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Rice demands higher nitrogen fertilizer during grain filling stage under elevated atmospheric CO_2 condition

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Abstract

An experiment was conducted in open top chamber (OTC) to determine the response of rice to elevated carbon dioxide (eCO_2) under varying time of nitrogen (N) application. Rice was grown in OTC with 500 ppm CO_2 (eCO_2), 450 ppm CO_2 (intermediate CO_2, iCO_2), ambient CO_2 (aCO_2) and open field (OF, 380 ppm CO_2). The timings of N application were N1 = $1/3^{rd}$ N at early tillering (ET) + $1/3^{rd}$ at active tillering (AT) + $1/3^{rd}$ before panicle initiation (PI) stage, N2 = $1/3^{rd}$ N at ET + $1/3^{rd}$ before PI + $1/3^{rd}$ at booting stage (BS), and N3 = $1/3^{rd}$ N at ET + $1/3^{rd}$ before PI + $1/3^{rd}$ at flowering stage (FS). The results revealed that photosynthesis (Pn), shoot and root dry matter (SDM and RDM) production, yield and yield components were favored at eCO_2 when N application scheduled from ET to FS of rice. Interestingly, the N application up to FS of rice showed significant improved grain fertility and reduced sterility under rising CO_2. However, rice plant accumulated and translocated more nutrients from shoot to grain under elevated CO_2 (eCO_2) condition. Moreover, higher grain amylose and lower protein was obvious at eCO_2. Collectively, rice yield increased by 18 to 20 % under eCO_2 with the application of N at FS of rice. These results indicate that to maximize rice yield under eCO_2, it is crucial to supply N at FS of rice in order to increase grain fertility and reduce spikelet sterility.

Keywords: climate change, carbon dioxide, grain sterility, photosynthesis, plant nutrition.

Introduction

Atmospheric CO_2 concentration, increasing very rapidly, is projected to reach 583.4 μmol mol^{-1} from its current 381 μmol mol^{-1} by the end of the 21^{st} century (IPCC, 2013) and the current trend of increasing is up to 10 times faster than previous (IPCC, 2019). The eCO_2 concentration would have a significant impact on climate and food production of the world through affecting plant growth, development, grain yield and quality directly (Ainsworth and Rogers, 2007). However, the eCO_2 will increase global surface temperatures approximately 4 °C compared at the end of the 21^{st} century (Solomon, 2007). Despite of favorable effect, rising temperature nullifies the positive effect of eCO_2 on grain yield of cereal crops (Masutomi et al., 2009). The negative effect of high temperature is due to impaired pollination that leads to spikelet sterility resulting reduced crop yield (Satak and Yoshida, 1978) and affect the inherent soil fertility (Lal, 2002).

The C_3 crops respond more strongly to the eCO_2 than C_4 crop (Ainsworth and Long, 2004; Jablonski et al., 2002). The Pn of crops increased significantly under eCO_2 resulting increase in biomass and yield of C_3 plants (Chunwu et al., 2016; Haque et al., 2005). On the other hand, stomatal conductance (Gs) and transpiration (Tr) rate of plants reduced under eCO_2 condition (Chunwu et al., 2016; Morgan et al., 2004). As a C_3 plant, growth and yield of rice (*Oryza sativa* L.) is markedly enhanced by eCO_2 (Pachauri et al., 2014). Previous studies have shown that leaf area, SDM, panicle and grain number per unit area and grain yield of rice were enhanced due to eCO_2 (Kim et al., 2001; Satapathy et al., 2015; Yang et al., 2006).

The eCO_2 has a dilution effect on nutrient uptake by the crop and a nutrient level in plants is decreased (Li et al., 2013). On the other hand, plants removed greater amount of nutrients from soil and translocated to the grain under eCO_2. Therefore, rice crops exhausted soil minerals to great extent leading to very low available nutrient content in soil after harvesting of the crops (Wang et al., 2011). Rice production also greatly influenced by proper nutrient management practice (Roy et al., 2015) and nutrient absorption of a crop is determined by the time of fertilizer application. Therefore, fertilizers should be applied at right amount and proper time. As mineral fertilizer, N is the main nutrient associated with yield (Jing et al., 2016). For synchronizing plants growth and reducing loss, N is recommended to apply in splits starting from transplanting to flowering. The application of N at early growth stage will helps to produce sufficient SDM, but application at PI stage increase rice grain yield (Subasinghe et al., 2008; Mamun et al., 2016). Therefore, the time of application be adjusted to achieve high yield under eCO_2 condition and high proportion of N should be applied at the late growth stage of rice, especially after PI stage (Wang et al., 2011; Yang et al., 2007). Early studies also suggested that recommended N might not be enough and higher amount should be applied for getting high yield under eCO_2 condition (Razzaque et al., 2009). The recommended practice of N management in rice cultivation is the three splits application from early tillering to 7 days before PI stage. This practice of N management did not work for increasing rice yield under eCO_2 condition (Razzaque et al., 2009), because under eCO_2 condition, the number of spikelets production increased significantly but filled grains reduced due to increasing sterility induced by high temperature (Aktar et al., 2006; Kim et al., 2001). Previous studies have shown that enriched CO_2 favored Pn, shoot growth and yield, but unfilled spikelets increased in rice (Yang et al., 2009). Razzaque et al. (2009) disclosed that rice used higher amount of N under eCO_2 condition. However, it is also important to understand the effect of timing of N application on grain fertility, reduce their sterility and grain yield under increased CO_2 condition. Thus, the objective of the study was to determine the effect of timing of N application on morpho-physiological parameters, yield traits, grain quality and nutrient uptake in rice under eCO_2 condition.

