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Intraspecific variation in the response of rice (*Oryza sativa* L.) to increased CO_2 and temperature: growth and yield response of 17 cultivars[1]

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Abstract

Seventeen rice (*Oryza sativa* L.) cultivars of contrasting ecosystems and origins were exposed to two CO_2 concentrations (373 [ambient] and 664 $\mu l\ l^{-1}$ CO_2 [elevated]) at two different day/night temperatures (29/21 °C and 37/29 °C) in glasshouses at the International Rice Research Institute phytotron during the dry seasons of 1994 and 1995. Growth at elevated CO_2 (as determined by total plant biomass at maturity) increased by an average of 70% and 22%, respectively, for all cultivars for growth temperatures of 29/21 °C and 37/29 °C relative to the ambient CO_2 treatment. At the 29/21 °C optimal growth temperature, grain yield increased on average *c.* 50% with enriched CO_2. In contrast, at the higher growth temperature (37/29 °C), grain yield was almost zero, presumably due, in part, to temperature-induced infertility (i.e. the percentage of filled spikelets was $<1\%$). Among cultivars, IAC 165, a tropical japonica from Brazil, showed the largest relative increase in both biomass and grain yield. While the range of responses to increased CO_2 and/or temperature were quite large (e.g. 10–250%) and may not be applicable to field conditions, data indicate that lines are available which could maximize productivity as CO_2 concentration increases. Additional work, however, would be needed to identify cultivars which would maintain maximum yields in a high CO_2, high temperature environment.

Key words: CO_2 concentration, rice, temperature, intraspecific variation.

Introduction

Carbon dioxide has risen from a preindustrial concentration (*c.* 270 $\mu l\ l^{-1}$) to a current estimate of approximately 365 $\mu l\ l^{-1}$ (Conway *et al.*, 1994). As the need for fossil-fuel energy increases with increasing population, it is generally accepted that CO_2 concentrations will reach a mean of *c.* 600 $\mu l\ l^{-1}$ sometime during the 21st century (Conway *et al.*, 1994). Since plants possessing C_3 metabolism (i.e. 95% of all plant species) are currently CO_2 limited, significant increases in growth and development could occur for a wide range of cultivated and native plant species. Interspecific differences in the potential response to increasing CO_2 are, in fact, well documented (Kimball, 1983; Cure and Acock, 1986; Ziska *et al.*, 1991).

Little attention, however, has been given to intraspecific variation in plant response to increasing CO_2 concentration either by itself or in conjunction with other potentially changing environmental parameters (Wulff and Alexander, 1985; Ziska and Teramura, 1992; Curtis *et al.*, 1994). As CO_2 concentration increases several general circulation models (GCMs) predict that current mean temperatures will rise by 2–5 °C (Gutowski *et al.*, 1988; Cohen, 1990). It is important, therefore, to examine genetic diversity with respect to increasing CO_2 and temperature since both parameters could increase concurrently. Intraspecific variation could be used to select for optimal cultivars which would maximize commercial productivity in a high CO_2, high temperature environment. Such information would be especially valuable for plant breeders in selecting lines within agronomically important species.

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Abbreviations: CO_2, carbon dioxide; DAS, days after sowing; FS, filled spikelets; *PAR*, photosynthetic active radiation; PE, panicle emergence.

Among agronomically important species, rice supplies approximately two billion people with 40% of their daily calorific needs (see Table 1.1, Matthews *et al.*, 1995). Many of the countries dependent on rice have a limited ability to maintain adequate calorific needs if rice production falls below consumption. For future climatic conditions, rice breeders may wish to select cultivars of rice based on maximization of growth and reproductive output. Previous work on the response of two cultivars to elevated CO_2 under optimal temperature conditions (Ziska and Teramura, 1992) has demonstrated that intraspecific variation with respect to growth and productivity is possible; however, the range of the response to CO_2 and the sensitivity of this response to increasing temperature was not examined.

In the current experiment, the growth characteristics of seventeen rice cultivars of contrasting morphologies and origins were examined. The primary objective of this study was to determine the range of response in plant biomass and grain yield as CO_2 and/or temperature increased. A secondary objective was to determine if sufficient variability existed so as to select for rice genotypes which could maximize productivity with future increases of CO_2 and/or temperature.

