

## BRIEF COMMUNICATION

**Elevated CO<sub>2</sub> concentration enhances the role of the ear to the flag leaf in determining grain yield of wheat**C.-W. ZHU<sup>\*,+</sup>, J.-G. ZHU<sup>\*</sup>, G. LIU<sup>\*</sup>, Q. ZENG<sup>\*</sup>, Z.-B. XIE<sup>\*</sup>, J. PANG<sup>\*\*</sup>, Z.-Z. FENG<sup>\*\*</sup>, H.-Y. TANG<sup>\*</sup>, and L. WANG<sup>\*</sup>*State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing, 210008, P.R. China<sup>\*</sup>**Department of Global Agricultural Sciences, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Japan<sup>\*\*</sup>***Abstract**

Net photosynthetic rate ( $P_N$ ) of ear and flag leaf during grain filling stage and grain yield of plants with non-darkened or darkened flag leaf or darkened ear were examined in two different CO<sub>2</sub> concentrations: ambient (AC) and AC+200  $\mu\text{mol mol}^{-1}$  (EC). Ear showed much higher enhancement (56 %) of  $P_N$  than flag leaf (23 %) under EC. Moreover, CO<sub>2</sub> enrichment shortened the photosynthetic duration of flag leaf relative to ear. In this way the ratio of ear to flag leaf contribution to grain yield increased from 1.18 (AC) to 1.39 (EC).

*Additional key words:* net photosynthetic rate; *Triticum aestivum*.

The rapid increase in atmospheric CO<sub>2</sub> (~21 % since 1960) is likely to have a direct effect on C<sub>3</sub> crop growth since it represents an increase in the raw material (carbon) needed for plant photosynthesis (Kerr 2001, Pérez *et al.* 2007). The higher CO<sub>2</sub> required to saturate photosynthesis of ear may lead to a higher enhancement of the net photosynthesis (Knoppik *et al.* 1986, Long 1991). As CO<sub>2</sub> concentration continues to rise, the role of the ear relative to the flag leaf may rise in supplying assimilates to grain of wheat. However, photosynthetic activity of wheat has traditionally been studied using leaves under elevated CO<sub>2</sub> conditions (EC), neglecting ears, thus few studies on comparing photosynthetic responses of wheat ear and flag leaf to EC were carried out under field condition (Ainsworth and Long 2005). Therefore, to date, the role of ear relative to flag leaf in determining grain yield at projected CO<sub>2</sub> concentration is not elucidated for wheat. The current study tested the hypothesis that EC enhances the role of ear to flag leaf

contribution to grain yield.

The experiment was conducted in free-air CO<sub>2</sub> enrichment (FACE) system, which is located at Zhongcun village (119°42'0"E, 32°35'5"N), Yangzhou city, Jiangsu province, China, a typical region for winter wheat production. Three experiment rings were fumigated with EC and other three maintained at AC. The running and controlling systems for these facilities were the same as used in a Japanese FACE site (Okada *et al.* 2001). Winter wheat (*Triticum aestivum* L. cv. Yangmai 14) was sown on 20 November, 2006 at a density of 300 seedlings per m<sup>2</sup> with a row space of 20 cm, and harvested on 1 June, 2007. For each ring, from 1 week after anthesis to maturity, the ears of eight main culms and the flag leaves of eight other randomly selected main culms were kept in the dark by covering with aluminum foil, with 1-mm-diameter holes (at least 15 mm apart, and representing about 0.3 % of the covering area) to prevent accumulation of ethylene and water vapour. Eight other

Received 31 August 2007, accepted 6 February 2008.

<sup>+</sup>Author for correspondence; fax: +86-25-8688028, e-mail: jgzhu@issas.ac.cn

*Abbreviations:* DAG – days after grain filling; FACE – free-air CO<sub>2</sub> enrichment;  $P_N$  – net photosynthetic rate.

*Acknowledgment:* The work was supported by the Knowledge Innovation Program of Chinese Academy of Sciences (grant no. KZCX3-SW-440) and the Key Projects of National Natural Science Foundation of China (grants no. 30470334, 40571157). The main instruments and apparatus of the FACE system were supplied by National Institute of Agro-Environmental Sciences and Agricultural Research Center of Tohoku Region (Japan).

non-darkened main culms were tagged at the same ring. The mass of grains and the number of grains per ear were measured at maturity for the control, ear-darkened, and flag leaf-darkened main culms. The portable infra-red analyser *LI-6400* (*LI-COR*, USA) was used. A gas exchange chamber designed to contain the whole organ was used for the ear, and standard leaf chamber was used for blade. For each sampling date, flag leaf and ear from four to six culms were used. Measurements were performed from 10:30 to 14:00 (Beijing time) on sunny days. Data were analyzed as a completely randomized split plot design with the different concentrations of CO<sub>2</sub> as the main plots. *T*-test was used to check significance of differences with respect to EC. Unless otherwise stated, the differences for any measured parameter were significant at the  $p < 0.05$  level.

