; Wittwer, 1970, 1980, 1981, 1983; Newman, 1980; Rosenberg, 1982). Major agricultural areas, including the primary grain belts of the world, may experience warmer and drier

climates (Gates et al., 1983). For many crops, negative effects of climatic change may be partially mitigated by positive effects of increased photosynthetic rates and decreased transpiration (Strain and Cure, 1985; Paez, 1983, 1984; King and Greer, 1986). However, such amelioration of negative effects for species such as maize (*Zea mays* L.), that use the C4 photosynthetic pathway, may not occur. Positive CO₂ effects for maize through increased photosynthesis are unlikely because the C4 photosynthetic pathway is not CO₂-limited.

Most studies regarding CO₂ effects on maize have concerned biomass production because of the socioeconomic importance of yield (Ford and Thorne, 1967; Rogers et al., 1983a; Patterson and Flint, 1980; Surano et al., 1988; King and Greer, 1986; Wong, 1979; Gardner et al., 1981). Few studies have examined CO₂ effects on maize morphology and phenology. Even fewer studies have examined the combined effects of elevated CO₂ concentrations and water stress (Lemon, 1983). Additionally, most previous studies did not expose maize for entire growing seasons and/or were not conducted in the field (Surano et al., 1988).

It is generally agreed that maize grown under water stress may be stunted. Gardner et al. (1981) stated that the stem height of water-stressed maize plants was 50 cm less than that of well-watered plants. However, the stem height of maize has been shown to increase when the plants are grown under well-watered elevated CO₂ conditions (Ford and Thorne, 1967; Patterson and Flint, 1980). King and Greer (1986) showed that water-stress stunted maize, but elevated CO₂ levels reduced the degree of stunting. Similar amelioration of stunting by elevated CO₂ levels has also been demonstrated in tomato (*Lycopersicon esculentum* Mill.) (Paez et al., 1983). Stem diameters may also be affected by elevated CO₂ levels (Acock and Allen, 1983).

One study showed increased leaf area production for maize (Patterson and Flint, 1980). However, numerous studies of CO₂ effects on maize leaf area reported no increases (Ford and Thorne, 1967; Rogers et al., 1983a; Wong, 1979; King and Greer, 1986). Paez (1984) stated that reductions in leaf area in pea (*Pisum sativum* L.) due to water stress were compensated by elevated CO₂ levels. However, King and Greer (1986) indicated that elevated CO₂ levels were unable to ameliorate water stress-induced leaf area reductions in maize.

Baker and Enoch (1983) generalized that phenological rates increase in plants grown under elevated CO₂. However, Hesketh and Hellmers (1973) reported a decrease in maize phenological rate under elevated CO₂, while King

and Greer (1986) showed no change. Gardner et al. (1981) showed that water-stressed maize developed faster. King and Greer (1986) indicated that water stress caused a reduction in maize phenological rate, and that elevated CO₂ did not mitigate water-stress effects on phenology.

Morphological and phenological expressions of the interacting effects of elevated CO₂ and water stress on field-grown maize may be important. Negative effects of water stress might be alleviated under elevated CO₂. If elevated CO₂ levels cause increased stem heights, plants may have a tendency to lodge. Carbon dioxide may cause reduced leaf transpiration rates. But if CO₂ also causes increased leaf area, plants may actually have greater consumptive water use because they have more total transpiring area (Kimball, 1985; Chaudhuri, 1986). Taller plants with greater leaf area may be able to shade out competitors with greater efficiency, especially if the increased height and leaf area are produced earlier under elevated CO₂. However, if plants become taller and have greater leaf area, future planting densities may need adjustment, resulting in reduced yields per area planted.

Plants with CO₂-induced increases in phenological rates may have shortened life cycles and therefore be able to avoid periods of late-season drought. Earlier production of yield could result in cost savings and possibly allow double-cropping. Phenological delays resulting in longer rotation times may require increased production costs. Additionally, crops grown until late in the season may be more susceptible to drought, pests and low temperatures.

The effects of elevated CO₂ levels and water stress on the morphology and phenology of maize must be understood before any analysis of future elevated CO₂ effects can be completed. Presented here are the results of morphological and phenological measurements made on a maize crop subjected to long-term elevated CO₂ concentrations and water stress in open-top exposure chambers under otherwise normal field conditions. This study was conducted as part of an experiment examining a wide range of elevated-CO₂ and water-stress effects on maize. Results from other aspects of the study are reported elsewhere (Surano and Houpis, 1988; Surano et al., 1988).

MATERIALS AND METHODS

A detailed accounting of materials and methods for this experiment can be found in Surano et al. (1988). That document contains descriptions of the maize cultivar, cultural practices, field chambers, CO₂ exposure procedures, and

atmospheric sampling protocols. These topics are summarized below and are followed by a detailed discussion of morphological and phenological measurements.

Maize was field-grown at Livermore, California, in standard open-top exposure chambers (Heagle et al., 1973, 1979; Rogers et al., 1983b). Each experimental treatment consisted of one of 4 CO₂ concentrations and one of 2 levels of applied water. The experiment used a complete factorial design with 2 replications, for a total of 16 chambers. The exposures were designed to track ambient CO₂ concentrations seasonally and diurnally. The CO₂ treatment set-point concentrations were ambient +0, ambient +75, ambient +150, and ambient +300 μLL^{-1} . The seasonal mean ambient CO₂ concentrations was 350 μLL^{-1} . The seasonal mean daytime CO₂ treatment concentrations were 348, 431, 506 and 656 μLL^{-1} , respectively. The water treatments were well-watered (WW; 340-360 mm water in 6 irrigations) and water-stressed (ws; 150-180 mm water in 3 irrigations). The treatments began at emergence (20 June 1983) and were continuous through harvest (25 September 1983).

A hybrid maize cultivar (*Zea mays* L., cv. Funk G4040) was planted on a well-drained Rincon soil (Typic Palexeralf). Sixteen experimental plots were established. Each plot contained a randomly placed exposure chamber and an associated non-chambered control plot, termed a companion plot. Each chamber and companion plot contained 3 rows of 16-20 plants each. Separate drip-irrigation systems in each experimental area provided even distribution of water during irrigations.

Pure CO₂ was injected continuously into the chamber fan inlet air streams to increase the atmospheric concentrations of CO₂ in the treatment chambers. Carbon dioxide treatment concentrations were manually controlled by adjustment of the amount of pure CO₂ delivered to each chamber. Samples of ambient air and chamber atmospheres were drawn continuously from the chamber centers at a height of 1 m and were analyzed for CO₂ concentration with an infrared gas analyzer. Chamber CO₂ concentrations were sampled for 1 minute every 20 minutes. Ambient CO₂ concentrations were monitored continuously and averaged in 10-min intervals.

Weekly morphological measurements of stem height and stem diameter were made nondestructively on all plants in the middle row of each chamber and companion plot. Stem height was measured from the plant base to the tip of the highest outstretched leaf or tassel. Basal stem diameter was measured at two

perpendicular positions with calipers. Data from the two basal diameter measurements was averaged for each plant. A portable leaf area meter (Model LI-3000, LI-COR Inc., Lincoln, Nebraska) was calibrated and used to determine the leaf area of plants in situ on live leaves. Leaf area measurements were made on all plants from the middle row of each chamber after vegetative growth had ceased and plants were in the reproductive growth stages.

All morphology data collected from the chambers was normalized with data from the associated companion plots (see Surano et al., 1988). This normalization of the chamber data corrected for both field position and chamber effects.

Two-factor analyses of variance were performed on the morphology data (Sokal and Rohlf, 1969). The factors in the ANOVAs were CO₂ concentration and water treatment. Separate ANOVAs were run for each sampling date to determine the onset of treatment effects and if the effects persisted through the season. Fischer's Least Significant Difference multiple range test was used to test for significant differences between means of morphology data from different dates (Snedecor and Cochran, 1967).

Phenological stages of development were determined weekly by estimation of the percentage of all plants in a chamber or companion plot that had reached particular growth stages as defined by Ritchie and Hanway (1982). The collective grouping of plants in a chamber was said to have reached a particular phenological stage when at least 51% of the plants in the chamber had reached that particular stage. Vegetative phenological stages were based on the number of fully expanded leaves and were numbered V1-V17. When the tassel was exposed, a plant was said to be in the VT (tasseling) stage. When silks became visible, plants were said to be in the R1 (silking) stage. Other reproductive phenological stages (R2-R6) were difficult to determine, because limited numbers of ears were available for analysis. Exact determinations of the reproductive stages is based on kernel morphology and would have required destructive sampling of ears. Best estimates of the plants in these stages were made without ear destruction. However, all plants were in the R5 (dent) or R6 (physiological maturity: black layer formation) at final harvest.

Non-reproductive phenological stages were also difficult to quantify. The vegetative growth stages were based on fully expanded leaves. At any one time, a maize plant may have several leaves in partial expansion, often making the determination of vegetative growth stage somewhat subjective. Therefore, strict

statistical analyses were not warranted. Instead, the stages of growth of each treatment combination were plotted against time to see if any obvious trends could be discerned. However, one growth stage was easily determined. The VT (tasseling) stage was chosen as an objective measure of phenological development. Plants either had tassels or they did not. The percentages of plants showing tassels from each replication of each treatment combination were plotted against time and linear regression equations were fit to the data. The regression equations were used to estimate the day of the year that a given treatment would have 50% and 90% of its plants in the VT stage.

RESULTS

The ANOVA results for stem height are given in Table 1. Carbon dioxide and the CO₂ x water treatment interaction were insignificant throughout the season. However, beginning at mid-season and persisting through the remainder of the growing season, water stress caused a significant decrease in maize stem height (Figure 1). In the early stages of growth, stem heights significantly increased as the season progressed in both water treatments. However, in early August, plants in the ws treatment had significantly shorter stems than those in the WW treatment. By mid-August, plants in both treatments had achieved their maximum heights and the ws plants remained significantly shorter than those in the WW treatment. Plants in the WW treatment had a mean mature stem height of 285 cm, while those in the ws treatment had a mean mature stem height of 215 cm.

The ANOVA results for stem diameter are presented in Table 2. Carbon dioxide level and the CO₂ x water treatment interaction were not statistically significant in affecting stem diameter. Water treatment was a statistically significant factor. However, unlike the analysis for stem height, water treatment did not show any significant seasonal trends. The mean stem diameters for plants in the two water treatments over the growing season are shown in Figure 2. Water treatment was insignificant early in the season. In early August water treatment was a significant factor, but at the next measurement date water treatment was insignificant. By mid-August, water treatment was again a significant factor in determining stem diameter and continued to be a significant factor until early September, when it once again became insignificant. Plants in the WW treatment had a mean mature stem diameter of 3.6 cm, while those in the ws treatment had mean mature stem diameter of 3.0 cm.

Table 1. p values for 2-factor analyses of variance on stem height at various dates for maize subjected to elevated CO₂ and water stress in 1983. Values ≤ 0.05 are statistically significant.

Date	source of variation		
	CO ₂	Water	CO ₂ x Water
13 July 1983	0.4792	0.8606	0.3406
20 July 1983	0.6827	0.8554	0.2162
27 July 1983	0.4529	0.6436	0.3782
3 August 1983	0.3326	0.0056	0.9751
9 August 1983	0.3501	0.0041	0.8571
16 August 1983	0.1269	0.0007	0.4306
23 August 1983	0.2524	0.0004	0.3591
30 August 1983	0.2193	0.0003	0.3550
6 September 1983	0.2511	0.0009	0.3843
13 September 1983	0.1727	0.0002	0.3647

Figure 1. Seasonal stem heights of well-watered (WW) and water-stressed (ws) maize plants grown in open-top exposure chambers at Livermore, CA, 1983. Points labeled with the same letter are not significantly different.

Table 2. p values for 2-factor analyses of variance on stem diameter at various dates for maize subjected to elevated CO₂ and water stress in 1983. Values ≤ 0.05 are statistically significant.

Date	source of variation		
	CO ₂	Water	CO ₂ x Water
13 July 1983	0.1306	0.1408	0.0516
20 July 1983	0.6438	0.1450	0.4103
27 July 1983	0.0903	0.4464	0.1288
3 August 1983	0.1142	0.0245	0.4746
9 August 1983	0.7987	0.1335	0.4311
16 August 1983	0.0618	0.0039	0.7104
23 August 1983	0.0780	0.0038	0.3397
30 August 1983	0.0812	0.0056	0.0809
6 September 1983	0.2061	0.0715	0.5249

Figure 2. Seasonal stem diameters of well-watered (WW) and water-stressed (ws) maize plants grown in open-top exposure chambers at Livermore, CA, 1983. Points labeled with the same letter are not significantly different.

Carbon dioxide and the CO₂ x water treatment interaction were also insignificant factors in determining leaf area ($p \leq 0.80$ and 0.83 , respectively). Water stress significantly reduced leaf area ($p \leq 0.01$). Plants in the WW treatment had a mean mature leaf area of 5190 cm² plant⁻¹, while those in the ws treatment had a mean mature leaf area of 4690 cm² plant⁻¹.

The plots of phenological stages through the season are shown in Figure 3. There does not appear to be any discernable difference between the phenological rates of plants in the various CO₂ treatments in the WW treatment. However, the development of plants in the ambient +300 μLL^{-1} CO₂ treatment initially lagged behind but then increased in rate and overtook other CO₂ treatments. In the ws treatments, it appears that the development of plants in the ambient +0 μLL^{-1} CO₂ treatment consistently lagged behind those in the other CO₂ treatments. The delay occurred early and persisted throughout the season.

The phenology regression equations and their respective estimations of the day of the year that 50% and 90% of plants reached the VT stage are given in Table 3. These data show that the phenological development of the ws treatments was delayed. Approximately 50% of the plants in the WW treatments reached VT by day 218, and 90% of them reached VT by day 226. Under water stress, 50% of the plants in CO₂ treatments other than ambient +300 μLL^{-1} reached VT by day 221, and 90% reached VT by day 228. There is some indication that plants in the ws ambient +300 μLL^{-1} CO₂ treatment may have had their water stress-induced phenological retardation ameliorated. The number of days for those plants to reach VT corresponds well with the number of days needed by plants in the WW CO₂ treatments.

DISCUSSION

Elevated CO₂ had no effects on the morphology of maize, regardless of water treatment. Water stress, however, severely affected maize morphology. The degree of water stress in this experiment was extreme. It is not surprising that plants grown with half of the amount of water normally supplied to a well-watered crop were stunted and produced less leaf area.