Table 1. *List and origin of cultivars grown at two elevated* CO_2 *concentrations (373* $\mu l\ l^{-1}$ *and 664* $\mu l\ l^{-1}$*) at two different day/night temperature (29/21 °C and 37/29 °C)*

Additional details of the experimental treatments are given in the text.

Cultivar	Origin	Comments
1. Azucena	Philippines	Upland, blast and drought resistance
2. IAC 165	Brazil	Upland, blast and drought resistance
3. IRAT 104	Ivory coast	Upland
4. IR28	IRRI	Lowland, salt susceptible
5. IR30	IRRI	Lowland
6. IR36	IRRI	Lowland
7. IR46	IRRI	Lowland, moderate drought tolerance
8. IR64	IRRI	Lowland, drought susceptible
9. IR72	IRRI	Lowland, widely adapted cultivar
10. IR74	IRRI	Lowland, tungro resistance
11. ITA 186	IITA	Upland, drought resistance
12. Kinandang patong	Philippines	Upland
13. MGL-2	India	Upland, drought resistance
14. N22	India	Upland, heat and drought tolerant
15. OS4	West Africa	Upland, blast resistant, deep roots
16. Salumpikit	Unknown	Upland, drought resistance
17. YRL-39	Australia	Lowland, panicle height < canopy height

Materials and methods

Seed of 17 rice (*Oryza sativa* L.) cultivars were obtained from the International Rice Research Institute (Los Baños, Philippines). These cultivars represent a range of japonica and indica types from lowland to upland ecosystems (e.g. Salumpikit versus IR36), origins (e.g. IRAT 104 versus MGL-2) with contrasting morphologies (e.g. YRL-39 versus IR72). A description of the individual cultivars used is given in Table 1.

Seeds from each cultivar were pre-germinated at 30 °C and five seedlings transplanted to circular PVC pots (25 cm diameter, 24 l) filled with local soil (Maahas clay) 2–3 d after germination. Plants were thinned to one plant per pot at 10 d after sowing (DAS). Plants from a given cultivar were grouped together but groups spaced so as to minimize mutual shading. Pots within a given cultivar were separated by a distance of *c.* 30 cm. Both pots within a group and groups were rotated weekly inside a glasshouse until flowering to minimize border effects. All pots were flooded to 3 cm at 20 DAS with nutrient solution (Yoshida *et al.*, 1976) without nitrogen and pots were drained and new solution added on a weekly basis. Weekly measurements of chlorophyll content were made using the SPAD (model 502, Minolta Corp., Japan) to determine if the plants were receiving adequate nitrogen (Peng *et al.*, 1995). Nitrogen was applied separately as ammonium sulphate based on SPAD readings (about once every 2 weeks until flowering). While nitrogen applied did vary depending on cultivar, for a given cultivar the amount of N applied did not vary between treatments. For all cultivars and treatments, SPAD levels remained above 37 (i.e. optimal N levels, see Peng *et al.*, 1995) until flowering. All other standard cultural practices with respect to pests and diseases were followed.

