Effects of CO₂ and Temperature on Rice: A Summary of Five Growing Seasons

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Abstract

Projected future climate change includes a strong likelihood of increased atmospheric carbon dioxide concentration ([CO₂]) and possible increases in air temperatures. Since 1987, several [CO₂] and temperature experiments have been conducted on rice (*Oryza sativa*, L., cv. IR-30) in outdoor, naturally-sunlit, environmentally controlled, plant growth chambers by USDA-ARS and the University of Florida, at Gainesville, Florida, USA. The objectives of this paper are to summarize some of the major findings of these experiments. Among these experiments, [CO₂] ranged from 160 to 900 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air while temperature treatments ranged from 25/18/21 to 40/33/37°C (daytime dry bulb air temperature / nighttime dry bulb air temperature / paddy water temperature). Total growth duration was shortened by 10 to 12 days across a [CO₂] range from 160 to 500 $\mu\text{mol mol}^{-1}$ due to a shortened vegetative phase of development and a reduction in the number of mainstem leaves formed prior to panicle initiation. Photosynthesis, growth, and final grain yield increased with [CO₂] from 160 to 500 $\mu\text{mol mol}^{-1}$ but were very similar from 500 to 900 $\mu\text{mol mol}^{-1}$. Carbon dioxide enrichment from 330 to 660 $\mu\text{mol mol}^{-1}$ increased grain yield mainly by increasing the number of panicles plant⁻¹ while increasing temperature treatment above 28/21/25°C resulted in decreased grain yield due largely to a decline in the number of filled grain panicle⁻¹. Evapotranspiration decreased and water-use efficiency increased with increasing [CO₂] treatment while the reverse trends were found with increasing temperature treatment. These results indicate that future increases in [CO₂] are likely to benefit rice production by increasing photosynthesis, growth, and grain yield while reducing water requirements. In warmer areas of the world, possible future increases in air temperature may result in yield decreases and increased water requirements.

Key Words: carbon dioxide, growth, yield, photosynthesis, evapotranspiration.

Introduction

Global atmospheric carbon dioxide concentration ([CO₂]) is currently increasing at an increasing rate (Keeling et al. 1989). Current [CO₂] (about 355 $\mu\text{mol mol}^{-1}$) has been projected to increase to about 670 to 760 $\mu\text{mol mol}^{-1}$ by the year 2075 due mainly to the continued burning of fossil fuels (Rotty & Marland 1986). As a result of this rise in [CO₂] and other "greenhouse gasses", several atmospheric general circulation models have predicted significant increases in global air temperature (Hansen et al. 1988). Most published studies on [CO₂] and temperature effects on plants have dealt mainly with temperate crop species while tropical plants have received less attention. Since both [CO₂] and temperature can have large effects on plants, it is important to quantify the effects of these climate variables on food crops such as rice. The objectives of this paper are to summarize some of the major research findings from this location on the effects of [CO₂] and temperature on rice (*Oryza sativa* L., cv. IR-30).

Materials and Methods

Controlled-Environment Chambers

Rice (*Oryza sativa*, L., cv. IR-30) plants were grown season-long in six controlled environment chambers described by Jones et al. (1984). These chambers were located outdoors and were exposed to natural sunlight. They were constructed of a clear cellulose acetate roof with polyester film (Mylar) walls (ALMAC Plastics Inc., Atlanta, GA). Above ground chamber dimensions were 2.0 by 1.0 m in cross section by 1.5 m in height. The chamber tops were attached to an aluminum vat (1.9 by 0.8 m in cross section and 0.6 m deep) which was filled with soil to a depth of 0.5 m. This vat provided a water-

tight, flooded root environment for growing rice in paddy culture. A dedicated computer operating in real time was used to maintain environmental control in each of the chambers and record plant responses (photosynthesis and evapotranspiration rates) and environmental data (air temperature, humidity, [CO₂], paddy water temperature and solar radiation) to magnetic disc every 300 s. Signals from an array of sensors in each chamber were monitored at specific time intervals and used in control algorithms to actuated various devices in order to maintain desired environmental control. Shown in Table 1 are summaries of the [CO₂] and temperature set points maintained for the five season-long experiments conducted on rice at this location. Among these experiments [CO₂] ranged from 160 to 900 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air while temperature treatments ranged from 25/18/21 to 40/33/37°C (daytime dry bulb air temperature / nighttime dry bulb air temperature / paddy water temperature) (Table 1).

