PHOTOSYNTHESIS, GROWTH AND PRODUCTIVITY OF RICE UNDER ELEVATED CO_2

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SUMMARY

A field experiment was conducted to compare the changes in photosynthesis, growth and productivity of rice at elevated CO_2 concentration with that of the plants grown under ambient CO_2 and field conditions. Thirty-five days old seedlings of rice (*Oryza sativa*) cv. BRRIdhan 39 were transplanted in three growing environments – (i) open top chamber (OTC) with elevated CO_2 (570 ± 50 ppm), (ii) OTC with ambient CO_2 (~ 360 ppm) and (iii) in the open field. Leaf photosynthesis rate (Pn) of rice was measured at successive growth stages viz. vegetative, panicle initiation, flowering, early maturity, mid-maturity and maturity stages. It was observed that Pn increased from vegetative stage to flowering stage and then declined gradually towards the maturity stage in this cultivar. Elevated CO_2 profoundly increased the Pn rates at all growth stages of rice, the highest Pn (40.02 µmol m^{-2} s^{-1}) being observed at flowering stage. Elevated CO_2 also enhanced biomass accumulation resulting in nearly 38% and 35% higher dry matter than ambient and field-grown rice, respectively. Compared to the plants grown in OTC at ambient CO_2 or grown in the field, elevated CO_2 treated plants had more favourable partitioning of dry matter into panicles. Consequently, plants with elevated CO_2 produced higher seed yield (19.624 g $hill^{-1}$) than the ambient (15.543 g $hill^{-1}$) and field (15.682 g $hill^{-1}$) grown rice.

Key words **: Elevated CO_2, growth, photosynthesis, productivity, rice.**

INTRODUCTION

There has been an increasing trend in the atmospheric CO_2 concentration since preindustrial period due to burning of fossil fuels and deforestation (Clark *et al.* 1982). Presently the CO_2 concentration in the atmosphere is around 370 ppm which is expected to become double of pre-industrial CO_2 concentration by the middle of present century (Watson *et al.* 1990, Hougton *et al.* 1996, Olszyk and Wise 1997). Different crops respond differently to elevated CO_2 concentration (Ghildiyal and Sharma-Natu 2000). In general, C_3 plants species respond favourably to elevated CO_2 compared to C_4 species. Elevated CO_2 can cause an increase in biomass and yield ranging between 10 and 40% in many C_3 crops (Kimball 1983, Mitchell *et al.* 1993, Weigel *et al.* 1994, Ravi *et al.* 2001, Sharma-Natu *et al.* 2004). Such a variation in the performance of C_3 species under elevated CO_2 results from the variations in photosynthesis rates and sink strength of the species (Poorter 1993, Reddy *et al.* 1995, Biswas *et al.* 1996, Sharma-Natu *et al.* 1997, 2004). As a C_3 plant, rice also showed a positive response to elevated CO_2 concentration (Ziska *et al.* 1996). However, there is lack of information on stage dependent photosynthetic response and its relationship to the productivity of indica rice under elevated CO_2 condition, especially in the long term study. Such study would be helpful to develop a realistic model to predict crop response pattern to global climate conditions. The present study was undertaken to observe the periodical response of photosynthesis, growth and productivity of rice under elevated CO_2 concentration.

MATERIALS AND METHODS

A field experiment was carried out at the Bangabandhu Sheikh Mujibur Rahman Agricultural University, Gazipur, Bangladesh during wet season of 2000. Thirty-five day old rice seedlings of rice cv. BRRIdhan 39 were transplanted under three growing conditions - open top chamber (OTC) with elevated CO_2 (570 ± 50 ppm), OTC with ambient CO_2 (~ 360 ppm) and open field as a control treatment. Details of the construction and operation of the OTC have been provided elsewhere (Leadley and Drake 1993, Uprety 1998). Diameter of the OTC was 3 m and 280 hills of rice were accommodated in a planting configuration of 25 cm × 10 cm. Single seedling per hill was transplanted on 20 July, 2000. A fertilizer dose of 90-20-60-20-3.5 kg N, P, K, S and Zn ha^{-1} was applied. Entire amount of all the fertilizers excepting N was applied prior to transplanting, while N was applied in three equal splits 4, 21 and 52 days after transplanting (DAT). Adequate plant protection measures were taken to keep the crop free from insect-pests and weeds.