Six to eight pots per cultivar (depending on seed availability) were randomly assigned to one of four environmental treatments. These were (1) ambient CO_2 ($373 \pm 3.9\ \mu l\ l^{-1}$) at an optimal growth temperature of 29/21 °C (day/night); (2) elevated CO_2 ($664 \pm 32\ \mu l\ l^{-1}$) at the same temperature; (3) ambient CO_2 at the high growth temperature of 37/29 °C; (4) elevated CO_2 at the high growth temperature. All environmental treatments were maintained within individual, naturally sunlit glasshouses which are part of the IRRI phytotron. The highest growth temperature was chosen as being approximately 2–3 °C above current maximum temperatures encountered in the field during the dry season at IRRI. Previous experience within the IRRI phytotron has shown 29/21 °C to be the optimal growing temperature for many different rice cultivars (Yoshida *et al.*, 1976). CO_2 concentration was monitored using a Li-Cor (Model 6252, Lincoln, NE, USA) IRGA set in the absolute configuration. Elevated CO_2 was maintained by using a CO_2 feedback injection system which consisted of the IRGA, CR-10 data logger and proportional solenoid controller. This system was designed to inject CO_2 if the difference between the desired and actual value was greater than 10%. For the elevated CO_2 treatment, this value was the ambient concentration plus 300 $\mu l\ l^{-1}$; the difference between the desired set point (673 $\mu l\ l^{-1}$) and the actual value (664 $\mu l\ l^{-1}$) was $\leq 10\ \mu l\ l^{-1}$ when averaged over the experimental period. Air temperature and humidity were controlled using a water cooled system attached to a Chessel microprocessor controller (Gauri International Corp., Victoria, Australia). Temperature and CO_2 concentration in the glasshouse were checked at 5 min intervals by a datalogger (CR-10, Campbell Scientific). Because only two glasshouses were available, the same experiment was repeated twice at day/night temperatures of 29/21 °C and 37/29 °C during the dry seasons of 1994 and 1995. Cumulative total radiation for the 1994 and 1995 dry seasons (approximately 120 d) was 2827 and 2803 mJ m^{-2}, respectively, during the period of experimentation. For all experiments, day temperatures were maintained from 09:00 h until 17:00 h, night temperatures from 19:00 h until 07:00 h. The time periods from 07:00–09:00 h and 17:00–19:00 h were periods of temperature transition where the difference between day and night temperature was reduced by half each hour (e.g. for a 21 °C night temperature, a 4 °C increase in temperature by 08:00 h to 25 °C and 29 °C by 09:00 h). All temperatures were maintained at the set point ±0.9 °C. Relative humidity was maintained at 70±5% for each day/night temperature (e.g. approximate dew point temperatures of 31 and 23 °C for day temperatures of 37 and 29 °C, respectively).

For all cultivars, time to initial and 50% panicle emergence (PE) was observed. Because the number of plants was limited, destructive sampling was limited to maturity. Maturity was determined when >50% of the panicles had senesced for an individual cultivar. Plants were then cut at soil level and separated into roots, stems, culms, leaf lamina, and panicles (if present). Roots were carefully washed and separated using multiple screens. Total dry weight was obtained separately from roots, and included leaf laminae, stems (including leaf sheaths), and panicles for green and senesced material. All material was dried at 70 °C for 72 h (or until changes in dry weight were constant) and dry weights obtained. In addition, grain (seeds) were removed separately and the number of spikelets per panicle and the number of viable seed per panicle were determined for each pot. Viable seed was determined by pinching each floret to determine if the grain had filled. The ratio of unfilled to filled grain was presumed to reflect the degree of seed set and floral sterility.

Plant data were analysed as a completely randomized design using a two-way ANOVA (LSTAT, IRRI) and Duncan's multiple range test (DMRT). Unless otherwise stated, differences were determined as significant at the $P \leq 0.05$ level.

Results

Among all cultivars, the range of plant growth response to elevated CO_2 and temperature (as determined by total plant biomass at maturity) varied significantly (Table 2). When ranked from least to greatest stimulation, IAC 165, a tropical japonica type from Brazil, showed the greatest stimulation at either growth temperature (265% and 181% at the 29/21 °C and 37/29 °C growth temperatures, respectively); while conversely, cultivars MGL-2, ITA 186, IR64, IR74, and IR46 showed no significant response at either growth temperature (Fig. 1). Overall, the degree of stimulation and the number of cultivars showing significant enhancement with elevated CO_2 decreased at the higher growth temperature of 37/29 °C (e.g. 12 out of 17 cultivars with an average stimulation of 70% versus 8% out of 17 cultivars with an average stimulation of 23% for the 29/21 °C and 37/29 °C growth temperatures, respectively) (Table 1; Fig. 1). In comparing the different components of total plant weight with respect to CO_2 at the optimal (29/21 °C) and elevated (37/29 °C) temperature, roots demonstrated the largest increase with elevated CO_2 (142% versus 59%), followed by tiller (97% versus 27%), panicle (54% versus 49%), and leaves (46% versus 5%) when averaged over all cultivars. Because of the greater stimulation in roots relative to above-ground dry matter, root/shoot ratios, on average, also increased by *c.* 20% for all cultivars. Interestingly, with the exception of IAC 165, the ranking of cultivars with respect to CO_2 stimulation was greatly altered with the increase in growth temperature (Fig. 1).