In all five of these experiments (Table 1), dew-point air temperature (General Eastern Model 1100 DP dew-point hygrometer, Watertown, MA) was controlled by driving a bypass valve which determined the rate of flow of chilled water through cooling coils. The condensate from the cooling coils passed through tipping bucket rain gauges monitored by the computer to calculate evapotranspiration (ET) rate over 300 s intervals. Dry bulb air temperature was controlled by turning computer-controlled electrical resistance heaters on and off (experiments I, II, and V) or by regulating the flow of hot water through air heat exchanger coils located in the duct work of the chambers with computer controlled 3-way valves (experiments III and IV). Dry bulb air temperature was measured with a shielded thermocouple located in the air stream of the upper ductwork near the top of each chamber. Paddy water temperatures were also measured with a thermocouple located in the paddy flood water at a point 25 mm above the flooded soil surface. Paddy flood water depth was maintained at 50 mm above the soil surface using a float actuated watering valve. Flood water temperature was maintained using resistance heaters consisting of plastic coated nichrome heating wires wrapped around nine 0.8-m-long aluminum rods and placed between the rows within the flood water (experiments I and II). In experiments III, IV and V, paddy flood water was controlled using a paddy water heat exchanger consisting of two submerged copper manifolds, 0.29 m in diameter and 1.9 m in length that supplied hot (65 - 75°C) or cold (15-18°C) water to nine submerged copper cross members, 0.16 m in diameter and 0.8 m in length. A simple feedback control algorithm permitted the injection of either hot or cold water into the paddy water heat exchanger through computer controlled solenoid valves.

Table 1. Treatment structures for experiments conducted on rice (cv. IR-30) in outdoor, naturally sunlit, controlled environment chambers.

Experiment Designation	Planting Date	[CO ₂] $\mu\text{mol mol}^{-1}$	Temperature ¹ (°C)	Comments
RICE I	22 Jan. 1987	160 250 330 500 660 900	31/31/27	Photoperiod extended to > 18 h until 2 March
RICE II	23 June 1987	160 250 330 500 660 900	31/31/27	Natural Photoperiod
RICE III	10 Oct. 1988	330 660	28/21/25 34/27/31 40/33/37	Full factorial: CO ₂ x Temperature
RICE IV	14 July 1989	660	25/18/21 28/21/25 31/24/28 34/27/31 37/30/34	One additional chamber at 330 $\mu\text{mol mol}^{-1}$ and 28/21/25°C
RICE V	8 June 1990	330 660	28/21/25	Full factorial: 2 CO ₂ x 3 N fertilizer rates

¹ Temperature treatments are expressed as daytime dry bulb air temperature / nighttime dry bulb air temperature / paddy water temperature.

Daytime [CO₂] was maintained using the computer controlled CO₂ injection system described by Jones et al., (1984). Pure CO₂ was injected from high pressure cylinders in order to replace the CO₂ taken up by the plants during photosynthesis. A similar injection system was used to maintain subambient [CO₂] (160 and 250 $\mu\text{mol mol}^{-1}$, Table 1) levels by injecting CO₂ free air during periods of low photosynthetic rates experienced early in the growing season prior to canopy closure or during periods of low light intensity. Solar irradiance above the chambers was measured with a pyranometer (Eppley Laboratories, Inc., Model 8-48, Newport, RI) and converted to photosynthetic photon flux density (PPFD) inside the chambers. Canopy net photosynthetic rate (Pn) was calculated from CO₂ mass balances over 300-s intervals while PPFD and ET were integrated over the same time interval. Water-use efficiency (WUE) was calculated from these data as the ratio of Pn to ET.

Plant Culture

In all five experiments (Table 1), rice was direct seeded by hand into 11 rows 0.18 m apart in each chamber. The plants were thinned to 235 plants m^{-2} , and flood water was applied at the second leaf stage. Specific control setpoints for each chamber (Table 1) were also initiated at this time. Shades made of black, densely-woven, polypropylene fibers were maintained at canopy height along the outside of each chamber to provide a light environment similar to that induced by border rows in a field crop. The chambers were fertilized with N, as urea and P and K prior to flooding. Additionally, urea-N was applied in 2 or 3 split applications during the growing season.