Stem heights did not increase due to elevated CO₂ levels under well-watered conditions. This disagrees with previous reports of CO₂-induced maize stem height increases (Patterson and Flint, 1980; Ford and Thorne, 1967). However, those previous experiments were conducted in controlled environment chambers under less than full light conditions. Additionally, those experiments

Figure 3. Growth stages of well-watered (WW) and water-stressed (ws) maize at various CO₂ concentrations during the 1983 growing season at Livermore, CA. Carbon dioxide concentrations are expressed as μLL^{-1} above ambient background concentrations.

did not expose the crops to elevated CO₂ levels for the entire growing seasons. In another study, sorghum (*Sorghum bicolor* (L.) Moench.), another C₄ crop species, did not exhibit stem height increases under elevated CO₂ (Chaudhuri et al., 1986). Water stress alone caused a 70 cm reduction in stem height. This is an even greater reduction than previously reported (Gardner et al., 1981).

The effects of CO₂ were unable to even partially mitigate water stress-induced stem height, stem diameter, and leaf area changes. Partial mitigation of water stress effects on biomass production was demonstrated in this same experiment (Surano et al., 1988) and was shown for maize stem height in another study (King and Greer, 1986).

Stem diameter measurement proved to be a poor indicator of morphological change. Early in the season water treatment was an insignificant factor with respect to stem diameter. However, at this time the plants were small and the availability of water was high, due to pre-emergence saturation of the entire field soil profile (Surano et al., 1988). Once the plants achieved sufficient size and significant evapotranspiration had occurred, water stress-induced stem diameter effects were detected. However, after first detection of water-treatment

Table 3. Regression models predicting the day of the year (t) that each treatment would display a given percentage (%) of its plants in the VT (tasseling) stage of growth. The t_{90} and t_{50} values represent the number of days (based on the regression model) required for each treatment to have 90 and 50% of its plants, respectively, in the VT stage.

Treatment	Regression Equation	r^2	t_{90}	t_{50}
+0 ws	%=-1386 + 6.5t	0.83	227	221
+75 ws	%=-1141 + 5.4t	0.83	228	221
+150 ws	%=-1305 + 6.1t	0.88	229	222
+300 ws	%=-1302 + 6.2t	0.81	225	218
+0 WW	%=-1081 + 5.2t	0.82	225	218
+75 WW	%=-730 + 3.6t	0.68	228	217
+150 WW	%=-1368 + 6.5t	0.92	224	218
+300 WW	%=-1525 + 7.1t	0.99	227	221

effects on stem diameter on 3 August, the effect of water treatment on stem diameter was insignificant on 9 August and 6 September. These dates corresponded with dates of ws-treatment irrigations, which were conducted on 6 August and 2 September. Stem diameter can be affected by available water and may vary as soil water conditions change. Stem diameter variations exhibiting varying degrees of plasticity may be seen both seasonally and diurnally.

Leaf area was also unaffected by CO_2 treatments. This agrees with previously published reports (Wong, 1979; Rogers et al., 1983a; King and Greer, 1986). Water stress alone caused reductions in leaf area similar to those reported by King and Greer (1986). Carbon dioxide exposures were unable to compensate for water stress-induced leaf area reduction, again in agreement with King and Greer (1986). The potential for greater consumptive water use was not realized because leaf area did not increase and transpiration rates declined under elevated CO_2 (Surano and Houppis, 1988). This resulted in conservation of water and increased water-use efficiency (Surano et al., 1988).

An apparent discrepancy exists with respect to leaf biomass and leaf area data from this experiment. Leaf biomass production was reported to be unaffected by water stress (Surano et al., 1988), while leaf area was reduced. It is unlikely that specific leaf weights would be so severely affected by water stress. The discrepancy is resolved when one realizes that only live tissue was sampled for leaf area, but all leaf tissue was collected, dried and weighed for

biomass determinations. As the season progressed, plants under water stress exhibited senescence of older leaves. These leaves remained attached to the stems and were harvested for leaf biomass determinations at the final harvest, but were not sampled for leaf area.

In agreement with a previous study, elevated CO₂ did not affect the phenological development of maize grown under well-watered conditions (King and Greer, 1986). Again in agreement with King and Greer (1986), water stress may have caused a slight delay in phenological development of maize. However, unlike that reported by King and Greer (1986), elevated CO₂ in this experiment may have caused partial mitigation of water stress effects on maize phenology.

The subjectivity and degree of resolution of the phenological measurements, as well as the small nature of changes, make it impossible to make conclusive statements about phenological effects. If effects do exist, they are probably small, probably on the order of a few days. Therefore, the potentials for reduced or increased production costs, double-cropping, and avoidance of drought, pests, etc. under elevated CO₂ concentrations probably do not exist.

CONCLUSIONS

Severe water stress caused reductions in stem height, stem diameter and leaf area production of field grown maize. However, stem diameter was a poor measure of morphological change because effects changed as water availability was altered throughout the season. Elevated CO₂ levels had no effect on the morphology of maize, regardless of water treatment. Elevated CO₂ was therefore unable to mitigate water stress effects on maize morphology.

Maize grown under future elevated CO₂ concentrations will be unlikely to lodge since stem height does not increase under elevated CO₂. Leaf area will probably not increase, so planting densities will not need adjustment. Consumptive water use will decline, because transpiration rates will decrease through CO₂-induced stomatal closure and total transpiring area will not increase.

Phenological development of maize was possibly delayed under water stress. Carbon dioxide concentrations at ambient +300 μLL^{-1} may have allowed water-stressed plants to develop at rates similar to those of well-watered plants. The small nature (2-3 days) of phenological changes is probably insignificant with respect to maize production.

Maize will continue to develop at similar rates under future elevated CO₂ concentrations, and its morphology will not be significantly altered unless water stress becomes severe.

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**THE CARBON ECONOMY OF A MAIZE CROP
EXPOSED TO ELEVATED CO₂ CONCENTRATIONS AND WATER STRESS
DETERMINED FROM ELEMENTAL ANALYSES**

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ABSTRACT

Maize crops, grown in open fumigation chambers under field conditions, were exposed to four levels of atmospheric CO₂ and two levels of water. Photosynthetic and respiratory activities were assessed from elemental analyses of aboveground biomass. Elemental composition varied little with CO₂ or water treatment. The mean elemental composition of organic materials per 100 g biomass at a harvest during grain filling was C_{3.63} H_{6.04} N_{0.093} O_{2.87} S_{0.002}. (The balance of the mass, 3.08 g, was due to minerals.) That material had more C and H and less N and was more reduced chemically than preanthesis biomass. While crop growth rates were affected by CO₂ and water, the growth respiration factor (0.11 g C g⁻¹ biomass) and the fraction of estimated gross photosynthesis used in growth respiration were small and unaffected by treatment. It is estimated that net carbon storage amounted to 53% of gross photosynthesis while 14% went to growth respiration and 33% went to maintenance.

INTRODUCTION

The global rise in atmospheric CO₂ concentration may also bring changes in precipitation and temperature features of our climates. It is anticipated the N. American maize belt will experience higher temperatures and less rainfall than at present (Manabe et al., 1981). How agricultural production may respond is a matter of some concern.

The maximum photosynthesis rates of crops with a C3 photosynthetic system are limited by present CO₂ levels. Such crops can be expected to have a greater direct growth response to elevated CO₂ than those with C4 systems which are not so limited by CO₂ concentrations. In C4 crops such as maize, stomatal conductance declines with increases in CO₂ (Goudriaan and van Laar, 1978) and photosynthesis rate is maintained or increases some while transpiration declines.

Surano and Shinn (1984) proposed that the improved water use efficiency (WUE) of maize expected with elevated CO₂ would be an important factor allowing it to persist as a crop in climates with limited rainfall. They conducted a detailed field experiment at Livermore, California (USA) to document the behavior of maize with variations in atmospheric CO₂ and soil moisture supply. They found that increasing CO₂ increased WUE independent of water supply while development and yield were largely unaffected. Their measurements involved

only the dry weights of the plants and questions remain about whether changes in biochemical composition and respiratory metabolism also occurred.

The carbon economy of higher plants is defined by the relative rates of carbon fixation and reduction in photosynthesis on one hand and by carbon loss in respiration on the other. The oxidation level of carbon in substrate CO_2 is +4 while that of carbon in newly assimilated simple carbohydrates such as glucose is 0. The biomass synthesized from that assimilate is a complex of organic substances. Some substances are more reduced than glucose, some like cellulose are at the same level while others are more oxidized (e.g. organic acids). Taken together, biomass is generally more reduced (ΔH_c near 17 kJ g^{-1} for herbaceous material) than glucose ($\Delta H_c = 15.6 \text{ kJ g}^{-1}$).

Most of the reductant and energy for these syntheses is obtained by respiring a portion of the assimilated carbohydrate. That component of respiration can be termed synthesis respiration. Additional costs such as turnover of synthetic enzymes and messenger RNA, long-distance transport and ion uptake may be added to synthesis costs to yield growth and respiration (R_g) (Penning de Vries et al., 1974). The remaining component of the respiratory losses can be attributed to maintenance (R_m) of the existing system (Penning de Vries et al., 1975). Penning de Vries et al. (1974) offered a method for the calculation of R_g and production values (PV; g product per g glucose substrate used in synthesis) for individual organic products and for major classes such as lipids and proteins based on least-cost biochemical pathways. Similar values can be calculated for complex biomass given proximate analyses of the biomass and allowances for mineral uptake and transport.

McDermitt and Loomis (1981) offered an alternative approach in which the calculation of R_g as well as heat of combustion are based on elemental rather than proximate analyses. The basis of their approach is the assumption that the empirical elemental formula for 100 g of product biomass (1 mol),

should balance electrochemically. The reduction level of that formula biomass can be calculated:

$$r = 2x - h - 5n - 6s \quad (\text{Eq. 1})$$

where 5 and 6 are the oxidation numbers of the NO_3^- -N and SO_4^{2-} -S substrates. The value of r relates directly to the amount of respiration which occurred during biosynthesis. In addition, the coefficient c corresponds to the amount of

substrate required for carbon skeletons so the total glucose requirement for synthesis is predicted by:

$$\text{Glucose Equivalent (GE)} = c/6 - r/24 \text{ (mol glucose per mol}^{-1} \text{ biomass)} \quad (\text{Eq. 2})$$

since each glucose contains 6 carbons and 24 electrons are released in respiration (equivalent to 36 ATP or 12 NADH₂). The inverse of GE can be expressed as a Glucose Value (GV) equal to the g biomass formed per g glucose consumed, i.e. in the same units as PV. A theoretical comparison of calculated PVs and GVs revealed as apparent constancy for biomass formation (McDermitt and Loomis, 1981):

$$\text{PV} = 0.88 \text{ GV} \quad (\text{Eq. 3})$$

where 0.88 (termed the growth efficiency, Eg) relates to energy losses in metabolism. In an experimental study with sorghum (*Sorghum bicolor* Moench.), Lafitte (1985) obtained a constant value for Eg near 0.84 ± 0.02 .

The present experiment was conducted as a part of the experiment by Surano and Shinn (1984). Following McDermitt and Loomis (1981), we employed elemental analyses of the maize biomass to learn whether CO₂ or moisture levels influenced the reduction level (i.e., the biochemical composition) of the crop. That approach allowed us to also construct a budget for the carbon economy of the crop which included Rg.

MATERIALS AND METHODS

The plots at Livermore, California (37°42'N, 121°42'W) were sited on a well-drained Rincon soil (Typic Palexeralf; Welch et al., 1966). The land was fertilized uniformly with 327 kg N, 78 kg P and 149 kg K per ha, ridged into 76-cm rows and pre-irrigated to fill the profile. Kernels of hybrid maize (early maturing cv. Funk G4040) were planted on 13 June 1983 at a density of 5.4 kernels m⁻¹ (71,000 plants ha⁻¹). Final stand was close to the planted density. The treatments were arranged in a randomized complete block design with two water treatments, four CO₂ levels and two replications. Each plot was 7.6 by 9.8 m.

CO₂ was controlled in open-top, transparent exposure chambers as described by Rogers et al. (1983). Each chamber was 3 m in diameter and 3.3 m high, enclosing about 50 plants. Turbulent air enriched in CO₂ was delivered at

ground level; the upper 0.9 m of the chamber was formed as a frustrum with the diameter narrowing to 2.1 m to limit fluctuations in CO₂ concentration. CO₂ fumigation began 20 June. Between then and 25 September, average daytime concentrations were 348 (near ambient), 431, 506 and 656 ppm (v/v) while average nighttime values were 373, 457, 535 and 686 ppm. These treatments are referred to here as ambient, +75, +150 and +300, respectively. The seasonal averages for day and night temperatures within the chambers were 27±3°C and 18±3°C, respectively (Surano and Shinn, 1984).

Water was supplied in a uniform manner through a drip-irrigation system. Well-watered plots (W) received 340 to 360 mm of water in six post-emergence irrigations and water stressed plots (w) received 150 to 180 mm of water in three irrigations. Surano and Shinn (1984), using neutron probe methods, found little influence of CO₂ level on seasonal water use (mean of 365 mm for the W treatment and 245 mm for the w treatment). Water-use efficiency (WUE) was affected little by irrigation level, but increased as CO₂ increased. With ambient CO₂, 52 kg of aboveground dry matter was produced per mm whereas 70 kg mm⁻¹ was obtained with +300 CO₂. The treatments did not affect developmental rates. More details are provided by Surano and Shinn (1984).

Plant samples were collected on 2 August (harvest 1; 47 days after planting (DAP) as tassels emerged) and 20 September (harvest 2; 96 DAP, near the end of the effective grain-filling period while the leaves were still green). Two representative plants were harvested at ground level from near the center of each plot. Dry weights were determined after oven drying. Subsamples were dried by lyophilization and ground to pass a 0.4 mm screen for elemental analyses.

Carbon, H, and N contents of the lyophilized material were determined by the Dumas combustion method by the University of California (Berkeley) Microanalytical Laboratory. The oxygen content of the tissue was calculated as the difference between the original weight and the C, H, N and mineral contents excluding the inorganic oxygen of PO₄³⁻, NO₃⁻, and SiO₂. Contents of S, P, K, Mg, Ca, Na, Fe, Al, Mn, B, Cu, and Zn were determined by atomic absorption by the A&L Western Agricultural Laboratory, Modesto, California. Separate determinations of NO₃-N (Thayer and Huffaker, 1980), SO₄-S, Cl and SiO₂ were made in our own laboratory. Sulfate and Cl were present only in traces. Silica was determined using traditional methods of NaOH fusion with ashed material and spectrophotometric assay of SiO₂ in the resulting solution (Fox et al., 1969).