Table 2. *Effect of temperature and CO_2 on total plant biomass (stems, leaves, panicles, and roots) of different rice cultivars (by alphabetical order)*

Different letters for each cultivar indicate significant differences at the $P \leq 0.05$ level with respect to either CO_2 or temperature (DMRT, $n = 6$–8).

ultivar	373 μl l^{-1}	664	373 ^{1}	664 μl l
		(g/plant)		
Azucena	196.3 bc	321.6 a	157.4 c	222.7 b
IAC 165	94.4 c	342.6 a	87.8 c	247.4 b
IRAT 104	175.0 b	270.1 a	126.4 c	205.0 b
IR28	96.9 bc	154.0 a	81.1 c	117.8 b
IR30	103.7 bc	211.1 a	94.1 c	123.3 b
IR36	92.5 c	211.9 a	130.4 b	178.1 a
IR46	152.1 a	166.2 a	128.9 a	145.2 a
IR64	101.6 b	132.5 ab	166.7 a	136.2 ab
IR72	116.1 b	208.2 a	118.1 b	171.0 a
IR74	193.3 a	244.4 a	176.8 a	180.8 a
ITA 186	112.9 a	139.0 a	99.5 ab	84.2 b
Kinandang Patong	161.4 b	295.5 a	162.3 b	195.3 b
MGL-2	231.3 a	290.1 a	216.5 ab	179.3 b
N22	86.4 c	217.8 a	158.0 b	125.4 bc
OS4	180.1 b	326.4 a	140.6 b	162.0 b
Salumpikit	195.6 b	350.7 a	260.0 b	309.8 ab
YRL-39	77.8 b	141.5 a	55.9 b	107.1 ab

At the higher growth temperature, the percentage of filled spikelets (as determined by counting all individual grains within the panicle) was reduced to almost zero. Only N22 produced any significant amount of seed (*c.* 3%) (Table 3). At the high CO_2 concentration, high growth temperature treatment, no cultivar produced any viable seed (Table 3). At the optimal growth temperature however, the elevated CO_2 concentration resulted in a significant increase in the percentage of filled spikelets for six cultivars, IRAT 104, IR36, IR64, IR72, MGL-2, and YRL-39, and a significant decrease in one cultivar, ITA 186 (Table 3). When averaged over all cultivars the increase in the percentage of filled spikelets with increasing CO_2 concentration was slight but non-significant (72% versus 77%).

The time to 50% panicle emergence was, in general, decreased on average with both increasing CO_2 and temperature (with the exception of cv. IAC 165 and IR36) (Table 4). In addition, there appeared to be a synergistic effect in reducing the time to PE between increasing CO_2 and temperature for 9 of the 17 cultivars. When averaged over all cultivars, the number of days decreased from 97 to 89 and 91 to 81 for the ambient and high CO_2 treatments at the 29/21 °C and 37/29 °C growth temperatures, respectively (Table 4).

As with total plant biomass, the response of grain yield to increasing CO_2 varied greatly (Table 5). When ranked, IAC 165 and N22 show the largest percentage stimulation