Leaf photosynthesis rates were measured several times at vegetative, panicle initiation, flowering, early maturity, mid maturity and maturity stages with the help of a portable photosynthesis-measuring device (LICOR 6200, Lincoln, Nebraska). Photosynthesis rates were measured on the uppermost fully expanded leaf of the mother shoot on clear sunny days between 11:00 and 13:00 hours. Plants were sampled periodically to determine leaf area and dry matter accumulation into different components of rice. Leaf area of sampled plants was measured with an automatic leaf area meter (Model AAM-7 Hayashi Dehnco Co. Ltd. Tokyo, Japan). The above-ground portion of the plants was partitioned into leaf, leaf sheath, stem and panicle and oven dried at 70°C for 72 hours and weighed. At maturity, seed yield and associated attributes were recorded. Ten replicates of each treatment were taken for every observation. Data were analysed statistically by analysis of variance and means were compared by least significant difference (LSD) test wherever necessary (Gomez and Gomez 1984).

RESULTS AND DISCUSSION

Leaf photosynthesis rates (Pn) of the uppermost fully expanded leaves in the rice cultivar were measured several times in the growing season beginning from vegetative till the maturity stage in all three treatments. Rice plants grown at elevated CO_2 exhibited significantly increased Pn rates compared to ambient and field grown plants throughout the growing period. Irrespective of treatment difference, Pn rates increased gradually reaching a peak at flowering stage and thereafter declined sharply (Fig. 1). The results are in partial agreement with Palit *et al.* (1979) who measured Pn of rice from flowering and noticed higher Pn rate at flowering that decreased gradually as grain filling progressed. The possible reason for decline in Pn rates at later stage of rice growth may be associated with the decline of leaf N concentration as there is a strong relationship between Pn and leaf N content of field grown rice (Peng *et al.* 1995). The decline of Pn rates also might have accompanied with the loss of integrity of leaf chloroplast as the leaf age advanced (Thornton and Wample 1980) and due to inadequate sink demand for

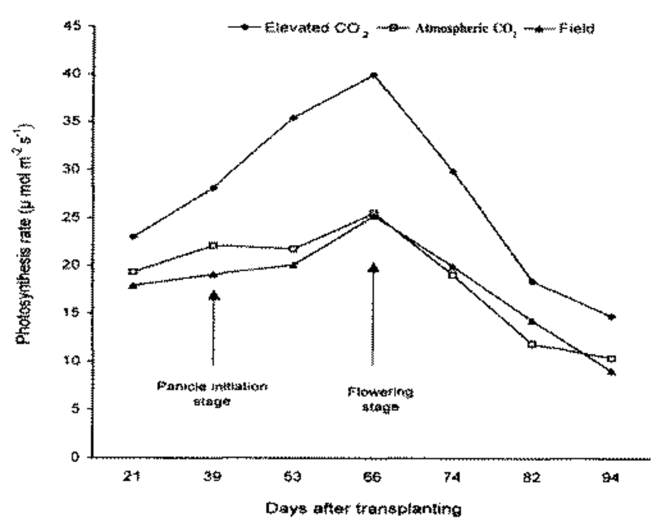

Fig. 1. Photosynthesis rate of rice at successive growth stages under elevated CO_2 (OTC), atmospheric CO_2 (OTC) and open field conditions

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photosynthates (Delgado *et al.* 1994). As CO_2 is the substrate of photosynthesis, it was expected that increasing atmospheric CO_2 would increase Pn rates. Higher Pn rates of crops grown under elevated CO_2 have also been reported by Ziska and Teramura (1992) and Uprety and Mahalaxmi (2000). In the present study, CO_2 enrichment increased Pn rates by 29, 58 and 62 per cent, respectively in successive three growth stages compared to that of field grown plants. The differences in Pn rates widened as the growth progressed suggesting that elevated CO_2 favoured sustaining higher Pn rates during the generative and grain filling phases. Plants grown at ambient CO_2 condition in OTC tended to maintain a slightly higher Pn rates than the field grown plants which might be due to slightly higher (2-3°C) temperature within the chamber (Uprety 1998).

