Rice yield enhancement by elevated CO_2 negatively correlates with hastened occurrence of heading –Results form five years chamber studies-

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Abstract

Rice (*Oryza sativa* L.) yield enhancement by elevated CO_2 concentration ([CO_2]) has often been reported to a varying degree ranging. To identify possible reasons for the variation in yield enhancement by elevated CO_2, we analysed the results from the experiments conducted in six naturally sunlit, controlled environment chambers for five years (from 1998 to 2002). Rice plants (cv. Nipponbare) were grown season-long under ambient (354-383/397-448 ?mol mol^{-1}; day/night) and elevated (670-721/702-780 ?mol mol^{-1}) [CO_2] each in three chambers. Air temperature inside the chambers was controlled at the outside level. Relative humidity was kept 77-80 %. Total nitrogen application was 8 g m^{-2} in 1998 and 1999, and 12 g m^{-2} in 2000-2002. In 2001, two subplots in which the timing of top-dressing was different were made in all chambers.

Final total dry weight was significantly increased by 8.0-18.7% by elevated [CO_2] in all five years. Enhancement of final total dry weight by elevated [CO_2] at each N level was similar across years. Days to heading were significantly shortened by 2.6-8.0 days. Grain yield was significantly increased by elevated [CO_2] by a varying degree ranging from 4.1 to 22.4 %, but the relationship between grain yield and final total dry weight enhancements was not clear. On the other hand, a strong negative relationship was found between grain yield enhancement and the days to heading hastened by elevated [CO_2]. These suggest that degree of acceleration of plant development can have a significant impact on the rice yield responsiveness to elevated [CO_2].

Media summary

Grain yield enhancement of rice by elevated CO_2 was negatively correlated with hastened occurrence of heading.

Key Words

Elevated CO_2, Rice, Yield, Growth

Introduction

Elevated CO_2 concentration ([CO_2]) increases growth and yield of many agricultural crops but with a varying degree (Kimball 1983). Rice (*Oryza sativa* L.) is generally less responsive to elevated [CO_2] compared to other crop species (Kimball et al. 2002), but variation exists in the degree of enhancement by elevated [CO_2] among previous studies of rice, ranging from 4 % up to 44 % (Baker and Allen 1993, Nakagawa and Horie 2000, Kim et al. 2003a). The difference in the magnitude is partially due to experimental methods, but the range in responses of growth and yield to elevated [CO_2] also depends on factors such as nitrogen (N) level, air temperature and cultivar.

We have been examining the response of rice growth and gas exchange to elevated [CO_2] under controlled environment (Climatron) chambers (Sakai et al. 2001). During the last five growing seasons, we have observed a varying degree of responses to elevated [CO_2] even under the same experimental conditions. Identifying reasons for this variability in yield response will provide us with options for better adaptability of rice to possible future environments.

Methods

Controlled environment chambers

The experiments were conducted in six naturally sunlit, controlled environment chambers (Climatron) for five years (from 1998 to 2002). Details of the chamber system were described in Sakai et al. (2001). Briefly, chamber dimensions were 4x3x2 m (LxWxH). Each chamber housed two stainless-steel containers (1.5x1.5x0.3m) filled with paddy soil. Air temperature and relative humidity in each chamber were controlled by electrical resistive heaters (with a bubbling system for humidification) and cold-water heat exchangers. Daytime [CO_2] was maintained by a computer-controlled pure CO_2 injection system, which compensated for CO_2 uptake by rice canopy. Night-time [CO_2], which increased due to plant respiration, was kept below 100 ?mol mol^{-1} higher than the daytime [CO_2] by a computer-controlled air ventilation system, which introduced ambient air to reduce [CO_2].

Plant culture and growth condition

In all five years, rice plants (cv. Nipponbare) were grown season-long under ambient (354-383/397-448 ?mol mol^{-1}; day/night) and elevated (670-721/702-780 ?mol mol^{-1}) [CO_2] each in three chambers. Germinated seeds of rice were sown to seedling trays (cell size, 1.5x1.5cm) on 20 April (1998-2001) and 23 April (2002), and seedlings were grown in Climatron chambers under 350 or 650 ?mol mol^{-1} [CO_2], with air temperature and relative humidity controlled at 23 ?C and 80 %, respectively for about a month. They were then transplanted in the containers in chambers with 3 seedlings per hill at a 20?20 cm spacing on 15 May (1998-2000 and 2002) and 25 May (2001). Total nitrogen (N) application was 8 g m^{-2} in 1998 and 1999, and 12 g m^{-2} in 2000-2002. All containers received the same amount of N at the same timing in each year (Table 1), except in 2001, where the timing of second topdressing was different between containers in all chambers: the second top-dressing was applied at the panicle initiation stage in one container and at the heading stage in the other container. In all years, 15 g of P_2O_5 m^{-2} and 15 g m^{-2} of K_2O were applied just before transplanting. Air temperature inside the chambers was controlled at the outside level. Relative humidity was kept 77-80 %. When rice plants in ambient [CO_2] chambers reached physiological maturity (always later than in elevated [CO_2]), rice plants were harvested simultaneously in both [CO_2] treatments.