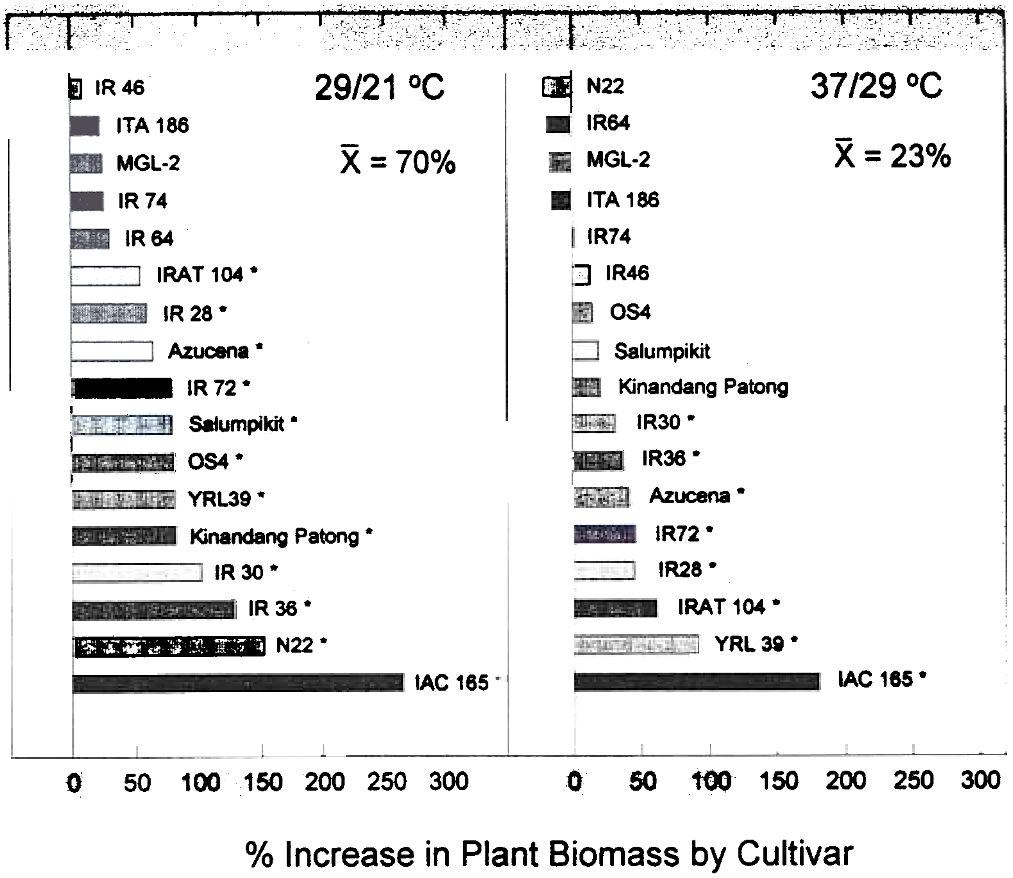

Fig. 1. Percentage increase in total plant biomass (roots, stems, leaves, and panicles) at maturity for 17 rice cultivars at two different CO_2 concentrations (ambient, 373 μl l^{-1} and elevated 664 μl l^{-1}) and two different growth temperatures 29/21 °C and 37/29 °C). Actual numbers for plant biomass are given in Table 2. *Indicates a significant increase in total biomass for a given CO_2 treatment for a given growth temperature (Students unpaired *t*-test).

(350% and 241%, respectively) (Fig. 2), with N22 showing the largest absolute increase in grain yield at the elevated CO_2 concentration (125.5 g $plant^{-1}$). The grain yield response of IAC and N22 was several times greater than the next cultivar, YRL-39 (Fig. 2). Overall, the number of cultivars showing a significant enhancement of grain yield with elevated CO_2 at 29/21 °C (14 out of 17) was slightly greater than the number showing a significant enhancement in total plant weight (12 out of 17) for this same temperature (Figs 1, 2). In general, there was good agreement between stimulation of biomass and grain yield as CO_2 concentration increased at the optimal temperature (29/21 °C) (Figs 1, 2); although when averaged for all cultivars, the percentage increase in grain weight with increasing CO_2 concentration was less (48%) compared to that of total biomass (70%) (Figs 1, 2). The average increase in grain yield among all cultivars as CO_2 concentration increased was due primarily to the increase in panicle weight (54%) due, in turn, to an increase in tiller number (55%). No net change in individual grain weight was observed (data not shown) with CO_2 concentration.

Although grain yield responded favourably to increasing CO_2 (at the optimal growth temperature of 29/21 °C), harvest index (HI), the ratio of grain weight to total plant weight (including roots), on average, did not change (0.42 and 0.39 for the ambient and elevated treatments, respectively). Among cultivars, seven showed a significant reduction in HI, while only four, IAC 165, IR46, IR64, and N22 showed a significant increase. For all cultivars, N22 showed the largest response to CO_2 concentration with a harvest index of 0.60 (Table 5).

