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Photosynthesis and Yield of Southern U.S.A. Rice Cultivars in Response to CO_2 and Temperature

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Abstract

This study was conducted to determine the effects of atmospheric carbon dioxide concentration (CO_2) and air temperature on four Southern USA rice cultivars. In 2000, 'Cocodrie', 'Cypress' and 'Jefferson' were grown season-long in outdoor, naturally sunlit, controlled environment chambers in constant day/night air temperature regimes from 24 to 40°C under an elevated CO_2. In 2002, the rice cultivar 'Lamont' was grown with day/night air temperature treatments of 19/15 to 35/31°C under elevated CO_2. The CO_2 enrichment increased grain yield by 46 to 71% among the three cultivars in 2000. In 2002, CO_2 enrichment resulted in a non-significant increase in seed yield for the MC but more than doubled RC yields. We conclude that: i) these four USA rice cultivars may be more sensitive to high temperature stresses on reproductive development than some previously studied Asian rice cultivars; ii) the wide range in grain yield responses to CO_2 among these four cultivars points to the potential for breeding rice cultivars that are more responsive to expected future global levels of atmospheric CO_2 and; iii) elevated CO_2 may result in enhanced ratoon crop growth and yield.

Key words: Acclimation, Climate Change, Rice-ratooning

1. Introduction

Rice is the world's most important grain crop in terms of direct human food consumption. Although most rice is consumed in the countries in which it is produced, the United States accounts for 20 to 25 percent of the world trade in rice. To meet future food requirements in Asia, increases in rice yield will probably come from increases in rice yield per unit land area rather than an expansion of total rice acreage due to a lack of new land in Asia suitable for cultivating rice (Cassman, 1999). Based on both historical yield records and by comparing grain yields in cultivar trials, Peng et al., (1999; 2000) estimate that the yield potentials of the indica inbred lines developed by the International Rice Research Institute (IRRI) have not changed for the last 30 years. Due to the leveling-off or plateau in rice grain yields experienced in many Asian countries in recent years, coupled with an expanding human population, the USA world market share in rice trading could expand in the future.

The current rise in global atmospheric CO_2 has been well documented (Keeling et al., 1995). A primary direct effect of elevated CO_2 on plants with the C_3 carbon fixation pathway, such as rice, is usually an increase in net photosynthesis which often leads to increases in growth and final grain yield.

As instrumentation for measuring leaf-level photosynthesis became increasingly available, single-leaf photosynthesis of rice and other crops was extensively examined in the 1960's and '70's. Because of a lack of correlation between single-leaf photosynthesis and yield, extensive efforts to breed crop cultivars with high leaf photosynthesis failed to result in the release of higher-yielding crop cultivars (Nelson, 1988) and in fact even led to some cultivars with lower yield potential (Evans, 1990). However, leaf-level photosynthesis (A_{leaf}) measurements, especially A_{leaf} vs. light and A_{leaf} vs. C_i (C_i, substomatal CO_2 concentration) are essential to understanding leaf-level biochemistry of photosynthesis and photosynthetic responses to environmental variables. In contrast with A_{leaf}, canopy photosynthesis or canopy net assimilation (A_{can}) *does* correlate with crop biomass production and it is generally agreed that it is this parameter, A_{can}, that needs to increase in order to achieve the required future rice grain yield enhancements (Peng, 2000).

Previous studies by Ziska and Teramura (1992) and Ziska et al. (1996) indicate that there is considerable variability among current rice cultivars in their responses to CO_2 and temperature. Recently, Baker (2004) found large differences in the growth and grain yield responses of four Southern USA rice cultivars in response to CO_2 and temperature. In this paper, we briefly summarize these findings and present recently analyzed canopy photosynthesis data that help explain the differences in yield responses to CO_2 and temperature of these Southern USA rice cultivars.

2. Materials and Methods

2.1 SPAR chambers

Experiments were conducted in the Soil-Plant-Atmosphere-Research (SPAR) facility at Beltsville, Maryland. This facility is comparable in design and operation to similar outdoor experimental systems at the University of Florida (Pickering et al. 1994), Corvallis, Oregon (Tingey et al., 1996) and Mississippi State University (Reddy et al. 2001). This facility consists of 18 naturally sunlit, SPAR chambers, six of which were available for use in these experiments. These chambers control atmospheric CO_2 con-

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centration, air temperature and humidity while measuring canopy photosynthesis at 300 s intervals. A physical description of the operation of these SPAR chambers is given by Baker (2004) and Baker et al. (2004).