The mainstem of five replicate plants in each chamber was tagged with a small plastic loop prior to flooding. Stage of leaf development was determined after Haun (1973) for these tagged mainstems. At final harvest, growth attributes, grain yield, and yield components of each of 30 (experiment I) or 45 (experiments II - V, Table 1) sampled plants from each chamber were measured. For each plant, the number of panicles and individual grains were counted. Total above ground biomass and grain mass were determined after oven drying.

Results and Discussion

Development

The effects of a wide range of [CO₂] on rice mainstem leaf developmental rates are shown in Table 2 for the RICE I and II experiments. In the RICE II experiment, the number of mainstem leaves at panicle initiation and final number of mainstem leaves decreased from the 160 to the 500 $\mu\text{mol mol}^{-1}$ [CO₂] and remained similar from 500 to 900 $\mu\text{mol mol}^{-1}$ (Table 2). In this experiment, panicle initiation and boot stage occurred 10 to 12 days earlier in the superambient (500, 660, and 900 $\mu\text{mol mol}^{-1}$) compared with the 160 $\mu\text{mol mol}^{-1}$ [CO₂] treatment (Baker et al. 1990a). These results indicate that in the RICE II experiment, plant developmental rate was accelerated up to the 500 $\mu\text{mol mol}^{-1}$

Table 2. Effects of [CO₂] on the phyllochron interval and main stem leaf stage under two different photoperiods (see Table 1). Adapted from Baker et al. (1990a).

[CO ₂] treatment ($\mu\text{mol mol}^{-1}$)	Vegetative phase phyllochron interval		Main stem leaf stage at panicle initiation		Final main stem leaf number	
	--- days leaf ⁻¹ ---		----- Number of main stem leaves -----			
	I	II	I	II	I	II
160	4.1	3.6	12.1	12.9	15.4	15.3
250	4.1	3.7	12.0	12.0	14.6	14.2
330	3.6	3.3	11.8	11.6	14.8	13.6
500	3.4	3.8	12.1	10.7	14.8	13.0
660	3.3	3.6	12.2	10.5	14.6	12.8
900	3.6	3.6	12.0	10.5	14.6	12.8
LSD _{0.05}	0.6	NS	NS	0.8	NS	0.8

due to a shortening of the vegetative phase of development and a reduction in the number of mainstem leaves formed during vegetative development prior to panicle initiation. In the RICE I experiment, the effects of $[CO_2]$ on the number of mainstem leaves formed at panicle initiation (Table 2) and on the timing of panicle initiation and boot stage (Baker et al. 1990a) were small. This lack of developmental response to $[CO_2]$ in the RICE I experiment was attributed to the artificially extended photoperiod forcing the plants to remain vegetative, especially in the superambient $[CO_2]$ treatment (Baker et al. 1990a).

Overall, in these five experiments, temperature treatments ranging from 25/18/21 to 40/33 37°C greatly influenced developmental rate and total growth duration while the effects of $[CO_2]$ enrichment from 330 to 660 $\mu\text{mol mol}^{-1}$ were comparatively small. For example, number of days to anthesis was shortened by approximately 10 days across the temperature treatment range from 25/18/21 to 34/27/31°C for the RICE IV experiment (data not shown).

Growth and Yield

In the RICE I and II experiments, total above ground biomass, root biomass, tillering and final grain yield were all increased with increasing $[CO_2]$ treatment, with the greatest increase occurring across the 160 to the 500 $\mu\text{mol mol}^{-1}$ $[CO_2]$ treatment range followed by similar response to $[CO_2]$ from 500 to 900 $\mu\text{mol mol}^{-1}$ (Baker et al. 1990b). The increased growth under $[CO_2]$ enrichment is often associated with increased tillering in rice (Imai & Murata 1976; 1979a,b; Imai et al. 1985; Baker et al. 1990b). As a result, CO_2 enriched rice plants often produce greater grain yield due to an increase in the number of panicles (Imai et al. 1985; Baker et al. 1990b).