This method yielded organic O contents near 45% of the dry matter. More direct methods for O such as activation analysis and the Dumas oxygen method worked poorly with our material. Water, of course, is a serious contaminant for all these methods through either weight dilution or oxygen addition and great care was taken in drying and for maintenance of dessication. C, H and N analyses were reported to four significant figures while the other analyses and plant data were carried to three. To avoid systematic rounding errors, atomic weights were introduced at five significant figures and the calculations were carried at 15 before rounding for presentation here.

RESULTS

The empirical formulae of the biomasses are reported in Table 1. Increasing CO₂ level had little influence on elemental composition except for a slight dilution of nitrogen and a slight increase in oxygen at harvest 1. Oxygen declined slightly with increasing CO₂ at harvest 2. More dramatic changes occurred with age: the concentrations of both carbon and hydrogen were significantly greater while nitrogen was less at harvest 2 ($P < 0.010$).

Those formulae give the skeletal carbon content (c) and serve as the basis for calculation of reduction level (r). Both are required in the calculation of the amount of glucose used in the production of the tissue (GE) (Table 2). The maize biomasses were all more reduced than glucose so the values of r are negative. The biomass was generally more reduced at harvest 2 than at harvest 1 ($P < 0.1$) following the increase in hydrogen. There was a trend toward a decrease in the reduction level with water stress, particularly at the first harvest, but that effect was not significant. CO₂ level had no direct effect on r but the interaction between CO₂ treatment and harvest date was significant ($P < 0.025$). At harvest 1, r appears to have declined with increasing CO₂. At harvest 2, that trend was reversed.

GE values tended to follow the trends in the r values, but they were influenced much more directly by carbon concentration (very strong positive correlation). More glucose was required for the synthesis of a unit of biomass from harvest 2 (high carbon, low nitrogen) than from harvest 1 ($P < 0.010$). Water stress and CO₂ level had no effect on GE but a significant interaction between harvest date and CO₂ was again observed.

Yields of aboveground biomass and estimates of cumulative net photosynthesis and respiration associated with growth also are presented in

Table 1. Elemental formulae for aboveground biomass of maize grown with variation in supplies of CO₂ and water (means of two replicates).

Treatment		Elemental Formula					Mean
Water	CO ₂						
<u>Harvest 1</u>							
W	ambient	C _{3.51}	H _{5.78}	N _{0.163}	O _{2.82}	S _{0.0012}	C _{3.51} H _{5.76} N _{0.133} O _{2.84} S _{0.0018}
	+75	C _{3.56}	H _{5.75}	N _{0.119}	O _{2.82}	S _{0.0014}	
	+150	C _{3.53}	H _{5.81}	N _{0.168}	O _{2.84}	S _{0.0020}	
	+300	C _{3.44}	H _{5.68}	N _{0.131}	O _{2.87}	S _{0.0023}	
w	ambient	C _{3.50}	H _{5.58}	N _{0.153}	O _{2.86}	S _{0.0016}	C _{3.50} H _{5.70} N _{0.130} O _{2.87} S _{0.0015}
	+75	C _{3.49}	H _{5.60}	N _{0.136}	O _{2.85}	S _{0.0016}	
	+150	C _{3.49}	H _{5.76}	N _{0.132}	O _{2.87}	S _{0.0016}	
	+300	C _{3.53}	H _{5.89}	N _{0.101}	O _{2.90}	S _{0.0014}	
<u>Harvest 2</u>							
W	ambient	C _{3.63}	H _{6.05}	N _{0.089}	O _{2.88}	S _{0.0017}	C _{3.63} H _{6.07} N _{0.088} O _{2.87} S _{0.0018}
	+75	C _{3.62}	H _{6.06}	N _{0.087}	O _{2.88}	S _{0.0020}	
	+150	C _{3.64}	H _{6.05}	N _{0.089}	O _{2.85}	S _{0.0014}	
	+300	C _{3.65}	H _{6.13}	N _{0.088}	O _{2.85}	S _{0.0019}	
w	ambient	C _{3.59}	H _{5.99}	N _{0.096}	O _{2.89}	S _{0.0020}	C _{3.62} H _{6.00} N _{0.098} O _{2.87} S _{0.0020}
	+75	C _{3.63}	H _{5.99}	N _{0.095}	O _{2.89}	S _{0.0022}	
	+150	C _{3.62}	H _{5.91}	N _{0.101}	O _{2.86}	S _{0.0022}	
	+300	C _{3.66}	H _{6.10}	N _{0.099}	O _{2.84}	S _{0.0016}	

Molar formula weights for substances of unknown molecular weight or composition are 100 g including minerals.

Table 2. The biomass yields on 20 September were in the range of 13 to 22 t ha⁻¹. Yields tended to be greater with elevated CO₂, particularly for the stressed plants; reduction in water supply reduced yield sharply. The standing biomasses also are presented in terms of elemental carbon under the heading Pnet (net photosynthesis). The sum of Pnet and Rg ("production photosynthesis") is also included. Respiration associated with growth (Rg) was estimated following McDermitt and Loomis (1981) using $E_g = 0.84 \pm 0.02$ (Lafitte, 1985) so that

$$R_g = 0.137GE - 0.030r \text{ (kg C kg}^{-1} \text{ new biomass) (Eq. 4).}$$

Table 2. Standing crops of maize, grown with variations in supplies of CO₂ and water, expressed as dry matter and as carbon (Pnet; kg C/ha) and the estimated growth respiration (Rg) and production photosynthesis (Pnet + Rg) required in their production. Specific Rg=0.137GE- 0.03r where GE (Glucose Equivalent) and r (reduction level) were calculated from the elemental analyses of Table 1.

Treatment		Rg calculation			Standing Crop Characteristics			
Water	CO ₂	r (mol elect [100g] ⁻¹)	GE (mol glucose [100g] ⁻¹)	Specific Rg (g C g ⁻¹ DM)	Dry Matter (kg/ ha)	Pnet (kg C/ ha)	Rg (kg C/ ha)	Pnet + Rg (kg C/ ha)
Harvest 1								
W	Ambient	-0.959	0.624	0.114	8590	3620	980	4600
	+75 ppm	-0.709	0.623	0.107	8760	3490	870	4360
	+150 ppm	-0.733	0.619	0.107	8800	3730	940	4670
	+300 ppm	-0.603	0.599	0.100	5680	2350	570	2920
	Mean	-0.751	0.616	0.107	7810	3290	840	4130
w	Ambient	-0.634	0.609	0.103	4970	2090	510	2600
	+75 ppm	-0.593	0.606	0.101	6040	2530	610	3140
	+150 ppm	-0.687	0.609	0.104	5960	2500	620	3120
	+300 ppm	-0.614	0.613	0.102	6890	2920	710	3630
	Mean	-0.632	0.610	0.102	5960	2510	610	3120
Harvest 2								
W	Ambient	-0.749	0.635	0.110	18700	8140	2050	10190
	+75 ppm	-0.745	0.635	0.109	21000	9140	2300	11440
	+150 ppm	-0.799	0.640	0.112	21200	9260	2370	11630
	+300 ppm	-0.874	0.644	0.115	21900	9600	2510	12110
	Mean	-0.792	0.639	0.111	20700	9030	2300	11330
w	Ambient	-0.697	0.628	0.107	13600	5870	1450	7320
	+75 ppm	-0.710	0.634	0.108	14600	6360	1580	7940
	+150 ppm	-0.708	0.633	0.108	13700	5960	1480	7440
	+300 ppm	-0.925	0.647	0.116	17000	7460	1980	9440
	Mean	-0.760	0.636	0.110	14700	6410	1620	8030

This value was multiplied by the standing crop to yield an estimate of growth respiration for the crop. Specific Rg varied little from 0.11.

In the interval between harvests 1 and 2, crop growth rates (CGR) differed markedly between water treatments: 263 kg dry matter ha⁻¹ day⁻¹ in W versus only 179 kg in w (Table 3). The means for the CO₂ treatments were variable,

increasing from 191 to 248 kg dry matter ha⁻¹ day⁻¹ with increasing CO₂. However, that was mainly due to an unusual gain in the W+300 treatment after a low yield in that treatment on 2 August, making the effect suspect.

We assumed that the specific maintenance respiration rate was 0.005 kg C kg⁻¹ biomass day⁻¹ and that it did not vary with age or treatment. That value was derived from McCree's (1983) work with sorghum in the vegetative stage. His whole-plant maintenance coefficient, 0.02 kg C kg C⁻¹ day⁻¹ at 30°C, translates to about 0.008 kg C kg biomass⁻¹ day⁻¹. The 0.008 value, corrected with Q₁₀=2 for the sinusoidal diurnal temperature variation at the experimental site, yielded 0.005 as the estimate for the mean daily specific maintenance rate. Estimated crop R_m for the W treatment averaged 71 kg C ha⁻¹ day⁻¹ between harvests 1 and 2 (Table 3) (mean biomass near 14,250 kg ha⁻¹) while that for the w treatment (mean biomass near 10,350 kg ha⁻¹) was 57 kg C ha⁻¹ day⁻¹.

DISCUSSION

Among the principal findings from this research was that the elemental composition of maize biomass was affected only a small amount by harvest date and even less by water and CO₂ treatments. In fact, our results were little different from those of Latshaw and Miller (1924) for maize grown in Kansas (USA). Comparing the mean result for harvest 2 with Latshaw and Miller's data for a similar stage of growth:

Mean for harvest 2:	C _{3.63}	H _{6.04}	O _{2.87}	N _{0.093}	S _{0.002}
Latshaw and Miller:	C _{3.63}	H _{6.18}	O _{2.78}	N _{0.104}	S _{0.005}

It seems that the elemental composition of maize biomass is little changed by 60 years of plant breeding and little affected by the differences between California and Kansas environments.

The mean reduction level (r) for all observations was -0.73, i.e., the biomass contained 0.73 mol more electrons per 100 g than glucose. Specific heats of combustion calculated from r and GE with equations developed by McDermitt and Loomis (1981) averaged 16 kJ g⁻¹ for data from harvest 1 and 17 kJ g⁻¹ for harvest 2 compared to 15.6 kJ g⁻¹ for glucose. The difference between harvests was significant (P<0.050). The small reduction relative to glucose derives from the modest levels of H and N found in the empirical formulae

Table 3. Daily Crop Growth Rates (CGR) in terms of dry matter and carbon for maize crops for the interval harvest 1 to harvest 2 (49 days) when grown with variations in supplies of CO₂ and water. Daily values of R_g, P_{net} and estimated maintenance respiration (R_m) were summed to provide an estimate of gross photosynthesis (P_g) in terms of carbon.

Treatment		CGR	CGR (P _{net})	R _g	R _m *	P _g
Water	CO ₂	(kg DM/ ha / day)	(kg C/ ha / day)	(kg C/ ha / day)	(kg C/ ha / day)	(kg C/ ha / day)
W	ambient	206	92	22	68	173
	+75 ppm	262	115	29	73	217
	+150 ppm	253	113	29	75	217
	+300 ppm	331	148	40	69	256
	mean	263	117	30	71	218
w	ambient	176	77	19	46	143
	+75 ppm	175	78	20	52	150
	+150 ppm	158	71	18	49	137
	+300 ppm	206	93	26	60	178
	mean	179	80	20	52	152
Relative Values (%)						
W	ambient		51	12	37	100
	+75 ppm		53	14	34	100
	+150 ppm		52	14	35	100
	+300 ppm		58	16	27	100
	mean		53	14	33	100
w	ambient		54	14	32	100
	+75 ppm		52	13	34	100
	+150 ppm		51	13	36	100
	+300 ppm		52	15	33	100
	mean		52	14	34	100

* Specific R_m = 0.005 g C/ g biomass / day after adjustment for diurnal variations in temperature. Biomass was assumed to increase in a linear manner from harvest 1 to harvest 2.

(Table 1) indicating the presence of only small amounts of strongly reduced compound such as lipids and amino nitrogen. That conclusion is not unexpected since we know that maize biomass normally is dominated by carbohydrates

(cellulosic material, starch and sugars) (Subcommittee on Feed Composition, 1982).

Proximal analyses of various biochemical classes are needed if we are to fully explain the variations in r . It may be possible to estimate biochemical composition from elemental analyses. Gnaiger and Bitterlich (1984), for example, offered a mathematical protocol for predicting contents of protein, lipid, carbohydrate and residual water from C, H, and N analyses. (Residual water, chemically bound to free amino acids, sugars and other materials, remains in samples after drying.) The first step involves assignment of portions of the C, H, and N contents to nitrogenous compounds using an empirical formula for protein. Applied to our data, their method predicted that protein varied from 7 to 14% of the organic fraction while 80 to 90% was carbohydrate. The results for water and lipid, however, were erratic (e.g., negative values for lipids).

We obtained a better estimate of the carbohydrate fraction after first making empirical corrections for lignin, lipid, organic acids and water. Empirical formulae for nitrogenous compounds in maize leaves and grain were used. With this approach, the residual portions of C, H, and N matched reasonably with those expected in carbohydrates. The sum of the residual C, H, and O varied from 67 to 77% of the organic material with the lowest values occurring at harvest 1 at the lower levels of CO_2 . The overall mean composition was 10% protein and 74% carbohydrate in addition to minerals and the assumed contents of lipid, lignin, organic acids and water.

The interaction between CO_2 level and harvest date on r values was explained in part by that analysis. Carbohydrate content tended to increase with increasing CO_2 at harvest 1 but not at harvest 2. It is dangerous to proceed too far with these estimates of composition, however, since the calculations are sensitive to O content and to assumptions about residual water and the elemental composition of protein (the N content of plant proteins ranges between 14 and 18%).

Our construction of the carbon economy of the maize crops (Table 2 and 3) encountered additional variability in production estimates due to the limited sample size. This is particularly evident in the low yield for W+300 at harvest 1. Specific R_g is independent of that problem, however, and the small values there (0.10 to 0.12 g C g⁻¹) reflect the small values for r found from the elemental analyses. A strong correlation between R_g and r ($r^2 = 0.92$) indicated that variations in r were dominant over GE in Equation 4.

Net photosynthesis is rather clearly defined here by the absolute C content of the biomass. Since chemical bond energy is conserved in metabolism, a better picture emerges when the r value or heat of combustion is also known. The theoretical basis for the calculation of r and specific R_g is sound. Those values are influenced so strongly by final composition that uncertainties about the value of E_g and its influence on Equation 4 have small effect. The principal uncertainties about photosynthesis in maize are seen to lie more with R_m rather than with R_g or net photosynthesis.