2.2 Plant culture- 2000

For these experiments, a dark red Christiana clay top soil was placed into plastic containers 0.0189 m^3 in volume and 0.4 m tall. Prior to planting rice, each container was filled with soil to within 0.07 m of the container top in order to allow the later application of a 0.05 m permanent flood above the soil surface. Water was supplied to each container with a computer-controlled drip irrigation system. The Southern USA rice cultivars utilized in 2000 were 'Cocodrie', 'Cypress' and 'Jefferson'. These cultivars are commonly grown in the rice growing regions of Texas and Louisiana, USA. Three plastic containers per cultivar (9 containers total per chamber) were placed into the chambers on the day of planting. The 9 containers per chamber were arranged in three rows of three containers, simulating a 0.3 m x 0.3 m hill arrangement with a combined total of 36 plants m^{-2} after thinning. Eight seeds per container for each cultivar were planted on 29 June 2000. The rice was thinned to 4 plants per container on 10 July and the 0.05 m flood water was applied. All six chambers were maintained at a constant day/night air temperature of 30°C until 7 July to facilitate uniform emergence.

Five chambers were maintained from planting to final harvest at a daytime CO_2 treatment of 700 μmol CO_2 mol^{-1} air while one additional chamber was controlled to 350 μmol mol^{-1}. Constant day/night air temperature treatments of 24, 28, 32, 36 and 40°C were initiated in the 700 μmol mol^{-1} CO_2 treatment on 7 July while the 350 μmol mol^{-1} CO_2 treatment was controlled to 28°C. Plants in the 40°C temperature treatment died during early vegetative growth and the air temperature and CO_2 treatments were terminated in this chamber.

2.3 Plant culture- 2002

Seeds of the rice cultivar 'Lamont" were sown in greenhouse flats (cell size 6.0 x 6.0 x 6.0 cm) filled with a commercial peat-vermiculite mix on 17 April 2002. Twelve seedlings with about 1.5 main-stem leaves were transplanted into each of nine containers within each of the six outdoor controlled environment chambers on 26 April. Plants were thinned to a uniform 8 plants per container by removing 2 plants from each container on both 6 and 20 May. This resulted in a final plant population of 72 plants m^{-2} in each chamber.

A constant day/night air temperature of 30°C was maintained from 26 to 29 April to promote uniform establishment. Five chambers were maintained from 29 April to final harvest at a daytime [CO_2] treatment of 700 μmol CO_2 mol^{-1} air while one additional chamber was controlled to 350 μmol mol^{-1} and 27/23°C. In the 700 μmol mol^{-1} [CO_2] treatment, day/night air temperature treatments were set to 19/15, 23/19, 27/23, 31/27 and 35/31°C. The day/night thermoperiod for this experiment was 15/9 h.

To test for possible photosynthetic acclimation, a short-term [CO_2] cross-switching experiment was conducted in the 2002 experiment. Prior to dawn, the [CO_2] in each chamber was controlled to 169, 256, 355, 501, 700 and 999 μmol (CO_2) mol^{-1} air from 1 to 6 June 2002, respectively. In this way, photosynthetic light response of the long-term 350 and 700 μmol mol^{-1} [CO_2] treatments could be compared at a range of common short-term [CO_2]. After 13.00 hours, the [CO_2] control setpoint was returned to its original long-term growth concentration treatment.

3. Results and Discussion

3.1 Yield 2000

Shown in Table 1 are the yield and final above-ground biomass for the 350 and 700 μmol mol^{-1} treatments grown at 28°C in the 2000 experiment. The effects of CO_2 enrichment on grain yield amounted to gains of 46, 71 and 57% for Cocodrie, Cypress and Jefferson, respectively. The CO_2 enrichment increased grain yield largely through increases in the number of filled grains per panicle and an increase in individual seed mass of about 1 to 2 mg per seed (Baker, 2004). The CO_2 enrichment also increased above-ground biomass and harvest index. Among the three cultivars, Cypress had the highest grain yield, due mainly to the production of more panicles per plant compared with the other two cultivars.

Table 1. Grain yield, above-ground biomass and harvest index for three USA rice cultivars grown at 28°C and two CO_2 concentrations. (Adapted from Baker, 2004).