Discussion

While phytotron glasshouse studies are advantageous in examining the responses of a large number of cultivars, it is recognized that the response of both biomass and yield to CO_2 and/or temperature will vary considerably between phytotron and field studies. These differences are due to greater light interception by individual plants within greenhouses (Nakagawa *et al.* 1994) as well as differences in soil, insects, windspeed, etc. As a result, the relative stimulation of biomass and grain yield in response to CO_2 and/or temperature in the current phytotron

Table 3. *Effect of temperature and CO_2 on the percentage of filled spikelets for 17 different rice cultivars*

*Indicates a significant difference at the $P \leq 0.05$ level for a given CO_2 treatment for a given day/night temperature for each cultivar (Students unpaired *t*–test, $n = 6–8$). For all cultivars, higher growth temperature resulted in a significant reduction in filled spikelets relative to the optimal temperature at 29/21 °C for either CO_2 concentration.

Cultivar	29/21 °C		37/29 °C	
	373 µl l^{-1}	664 µl l^{-1}	373 µl l^{-1}	664 µl l^{-1}
Azucena	82.8	76.4	0.0	0.0
IAC 165	68.2	68.8	0.2	0.0
IRAT 104	77.7	89.8*	0.0	0.0
IR28	62.6	64.0	0.3	0.0
IR30	62.0	61.1	0.0	0.0
IR36	64.3	81.1*	0.0	0.0
IR46	68.2	73.3	0.0	0.0
IR64	59.5	77.5*	0.1	0.0
IR72	60.1	73.7*	0.0	0.0
IR74	78.6	81.2	0.4	0.0
ITA 186	86.8	75.6*	0.0	0.0
Kinandang Patong	81.7	76.1	0.0	0.0
MGL-2	67.5	76.0*	0.0	0.0
N22	78.4	78.8	2.9	0.1*
OS4	86.7	84.8	0.0	0.0
Salumpikit	88.4	88.3	0.0	0.0
YRL-39	57.3	69.3*	0.0	0.0

Table 4. *Effect of temperature and CO_2 on the number of days to 50% panicle emergence for 17 different rice cultivars*

Different letters for each cultivar indicate significant differences at the $P \leq 0.05$ level with respect to either CO_2 or temperature (DMRT, $n = 6–8$).

Cultivar	29/21 °C		37/29 °C	
	373 µl l^{-1}	664 µl l^{-1}	373 µl l^{-1}	664 µl
Azucena	104 a	102 a	103 a	93 b
IAC 165	78 b	93 a	68 c	86 b
IRAT 104	106 a	97 b	95 b	82 c
IR28	92 a	77 b	80 ab	67 c
IR30	93 a	78 b	87 a	75 b
IR36	93 b	104 a	81 c	103 a
IR46	109 a	93 b	109 a	77 c
IR64	96 a	81 bc	90 b	76 c
IR72	97 a	89 b	84 b	76 c
IR74	114 a	107 a	108 a	95 b
ITA 186	98 a	79 b	79 b	74 b
Kinandang Patong	104 a	94 b	99 ab	90 b
MGL-2	105 a	77 b	95 a	62 c
N22	75 a	68 b	78 a	70 b
OS4	102 a	94 b	89 b	90 b
Salumpikit	97 a	89 b	94 ab	70 c
YRL-39	95 a	85 b	102 a	82 b

Table 5. *Effect of CO_2 on grain yield (g plant^{-1}) and harvest index (HI, grain yield/total plant biomass) at maturity for the 29/21 °C growth temperature*

No appreciable grain yield was observed at the higher growth temperature 37/29 °C at either CO_2 concentration. *Indicates a significant increase in total grain weight or HI with an increase in CO_2 (Students unpaired *t*–test).