In Fig. 1 are comparisons of average grain yield for the RICE I and II experiments and canopy net photosynthesis (Pn) at 1500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ on day 61 of RICE II both normalized to the values obtained in the 330 $\mu\text{mol mol}^{-1}$ $[CO_2]$ treatments. A Michaelis-Menten rectangular hyperbola, modified by adding a Y-intercept term, was fit to these data after Allen et al. (1987) using the NLIN procedure provided by the SAS Institute (Cary, NC):

$$Y = (Y_{\text{max}} * [CO_2]) / ([CO_2] + K_m) + Y_i \quad (1)$$

Fig. 1. Rice grain yields and canopy net photosynthesis responses to $[CO_2]$ normalized to the values obtained from the 330 $\mu\text{mol mol}^{-1}$ $[CO_2]$ treatment. The percent variation explained by the rectangular hyperbola model was 90 and 96% for grain yield and photosynthesis, respectively.

where Y is yield or Pn; $[CO_2]$ is carbon dioxide concentration; Y_{max} is the asymptotic response limit of $(Y - Y_i)$ at high $[CO_2]$; Y_i is the intercept on the y axis; and K_m is the value of substrate concentration (eg. $[CO_2]$ at which $(Y - Y_i) = 0.5 * Y_{\text{max}}$). Parameters of $Y_{\text{max}} = 2.24$, $K_m = 284 \mu\text{mol mol}^{-1}$, and $Y_i = -0.13$ were obtained for relative grain yield (Fig. 1) with an asymptotic relative yield response ceiling ($Y_{\text{max}} + Y_i$) of 2.11 at infinite $[CO_2]$. For Pn parameters were 3.96, 70.83 $\mu\text{mol mol}^{-1}$, and -2.21, for Y_{max} , K_m , and Y_i , respectively with a relative Pn response ceiling of 1.75 at infinite $[CO_2]$. Using these parameters to calculate percentage increase in relative response at a $[CO_2]$ of 660 $\mu\text{mol mol}^{-1}$ over that obtained at 330 $\mu\text{mol mol}^{-1}$ resulted in 44% ($Y = 1.44$) and 36% ($Y = 1.36$) increases for grain yield and Pn, respectively. However, it should be noted that other environmental factors as temperature, light and mineral nutrition may strongly influence the shape of the curves shown in Fig. 1. Across a relatively wide temperature range from 25/18/21 to 37/30/34°C, Baker et al.

(1992a) found only a slight apparent temperature optimum for biomass production in the mid-temperature ranges. Plants grown at 40/33/37°C were found to be near the upper temperature limit for survival. Temperatures greater than 35°C for more than one hour at anthesis induce a high percentage of spikelet sterility (Yoshida 1981). In the 40/33/37°C treatments, plants in the 330 $\mu\text{mol mol}^{-1}$ [CO₂] treatment died during internode elongation while plants in the 660 $\mu\text{mol mol}^{-1}$ [CO₂] treatment produced small, abnormally shaped panicles that were sterile (Baker et al. 1992b).

Final above ground biomass, grain yield and yield components for the five rice experiments are shown in Table 3 for [CO₂] treatments of 330 and 660 $\mu\text{mol mol}^{-1}$. While these experiments differ mainly in the time of year they were conducted (Table 1) and utilized different soil types, several trends in plant responses to [CO₂] and temperature are apparent. At both [CO₂] treatments, grain yield was highest in the 28/21/25°C temperature treatment followed by a decline to zero yield in the 40/33/37°C treatment. The [CO₂] enrichment from 330 to 660 $\mu\text{mol mol}^{-1}$ increased grain yield by increasing the number of panicles plant⁻¹ while filled grain panicle⁻¹ and individual seed mass were less affected. As with grain yield, temperature effects on yield components were large and highly significant. Panicles plant⁻¹ increased while filled grain panicle⁻¹ decreased sharply with increasing temperature treatment. Individual seed mass was stable at moderate temperatures but tended to decline at temperature treatments above 34/27/31°C. Final above ground biomass and harvest index were increased by [CO₂] enrichment while harvest index declined sharply with increasing temperature treatment. Overall, there were no significant interactive effects between [CO₂] and temperature on grain yield, yield components, or final above ground biomass (Table 3). Utilizing polynomial regression equations to describe the relationship between the grain yield and temperature in Table 3, Baker et al. (1993) found that a linear interpolation across predicted grain yields at 26 and 36°C resulted in grain yield declines of approximately 9.6 and 10.1% for each 1°C rise in temperature for the 330 and 660 $\mu\text{mol mol}^{-1}$ [CO₂] treatment, respectively.