Table 1. Summary of CO_2 concentration, average air temperature and relative humidity, and nitrogen application for five years of the experiment (1998-2002).

Year	Treatment	[CO_2] Day	Night	Mean air T[1)]	Mean RH[2)]	Basal N applied	Top-dressed N	Growth duration[4)]
		(μmol mol^{-1})		(?C)	(%)	(g m^{-2})	(gN m^{-2})	(days)
1998	Ambient	354	397	23.4	79.6	5.0	3.0 (56) [3)]	151
	Elevated	670	703					

1999	Ambient	366	409	25.1	78.6	5.0	1.5 (47)	1.5 (57)	142
	Elevated	695	750						
2000	Ambient	370	435	25.3	79.6	7.0	2.5 (31)	2.5 (60)	136
	Elevated	721	779						
2001	Ambient (NT)[5)]	377	446	24.4	77.3	6.0	3.0 (32)	3.0 (61)	131
	Elevated (NT)	700	761						
	Ambient (LT)	377	446	24.4	77.3	6.0	3.0 (32)	3.0 (84)	131
	Elevated (LT)	700	761						
2002	Ambient	383	448	24.0	76.8	6.0	3.0 (33)	3.0 (57)	138
	Elevated	706	780						

[1)] Mean air temperature during the growing season, [2)] Mean relative humidity during the growing season, [3)] Values in parenthesis are days after transplanting when nitrogen was top-dressed. [4)] Rice plants were harvested at the day of maturity under ambient CO2 concentration simultaneously in both CO2 treatments. [5)] NT: normal top-dressing, LT: late top-dressing; nitrogen was applied at panicle initiation stage and at heading stage, respectively.

Total dry weight and yield determination

Three hills from each chamber were destructively sampled at harvest. At each hill, a block of soil with a size of 20x20x15 cm (LxWxD) was dug up, and the soil was gently washed away from the roots with running water. Plant samples were then oven-dried at 80 ?C for three days and the dry weights were measured. To determine grain yield, 12 hills (1998), 15 hills (1999, 2000) and 10 hills (2001, 2002) from each chamber (from each container only in 2001) were harvested. After air drying for one month, panicle number was counted and the spikelets were threshed carefully. Filled spikelets were selected using a salt solution with specific gravity of 1.06 (1998-2000) or an airflow machine (2001, 2002), and counted. Filled spikelets were them oven-dried at 80?C in for one week. Grain yield was expressed as the dry weight of filled unhusked grain.

Table 2. The effects of elevated [CO_2] on rice growth, yield and their related factors over five years.

Year	N applied (g m^{-2})	CO_2 Treat-ment	Days to heading	LAI at heading	Final total DW (g m^{-}	Panicle density (m^{-2})	Spikelet density (10^3 m^{-2})	Filled spikelet (%)	Single grain wt. (mg)	Grain yield[1)] (g m^{-2})

2)

1998	8	Ambient	100.3	5.77	1785	431	28.1	86.9	22.4	552
		Elevated	97.7	5.22	1940	467	32.6	92.8	22.4	676
		%change[2)]	-2.7	-9.4	8.7	8.4	15.8	6.8	-0.1	22.4
1999	8	Ambient	93.0	5.52	1797	502	30.2	92.7	23.5	658
		Elevated	87.3	5.91	1940	499	33.9	89.7	23.5	713
		% change	-6.1	7.1	8.0	-0.6	12.2	-3.2	-0.1	8.4
2000	12	Ambient	86.5	8.32	1810	543	35.2	93.7	23.0	771
		Elevated	80.7	7.28	2149	529	41.1	88.9	23.2	846
		% change	-6.7	-12.5	18.7	-2.6	16.7	-5.1	0.7	9.5
2001	12	Ambient	81.7	8.41	2067	519	37.7	93.9	21.5	762
	(NT)[3)]	Elevated	77.3	7.80	2285	529	39.0	95.9	22.5	842
		% change	-5.3	-7.3	10.6	1.9	3.5	2.2	4.7	10.5
	12	Ambient	80.3	8.83	2375	531	35.8	96.0	23.0	793
	(LT)	Elevated	75.0	7.41	2616	563	37.6	96.7	23.1	839
		% change	-6.6	-16.1	10.1	6.1	4.9	0.8	0.2	5.8
2002	12	Ambient	89.0	9.09	2020	484	40.0	95.7	22.1	846
		Elevated	81.0	9.11	2236	499	40.2	94.6	23.1	880
		% change	-9.0	0.2	10.7	3.2	0.6	-1.2	4.6	4.1

ANOVA[4]								
CO_2	**	ns	**	**	*	ns	ns	*
Year	**	**	**	**	**	*	*	**
N	**	**	**	**	**	*	ns	**
CO_2*Year	ns	ns	ns	ns	ns	ns	ns	ns
CO_2*N	ns	ns	ns	ns	ns	ns	ns	ns

1) grain yield is expressed on a dry mass basis. 2) % change due to elevated [CO_2]. 3) See table 1. 4) * and **, significant at P<0.05 and P<0.01; ns, not significant.