Cultivar	Grain weight		Harvest index	
	373 µl l^{-1}	664 µl	373 µl l^{-1}	664 µl
Azucena	62.0	82.3*	0.34	0.28*
IAC 165	17.2	76.5*	0.14	0.24*
IRAT 104	58.6	86.0*	0.36	0.35
IR28	46.9	61.1*	0.50	0.42*
IR30	56.3	69.9	0.56	0.36*
IR36	51.5	78.7*	0.57	0.41*
IR46	56.5	74.9*	0.39	0.48 *
IR64	41.2	68.0*	0.42	0.55*
IR72	60.0	91.3*	0.54	0.47
IR74	83.6	77.8	0.46	0.35*
ITA 186	36.8	33.4	0.34	0.26*
Kinandang Patong	59.1	91.5*	0.38	0.33
MGL-2	93.1	122.3*	0.42	0.45
N22	36.8	125.5*	0.45	0.60*
OS4	58.0	81.8*	0.34	0.27*
Salumpikit	87.3	106.5*	0.48	0.33*
YRL-39	40.5	71.1*	0.54	0.53

experiment (e.g. 70% stimulation) was much larger on average, than those observed in previous field experiments (10–30%, Baker *et al*., 1990, 1992; Horie, 1993). Although direct comparisons of biomass or yield between glasshouse and field experiments are difficult, the range of the vegetative and reproductive responses observed among cultivars in the present study indicated that sufficient intraspecific variation exists in rice to select for optimal productivity with future increases in CO_2 concentration. For the rice cultivars tested, IAC 165 and N22 appear to be particularly promising, with a 2–4-fold increase in grain yield with increasing CO_2 concentration at the 29/21 °C growth temperature. It is unclear, however, from the current number of cultivars examined, whether varieties could be found which maximize productivity if CO_2 and temperature increase concurrently.

In the current experiment, no synergism was observed between CO_2 and temperature with respect to stimulation of either plant biomass or grain yield at maturity. (Indeed, a reduction in the relative effect of CO_2 at the higher growth temperature was observed for almost all cultivars.) This was somewhat surprising since at the biochemical level, increasing CO_2 concentration not only directly stimulates ribulose 1,5 bisphosphate carboxylase-oxygenase (Rubisco), but also inhibits carbon loss via photorespiration (i.e. the oxygenase portion of Rubisco). Therefore, as temperature rises and carbon lost through photorespiration increases, elevated CO_2 should result in a greater stimulation of net photosynthesis as determined by CO_2 uptake at the single leaf level (for reviews see Long, 1991; Potvin, 1994). What are the unique aspects of rice growth and development which could be altered by increasing temperature in such a way as to limit the response to increasing CO_2 concentration?

In rice, accumulation of vegetative biomass is relatively constant up to day temperatures of 45 °C, provided water is not limiting (De Datta, 1981). However, for rice, high day-time temperatures (in excess of 33 °C, see Fig. 8,