Table 3. Rice grain yield, components of yield, total above ground biomass and harvest index for rice grown season-long in five separate experiments. Adapted from Baker et al. (1993).

CO ₂ $\mu\text{mol mol}^{-1}$	Temperature (°C)	Mean air temp. (°C)	Grain yield Mg/ha	Panicle plant ⁻¹ no/plant	Filled grain no/panicle	Grain mass mg/seed	Biomass g/plant	Harvest index	Experiment No.
330	28/21/25	24.2	7.9	5.1	34.5	17.4	7.3	0.47	RICE III
	28/21/25	25.1	6.6	3.9	39.6	17.5	6.5	0.44	RICE IV
	28/21/25	25.1	8.0	4.0	47.5	18.5	8.1	0.43	RICE V
	31/31/27	31.0	5.2	5.9	23.0	17.1	5.5	0.42	RICE I
	31/31/27	31.0	4.3	5.4	19.0	17.9	7.2	0.26	RICE II
	34/27/31	30.2	4.2	7.7	15.2	16.2	5.6	0.43	RICE III
	40/33/37	36.2	0.0	-	-	-	-	-	RICE III
660	25/18/21	22.1	8.4	4.4	46.0	18.2	7.8	0.47	RICE IV
	28/21/25	24.2	8.4	5.0	37.7	18.0	7.9	0.46	RICE III
	28/21/25	25.1	10.4	4.2	58.3	18.3	8.9	0.50	RICE IV
	28/21/25	25.1	10.1	4.4	54.2	19.0	9.3	0.47	RICE V
	31/31/27	31.0	6.8	6.9	25.1	17.2	7.5	0.40	RICE I
	31/31/27	31.0	6.4	6.0	24.8	18.4	9.3	0.29	RICE II
	34/27/31	30.2	4.8	6.5	18.5	16.7	6.3	0.32	RICE III
	34/27/31	31.1	3.4	7.5	12.9	16.3	8.1	0.18	RICE IV
	37/30/34	34.1	1.0	8.0	3.0	14.2	7.1	0.06	RICE IV
	40/33/37	36.2	0.0	-	-	-	-	-	RICE III
F-Values									
CO ₂ concentration			4.2 *	4.3 *	0.4 NS	0.1 NS	13.1 **	4.6 *	
Temperature			51.8 **	22.6 **	51.1 **	27.0 **	3.2 *	32.8 **	
CO ₂ * Temperature			1.9 NS	1.7 NS	1.3 NS	0.3 NS	0.2 NS	1.9 NS	

**, * Significant at the 0.01 and 0.05 probability levels, respectively. NS = Not significant.

¹ Mean air temperature is the average of day and night temperature adjusted for thermoperiod.

Gas exchange

Shown in Fig. 2 is an example of Pn vs. PPFD for the six [CO₂] treatments on day 60 of the RICE II experiment. In all five experiments, following complete canopy closure, the Pn light response curve was essentially linear and showed little tendency towards light

Fig. 2. Canopy net photosynthetic rate (P_n) vs. incident photosynthetic photon flux density (PPFD) for six daytime $[CO_2]$ treatments on day 60 of the RICE II experiment.

Fig. 3. Canopy net photosynthetic rate (P_n) vs. incident photosynthetic photon flux density (PPFD) for two daytime $[CO_2]$ treatments and five daytime temperature treatments on day 60 of the RICE IV experiment.

saturation. This is likely due to the high plant population used in these studies and the very erect leaf orientation of the rice cultivar IR-30 permitting more efficient distribution of light with depth in the canopy. As in Fig. 1, at high light, P_n increased with increasing $[CO_2]$ up to the $500 \mu\text{mol mol}^{-1}$ and was very similar from 500 to $900 \mu\text{mol mol}^{-1}$ (Fig. 2).