While R_m was estimated only crudely, it appeared to constitute a large fraction (ca. 33%) of crop photosynthesis during the measurement period. Wilson et al. (1980) found that specific R_m for young sorghum plants declined significantly during a drying cycle. Whether that was due to dilution of metabolic components through the accumulation of carbohydrate or to less ion leakage from roots and whether it would also occur in adapted plants over a growing season are unknown. Allowance for that effect would lower the estimates of R_m and gross photosynthesis shown in Table 3 for the stressed plants unless offset by higher temperatures. Our findings are also limited by the absence of data for the root systems. Surano and Shinn (1984) found from a partial sampling that root production increased with CO_2 level in the well watered crops. Inclusion of root data would increase all of the estimates of carbon exchange by an amount proportional to root mass (i.e., by perhaps 15 to 20%).

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Appendices

1983 LLNL Elevated CO₂/Water Stress Maize Experiment

Chamber Number	Designed CO ₂ Set Point μL/L > ambient (A)	Daytime CO ₂ Concentration μL/L > ambient (A)	Seasonal Mean Daytime CO ₂ μL/L	Water Treatment
1	A+150	A+156	509	stress
2	A+75	A+81	434	stress
3	A+0	A-3	350	stress
4	A+75	A+78	431	W W
5	A+0	A-3	350	stress
6	A+300	A+303	656	stress
7	A+75	A+80	433	stress
8	A+300	A+304	657	W W
9	A+300	A+305	658	stress
10	A+150	A+154	507	stress
11	A+0	A-5	348	W W
12	A+75	A+80	433	W W
13	A+300	A+305	658	W W
14	A+150	A+154	507	W W
15	A+0	A-2	351	W W
16	A+150	A+153	506	W W
Ambient	A	A	353	-

CO ₂ Level	Stress Plots	W.W. Plots
0	3; 5	11; 15
75	2; 7	4; 12
150	1; 10	14; 16
300	6; 9	8; 13

Appendix 1. Treatments and Experimental Field Map

Chambers	humic	CEC	base sat	pH	P	K	Ca	Mg	Mn	Zn	Cu	NO3
13-16	%vol	meq (100 cm ³) ⁻¹	% of CEC		ppm	ppm	ppm	ppm	ppm	ppm	ppm	ppm
1	1.0	18.1	98	6.9	144	515	2647	352	8.4	6.8	2.5	2.1
2	1.4	16.8	95	6.9	48	257	2305	349	6.7	9.5	2.2	3.2
3	0.9	17.3	98	6.9	154	465	2512	329	8.4	6.2	2.0	1.8
4	1.1	18.4	98	7.1	84	326	2647	413	6.4	13.0	2.0	2.5
5	0.9	17.8	98	6.8	183	486	2609	384	9.3	8.3	2.8	2.2
6	1.3	14.9	95	6.7	58	254	2056	285	7.3	10.4	2.3	1.6
mean	1.1	17.2	97	6.9	112	384	2463	352	7.8	9.0	2.3	2.2
SD	0.2	1.3	2	0.1	56	119	238	44	1.1	2.5	0.3	0.6
9-12												
1	1.3	18.3	96	6.8	71	359	2590	341	7.3	5.4	2.4	1.7
2	1.2	16.4	95	6.7	24	187	2337	310	7.4	10.2	2.2	0.8
3	1.0	19.1	96	6.9	113	396	2656	376	7.0	4.9	2.3	1.0
4	0.8	16.8	95	7.0	57	225	2305	368	7.1	9.8	2.1	0.9
5	1.1	18.7	96	6.6	39	308	2444	313	7.8	2.9	2.5	2.5
6	1.1	15.3	95	6.8	65	231	2152	281	7.1	9.9	2.2	0.8
mean	1.1	17.4	96	6.8	62	284	2414	332	7.3	7.2	2.3	1.3
SD	0.2	1.5	1	0.1	31	83	188	37	0.3	3.2	0.1	0.7
5-8												
1	1.1	16.7	93	6.4	39	255	2218	313	8.4	2.3	2.1	0.8
2	1.1	19.2	96	6.8	27	177	2787	385	7.2	6.0	2.1	0.8
3	1.1	15.0	95	6.7	36	120	2174	225	6.9	20.5	1.9	0.8
4	1.1	16.9	95	6.7	38	157	2351	374	7.7	4.8	1.9	0.9
5	0.9	15.2	95	6.9	145	527	2010	266	7.4	5.2	2.1	0.9
6	1.4	15.7	90	6.3	52	314	2163	256	8.8	3.3	2.6	1.7
mean	1.1	16.5	94	6.6	60	258	2284	303	7.7	7.0	2.1	1.0
SD	0.2	1.6	2	0.2	14	149	270	66	0.7	6.7	0.3	0.4
1-4												
1	0.9	18.4	93	6.5	46	330	2498	314	8.3	2.7	2.4	1.7
2	1.0	20.1	96	6.9	28	187	2876	433	6.9	9.8	2.1	1.6
3	1.0	15.1	92	6.4	45	317	1970	267	10.3	3.0	2.5	1.0
4	1.0	19.6	96	6.9	25	170	2838	404	7.0	6.3	2.1	0.8
5	1.1	12.8	91	6.4	42	263	1633	210	9.2	2.1	2.0	0.8
6	1.0	13.4	94	6.8	36	150	1857	254	6.9	5.8	2.2	0.8
mean	1.0	16.6	94	6.7	37	236	2279	314	8.1	5.0	2.2	1.1
SD	0.1	3.2	2	0.2	9	78	531	88	1.4	2.9	0.2	0.4

Appendix 2. Preplant Soil Analysis

1983 LLNL Elevated CO₂/Water Stress Maize Experiment

deviations from ambient in $\mu\text{L/L}$
7/1-9/19 diurnal hourly
means

CHAM +CO ₂	3	5	11	15	2	7	4	12	1	10	14	16	6	9	8	13	
Hour	S	S	W	W	S	S	W	W	S	S	W	W	S	S	S	S	Ambi ent
5	7	8	0	4	94	80	91	89	177	171	167	162	322	329	322	320	366
6	2	1	-2	0	81	75	79	80	165	161	158	154	314	320	313	312	362
7	-4	-4	-3	-1	71	71	73	77	148	149	149	146	299	304	297	298	359
8	-6	-6	-6	-4	75	76	77	80	149	151	152	151	301	303	301	299	352
9	-8	-9	-10	-8	72	75	75	77	151	149	148	149	294	301	301	293	352
10	-10	-10	-12	-10	73	75	74	76	154	149	150	149	298	299	301	294	351
11	-8	-8	-11	-9	76	77	75	77	154	150	149	150	299	297	299	297	350
12	-7	-7	-11	-9	78	79	75	76	154	150	148	150	300	296	300	299	349
13	-7	-7	-10	-8	79	79	75	75	152	147	149	150	298	295	298	303	348
14	-6	-6	-8	-7	79	80	75	76	151	146	148	150	297	294	294	300	348
15	-4	-5	-5	-4	80	81	76	77	151	147	149	151	297	296	294	303	348
16	-3	-4	-4	-2	81	81	76	78	150	149	150	152	298	297	296	306	348
17	-4	-1	0	3	84	85	79	81	155	155	156	156	301	302	302	311	349
18	3	4	4	10	91	90	85	90	162	166	169	163	311	317	314	322	352
19	9	8	7	13	97	94	90	95	169	173	174	168	319	324	321	325	355
20	6	6	3	12	95	90	90	95	169	172	174	165	317	325	321	323	361
21	6	8	2	9	96	87	87	91	170	171	173	163	316	327	317	324	365
22	9	10	2	8	97	84	90	92	172	169	168	162	313	321	316	317	368
23	6	9	0	7	96	83	90	91	173	168	167	160	315	323	317	316	370
0	8	10	1	8	96	82	91	92	172	169	166	161	313	321	315	312	369
1	8	11	1	9	97	82	92	92	172	168	167	161	312	319	315	313	369
2	8	8	1	9	96	79	91	89	173	168	166	160	319	325	319	318	368
3	7	9	0	8	95	76	90	89	174	167	166	158	315	323	317	315	370
4	7	8	0	6	96	78	93	90	177	171	169	162	324	333	324	324	367
Day Av	-3	-3	-5	-2	81	80	78	80	156	154	154	153	303	305	304	305	353
Day SD	5.7	5.8	5.8	7.1	7.8	6.0	5.7	6.1	8.4	9.0	8.7	6.2	8.8	11.6	9.3	10.3	5.6
CONC	350	350	348	351	434	433	431	433	509	507	507	506	656	658	657	658	353
Nite Av	7	9	1	8	96	82	90	91	172	169	168	161	316	324	318	318	367
Nite SD	1.1	1.5	1.1	1.7	0.7	4.4	1.7	1.9	2.3	1.7	3.0	2.0	3.7	4.1	3.0	4.6	2.9
CONC	374	376	368	375	463	449	457	458	539	536	535	528	683	691	685	685	367

Appendix 3. Seasonal Mean CO₂ Concentration

C.P.	CO2	water	#	row	stem	lvs	#mat	#imm	# total	mat	imm	total	grain	AGB
			plants		DW	DW	10 ⁴	10 ⁵	ears	DW	DW	ears	DW	DW
					10 ⁶	10 ⁵	per ha	per ha	10 ⁵	10 ⁶	10 ²	10 ⁶	10 ⁶	10 ⁷
					g/ha	g/ha			per ha	g/ha	g/ha	g/ha	g/ha	g/ha
1	A+0	ws	15	west	6.43	3.28	3.31	1.37	1.70	2.71	0.71	2.71	2.23	0.95
1	A+0	ws	12	middle	6.15	3.76	2.37	1.54	1.78	1.26	2.17	1.26	1.03	0.78
1	A+0	ws	12	east	6.12	3.45	3.55	1.12	1.48	3.59	0.06	3.59	2.95	1.01
2	A+0	ws	12	west	6.63	3.25	4.14	1.07	1.48	3.28	0.74	3.28	2.76	1.02
2	A+0	ws	12	middle	7.49	3.97	2.37	2.07	2.31	3.28	3.40	3.28	2.76	1.12
2	A+0	ws	15	east	6.19	2.66	5.21	0.38	0.90	7.38	0.05	7.38	6.22	1.38
3	A+0	ws	12	west	5.24	3.14	6.51	0.18	0.83	6.50	0.12	6.50	5.17	1.21
3	A+0	ws	12	middle	3.70	2.77	2.96	1.30	1.60	1.80	2.66	1.80	1.43	0.58
3	A+0	ws	12	east	4.76	3.32	3.55	0.77	1.12	3.19	0.01	3.19	2.54	0.83
4	A+0	WW	12	west	6.66	3.33	6.51	1.36	2.01	6.25	3.14	6.25	4.92	1.32
4	A+0	WW	12	middle	5.68	3.15	6.51	1.01	1.66	4.39	3.18	4.39	3.45	1.04
4	A+0	WW	12	east	6.22	3.71	5.33	1.01	1.54	6.14	0.26	6.14	4.83	1.27
5	A+0	ws	12	west	6.83	4.25	2.96	0.95	1.24	3.26	7.20	3.26	2.69	1.05
5	A+0	ws	12	middle	6.30	3.81	1.18	1.95	2.07	0.73	5.60	0.73	0.60	0.74
5	A+0	ws	12	east	6.75	4.52	2.37	2.13	2.37	1.62	0.60	1.62	1.34	0.88
6	A+0	ws	12	west	5.99	3.52	2.96	1.60	1.89	2.92	3.13	2.92	2.41	0.93
6	A+0	ws	11	middle	6.12	3.87	3.87	1.55	1.94	3.51	1.69	3.51	2.90	1.00
6	A+0	ws	11	east	6.46	4.55	3.23	1.03	1.36	3.05	0.28	3.05	2.52	1.00
7	A+0	ws	12	west	6.24	3.40	5.33	1.07	1.60	5.84	1.25	5.84	4.71	1.24
7	A+0	ws	12	middle	5.14	2.94	1.78	1.12	1.30	1.74	4.70	1.74	1.41	0.72
7	A+0	ws	12	east	6.24	2.97	4.73	1.01	1.48	4.13	0.10	4.13	3.33	1.07
8	A+0	WW	12	west	5.01	3.14	4.73	1.30	1.78	4.08	4.41	4.09	3.34	0.94
8	A+0	WW	12	middle	7.80	4.20	5.92	0.59	1.18	6.90	3.31	6.90	5.63	1.51
8	A+0	WW	12	east	6.53	3.68	5.33	1.18	1.72	6.93	0.37	6.93	5.66	1.38
9	A+0	ws	12	west	7.61	3.85	3.55	0.95	1.30	3.81	4.07	3.81	2.88	1.18
9	A+0	ws	12	middle	5.72	2.82	2.96	1.07	1.36	1.25	2.69	1.25	0.94	0.73
9	A+0	ws	12	east	6.88	3.01	2.37	1.36	1.60	2.10	0.34	2.10	1.59	0.93
10	A+0	ws	12	west	6.81	4.07	3.55	1.36	1.72	2.14	5.06	2.14	1.67	0.94
10	A+0	ws	12	middle	5.91	3.53	1.18	2.37	2.49	0.44	5.71	0.44	0.34	0.67
10	A+0	ws	11	east	7.10	3.02	5.81	0.45	1.03	6.50	0.46	6.50	5.06	1.39
11	A+0	WW	12	west	8.46	4.38	6.51	0.89	1.54	9.55	0.79	9.55	7.81	1.84
11	A+0	WW	12	middle	6.35	3.11	7.10	0.36	1.07	7.61	1.23	7.61	6.23	1.43
11	A+0	WW	12	east	8.03	4.21	8.28	0.59	1.42	8.09	0.07	8.09	6.62	1.65
12	A+0	WW	12	west	8.57	3.05	7.10	0.12	0.83	11.61	0.36	11.61	9.20	2.05
12	A+0	WW	12	middle	7.11	2.91	4.73	0.89	1.36	4.34	4.10	4.34	3.44	1.17
12	A+0	WW	10	east	7.14	3.66	5.68	0.57	1.14	7.49	0.04	7.49	5.94	1.50
13	A+0	WW	12	west	7.87	4.02	4.73	1.30	1.78	4.80	2.67	4.80	3.64	1.31
13	A+0	WW	12	middle	7.41	3.61	5.92	1.89	2.49	3.86	3.15	3.86	2.93	1.16
13	A+0	WW	12	east	7.61	3.82	5.33	1.60	2.13	4.28	0.22	4.28	3.25	1.23
14	A+0	WW	12	west	7.47	3.72	6.51	0.41	1.07	7.11	1.72	7.11	5.62	1.50
14	A+0	WW	12	middle	7.04	3.20	5.92	0.65	1.24	4.74	4.62	4.74	3.74	1.21
14	A+0	WW	12	east	5.85	2.73	7.10	0.06	0.77	6.58	0.14	6.58	5.20	1.27
15	A+0	WW	12	west	7.09	2.38	7.10	0.06	0.77	9.58	0.32	9.58	7.55	1.69
15	A+0	WW	12	middle	6.28	2.64	5.92	0.83	1.42	4.78	4.67	4.78	3.77	1.13
15	A+0	WW	12	east	8.34	3.72	7.10	0.30	1.01	10.58	0.03	10.6	8.33	1.93
16	A+0	WW	12	west	8.24	4.91	4.14	1.42	1.83	4.11	2.71	4.11	3.37	1.28
16	A+0	WW	12	middle	6.01	2.42	4.73	0.65	1.12	4.72	0.61	4.72	3.88	1.10
16	A+0	WW	12	east	5.31	2.37	5.92	0.18	0.77	6.32	0.23	6.32	5.20	1.19
mean	ws				6.20	3.49	3.41	1.24	1.58	3.17	2.20	3.17	2.56	0.97
mean	WW				7.00	3.42	6.01	0.80	1.40	6.45	1.76	6.45	5.15	1.38