CO_2 μmol mol^{-1}	Cultivar	Yield g/plant	Biomass g/plant	Harvest index
350	Cocodrie	14.5	50.1	0.29
	Cypress	18.0	61.9	0.29
	Jefferson	12.8	44.1	0.29
700	Cocodrie	21.2	70.1	0.31
	Cypress	30.8	90.5	0.34
	Jefferson	20.1	59.4	0.34
		F-values		
	CO_2	14.9**	10.9**	9.1**
	Cult	4.5*	5.0*	1.1 NS
	CO_2 * Cult	0.7 NS	0.4 NS	0.7 NS

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

The temperature treatments had large effects on growth and yield. In all three cultivars the plants in the 40°C treatment died during vegetative growth and there was no living above-ground biomass at final harvest (Baker, 2004). Plants in the 36°C treatment survived to produce panicles, but none of the panicles in this treatment produced grain for any of the three cultivars. The 28°C temperature treatment appeared to be closest to the optimum temperature for grain yield, above-ground biomass and harvest index.

3.2 Yield 2002

For the cultivar Lamont in the 27/23°C treatment, CO_2 enrichment resulted in a non-significant 12% increase in MC seed yield (Table 2). All other MC growth and yield measurements were similarly unaffected by CO_2 enrichment except for filled grain number per panicle which was barely significantly higher ($P \leq 0.05$) than filled grain number of the ambient CO_2 treatment (Baker 2004). Temperature effects on MC yield and yield components were large. Plants in both the 19/15 and 35/31°C temperature treatments survived to produce panicles but failed to fill any grain. Both MC grain yield and numbers of filled grains per panicle were highest in the 27/23°C temperature treatments.

Table 2. Main crop grain yield, above-ground biomass and harvest index for the rice cultivar 'Lamont' grown in five day/night air temperature treatments and two CO_2 concentrations. (Adapted from Baker, 2004).

CO_2 (μmol mol^{-1})	Temp. °C	Yield g/plant	Biomass g/plant	Harvest index
350	27/23	16.9	33.7	0.53
700	19/15	0.0	22.4	---
	23/19	8.9	28.1	0.29
	27/23	19.0	33.5	0.57
	31/27	14.4	34.5	0.41
	35/31	0.0	22.4	---
LSD (Temp)*		3.4	5.0	0.07
LSD (CO_2)		NS	NS	NS

*Least significance difference (LSD) with P-value ≤ 0.05 for comparing means among the five air temperature treatments (LSD (Temp)) at a CO_2 concentration of 700 μmol mol^{-1} or two CO_2 treatments at an air temperature treatment of 27/23 °C (LSD(CO_2)).

In contrast to the MC yields, RC yields were roughly doubled by CO_2 enrichment at the 27/23°C temperature treatment (Table 3). Above-ground biomass and harvest index were also significantly increased by CO_2 enrichment. In both the MC (Table 2) and RC (Table 3) plants in the 35/31°C temperature treatment survived to produce panicles but failed to fill any seed. The RC yields and above-ground biomass were significantly larger in the 31/27°C treatment compared with the other temperature treatments.

Table 3. Ratoon crop grain yield, above-ground biomass and harvest index for the rice cultivar 'Lamont' grown in four day/night air temperature treatments and two CO_2 concentrations. (Adapted from Baker, 2004).

CO_2 (μmol mol^{-1})	Temp. °C	Yield g/plant	Biomass g/plant	Harvest index
350	27/23	5.6	18.9	0.29
700	23/19	4.6	19.7	0.24
	27/23	11.4	24.7	0.46
	31/27	13.4	31.9	0.42
	35/31	0.0	22.8	---
LSD (Temp)*		1.6	3.2	0.03
LSD (CO_2)		2.0	NS	0.05

* Same as in Table 2.

3.3 Canopy net assimilation (A_{can})

An example of whole canopy A_{can} vs. PFD on 26 August 2000 for the [CO_2] and temperature treatments is shown in Fig. 1. Since all three cultivars were present in each chamber, Fig. 1 represents the combined A_{can} for all three cultivars and is presented in order to illustrate relative difference in A_{can} among the [CO_2] and air temperature treatments. Simple second order polynomials fit the data well with R^2 values ranging between 0.94 and 0.96. Data are not shown for the 40°C temperature treatment since the plants had died by this time in the growing season. At 28°C and at a PFD of 1600 μmol (photons) m^{-2} s^{-1}, [CO_2] enrichment increased A_{can} by about 41%. At 700 μmol mol^{-1} the temperature optimum for A_{can} appeared to be near 28 to 32°C with higher or lower temperature treatments resulting in lower A_{can} (Fig. 1).