At the leaf-level, elevated $[CO_2]$ not only increases photosynthesis but typically increases the leaf temperature optimum for photosynthesis rate in C_3 plants (Percy and Björkman, 1983; Long, 1991). At the canopy level, apparent photosynthesis has been shown to be relatively insensitive to air temperature across a rather broad air temperature range (Baker et al. 1972; Jones et al. 1985). Shown in Fig. 3 is an example of rice canopy P_n vs. PPFD across a daytime air temperature range from 25 to 37°C on day 60 of the RICE IV experiment. While $[CO_2]$ enrichment increased P_n at the 28°C treatment, P_n was very similar among the daytime air temperature treatments in the $660 \mu\text{mol mol}^{-1}$ $[CO_2]$ treatment. Many studies of canopy photosynthesis responses to air temperature show only small differences across a rather wide range of air temperatures. This may be due in large part to the increase in evaporative cooling of leaves as air temperature increases.

Daytime totals of ET and calculations of WUE vs. daytime $[CO_2]$ treatment are shown in Fig. 4 for day 61 of the RICE II experiment. Carbon dioxide enrichment results in partial stomatal closure, increased stomatal resistance and reduces both single leaf and whole canopy transpiration. In some plant species such as soybean, $[CO_2]$ enrichment increases canopy leaf area so that the surface area for transpiration also increases thereby offsetting some of the water savings from $[CO_2]$ enrichment (Jones et al. 1985; Allen et al. 1985). The measured leaf area index of the RICE II experiment ranged from 10.1 to 14.3 across the $[CO_2]$ treatments from 160 to $900 \mu\text{mol mol}^{-1}$. In general, ET declined with increasing $[CO_2]$ in the RICE II experiment (Fig. 4) especially from the 250 to $900 \mu\text{mol mol}^{-1}$ $[CO_2]$. Calculations of WUE increased with $[CO_2]$ treatment due to the decline in ET

Fig. 4. Comparison of daily totals of water-use efficiency (WUE) and evapotranspiration (ET) for six daytime [CO₂] treatments on day 60 of the RICE II experiment. Total PPFD was 39.4 mol (Photons) m⁻².

Fig. 5. Comparison of daily totals of water-use efficiency (WUE) and evapotranspiration (ET) for two daytime [CO₂] treatments and five daytime temperature treatments on day 58 of the RICE IV experiment. Total PPFD was 26.5 mol (Photons) m⁻².

across this [CO₂] treatment range and the increase in Pn with [CO₂] up to the 500 μmol mol⁻¹ treatment (Figs. 1 and 2).

The effects of air temperature treatment on daytime totals of ET and calculations of WUE are shown in Fig. 5 for day 58 of the RICE IV experiment. In the 28°C air temperature treatment, [CO₂] enrichment from 330 to 660 μmol mol⁻¹ resulted in a similar decrease in ET and increased WUE as shown in Fig. 4. Evapotranspiration was greatly influenced by air temperature treatment and was roughly doubled from the 25 to the 37°C temperature treatment (Fig. 5). Calculations of WUE declined from the 28 to the 37°C temperature treatment due to the sharp increase in ET (Fig. 5) and the relatively stable Pn across this temperature range (Fig. 3).

Summary

Total growth duration was shortened by 10 to 12 days across a [CO₂] range from 160 to 500 μmol mol⁻¹ due to a shortened vegetative phase of development and a reduction in the number of mainstem leaves formed during this period. Photosynthesis, growth, and final grain yield increased with [CO₂] from 160 to 500 μmol mol⁻¹ but were very similar from 500 to 900 μmol mol⁻¹. Carbon dioxide enrichment from 330 to 660 μmol mol⁻¹ increased grain yield mainly by increasing the number of panicles plant⁻¹ while increasing temperature treatment above 28/21/25°C resulted in decreased grain yield due largely to a decline in the number of filled grain panicle⁻¹. Evapotranspiration decreased and water-use efficiency increased with increasing [CO₂] treatment while the reverse trends were found with increasing temperature treatment. These results indicate that future increases in global atmospheric [CO₂] are likely to benefit rice production by increasing photosynthesis, growth, and grain yield while reducing water requirements and increasing water-use efficiency. In warmer areas of the world, possible future increases in air temperature may result in yield decreases and increased water requirements.

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