Appendix 4. Companion Plot Biomass Production

cham- ber	# plants	CO ₂	water	row	stem DW 10 ⁶ g/ha	C stem DW 10 ⁶ g/ha	lvs DW 10 ⁵ g/ha	C lvs DW 10 ⁵ g/ha	#mat 10 ⁴ per ha	C # mat 10 ⁴ per ha	# imm 10 ⁵ per ha	C # imm 10 ⁵ per ha	# total ears 10 ⁵ per ha	C #total ears 10 ⁵ per ha	mat DW 10 ⁶ g/ha
1	14	A +150	ws	west	5.19	5.17	2.69	2.69	2.03	2.25	1.32	1.22	1.52	1.44	1.77
1	12	A +150	ws	middle	7.05	7.01	4.28	4.27	3.55	3.93	0.77	0.71	1.12	1.10	2.58
1	17	A +150	ws	east	4.66	4.64	1.53	1.53	1.67	1.85	1.00	0.92	1.17	1.11	1.30
2	11	A +75	ws	west	6.37	5.83	2.96	3.14	5.16	4.51	0.97	1.02	1.48	1.48	4.65
2	11	A +75	ws	middle	5.97	5.47	3.03	3.20	3.87	3.38	1.23	1.30	1.61	1.64	5.58
2	12	A +75	ws	east	6.72	6.15	2.99	3.17	2.37	2.07	1.01	1.06	1.24	1.27	1.92
3	10	A +0	ws	west	7.70	10.45	3.12	3.54	5.68	4.46	0.78	1.29	1.35	1.74	6.17
3	12	A +0	ws	middle	6.98	9.48	2.61	2.96	4.73	3.72	0.77	1.27	1.24	1.64	5.54
3	13	A +0	ws	east	8.05	10.93	2.92	3.31	4.92	3.86	0.71	1.17	1.20	1.56	6.41
4	11	A +75	WW	west	6.40	7.24	3.44	3.46	7.75	7.61	0.13	0.09	0.90	0.85	9.49
4	14	A +75	WW	middle	6.24	7.06	2.92	2.93	3.55	3.49	1.32	0.94	1.67	1.29	3.67
4	15	A +75	WW	east	6.55	7.42	2.49	2.50	5.68	5.58	0.43	0.30	0.99	0.86	8.03
5	11	A +0	ws	west	6.53	6.11	3.40	2.83	1.94	3.04	2.00	1.48	2.19	1.78	0.96
5	12	A +0	ws	middle	4.97	4.65	2.39	1.99	1.18	1.86	0.89	0.66	1.01	0.84	1.00
5	9	A +0	ws	east	6.12	5.73	4.29	3.57	3.16	4.96	1.26	0.93	1.58	1.43	2.91
6	12	A +300	ws	west	9.03	9.04	3.22	2.82	5.33	5.41	0.41	0.37	0.95	0.91	5.91
6	11	A +300	ws	middle	8.10	8.11	3.49	3.06	5.81	5.90	0.71	0.63	1.29	1.22	7.96
6	12	A +300	ws	east	7.24	7.25	3.37	2.95	2.96	3.01	1.24	1.11	1.54	1.41	3.50
7	12	A +75	ws	west	6.79	7.17	2.93	3.29	4.14	3.58	1.01	1.17	1.42	1.53	5.47
7	13	A +75	ws	middle	4.54	4.79	2.19	2.46	2.73	2.36	1.31	1.53	1.58	1.76	2.73
7	10	A +75	ws	east	5.48	5.79	3.17	3.56	2.13	1.84	1.70	1.98	1.92	2.17	3.00
8	13	A +300	WW	west	4.91	5.34	2.26	2.10	6.55	7.39	0.55	0.43	1.20	1.17	5.68
8	11	A +300	WW	middle	8.46	9.19	3.80	3.53	5.16	5.82	1.16	0.91	1.68	1.49	5.60
8	15	A +300	WW	east	5.58	6.06	1.86	1.73	6.63	7.47	0.14	0.11	0.80	0.86	7.24
9	13	A +300	ws	west	7.65	7.04	2.13	2.31	2.73	3.15	1.53	1.69	1.80	2.00	2.59
9	12	A +300	ws	middle	7.39	6.80	2.50	2.70	2.37	2.73	2.31	2.54	2.54	2.82	2.09
9	13	A +300	ws	east	10.46	9.63	2.71	2.93	4.37	5.03	1.80	1.99	2.24	2.49	4.81
10	13	A +150	ws	west	7.46	7.00	2.91	2.87	3.82	3.71	1.09	0.97	1.47	1.34	2.78
10	10	A +150	ws	middle	6.45	6.06	3.77	3.71	1.42	1.38	1.92	1.71	2.06	1.84	1.85
10	14	A +150	ws	east	6.92	6.49	2.33	2.29	3.04	2.95	1.12	0.99	1.42	1.29	3.45
11	15	A +0	WW	west	6.62	6.09	3.08	2.70	5.68	4.67	0.28	0.37	0.85	0.84	9.61
11	16	A +0	WW	middle	5.94	5.46	2.09	1.84	5.77	4.75	0.13	0.17	0.71	0.65	7.64
11	12	A +0	WW	east	7.18	6.61	2.98	2.62	6.51	5.36	0.06	0.08	0.71	0.61	11.02
12	12	A +75	WW	west	7.33	6.75	3.10	3.30	5.92	6.09	0.59	0.90	1.18	1.51	10.19
12	7	A +75	WW	middle	6.72	6.19	5.00	5.33	7.10	7.30	0.00	0.00	0.71	0.73	11.46
12	14	A +75	WW	east	6.93	6.38	2.38	2.54	7.10	7.30	0.05	0.08	0.76	0.81	12.67
13	12	A +300	WW	west	8.20	7.52	3.59	3.21	7.10	8.01	0.41	0.21	1.12	1.01	9.41
13	13	A +300	WW	middle	8.54	7.83	3.01	2.70	6.01	6.78	0.93	0.47	1.53	1.14	7.78
13	18	A +300	WW	east	10.38	9.52	2.63	2.35	4.73	5.34	0.63	0.32	1.10	0.85	8.37
14	15	A +150	WW	west	8.24	8.51	2.27	2.42	6.63	6.11	0.19	0.40	0.85	1.02	9.20
14	15	A +150	WW	middle	6.88	7.10	2.47	2.63	4.73	4.37	0.71	1.52	1.18	1.95	5.06
14	14	A +150	WW	east	7.66	7.90	2.43	2.59	7.61	7.02	0.20	0.43	0.96	1.14	8.15
15	14	A +0	WW	west	8.27	8.01	3.47	4.08	5.58	5.00	1.01	2.06	1.57	2.56	8.74
15	10	A +0	WW	middle	4.82	4.66	3.75	4.40	5.68	5.09	0.64	1.30	1.21	1.81	5.31
15	16	A +0	WW	east	6.60	6.39	2.54	2.98	6.21	5.56	0.27	0.54	0.89	1.10	8.70
16	15	A +150	WW	west	6.86	7.37	2.40	2.54	6.15	7.49	0.33	0.35	0.95	1.10	9.08
16	12	A +150	WW	middle	5.77	6.20	2.32	2.46	6.51	7.93	0.36	0.38	1.01	1.17	10.07
16	10	A +150	WW	east	9.07	9.74	4.26	4.51	7.10	8.65	0.64	0.68	1.35	1.55	11.62

Appendix 5: Chamber Biomass Production (by row).

	C mat	imm	C imm	total ears	C total ears	grain	C grain	AGB	C AGB	root	ET-orig	WUE
cha m-ber	DW 10^7 g ha^{-1}	DW 10^2 g ha^{-1}	DW 10^2 g ha^{-1}	DW 10^6 g ha^{-1}	DW 10^7 g ha^{-1}	DW 10^7 g ha^{-1}	DW 10^7 g ha^{-1}	DW 10^7 g ha^{-1}	DW 10^7 g ha^{-1}	DW 10^6 g ha^{-1}	10^6 kg ha^{-1}	AGB /ET
1	0.22	1.45	3.26	1.77	0.22	0.14	0.18	0.72	0.77	0.98	3.10	2.5
1	0.32	4.08	9.17	2.58	0.32	0.21	0.26	1.01	1.07	0.98	3.10	3.5
1	0.16	0.09	0.19	1.30	0.16	0.11	0.13	0.61	0.65	1.16	3.10	2.1
2	0.32	1.19	1.88	4.65	0.32	0.40	0.26	1.13	0.94	1.79	3.20	2.9
2	0.38	3.28	5.16	5.58	0.38	0.48	0.31	1.19	0.98	1.03	3.20	3.1
2	0.13	0.10	0.16	1.92	0.13	0.16	0.11	0.89	0.74	3.35	3.20	2.3
3	0.51	1.60	3.79	6.18	0.51	0.54	0.45	1.42	1.58	1.21	3.30	4.8
3	0.46	1.67	3.96	5.54	0.46	0.48	0.40	1.28	1.43	0.76	3.30	4.3
3	0.53	0.12	0.29	6.41	0.53	0.56	0.47	1.48	1.65	0.98	3.30	5.0
4	1.10	1.12	0.90	9.49	1.10	0.66	0.78	1.62	1.85	1.65	5.90	3.1
4	0.42	7.42	5.96	3.67	0.42	0.26	0.30	1.02	1.16	1.74	5.90	2.0
4	0.93	0.07	0.06	8.03	0.93	0.56	0.66	1.48	1.69	3.08	5.90	2.9
5	0.16	6.96	3.43	0.96	0.16	0.08	0.13	0.78	0.85	2.19	3.50	2.4
5	0.17	1.75	0.86	1.00	0.17	0.08	0.13	0.62	0.68	1.47	3.50	1.9
5	0.49	0.77	0.38	2.91	0.49	0.24	0.39	0.95	1.03	1.34	3.50	2.9
6	0.59	0.16	0.21	5.91	0.59	0.49	0.48	1.53	1.52	1.56	3.50	4.3
6	0.80	0.76	0.99	7.96	0.80	0.66	0.65	1.64	1.64	0.94	3.50	4.7
6	0.35	0.01	0.02	3.50	0.35	0.29	0.29	1.11	1.10	1.88	3.50	3.2
7	0.44	1.55	1.69	5.47	0.44	0.45	0.37	1.26	1.21	0.89	3.10	3.9
7	0.22	1.54	1.68	2.73	0.22	0.23	0.18	0.75	0.72	1.03	3.10	2.3
7	0.24	0.16	0.17	3.00	0.24	0.25	0.20	0.88	0.85	2.73	3.10	2.7
8	0.61	2.59	1.69	5.68	0.61	0.45	0.48	1.08	1.17	2.73	5.40	2.2
8	0.61	7.69	5.02	5.60	0.61	0.45	0.47	1.44	1.56	1.97	5.40	2.9
8	0.78	0.17	0.11	7.24	0.78	0.58	0.61	1.30	1.40	2.37	5.40	2.6
9	0.34	4.55	4.23	2.60	0.34	0.21	0.30	1.05	1.08	1.60	3.40	3.2
9	0.28	4.56	4.23	2.09	0.28	0.17	0.24	0.97	1.00	2.58	3.40	2.9
9	0.64	0.35	0.33	4.81	0.64	0.39	0.55	1.55	1.60	2.01	3.40	4.7
10	0.29	2.88	1.69	2.78	0.29	0.23	0.25	1.05	1.03	1.13	3.10	3.3
10	0.19	6.62	3.89	1.85	0.19	0.15	0.16	0.87	0.84	0.57	3.10	2.7
10	0.36	0.21	0.12	3.45	0.36	0.28	0.31	1.06	1.03	1.83	3.10	3.3
11	0.74	1.98	5.02	9.61	0.74	0.59	0.44	1.65	1.39	1.71	6.30	2.2
11	0.59	1.09	2.77	7.64	0.59	0.47	0.35	1.38	1.16	1.43	6.30	1.8
11	0.84	0.17	0.42	11.02	0.84	0.68	0.51	1.85	1.55	1.51	6.30	2.5
12	0.84	1.91	2.24	10.19	0.84	0.87	0.73	1.78	1.56	2.36	6.40	2.4
12	0.95	0.00	0.00	11.46	0.95	0.98	0.82	1.87	1.64	1.63	6.40	2.6
12	1.05	0.14	0.16	12.67	1.05	1.09	0.90	1.98	1.74	1.30	6.40	2.7
13	1.41	2.28	1.99	9.41	1.41	0.71	1.12	1.80	2.01	3.06	5.70	3.5
13	1.16	1.46	1.28	7.78	1.16	0.59	0.93	1.66	1.86	2.14	5.70	3.3
13	1.25	0.13	0.11	8.37	1.25	0.64	1.00	1.90	2.13	2.95	5.70	3.7
14	0.97	0.24	0.20	9.20	0.97	0.75	0.80	1.77	1.84	1.50	6.00	3.1
14	0.53	4.82	3.92	5.06	0.53	0.41	0.44	1.22	1.27	2.21	6.00	2.1
14	0.86	0.02	0.01	8.15	0.86	0.67	0.71	1.61	1.67	2.33	6.00	2.8
15	0.68	5.21	5.48	8.74	0.68	0.44	0.35	1.74	1.51	1.38	6.30	2.4
15	0.41	2.10	2.21	5.31	0.41	0.27	0.21	1.05	0.91	1.43	6.30	1.5
15	0.67	0.33	0.34	8.70	0.67	0.44	0.35	1.55	1.35	0.97	6.30	2.1
16	1.16	0.83	1.23	9.08	1.16	0.73	0.91	1.62	1.88	1.60	5.70	3.3
16	1.29	1.99	2.96	10.07	1.29	0.81	1.01	1.61	1.86	1.07	5.70	3.3
16	1.48	0.08	0.12	11.62	1.48	0.94	1.16	2.11	2.45	2.14	5.70	4.3