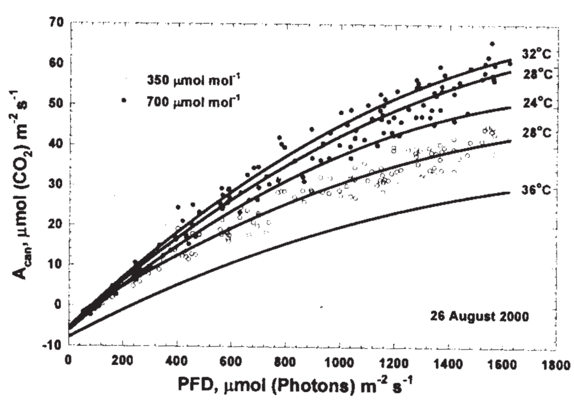

Fig. 1. Canopy net assimilation (A_{can}) vs. PFD for three cultivars of rice grown in four air temperature treatments. Canopy net assimilation represents the combined contributions of all three cultivars of rice in each chamber. Data points are for the ambient (open symbol) and elevated (closed symbol) [CO_2] treatments at 28°C air temperature treatment. The fitted curves are second order polynomials with R^2 values ranging from 0.94 to 0.99.

The seasonal trends in A_{can} measured at a PFD of 1400 μmol (photons) m^{-2} s^{-1} are shown in Fig. 2 for the rice cultivar Lamont in the 2002 experiment. As with MC grain yield in the 2002 experiment, CO_2 enrichment resulted in minor differences in A_{can} for the MC. Following MC harvest however, quite large differences in A_{can} were observed between the two CO_2 treatments for the RC.

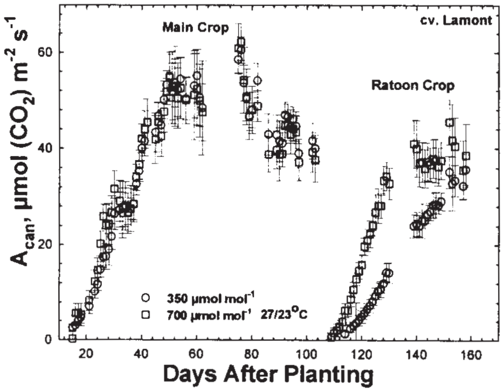

Fig. 2. Seasonal trends in canopy net assimilation rate (A_{can}) at PFD=1400 μmol (photons) m^{-2} s^{-1} for the rice cultivar Lamont grown in 2002. Error bars represent ± 95% confidence limit intervals.

Tests for A_{can} acclimation to long-term CO_2 enrichment of the MC in the 2002 experiment are shown in Fig. 3, where CO_2 was briefly changed over a wide range of short-term CO_2. The lower response curve of the long-term 700 μmol mol^{-1} treatment compared with that of the 350 μmol mol^{-1} indicates a down-regulation of A_{can} in response to CO_2 enrichment and may have been a factor in the relative lack of response to CO_2 enrichment for A_{can} of the MC and non-significant MC grain yield response (Table 2) in the 2002 experiment. The occurrence (or non-occurrence) of 'photosynthetic acclimation', also called 'down-regulation of photosynthesis', in response to CO_2 enrichment is a naturally occurring phenomenon that, due to a lack of understanding, limits our ability to predict plant and ecosystem responses to CO_2 enrichment.

In several studies with Asian cultivars, CO_2 enrichment increased grain yield largely through an increase in tillering and panicle numbers (Baker and Allen, 1993; Kim et al. 1996; Ziska et al. 1996; Kim 2001). Moya et al. (1998) found that grain yield enhancements due to CO_2 enrichment among three different Asian cultivars was related to relative tillering ability of a particular cultivar. In their study, the 'new plant type' (NPT2) cultivar, had a relatively fixed tiller number with large panicles, and was the least responsive cultivar to CO_2 enrichment.