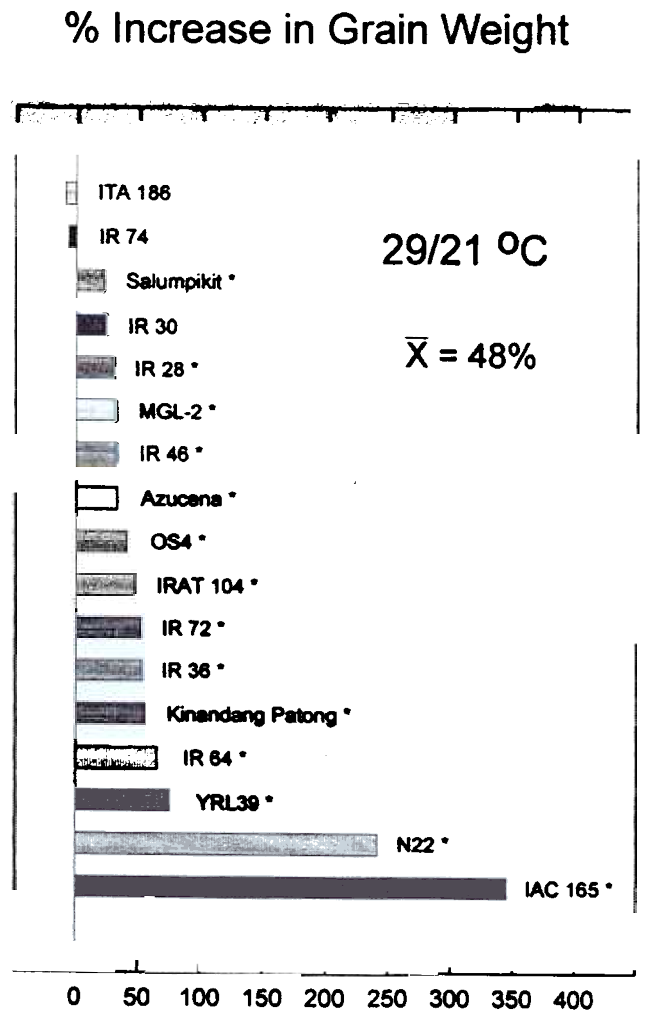

Fig. 2. Percentage increase in grain weight for the 29/21 °C temperature for 17 rice cultivars grown at two different CO_2 concentrations (ambient, 373 $\mu l\ l^{-1}$ and elevated 664 $\mu l\ l^{-1}$). Actual numbers for plant biomass are given in Table 4. *Indicates a significant increase in total biomass for a given CO_2 treatment for a given growth temperature (Students unpaired *t*–test).

Satake and Yoshida, 1978) may result in anther indehiscence, reduced pollen shedding and pollen tube germination with a subsequent decline in fertility and seed set. If pollen is artificially shed, fertility recovers (Satake and Yoshida, 1978). It has been demonstrated that the sensitivity of fertility and seed set to high temperature only occurs within a few hours after flowering. However, this would not explain the reduction in seed set for the N22 cultivar which is known to flower early in the morning and can tolerate day-time temperatures in excess of 40 °C while still producing viable grain (De Datta, 1981). It is conceivable, therefore, that higher mean daily temperatures (either due to increasing day or night temperature) could produce a similar result as a short-term exposure to higher temperatures during flowering for this cultivar. In addition to the direct effect of temperature on floral processes, high temperatures could have resulted in enhanced respiratory carbon loss and less assimilate needed for seed fill. However, if this were the case, then additional CO_2 and high temperature should have presumably resulted in a recovery of grain yield.

In the current experiment, a growth temperature of 37/29 °C resulted in a >95% elimination of viable seed in all cultivars tested. This developing seed represents a significant carbon sink for the rice plant. It has been suggested that in plants growing under enriched CO_2 conditions, removal or restriction of carbon sinks could result in photosynthetic insensitivity to CO_2 and a reduction in productivity (Stitt, 1991; Thomas and Strain, 1991; Webber *et al.*, 1994). Hence, for rice, the direct effect of temperature on removing reproductive sinks would be consistent with a limitation in the response to elevated CO_2, independent of any expected synergy of carbon acquisition at the biochemical level.

This sensitivity of reproduction to temperature in rice may, in part, explain some of the intraspecific variation in the response to CO_2 at different temperatures. N22 for example, demonstrates a large increase in seed yield (241%) and HI (33%) with increased CO_2 at 29/21 °C, but no response in either parameter at 37/29 °C. Conversely, IAC 165 (with the lowest HI of any cultivar) shows the largest stimulation in root development with increased CO_2 (approximately 10 ×, with a 35% increase in root/shoot ratio), which is not diminished as growth temperature increases. This suggests that other sinks, in addition to seeds, may play a role in determining the sensitivity of the growth response to elevated CO_2 and temperature. However, a simple ratio of sinks to sources (calculated as the ratio of root and panicle weight to total plant weight) was not sufficient to explain variation in cultivar response for a given CO_2 or temperature treatment (data not shown).

Nor can this variation be explained with respect to changes in the number of days to panicle emergence. Although increased CO_2 results in a presumably longer time for grain filling for IAC 165 (based on the longer time to 50% PE), N22 (with the second highest yield response), shows a significant reduction in time to PE as CO_2 increases.

Understanding the degree of stimulation of either biomass or grain yield with increasing CO_2 and/or temperature requires not only a knowledge of the size of carbon sources and sinks but also the regulation of carbon flux in order to optimize source and sink capacity (Woodrow, 1994). The current study demonstrates the range and variability of rice to potential changes in CO_2 and/or temperature; and was therefore useful as an initial screen to select for the most promising cultivars. However, a simple analysis of the growth and reproductive characteristics at maturity does not elucidate those physiological or developmental factors which could determine the absolute degree of sensitivity to future levels of CO_2 or temperature. It is hoped that further studies will be able to identify those factors which are crucial in determining selection criteria to maximize productivity among rice cultivars in response to a changing environment.

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