Appendix 5: Chamber Biomass Production (by row)

				stem	lvs	# mat ears	# imm ears	total # ears	mat ears	imm ears	total ears	grain	AGB	root	ET	WUE
cham -ber	CO ₂ Ambi- -ent +	water	row	DW 10 ⁷ g ha ⁻¹	DW 10 ⁵ g ha ⁻¹	10 ⁴ per ha	10 ⁵ per ha	10 ⁵ per ha	DW 10 ⁷ g ha ⁻¹	DW 10 ² g ha ⁻¹	DW 10 ⁷ g ha ⁻¹	DW 10 ⁶ g ha ⁻¹	DW 10 ⁷ g ha ⁻¹	DW 10 ⁶ g ha ⁻¹	10 ⁶ kg ha ⁻¹	AGB / ET
1	+150	ws	west	0.52	2.69	2.25	1.22	1.44	0.22	3.26	0.22	1.76	0.77	0.98	3.10	2.5
1	+150	ws	middle	0.70	4.27	3.93	0.71	1.10	0.32	9.17	0.32	2.57	1.07	0.98	3.10	3.5
1	+150	ws	east	0.46	1.53	1.85	0.92	1.11	0.16	0.19	0.16	1.30	0.65	1.16	3.10	2.1
2	+75	ws	west	0.58	3.14	4.51	1.02	1.48	0.32	1.88	0.32	2.61	0.94	1.79	3.20	2.9
2	+75	ws	middle	0.55	3.20	3.38	1.30	1.64	0.38	5.16	0.38	3.13	0.98	1.03	3.20	3.1
2	+75	ws	east	0.62	3.17	2.07	1.06	1.27	0.13	0.16	0.13	1.08	0.74	3.35	3.20	2.3
3	+0	ws	west	1.04	3.54	4.46	1.29	1.74	0.51	3.79	0.51	4.51	1.58	1.21	3.30	4.8
3	+0	ws	middle	0.95	2.96	3.72	1.27	1.64	0.46	3.96	0.46	4.04	1.43	0.76	3.30	4.3
3	+0	ws	east	1.09	3.31	3.86	1.17	1.56	0.53	0.29	0.53	4.68	1.65	0.98	3.30	5.0
4	+75	WW	west	0.72	3.46	7.61	0.09	0.85	1.10	0.90	1.10	7.77	1.85	1.65	5.90	3.1
4	+75	WW	middle	0.71	2.93	3.49	0.94	1.29	0.42	5.96	0.42	3.01	1.16	1.74	5.90	2.0
4	+75	WW	east	0.74	2.50	5.58	0.30	0.86	0.93	0.06	0.93	6.57	1.69	3.08	5.90	2.9
5	+0	ws	west	0.61	2.83	3.04	1.48	1.78	0.16	3.43	0.16	1.30	0.85	2.19	3.50	2.4
5	+0	ws	middle	0.46	1.99	1.86	0.66	0.84	0.17	0.86	0.17	1.35	0.68	1.47	3.50	1.9
5	+0	ws	east	0.57	3.57	4.96	0.93	1.43	0.49	0.38	0.49	3.94	1.03	1.34	3.50	2.9
6	+300	ws	west	0.90	2.82	5.41	0.37	0.91	0.59	0.21	0.59	4.84	1.52	1.56	3.50	4.3
6	+300	ws	middle	0.81	3.06	5.90	0.63	1.22	0.80	0.99	0.80	6.51	1.64	0.94	3.50	4.7
6	+300	ws	east	0.72	2.95	3.01	1.11	1.41	0.35	0.02	0.35	2.86	1.10	1.88	3.50	3.2
7	+75	ws	west	0.72	3.29	3.58	1.17	1.53	0.44	1.69	0.44	3.70	1.21	0.89	3.10	3.9
7	+75	ws	middle	0.48	2.46	2.36	1.53	1.76	0.22	1.68	0.22	1.85	0.72	1.03	3.10	2.3
7	+75	ws	east	0.58	3.56	1.84	1.98	2.17	0.24	0.17	0.24	2.03	0.85	2.73	3.10	2.7
8	+300	WW	west	0.53	2.10	7.39	0.43	1.17	0.61	1.69	0.61	4.78	1.17	2.73	5.40	2.2
8	+300	WW	middle	0.92	3.53	5.82	0.91	1.49	0.61	5.02	0.61	4.71	1.56	1.97	5.40	2.9
8	+300	WW	east	0.61	1.73	7.47	0.11	0.86	0.78	0.11	0.78	6.09	1.40	2.37	5.40	2.6
9	+300	ws	west	0.70	2.31	3.15	1.69	2.00	0.34	4.23	0.34	2.98	1.08	1.60	3.40	3.2
9	+300	ws	middle	0.68	2.70	2.73	2.54	2.82	0.28	4.23	0.28	2.40	1.00	2.58	3.40	2.9
9	+300	ws	east	0.96	2.93	5.03	1.99	2.49	0.64	0.33	0.64	5.53	1.60	2.01	3.40	4.7
10	+150	ws	west	0.70	2.87	3.71	0.97	1.34	0.29	1.69	0.29	2.47	1.03	1.13	3.10	3.3
10	+150	ws	middle	0.61	3.71	1.38	1.71	1.84	0.19	3.89	0.19	1.64	0.84	0.57	3.10	2.7
10	+150	ws	east	0.65	2.29	2.95	0.99	1.29	0.36	0.12	0.36	3.06	1.03	1.83	3.10	3.3
11	+0	WW	west	0.61	2.70	4.67	0.37	0.84	0.74	5.02	0.74	4.43	1.39	1.71	6.30	2.2
11	+0	WW	middle	0.55	1.84	4.75	0.17	0.65	0.59	2.77	0.59	3.52	1.16	1.43	6.30	1.8
11	+0	WW	east	0.66	2.62	5.36	0.08	0.61	0.84	0.42	0.84	5.08	1.55	1.51	6.30	2.5
12	+75	WW	west	0.67	3.30	6.09	0.90	1.51	0.84	2.24	0.84	7.27	1.56	2.36	6.40	2.4
12	+75	WW	middle	0.62	5.33	7.30	0.00	0.73	0.95	0.00	0.95	8.17	1.64	1.63	6.40	2.6
12	+75	WW	east	0.64	2.54	7.30	0.08	0.81	1.05	0.16	1.05	9.04	1.74	1.30	6.40	2.7
13	+300	WW	west	0.75	3.21	8.01	0.21	1.01	1.41	1.99	1.41	11.24	2.01	3.06	5.70	3.5
13	+300	WW	middle	0.78	2.70	6.78	0.47	1.14	1.16	1.28	1.16	9.29	1.86	2.14	5.70	3.3
13	+300	WW	east	0.95	2.35	5.34	0.32	0.85	1.25	0.11	1.25	9.99	2.13	2.95	5.70	3.7
14	+150	WW	west	0.85	2.42	6.11	0.40	1.02	0.97	0.20	0.97	8.00	1.84	1.50	6.00	3.1
14	+150	WW	middle	0.71	2.63	4.37	1.52	1.95	0.53	3.92	0.53	4.40	1.27	2.21	6.00	2.1
14	+150	WW	east	0.79	2.59	7.02	0.43	1.14	0.86	0.01	0.86	7.08	1.67	2.33	6.00	2.8
15	+0	WW	west	0.80	4.08	5.00	2.06	2.56	0.68	5.48	0.68	3.49	1.51	1.38	6.30	2.4
15	+0	WW	middle	0.47	4.40	5.09	1.30	1.81	0.41	2.21	0.41	2.12	0.91	1.43	6.30	1.5
15	+0	WW	east	0.64	2.98	5.56	0.54	1.10	0.67	0.34	0.67	3.47	1.35	0.97	6.30	2.1
16	+150	WW	west	0.74	2.54	7.49	0.35	1.10	1.16	1.23	1.16	9.08	1.88	1.60	5.70	3.3
16	+150	WW	middle	0.62	2.46	7.93	0.38	1.17	1.29	2.96	1.29	10.07	1.86	1.07	5.70	3.3
16	+150	WW	east	0.97	4.51	8.65	0.68	1.55	1.48	0.12	1.48	11.62	2.45	2.14	5.70	4.3

Appendix 6: Corrected Biomass Production (by row).

			stem	lvs	# mat ears	# imm ears	total # ears	mat ears	imm ears	total ears	grain		AGB	root	ET	WUE
chamber	CO2	water	DW 10 ⁷ g/ha	DW 10 ⁵ g/ha	10 ⁴ per ha	10 ⁵ per ha	10 ⁵ per ha	DW 10 ⁷ g/ha	DW 10 ² g/ha	DW 10 ⁷ g/ha	DW 10 ⁷ g/ha	DW 10 ⁷ g/ha	DW 10 ⁷ g/ha	DW 10 ⁶ g/ha	10 ⁶ kg/ha	AGB / ET
1	A+150	ws	0.56	2.83	2.68	0.95	1.22	0.24	4.21	0.24	0.19	0.83	1.04	3.10	2.7	
2	A+75	ws	0.58	3.17	3.32	1.13	1.46	0.28	2.40	0.28	0.23	0.89	2.06	3.20	2.8	
3	A+0	ws	1.03	3.27	4.01	1.25	1.65	0.50	2.68	0.50	0.44	1.55	0.98	3.30	4.7	
4	A +75	WW	0.72	2.97	5.56	0.44	1.00	0.82	2.31	0.82	0.58	1.57	2.16	5.90	2.7	
5	A+0	ws	0.55	2.79	3.29	1.02	1.35	0.27	1.56	0.27	0.22	0.85	1.67	3.50	2.4	
6	A+300	ws	0.81	2.95	4.77	0.70	1.18	0.58	0.41	0.58	0.47	1.42	1.46	3.50	4.1	
7	A+75	ws	0.59	3.10	2.59	1.56	1.82	0.30	1.18	0.30	0.25	0.93	1.55	3.10	3.0	
8	A+300	WW	0.69	2.46	6.90	0.48	1.17	0.67	2.28	0.67	0.52	1.38	2.35	5.40	2.5	
9	A+300	ws	0.78	2.65	3.63	2.07	2.44	0.42	2.93	0.42	0.36	1.22	2.06	3.40	3.6	
10	A+150	ws	0.65	2.96	2.68	1.22	1.49	0.28	1.90	0.28	0.24	0.97	1.17	3.10	3.1	
11	A+0	WW	0.61	2.39	4.93	0.21	0.70	0.72	2.74	0.72	0.43	1.37	1.55	6.30	2.2	
12	A+75	WW	0.64	3.72	6.90	0.33	1.02	0.94	0.80	0.94	0.82	1.65	1.76	6.40	2.6	
13	A+300	WW	0.83	2.75	6.71	0.33	1.00	1.27	1.13	1.27	1.02	2.00	2.72	5.70	3.5	
14	A+150	WW	0.78	2.55	5.83	0.78	1.37	0.78	1.38	0.78	0.65	1.59	2.01	6.00	2.7	
15	A+0	WW	0.64	3.82	5.22	1.30	1.82	0.59	2.68	0.59	0.30	1.26	1.26	6.30	2.0	
16	A+150	WW	0.78	3.17	8.02	0.47	1.27	1.31	1.44	1.31	1.03	2.06	1.60	5.70	3.6	

Appendix 7: Mean Biomass Production (by chamber)

	stem	lvs	# mat ears	# imm ears	total # ears	mat ears	imm ears	total ears	grain	AGB	root	ET	WUE
treatment	DW 10 ⁶ g/ha	DW 10 ⁵ g/ha	10 ⁴ per ha	10 ⁵ per ha	10 ⁵ per ha	DW 10 ⁷ g/ha	DW 10 ² g/ha	DW 10 ⁷ g/ha	DW 10 ⁶ g/ha	DW 10 ⁷ g/ha	DW 10 ⁶ g/ha	10 ⁶ kg/ha	AGB / ET
+0 ws	7.89	3.03	3.65	1.13	1.50	0.39	2.12	0.39	3.30	1.20	1.33	3.40	3.6
+75 ws	5.87	3.14	2.95	1.34	1.64	0.29	1.79	0.29	2.40	0.91	1.80	3.15	2.9
+150 ws	6.06	2.90	2.68	1.09	1.35	0.26	3.05	0.26	2.13	0.90	1.11	3.10	2.9
+300 ws	7.98	2.80	4.20	1.39	1.81	0.50	1.67	0.50	4.19	1.32	1.76	3.45	3.8
+0 WW	6.20	3.10	5.07	0.75	1.26	0.66	2.71	0.66	3.69	1.31	1.40	6.30	2.1
+75 WW	6.84	3.34	6.23	0.39	1.01	0.88	1.55	0.88	6.97	1.61	1.96	6.15	2.6
+150 WW	7.80	2.86	6.93	0.63	1.32	1.05	1.41	1.05	8.37	1.83	1.81	5.85	3.1
+300 WW	7.58	2.60	6.80	0.41	1.09	0.97	1.70	0.97	7.68	1.69	2.54	5.55	3.0

Appendix 8: Mean Biomass Production (by treatment)

1983 LLNL Elevated CO2/Water Stress Maize Experiment

STEM HEIGHT (cm)