$P_N$  of AC- and EC-grown flag leaves and ears were determined on six dates in April and May.  $P_N$  of flag leaves and ears were maximal on DAG 0 and then decreased with leaf age (Fig. 1). An enhancement of  $P_N$  in EC relative to AC was observed on DAG 0–20 but did not occur on DAG 25–28 in flag leaves and ears. Scatter plot and regression with 90 % confidence interval depict ambient *versus* FACE from parallel  $P_N$  for flag leaf [EC =  $-1.64 \pm 0.84 + 1.23 \pm 0.05$  AC] and ear [EC =  $-1.93 \pm 1.02 + 1.56 \pm 0.09$  AC] (DAGs 25 and 28 excluded). The 56 % enhancement of  $P_N$  for the ear was much larger than the parallel 23 % increase for flag leaf. Similarly, the ear showed a better performance of photosynthesis than the flag leaf in response to CO<sub>2</sub> enrichment (Knoppik *et al.* 1986, Wechsung *et al.* 2000). EC accelerated  $P_N$  decline of flag leaf and ear. At DAG 28, ear at the two CO<sub>2</sub> concentrations and flag leaf at EC were completely senesced, and only the flag leaf at AC was photosynthetically active (Fig. 1). Hence photosynthetic duration of flag leaf relative to ear was decreased due to CO<sub>2</sub> enrichment. The explanation was that senescence of flag leaf occurred earlier and was more pronounced than ear due to EC. And  $P_N$  of flag leaf, unlike  $P_N$  of ear, was less sensitive to higher temperature and drought under EC than under AC (Long *et al.* 2004).

The CO<sub>2</sub> enrichment increased the grain yield largely

through increases in the number of filled grains per panicle and individual seed mass due to increasing  $P_N$ . As expected, the darkening had large effects on growth and yield (Table 1). When the flag leaf was darkened, the grain yield remained at 58 and 75 % of not-darkened plant for AC and EC conditions, and when ear was darkened, the grain yield was only 49 and 54 %, respectively. EC enhanced the ratio of ear to flag leaf contribution to grain yield from 1.18 (AC: 58/49 %) to 1.39 (EC: 75/54 %) (Table 1).

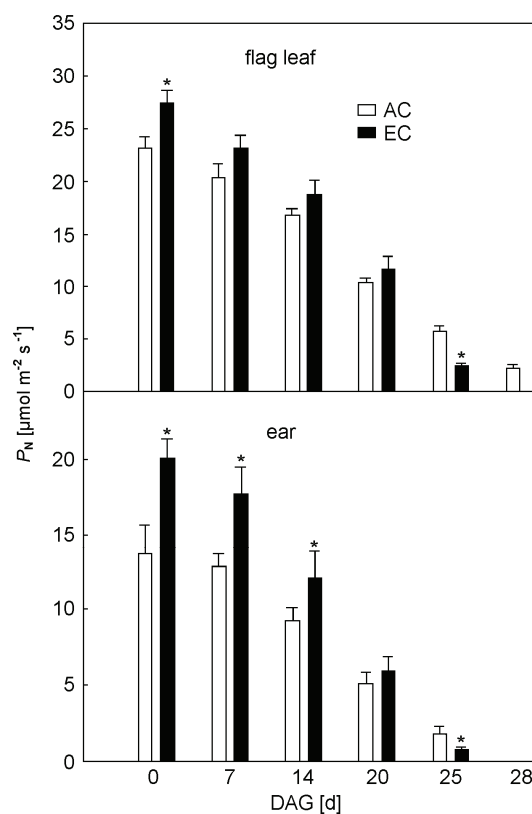


Fig. 1. Effects of CO<sub>2</sub> enrichment (EC) on net photosynthetic rate ( $P_N$ ) of flag leaf and ear. Gas exchange was measured from DAG 0 to DAG 28. \*significant difference relative to ambient CO<sub>2</sub>, AC (*t*-test,  $p < 0.05$ ). DAG: days after grain filling.

Table 1. Effects of darkening the flag leaf or the ear from one week after anthesis to maturity to yield components of wheat under two different CO<sub>2</sub> concentrations. Means  $\pm$ SD of three replicates. Values in parentheses are the percentage of mass compared with not-darkened plants.

	Darkened	Number of grain per ear	1 000-grain dry mass [g]	Grain yield per ear [g]	Ear/flag leaf contribution to grain yield
AC	nothing	37.54 $\pm$ 1.70	48.97 $\pm$ 0.48	1.84 $\pm$ 0.11	
	flag leaf	36.56 $\pm$ 1.42 (97)	29.27 $\pm$ 0.14 (60)	1.07 $\pm$ 0.04 (58)	1.18 $\pm$ 0.05
	ear	37.32 $\pm$ 1.70 (99)	25.72 $\pm$ 0.46 (53)	0.96 $\pm$ 0.04 (49)	
EC	nothing	41.42 $\pm$ 1.61	52.11 $\pm$ 0.66	2.16 $\pm$ 0.11	
	flag leaf	41.17 $\pm$ 1.71 (99)	39.33 $\pm$ 1.35 (75)	1.62 $\pm$ 0.12 (75)	1.39 $\pm$ 0.08
	ear	42.13 $\pm$ 2.08 (102)	27.55 $\pm$ 0.81 (51)	1.16 $\pm$ 0.11 (54)	

The enhancement of  $P_N$  observed for mid-day ear (56 %) and flag leaf (23 %) was higher than the final yield increase (17 %) due to EC. One explanation is a down-regulation of ear and flag leaf photosynthesis due to sink limitation resulting in an accumulation of starch and soluble sugars while N and ribulose-1,5-bisphosphate carboxylase/oxygenase contents are reduced under EC in the afternoon (Ainsworth and Long 2005). When ear was darkened, the increase of the final yield (22 %) was similar with enhancement of  $P_N$  of flag leaf (23 %) under EC, which meant an absence of the sink limitation. It

indicated that sink limitation was induced by ear photosynthesis at EC.

We found that the role of ear relative to flag leaf was larger in determining grain yield of wheat because ear had higher increase in  $P_N$  and relative duration of flag leaf photosynthesis was shortened under EC. Moreover, ear-sink-limitation was more severe under EC. The breeding strategies to increase whole-flag leaf photosynthesis are less effective in improving yield than increasing whole-ear photosynthesis and ear sink of wheat in future CO<sub>2</sub> concentrations in the atmosphere.

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