Photosynthesis and consequently the dry matter production is the function of leaf area development. Leaf area development of rice was influenced markedly by elevated CO_2 concentration. Compared with field grown plants or those grown in the OTC at ambient CO_2, plants treated with elevated CO_2 exhibited higher leaf area development throughout the growth period. Leaf area development peaked at the panicle initiation stage and thereafter it decreased over time in all the three treatments (Fig. 2). Elevated CO_2 increased and sustained leaf area by 93% at panicle initiation, 6.24% at flowering and 10.59% at maturity over field grown plants. Similar response of other crops to high CO_2 on leaf expansion was also reported by and Cure *et al.* (1989), Pal *et al.* (1997) and Uprety and Mahalaxmi (2000). At maturity stage, leaf area of rice under ambient condition dropped drastically reaching around 341 cm^2 per plant as compared to 682 cm^2 under elevated CO_2 and 617 cm^2 under field conditions. Therefore, percentage loss in leaf area from panicle initiation to maturity stage was much greater (78%) in the plants grown in chamber at ambient CO_2 and the least (39%) in the field grown plants. The high temperature induced "chamber effect" seems to be the cause of drastic reduction of post-anthesis leaf area of plants grown in the chamber at ambient CO_2 concentration. During pre-flowering phase the largest sink of an individual plant is the leaves (Sato 1974) and photosynthates produced at that time are mostly used for the formation and growth of leaves. The decline phase of leaf area coincided with the panicle development and grain filling of rice when competition for assimilates between leaf and panicle was most likely. Wada and Wada (1991) observed a close correlation between the decrease in leaf area and increase in sink size of rice during the later stages of growth. Enhancement of leaf senescence with the advance of growth stages is also attributed to decline of leaf area at the later part of rice growth.

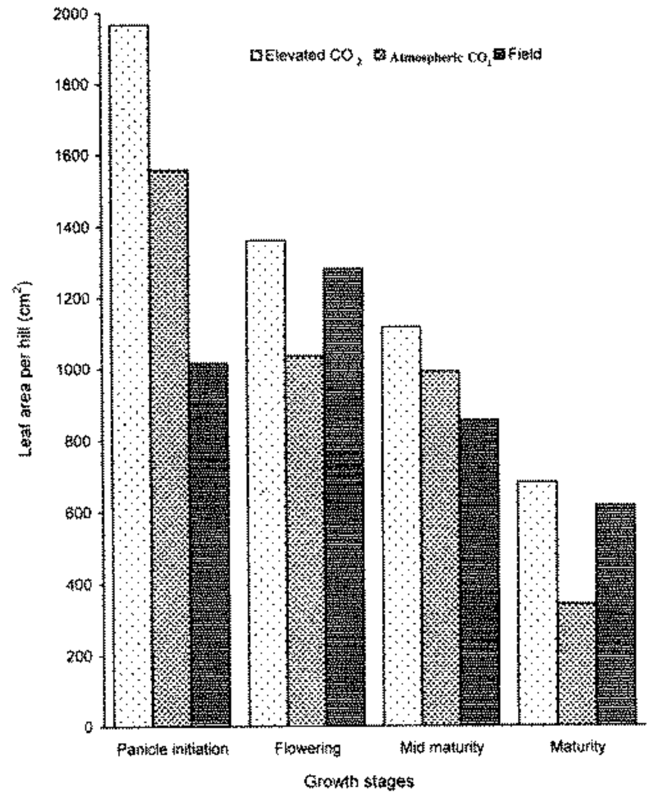

Fig. 2. Leaf area at different growth stages of rice under elevated CO_2 (OTC), atmospheric CO_2 (OTC) and open field conditions

Elevated CO_2 increased plant biomass gradually from panicle initiation to maturity stage of rice (Fig. 3). At maturity stage, the increase in total dry matter due to elevated CO_2 concentration was nearly 38% and 35% over ambient and field grown rice, respectively. Earlier, Baker *et al.* (1990) also reported promotion of dry matter production in rice due to elevated CO_2. It appears that higher sink demad due to grain filling triggered translocation of mass from the structural organs. However, the proportion of dry matter translocated from leaf and leaf sheath was lesser in the plants grown with elevated CO_2. The plants grown under elevated CO_2 accumulated more dry matter in the panicles than plants of other two