Date >	7/13	7/13	7/13	7/20	7/20	7/20	7/27	7/27	7/27	8/3	8/3	8/3	8/9	8/9	8/9
Cham-ber	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N
1	69	15	17	106	18	17	146	27	16	170	32	16	226	41	15
2	85	24	20	125	33	20	163	36	19	176	55	18	223	59	19
3	82	9	17	121	10	16	158	12	16	178	17	16	228	12	16
4	71	16	21	107	21	21	147	26	18	203	43	18	252	37	18
5	57	9	21	87	11	19	113	17	20	128	25	20	172	37	20
6	84	18	16	130	24	16	175	31	16	206	39	16	245	47	16
7	62	21	20	97	22	18	128	27	18	157	47	18	193	47	18
8	63	16	17	97	18	15	147	27	15	193	37	15	250	48	15
9	83	16	18	122	22	18	161	32	18	198	55	17	234	53	18
10	80	22	17	124	24	17	158	31	17	179	38	17	218	44	17
11	97	14	20	143	13	19	177	29	20	242	30	20	281	30	19
12	96	30	14	156	15	12	204	16	11	276	26	11	302	25	11
13	49	14	17	71	20	17	116	11	17	191	20	16	241	34	18
14	60	15	21	95	21	19	135	30	21	200	46	19	254	43	20
15	68	16	19	103	30	19	141	35	18	201	49	18	246	52	18
16	79	16	17	114	22	17	172	30	17	235	42	17	279	44	16
C.P.															
1	64	19	21	93	21	21	122	26	21	139	32	20	175	40	21
2	72	12	16	104	16	16	138	16	16	135	22	15	211	28	15
3	56	18	17	86	23	16	116	27	16	136	30	15	181	34	15
4	59	15	17	89	18	17	127	20	18	174	33	17	218	34	17
5	52	14	21	84	16	19	110	23	19	137	30	19	172	36	19
6	61	19	17	92	17	17	124	21	16	147	25	16	196	89	15
7	45	12	20	72	14	18	100	16	19	121	22	19	162	29	19
8	68	8	16	100	9	15	137	9	15	197	10	15	240	8	15
9	42	7	20	64	9	18	80	10	18	128	13	17	172	18	18
10	67	8	18	100	11	17	127	13	17	145	17	17	189	21	17
11	65	13	19	96	17	18	133	22	20	183	28	18	219	35	18
12	72	12	16	104	15	16	140	20	11	189	25	17	226	26	15
13	53	9	16	79	10	14	117	27	17	167	25	15	202	28	15
14	56	10	19	82	14	18	117	18	21	172	24	19	221	23	18
15	56	12	22	87	17	21	124	20	18	189	22	20	235	30	21
16	65	13	19	93	15	19	133	20	17	190	23	19	234	21	19

Appendix 9: Stem Height Measurement Data

1983 LLNL Elevated CO2/Water Stress Maize Experiment										STEM HEIGHT (cm)					
Date >	8/16	8/16	8/16	8/23	8/23	8/23	8/30	8/30	8/30	9/6	9/6	9/6	9/13	9/13	9/13
Cham- ber	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N
1	235	31	15	237	24	14	236	24	14	244	31	14	237	30	14
2	216	50	17	221	47	17	213	56	17	223	51	17	219	49	17
3	231	12	16	229	12	16	227	11	16	233	10	16	230	10	16
4	270	35	17	278	28	18	275	26	18	275	27	18	276	24	18
5	184	39	20	189	39	20	191	36	19	193	37	19	186	38	17
6	247	45	16	243	43	16	251	46	16	252	48	16	242	54	16
7	204	47	18	202	45	18	203	44	18	205	48	18	199	49	18
8	296	62	15	285	29	15	288	29	15	298	33	15	283	41	15
9	244	16	17	234	52	18	236	54	18	243	52	18	234	62	17
10	206	46	17	222	42	17	227	46	17	227	50	17	224	45	16
11	289	27	20	285	29	20	295	26	20	296	23	20	290	25	20
12	309	20	11	306	17	18	304	17	11	312	18	11	305	17	11
13	281	30	17	286	34	18	294	20	17	282	35	18	292	28	19
14	280	42	20	289	26	20	295	27	20	291	26	20	293	22	20
15	257	42	17	259	40	17	265	42	17	264	41	16	265	41	16
16	293	36	19	290	25	17	302	22	17	300	25	16	302	25	11
C.P.															
1	178	31	20	185	36	20	177	32	20	177	38	20	178	38	20
2	202	20	15	207	16	15	196	21	15	210	17	15	204	17	15
3	182	34	15	185	30	15	180	32	15	185	36	15	189	32	15
4	222	33	17	229	25	17	227	27	17	228	26	17	238	28	17
5	174	38	20	175	39	19	177	36	19	178	34	19	178	32	18
6	185	35	16	184	33	16	183	33	16	183	35	16	183	32	16
7	179	33	19	188	28	18	189	29	19	194	20	17	191	20	17
8	246	9	15	250	9	15	254	10	15	256	10	15	254	9	15
9	200	14	18	207	18	18	209	18	18	208	17	18	206	19	18
10	199	21	17	200	20	17	200	20	17	200	21	17	197	20	17
11	229	30	18	235	23	18	239	25	18	240	25	18	238	26	18
12	221	22	15	229	18	15	225	18	17	235	22	15	230	22	15
13	206	24	15	228	19	14	225	15	14	225	14	14	226	19	14
14	237	20	19	240	16	19	245	14	19	249	12	19	250	14	19
15	243	26	21	253	17	21	255	17	21	259	17	21	257	18	21
16	246	15	19	250	11	19	254	11	19	253	10	19	253	9	19

Appendix 9: Stem Height Measurement Data

1983 LLNL Elevated CO2/Water Stress Maize Experiment												Stem Height Means (cm)						M=Mean		
	7/13	7/13	7/20	7/20	7/27	7/27	8/3	8/3	8/9	8/9	8/16	8/16	8/23	8/23	8/30	8/30	9/6	9/6	9/13	9/13
Cham	M	corr	M	corr	M	corr	M	corr	M	corr	M	corr	M	corr	M	corr	M	corr	M	corr
-ber																				
1	69	62	106	99	146	137	170	166	226	235	235	247	237	245	236	252	244	265	237	254
2	85	68	125	104	163	135	176	177	223	193	216	200	221	204	213	205	223	204	219	205
3	82	84	121	122	158	156	178	178	228	230	231	238	229	237	227	238	233	242	230	232
4	71	74	107	110	147	149	203	213	252	259	270	281	278	290	275	291	275	293	276	282
5	57	63	87	90	113	118	128	127	172	182	184	198	189	207	191	204	193	208	186	199
6	84	79	130	123	175	162	206	191	245	228	247	250	243	253	251	259	252	264	242	252
7	62	79	97	117	128	147	157	176	193	217	204	214	202	206	203	203	205	203	199	199
8	63	86	97	123	147	189	193	291	250	346	296	382	285	363	288	366	298	373	283	360
9	83	113	122	166	161	231	198	210	234	248	244	229	234	216	236	213	243	224	234	217
10	80	69	124	108	158	143	179	168	218	210	206	194	222	212	227	214	227	218	224	217
11	97	92	143	136	177	171	242	242	281	288	289	292	285	290	295	297	296	300	290	296
12	96	82	156	137	204	187	276	267	302	300	309	323	306	320	304	325	312	323	305	323
13	49	57	71	82	116	127	191	209	241	268	281	315	286	300	294	314	282	305	292	314
14	60	66	95	106	135	148	200	212	254	258	280	273	289	288	295	290	291	284	293	285
15	68	75	103	108	141	146	201	194	246	235	257	245	259	245	265	250	264	248	265	251
16	79	75	114	112	172	166	235	226	279	268	293	275	290	278	302	286	300	288	302	290
C.P.																				
1	64		93		122		139		175		178		185		177		177		178	
2	72		104		138		135		211		202		207		196		210		204	
3	56		86		116		136		181		182		185		180		185		189	
4	59		89		127		174		218		222		229		227		228		238	
5	52		84		110		137		172		174		175		177		178		178	
6	61		92		124		147		196		185		184		183		183		183	
7	45		72		100		121		162		179		188		189		194		191	
8	68		100		137		197		240		246		250		254		256		254	
9	42		84		80		128		172		200		207		209		208		206	
10	67		100		127		145		189		199		200		200		200		197	
11	65		96		133		183		219		229		235		239		240		238	
12	72		104		140		189		226		221		229		225		235		230	
13	53		79		117		167		202		206		228		225		225		226	
14	56		82		117		172		221		237		240		245		249		250	
15	56		87		124		189		235		243		253		255		259		257	
16	65		93		133		190		234		246		250		254		253		253	
ws	57		87		115		136		182		187		191		189		192		191	
WW	62		91		129		183		224		231		239		241		243		243	

Appendix 10: Stem Height Means (by chamber)

1983 LLNL Elevated CO2/Water Stress Maize Expt.

Corrected Mean Ht.= (mean CP
stem ht. for the water treatment/plot
CP stem ht.) * chamber mean stem
ht.

Chm- bers	+0ws	+0ws	+75	+75	+150	+150	+300	+300	+0	+0	+75	+75	+150	+150	+300	+300
day	mean	corr.	mean	corr.	mean	corr.	mean	corr.	mean	corr.	mean	corr.	mean	corr.	mean	corr.
	ht.	ht.	ht.	ht.	ht.	ht.	ht.	ht.	ht.	ht.	ht.	ht.	ht.	ht.	ht.	ht.
194	68	72	74	73	75	65	83	93	83	85	81	76	69	70	56	57
201	103	104	112	111	115	103	126	140	123	123	125	118	104	108	83	84
208	133	134	146	141	152	139	168	189	160	159	169	163	152	156	131	132
215	150	149	167	178	175	167	202	200	223	218	231	232	217	219	192	193
221	197	202	208	205	222	221	239	237	264	260	271	274	265	261	245	249
228	205	216	210	207	220	219	245	238	274	268	285	298	286	274	288	297
235	207	220	211	205	229	228	238	232	273	267	292	305	289	283	286	286
242	207	220	208	204	231	232	243	233	281	273	286	305	298	288	291	292
249	211	224	214	203	235	240	247	241	282	274	289	304	295	286	289	292
256	207	216	209	202	230	235	238	232	279	274	287	298	296	287	288	292
C.P.																
194	54		57		65		51		60		65		61		61	
201	85		87		96		78		91		96		88		90	
208	113		117		124		101		129		132		124		126	
215	137		127		142		137		186		182		181		182	
221	176		184		181		183		228		222		228		221	
228	177		189		188		193		237		222		242		226	
235	179		197		192		196		245		229		245		239	
242	178		192		188		197		248		226		250		240	
249	181		202		188		196		250		231		251		241	
256	183		197		187		195		248		234		252		240	
Companion Plot			day		ws		WW									
Means																
			194		57		62									
			201		86		91									
			208		114		128									
			215		136		183									
			221		181		225									
			228		187		231									
			235		191		240									
			242		189		241									
			249		192		243									
			256		190		244									

Appendix 11: Stem Height Means (by treatment + day).

Appendix 12: Seasonal stem heights of maize plants from all treatments.

1983 LLNL Elevated CO ₂ /Water Stress Maize Experiment										STEM DIAMETER (cm)			M=Mean		
Date>	7/13	7/13	7/13	7/20	7/20	7/20	7/27	7/27	7/27	8/3	8/3	8/3	8/9	8/9	8/9
Cham	M	SD	N	M	SD	N	M	SD	N	M	SD	N	M	SD	N
-ber															
1	1.82	0.58	17	2.21	0.40	17	2.56	0.51	16	2.56	0.44	16	2.93	0.50	15
2	2.10	0.75	20	2.20	0.64	20	2.00	0.78	18	2.00	0.57	18	2.68	0.90	19
3	1.82	0.58	17	2.34	0.30	16	2.50	0.41	16	2.44	0.17	16	3.03	0.13	16
4	1.74	0.56	21	2.21	0.69	19	2.67	0.82	18	2.58	0.65	18	2.72	0.83	18
5	0.52	0.52	21	1.82	0.42	19	2.26	0.63	19	2.15	0.51	20	2.63	0.70	20
6	2.22	0.48	16	2.31	0.57	16	2.78	0.80	16	2.53	0.64	16	2.84	0.70	16
7	1.68	0.67	20	2.16	0.53	19	2.06	0.45	18	2.17	0.49	18	2.58	0.69	18
8	1.62	0.65	17	2.27	0.62	15	2.22	0.80	15	2.85	0.96	15	3.03	0.81	15
9	2.31	0.60	18	2.53	0.50	18	2.47	0.50	18	2.50	0.66	17	2.92	0.62	18
10	2.32	0.58	17	2.47	0.57	17	2.41	0.57	17	2.35	0.55	17	2.79	0.73	17
11	2.50	0.46	20	2.66	0.37	19	2.35	0.40	20	2.80	0.62	20	3.03	0.59	19
12	2.43	0.70	14	2.88	0.23	12	2.86	0.50	11	2.91	0.44	11	3.32	0.46	11
13	2.15	0.29	17	2.44	0.30	17	2.47	0.37	17	3.03	0.56	16	3.14	0.68	18
14	1.74	0.58	21	2.24	0.48	19	2.26	0.49	21	2.58	0.51	19	2.80	0.47	20
15	2.16	0.37	19	2.29	0.30	19	2.36	0.33	18	2.28	0.46	18	2.78	0.46	18
16	2.29	0.64	17	2.56	0.46	17	2.53	0.37	17	2.44	0.30	17	2.94	0.60	16
C.P.															
1	1.83	0.58	21	2.10	0.62	21	2.07	0.68	21	2.23	0.60	20	2.43	0.69	21
2	2.19	0.54	16	2.41	0.33	16	2.66	0.44	16	2.63	0.30	15	3.10	0.57	15
3	2.09	0.64	17	2.00	0.63	16	2.50	0.58	16	2.13	0.60	15	2.87	0.61	15
4	2.03	0.54	17	2.32	0.66	17	3.00	1.05	16	3.09	0.97	17	2.76	0.95	17
5	1.76	0.64	21	2.18	0.53	19	2.39	0.59	19	2.26	0.63	19	2.74	0.71	19
6	1.82	0.71	17	2.09	0.48	17	2.38	0.56	16	2.50	0.66	16	3.17	0.70	15
7	1.63	0.43	20	2.18	0.53	19	2.18	0.42	19	2.29	0.51	19	2.82	0.67	19
8	2.28	0.26	16	2.53	0.30	15	2.47	0.30	15	2.77	0.32	15	3.53	0.52	15
9	1.50	0.43	20	1.97	0.27	18	1.89	0.27	18	2.21	0.25	17	2.78	0.26	18
10	2.28	0.31	18	2.32	0.30	17	2.38	0.63	17	2.41	0.32	17	3.06	0.50	17
11	2.16	0.58	19	2.17	0.57	18	2.44	0.64	18	2.58	0.77	18	2.78	0.89	18
12	2.22	0.66	16	2.50	0.41	16	2.57	0.37	15	2.90	0.54	15	3.17	0.65	15
13	1.94	0.48	16	2.36	0.23	14	2.39	0.63	14	2.77	0.53	15	3.43	0.68	15
14	2.05	0.50	19	2.22	0.52	18	2.34	0.37	19	2.74	0.59	19	3.00	0.59	18
15	1.95	0.60	22	2.29	0.41	21	2.40	0.46	21	2.65	0.49	20	2.81	0.91	21
16	2.24	0.48	19	2.58	0.48	19	2.61	0.32	19	2.63	0.40	19	3.11	0.59	19

Appendix 13: Stem Diameter Measurement Data.