In the present study with Southern USA rice cultivars, CO_2 enrichment did not significantly affect final numbers of panicles (Baker, 2004). For the three cultivars most responsive to CO_2 enrichment in the

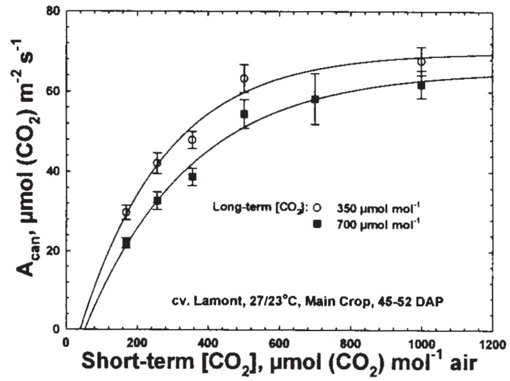

Fig. 3. Canopy net assimilation (A_{can}) vs. short-term CO_2 treatments of 169, 256, 355, 501, 700 and 999 μmol (CO_2) mol^{-1} air. Each datum is the solution of second order regression models of A vs. PFD with PFD set to PFD=1400 μmol (photons) m^{-2} s^{-1}. Error bars represent ± 95% confidence limit intervals.

2000 experiment, the number of filled grains per panicle was the largest yield component contributor to increased grain yield under CO_2 enrichment, followed in most cases by a modest but significant increase in individual seed mass.

Recent studies have shown that reproductive development is more sensitive to high temperature stresses than vegetative growth in rice. As daily mean temperatures increased above 26°C, rice grain yields were progressively reduced in both an *Indica* cultivar ('IR-30', Baker and Allen, 1993) and a *Japonica* cultivar ('Akihikari', Kim et al. 1996). Because flowering in rice usually occurs near midday, daytime maximum air temperature, rather than average daily temperature, is more relevant to the consideration of high-temperature-induced spikelet sterility. In these two previous studies, daytime air temperatures at or above 40-41°C resulted in zero grain yield. However, some yield was still produced at daytime air temperatures of 37°C (Baker and Allen, 1993) or as high as 39-40°C (Kim et al. 1996). The results of this study indicate that the upper daytime air temperature threshold for grain yield of these four USA rice cultivars is somewhere between 32 to 35°C.

Rice ratooning is practiced in many of the rice growing regions of the Southeastern USA. This practice involves harvesting the main crop (MC) and allowing the crop to re-grow for a second or ratoon crop (RC). The large RC yield increase from CO_2 enrichment (Table 3) may be explained by considering the effects of elevated CO_2 on carbohydrate metabolism in rice. In rice, remobilization of stored carbohydrates in the leaves and stem can contribute between 20 to 40% of the MC grain yield (Yoshida, 1972). Turner and Jund (1993) found a positive correlation between MC stem total nonstructural carbohydrate (TNC) content measured at MC harvest and subsequent RC grain yields. They suggested that high MC stem TNC should contribute to RC yields through beneficial effects on tiller regeneration processes following MC harvest. Several studies on rice have shown that CO_2 enrichment increases sucrose, starch and TNC concentrations in vegetative tissues (Vu et al. 1998; Widodo et al. 2003). Visual observations of the growing RC canopies indicated that under CO_2 enrichment, re-growth was faster and the canopies intercepted more light, especially at the beginning of re-growth.

A nearly universal finding in CO_2 enrichment studies, including those on rice, is increases in soluble carbohydrate or total nonstructural carbohydrate (TNC) concentration of leaves and other organs for plants grown under CO_2 enrichment (Rowland-Bamford, 1996; Vu et al. 1998). The increased TNC is often attributed to enhanced photosynthesis under CO_2 enrichment. Carbohydrate concentration is known to modulate the expression of many genes, including photosynthetic genes (Jang and Sheen, 1997). Long-term CO_2 enrichment for rice can result in decreases in the content of Rubisco and other photosynthetic pigments as well as decreases in Rubisco activity (Rowland-Bamford et al., 1991). Clearly, the mechanisms underlying photosynthetic acclimation and the resulting impacts on whole-canopy photosynthetic rates and resulting crop growth rates and final grain yield are areas in great need of further study.

4. Conclusions

The wide range in grain yield responsiveness to CO_2 enrichment found among these four USA rice cultivars points to the potential for selecting or developing high-yielding USA rice cultivars with the ability to take advantage of expected future global increases in CO_2. The findings presented here indicate that CO_2 enrichment could have potentially large positive effects on RC yields. Comparison of the results presented here with prior studies suggests that under CO_2 enrichment, these four USA rice cultivars may be more sensitive to high temperature stresses than previously studied Asian *indica* and *japonica* cultivars.

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