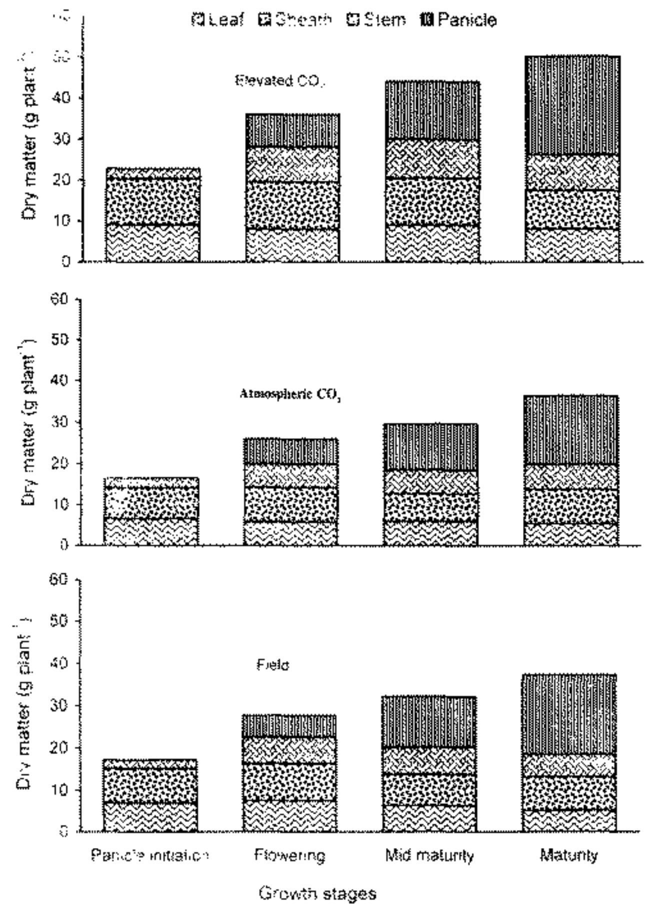

Fig. 3. Dry matter partitioning of rice at different growth stages under elevated CO_2 (OTC), atmospheric CO_2 (OTC) and open field conditions

treatments. At maturity, panicle dry weight was 23.93 g, 16.60 g and 18.79 g per plant under elevated CO_2, ambient CO_2 and field condition respectively. Further, the decrease of leaf dry matter from panicle initiation to maturity stage was 11.10% in elevated CO_2, 18.82% in ambient and 26.56% in field grown rice. Nearly, similar trend was observed in stem and leaf sheath dry matter. During post-anthesis period, gain in panicle dry matter is the result of the current photosynthesis and translocation of photo-assimilates from the structural organs of rice. Several authors (Palit *et al.* 1976, Evans 1992) also reported that grain yield of rice depends almost entirely on current photosynthesis. In the present study, high rate of photosynthesis during post-flowering phases (Fig. 1) perhaps contributed to the greater accumulation of photosynthates in the panicles and eventually resulted in higher panicle dry matter in plants grown in enriched CO_2 condition.

Grain yield is the product of mean individual grain weight and grain number. Elevated CO_2 enhanced both the parameters eventually resulting in significantly higher yield. Enriched CO_2 increased significantly panicles per hill and spikelets per panicle (Table 1) compared to ambient CO_2 and field grown plants. Our results compare favourably with the findings of Apel (1985). Similarly, the increase in grain yield of wheat under CO_2 enrichment is also primarily due to an increase in the number of ears per plant (Hocking and Meyer 1991, Sionit *et al.* 1992, Tuba *et al.* 1994). In our study, CO_2 enrichment increased seed size a little, which was expected as because the grain size in rice is fairly stable within a genotype (Yohida 1981). Weigel *et al.* (1994) reported that seed size remained unaffected in barely and decreased in wheat due to CO_2 enrichment. CO_2 enrichment adversely affected the ripening percentage of rice (Table 1). Sterility percentage of spikelets was 36.9% in elevated CO_2 grown plants as compared with 10.1% in ambient and 2.4% in field grown rice. Open top chamber, coupled with elevated CO_2 increased temperature under the chamber that might have increased the percent spikelet sterility and reduced the ripening percentage of rice. However, greater number of

Table 1. Yield and yield attributes of rice under elevated CO_2 (OTC) atmospheric CO_2 (OTC) and open field condition.

Treatments	Panicles hill^{-1}	Spikelet panicle^{-1}	Filled spikelet panicle^{-1}	Sterility (%)	Seed size (mg)	Grain yield (g hill^{-1})
Elevated CO_2	7.0	216.5	136.1	36.9	24.7	19.624
Ambient CO_2	5.6	138.2	109.1	10.1	23.3	15.543
Field condition	5.8	137.3	124.7	2.4	23.3	15.682
LSD (0.05)	0.95	21.28	14.06	4.83	0.79	1.223

panicles per hill and spikelets per panicle could offset the effect of sterility percentage on the grain yield.

In conclusion, CO_2 enrichment favoured photosynthesis and dry matter production resulting in significantly higher grain yield of rice. The increase in grain yield due to CO_2 enrichment may be explained from the promotional growth of biomass and the number of panicles per plant. Higher number of panicles per plant, larger number of spikelets per panicle and slightly higher seed size under elevated CO_2 compensated the negative effect of temperature on sterility and thereby increased the grain yield of rice.

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