1983 LLNL Elevated CO2/Water Stress Corn Experiment										STEM DIAMETER (cm)		
Date>	8/16	8/16	8/16	8/23	8/23	8/23	8/30	8/30	8/30	9/6	9/6	9/6
Chamber	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N
1	3.00	0.63	15	3.46	0.63	14	3.29	0.47	14	3.36	0.50	14
2	2.87	0.77	17	2.71	0.77	17	2.82	0.81	17	2.82	0.95	17
3	3.22	0.41	16	3.22	0.41	16	3.25	0.45	16	3.38	0.50	16
4	2.86	0.78	18	2.89	0.83	18	3.17	0.79	18	3.00	0.91	18
5	2.80	0.83	20	2.80	0.83	20	2.84	0.69	19	2.89	0.57	19
6	3.31	1.01	16	3.31	1.01	16	3.44	1.03	16	3.25	0.93	16
7	2.50	0.71	18	2.50	0.71	18	2.56	0.70	18	2.83	0.79	18
8	3.43	1.00	15	3.53	1.06	15	3.67	1.11	15	3.80	1.08	15
9	3.22	0.94	18	3.22	0.94	18	2.67	0.91	19	3.67	1.14	18
10	2.82	0.53	17	2.82	0.53	17	2.88	0.99	17	3.24	1.03	17
11	3.18	0.71	20	3.40	0.99	20	3.45	0.69	20	3.40	0.94	20
12	3.82	0.75	11	3.91	0.70	11	4.00	0.77	11	3.82	0.75	11
13	3.74	0.81	17	3.83	0.71	18	3.47	0.62	17	3.72	0.83	18
14	3.45	0.76	20	3.23	0.87	20	2.90	0.91	20	3.60	0.94	20
15	3.29	0.66	17	3.18	0.53	17	2.65	0.70	17	3.13	0.89	16
16	3.44	0.92	17	3.29	0.77	17	3.29	0.77	17	3.76	0.97	17
C.P.												
1	3.13	0.79	20	3.08	1.08	20	2.90	0.70	20	2.90	0.85	20
2	3.43	0.53	15	3.70	0.70	15	3.40	0.63	15	3.80	0.77	15
3	3.10	0.76	15	3.20	0.56	15	2.83	0.75	15	2.93	0.70	15
4	3.35	0.98	17	3.26	1.13	17	3.35	1.27	17	3.41	1.62	17
5	2.58	0.95	20	3.00	1.00	19	2.89	0.66	19	2.79	1.03	19
6	3.00	1.06	16	3.38	1.15	16	3.31	0.70	16	3.38	0.81	16
7	2.74	0.65	17	3.00	0.84	18	2.84	0.83	19	3.18	0.81	17
8	3.87	0.77	15	4.27	0.80	15	4.07	0.59	15	4.35	0.72	15
9	2.78	0.39	18	3.11	0.47	18	2.64	0.48	18	2.83	0.51	18
10	2.88	0.52	17	2.94	0.43	17	2.35	0.58	17	3.18	0.53	17
11	3.31	0.94	18	3.39	1.20	18	3.28	1.18	18	3.61	1.20	18
12	3.53	0.64	15	3.87	0.83	15	3.67	0.90	15	3.87	1.06	15
13	3.61	0.66	14	3.93	1.00	14	3.14	0.77	14	4.14	1.03	14
14	3.29	0.65	19	3.42	0.84	19	2.95	0.71	19	3.63	0.96	19
15	3.14	0.95	21	3.24	0.94	21	2.76	1.00	21	3.62	1.20	21
16	3.32	0.65	19	3.32	0.67	19	3.05	0.85	19	3.58	0.96	19

Appendix 13: Stem Diameter Measurement Data.

1983 LLNL Elevated CO2/Water Stress Maize Experiment										Stem Diameter Means (cm)						M=mean		
	7/13	7/13	7/20	7/20	7/27	7/27	8/3	8/3	8/9	8/9	8/16	8/16	8/23	8/23	8/30	8/30	9/6	9/6
Chm-ber	M	corr	M	corr	M	corr	M	corr	M	corr	M	corr	M	corr	M	corr	M	corr
1	1.82	1.88	2.21	2.27	2.56	2.85	2.56	2.68	2.93	3.46	3.00	2.83	3.46	3.57	3.29	3.28	3.36	3.62
2	2.10	1.81	2.20	1.97	2.00	1.73	2.00	1.77	2.68	2.48	2.87	2.47	2.71	2.33	2.82	2.40	2.82	2.32
3	1.82	1.64	2.34	2.52	2.50	2.31	2.44	2.67	3.03	3.03	3.22	3.07	3.22	3.20	3.25	3.32	3.38	3.60
4	1.74	1.81	2.21	2.26	2.67	2.25	2.58	2.31	2.72	3.03	2.86	2.93	2.89	3.18	3.17	3.11	3.00	3.32
5	0.52	0.56	1.82	1.80	2.26	2.18	2.15	2.22	2.63	2.76	2.80	3.21	2.80	2.96	2.84	2.84	2.89	3.24
6	2.22	2.30	2.31	2.38	2.78	2.69	2.53	2.36	2.84	2.57	3.31	3.26	3.31	3.11	3.44	3.01	3.25	3.00
7	1.68	1.95	2.16	2.14	2.06	2.18	2.17	2.21	2.58	2.63	2.50	2.70	2.50	2.65	2.56	2.61	2.83	2.78
8	1.62	2.10	2.27	2.47	2.22	2.57	2.85	3.44	3.03	3.30	3.43	4.29	3.53	4.22	3.67	4.24	3.80	4.51
9	2.31	2.91	2.53	2.77	2.47	3.01	2.50	2.64	2.92	3.02	3.22	3.42	3.22	3.29	2.67	2.93	3.67	4.05
10	2.32	1.92	2.47	2.30	2.41	2.34	2.35	2.27	2.79	2.62	2.82	2.89	2.82	3.05	2.88	3.55	3.24	3.18
11	2.50	2.44	2.66	2.91	2.35	2.43	2.80	3.00	3.03	3.35	3.18	3.29	3.40	3.60	3.45	3.45	3.40	3.56
12	2.43	2.31	2.88	2.73	2.86	2.81	2.91	2.78	3.32	3.22	3.82	3.71	3.91	3.62	4.00	3.58	3.82	3.73
13	2.15	2.34	2.44	2.45	2.47	2.61	3.03	3.03	3.14	2.81	3.74	3.55	3.83	3.50	3.47	3.63	3.72	3.39
14	1.74	1.79	2.24	2.39	2.26	2.44	2.58	2.60	2.80	2.87	3.45	3.59	3.23	3.39	2.90	3.23	3.60	3.75
15	2.16	2.34	2.29	2.37	2.36	2.49	2.28	2.38	2.78	3.04	3.29	3.59	3.18	3.52	2.65	3.15	3.13	3.27
16	2.29	2.16	2.56	2.35	2.53	2.45	2.44	2.57	2.94	2.91	3.44	3.55	3.29	3.56	3.29	3.54	3.76	3.97
C.P.																		
1	1.83		2.10		2.07		2.23		2.43		3.13		3.08		2.90		2.90	
2	2.19		2.41		2.66		2.63		3.10		3.43		3.70		3.40		3.80	
3	2.09		2.00		2.50		2.13		2.87		3.10		3.20		2.83		2.93	
4	2.03		2.32		3.00		3.09		2.76		3.35		3.26		3.35		3.41	
5	1.76		2.18		2.39		2.26		2.74		2.58		3.00		2.89		2.79	
6	1.82		2.09		2.38		2.50		3.17		3.00		3.38		3.31		3.38	
7	1.63		2.18		2.18		2.29		2.82		2.74		3.00		2.84		3.18	
8	2.28		2.53		2.47		2.77		3.53		3.87		4.27		4.07		4.35	
9	1.50		1.97		1.89		2.21		2.78		2.78		3.11		2.64		2.83	
10	2.28		2.32		2.38		2.41		3.06		2.88		2.94		2.35		3.18	
11	2.16		2.17		2.44		2.58		2.78		3.31		3.39		3.28		3.61	
12	2.22		2.50		2.57		2.90		3.17		3.53		3.87		3.67		3.87	
13	1.94		2.36		2.39		2.77		3.43		3.61		3.93		3.14		4.14	
14	2.05		2.22		2.34		2.74		3.00		3.29		3.42		2.95		3.63	
15	1.95		2.29		2.40		2.65		2.81		3.14		3.24		2.76		3.62	
16	2.24		2.58		2.61		2.63		3.11		3.32		3.32		3.05		3.58	
ws																		
ws	1.89		2.16		2.31		2.33		2.87		2.96		3.18		2.90		3.12	
WW																		
WW	2.11		2.37		2.53		2.77		3.07		3.43		3.59		3.28		3.78	

Appendix 14: Stem Diameter Means (by chamber).

Mean Stem Diameters from each treatment on each measurement day

Corr. Mean Diameter= (mean CP diameter for the water treatment/plot CP diameter)* chamber mean diameter

Chm- bers	+0ws diam.	+0ws corr.	+75 ws diam.	+75 ws corr.	+150 ws diam.	+150 ws corr.	+300 ws diam.	+300 ws corr.	+0 WW diam.	+0 WW corr.	+75 WW diam.	+75 WW corr.	+150 WW diam.	+150 WW corr.	+300 WW diam.	+300 WW corr.
194	1.17	1.15	1.89	1.87	2.07	1.90	2.27	2.58	2.33	2.39	2.09	2.07	2.02	1.98	1.89	1.88
201	2.08	2.15	2.18	2.05	2.34	2.28	2.42	2.57	2.48	2.63	2.55	2.50	2.40	2.37	2.36	2.28
208	2.38	2.24	2.03	1.93	2.49	2.58	2.63	2.84	2.36	2.46	2.77	2.51	2.40	2.45	2.35	2.44
215	2.30	2.44	2.09	1.98	2.46	2.47	2.52	2.49	2.54	2.69	2.75	2.54	2.51	2.59	2.94	2.94
221	2.83	2.90	2.63	2.55	2.86	2.99	2.88	2.78	2.91	3.19	3.02	3.13	2.87	2.89	3.09	2.72
228	3.01	3.13	2.69	2.57	2.91	2.86	3.27	3.34	3.24	3.44	3.34	3.33	3.45	3.57	3.59	3.29
235	3.01	3.08	2.61	2.47	3.14	3.31	3.27	3.20	3.29	3.56	3.40	3.42	3.26	3.47	3.68	3.22
242	3.05	3.08	2.69	2.50	3.09	3.40	3.06	2.97	3.05	3.32	3.59	3.35	3.10	3.39	3.57	3.25
249	3.14	3.42	2.83	2.53	3.30	3.39	3.46	3.48	3.27	3.41	3.41	3.54	3.68	3.85	3.76	3.34
Companions																
194	1.93		1.91		2.06		1.66		2.06		2.13		2.15		2.11	
201	2.09		2.30		2.21		2.03		2.23		2.41		2.40		2.45	
208	2.45		2.42		2.23		2.14		2.42		2.79		2.48		2.43	
215	2.20		2.46		2.32		2.36		2.62		3.00		2.69		2.77	
221	2.81		2.96		2.75		2.98		2.80		2.97		3.06		3.48	
228	2.84		3.09		3.01		2.89		3.23		3.44		3.31		3.74	
235	3.10		3.35		3.01		3.25		3.32		3.57		3.37		4.10	
242	2.86		3.12		2.63		2.98		3.02		3.51		3.00		3.61	
249	2.86		3.49		3.04		3.11		3.62		3.64		3.61		4.25	

Companion Plot Means	day	ws	WW
	194	1.89	2.11
	201	2.16	2.37
	208	2.31	2.53
	215	2.33	2.77
	221	2.87	3.07
	228	2.96	3.43
	235	3.18	3.59
	242	2.90	3.28
	249	3.12	3.78

Appendix 15: Stem Diameter (by treatment + day)

1983 LLNL Elevated CO2/Water Stress Maize Experiment

Leaf Area (cm2/plant)

Chm- ber	Plant 1	Plant 2	Plant 3	Plant 4	Plant 5	Plant 6	Plant 7	Plant 8	Plant 9	Plant 10	Plant 11	Plant 12	Plant 13	Plant 14	Plant 15	Mean
1	3494	4592	4596	5372	5183	4213	3460	4812	4638	3679	4740	4343	5250	5408	3434	4481
2	6553	5718	7048	6296	5534	5345	4819	3960	5359	4466	4589	3937	4735	3442	5208	5134
3	4952	5198	4992	4997	5150	5345	4997	5150	5345	4152	5455	5165	5059	5752	3954	5044
4	5233	3895	4680	4034	4565	5287	4034	4565	5287	5728	3984	4492	5380	4406	5555	4742
5	4142	4292	3730	3385	3925	4115	5183	4507	3449	5314	4441	3576	3998	4312	5731	4273
6	4278	6660	5926	4739	5408	4126	3282	5275	4446	3540	5663	4463	4145	5554	3833	4756
7	3169	4580	4781	3848	3349	3090	3275	3634	3762	3887	3679	4055	4812	3324	3794	3803
8	4530	6762	4660	4735	6436	4394	4990	6259	7116	5873	6823	4832	4576	5268	5063	5488
9	6058	4637	7436	5123	5257	4714	4668	3480	5686	4895	3205	4768	4918	3890	4853	4906
10	5222	6766	6173	4326	4535	3727	4208	4964	5182	4873	5436	6312	6209	5473	3718	5142
11	6708	7202	5976	5552	4954	5296	7322	6358	5206	6780	6514	5796	4769	6269	6287	6066
12	6869	6540	4872	3533	3052	3113	6770	6268	5648	5929	6169	5762	6302	7192	6666	5646
13	3266	4679	3397	3628	3674	4116	4876	5689	4982	4003	5113	5612	4960	6318	5698	4667
14	3865	5342	3329	4477	5165	3784	6737	7171	6008	6285	7234	5603	5366	7000	5920	5552
15	3734	4706	3898	3602	3911	3820	4745	4116	4660	4763	3614	4520	4423	4013	4633	4211
16	4667	6010	5636	3582	5506	4250	4618	4753	6062	5182	5646	5045	4784	6082	5461	5152

Appendix 16: Leaf Area Data

Corn Data

Corn Data

Appendix 17: Regression Models Predicting % of ws Plants in VT Stage.

Appendix 17: Regression Models Predicting % of ws Plants in VT Stage.

Corn Data

Corn Data

Appendix 18: Regression Models Predicting % of WW Plants in VT Stage.

Corn Data

Corn Data

Appendix 18: Regression Models Predicting % of WW Plants in VT Stage.

**DATE
FILMED**

5/6/94

END