Results

The seasonal mean air temperature during five years ranged from 23.4 (1998) to 25.3?C (2000). It was extremely cool summer in 1998. Contrary to 1998, it had been hot through the growing season in 1999 and 2000. In 2001, it was hotter than in 1999 and 2000 until panicle initiation stage, but was as cool as in 1998 after then. In 2002, air temperature was on a level with that in 1999 and 2000, but with some cool periods in tillering and grain filling stage.

Results of destructive sampling and yield determination of five years experiments are shown in Table 2. Days to heading were significantly shortened by elevated [CO_2] by 2.6-8.0 days. Although we did not determine the definitive dates of physiological maturity, hastened occurrence of heading events by elevated [CO_2] likely resulted in shorter growth duration in the elevated [CO_2] than in the ambient [CO_2] because grain filling in the elevated [CO_2] progressed under hotter condition than in the ambient [CO_2].

Leaf area index (LAI) at the heading stage was largely influenced by total N applied, but the effect of elevated [CO_2] was not significant though LAI was reduced in three years in the elevated [CO_2].

Final total dry weight was significantly increased by elevated [CO_2]. The enhancement of total dry weight was generally similar across years, but was slightly but consistently higher in years with larger N application, averaging 8 and 10 % for 8 and 12 g N m^{-2} application, respectively. Interestingly, the enhancement ratio was not altered when the timing of top-dressing was changed with the same total N application in 2001 though top-dressing at the heading stage increased total dry weight more than that at the panicle initiation stage in both [CO_2] treatments.

Both panicle and spikelet densities increased as a result of elevated [CO_2], but the effect was generally larger on spikelet density, indicating that spikelet per panicle was also increased by elevated [CO_2]. Filled spikelet percentage was generally high but significantly different among years with no consistent effect of elevated [CO_2]. The effect of elevated [CO_2] on single grain mass was noted, but about 5% enhancement was observed in two occasions with relatively small enhancement of spikelet density.

Elevated [CO_2] increased grain yields significantly, with a range of 4.1 to 22.4 % depending on the trials. The grain yield enhancement by elevated [CO_2] in some cases was larger than in biomass enhancement, but lower in other cases, and there was no clear association between them.

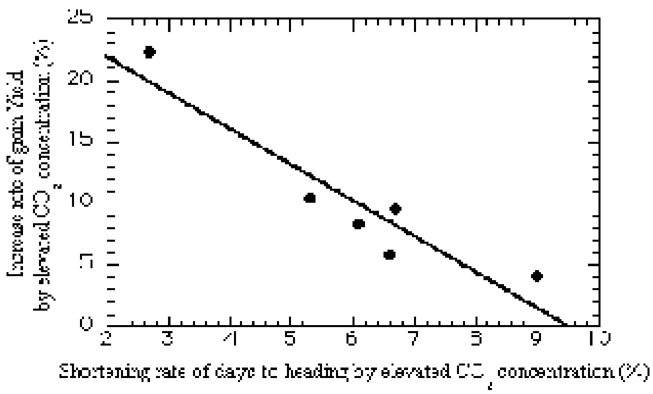

Figure 1. The relationship between the increase rate (%) of grain yield and the shortening rate (%) of days to heading by elevated CO_2 concentration in five years (1998-2002).

The variation in grain yield enhancement was closely correlated with the shortened days to heading by elevated [CO_2] (Figure 1). The earlier occurrence of heading in the elevated [CO_2] treatment seemed to have decreased the enhancement of spikelet density and filled spikelet percentage.

Implication and Conclusion

Final total dry weight was significantly increased by elevated [CO_2] in all five years, as has been observed in other studies with rice (Baker and Allen 1993, Nakagawa and Horie 2000, Kim et al. 2003a). Final total dry weight enhancement by elevated [CO_2] was similar among trials with the same N level despite a range of weather conditions experienced for the five years. This result suggests that conserved nature of the final total dry weight response to elevated [CO_2] is due to the limitation set by the amount of N available for rice plants in the range of N applied in this experiment. Grain yield enhancement, on the other hand, was more variable than that in biomass.

The strong negative relationship between grain yield enhancement and hastened occurrence of heading likely involves a number of different responses to CO2. Shorter days to heading might not have ensured enough time for reproductive organ development, so that the spikelet density response can be one source of variation in grain yield enhancement. Filled spikelet percentage can also be a source of variation because different timing of heading can result in different environmental conditions during the grain filling.

The mechanism by which elevated [CO_2] hastens occurrence of heading is not clear, but the present results suggest that degree of acceleration of plant development can have a significant impact on the rice yield responsiveness to elevated [CO_2].

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