Results and discussion

Photosynthetic traits

The combined effect of CO_2 and N application on Pn rate, Tr and Gs were statistically significant (Figure 1). The highest Pn rate was recorded under eCO_2 with N2. The Pn rates were 34.94, 34.81 and 37.51 μmol CO_2 m^{-2} s^{-1} under OF, which increased to 43.16, 45.57 and 43.78 μmol CO_2 m^{-2} s^{-1} under eCO_2 condition in N1, N2 and N3 treatment, respectively. The highest Tr was measured from OF with N3 treatment which was statistically similar to that of N1 and N2 under same growing condition. The lowest Tr was recorded from eCO_2 with N1 which was statistically similar to that of N2 under same condition. Significantly the highest Gs was recorded from OF with N2 (1.5 m mol m^{-2} s^{-1}) which was statistically similar to other two N treatments under same conditions. The Gs in eCO_2 reduced by 62, 67 and 58 % in N1, N2 and N3, respectively as compared to the OF (Figure 1). The influence of rising atmospheric CO_2 on Pn has been well documented for rice (Roy et al., 2012; Vicente et al.; 2017, Cai et al., 2018). It was found that the Pn of rice plant increases with increasing of atmospheric CO_2. Exogenous supply of CO_2 augmented its concentration inside rice leaf. As it is the substrate of Pn, it was expected that increasing CO_2 level in cellular level would increase Pn rate. The results were consistent with the findings of Chen et al. (2014) and Yuan et al. (2021). At high CO_2 level, the Tr is reduced because of a direct effect of Gs. The lower Tr and Gs of rice under eCO_2 conditions could be beneficial for the growth of rice (Chunwu et al., 2016). In a free air CO_2 enrichment study, Wall et al. (2001) demonstrated that sorghum growth under eCO_2 conditions was enhanced due to a decrease in Tr and Gs. The decreased Gs under eCO_2 was also reported by Wang et al. (2020) and Cai et al. (2018). Reduction in Gs might increase resistance to CO_2 diffusion into the leaf, thus partially offsetting the maximum stimulation of carboxylation rate.

Panicle and grain production

Panicle production and spikelet sterility varied due to interaction of CO_2 concentration and timing of N application (Figure 2). Rice produced higher number of panicle $hill^{-1}$ at iCO_2 with all N treatments. The number of panicles $hill^{-1}$ were 14 in OF with N1 which was increased to 17 in iCO_2 with N3. Rice produced higher percentage of sterile spikelets under increased CO_2 conditions in all N treatments. Under eCO_2 condition, rice produced 44, 37 and 40 sterile spikelets $panicle^{-1}$ in N1, N2 and N3, respectively. The total number of spikelets in OF ranged from 1716 to 1974, in aCO_2 1690 to 1824, in iCO_2 2220 to 2355 and in eCO_2 2432 to 2499 $plant^{-1}$ across the N treatments. However, the spikelets number was higher iCO_2 and eCO_2 with N3 treatment (Table 1). Higher number of filled grains $panicle^{-1}$ was recorded from the iCO_2 in all N treatments (Figure 2). Under iCO_2 condition, rice produced 110, 115 and 120 filled grains $panicle^{-1}$ in N1, N2 and N3, respectively. However, the filled grains numbers at OF condition were 99, 105 and 106 $panicle^{-1}$ in N1, N2 and N3, respectively. Moreover, from N1 to N3, the filled grains varied from 103 to 111 $panicle^{-1}$ at eCO_2. The production of total number of grains $hill^{-1}$ was the highest under eCO_2 with N3 (Table 1). However, grain fertility was the highest in eCO_2 with N3, where the spikelet sterility was the lowest. The grain size did not affect significantly due to the interaction of eCO_2 and N application timing. Numerically higher 1000-garin weight of rice was recorded from eCO_2 treatment in N3 treatment. Rice yield is the product of number of panicles $hill^{-1}$, number of grains $panicle^{-1}$ and weight of individual grain. The production of panicle bearing tillers was higher under iCO_2 (Figure 2). But rice produced 21.42, 13.33 and 21.42 % higher panicles under eCO_2 condition as compared to iCO_2, aCO_2 and OF, respectively in N3 treatment. Previous experiments have demonstrated that rice produced higher number of tillers and panicle at eCO_2 condition (Yang et al., 2006). The main reason for the increases in yield with rising CO_2 were due mainly to the increased panicles per unit area (Satapathy et al., 2015).

The eCO_2 significantly increased number of spikelets $panicle^{-1}$ as well as total number of spikelet $hill^{-1}$ of rice (Figure 2 and Table 1). The results are in agreement with the findings of Hamid et al. (2003) and Jagadish et al. (2007). Moreover, the significant increase in grain fertility by the eCO_2, compared to aCO_2 and OF, may be due to the combined effects of the changes in spikelets composition and source–sink ratio (Yang et al., 2006). A lower number of surviving spikelets $panicle^{-1}$ in turn resulted in a lower sink capacity. Therefore, the eCO_2 increases the sink capacity of rice. The present study denotes that the variation in spikelet number $panicle^{-1}$ was not due to spikelet differentiation $panicle^{-1}$ but mainly due to the enhancement of spikelets degeneration $panicle^{-1}$ under eCO_2 (Figure 2). The differentiated spikelets went down significantly while N applied upto PI stage (N1) at eCO_2 condition (Figure 2). The application of N up to PI stage improves vegetative growth and determines the number of spikelets, while the application of N after PI stage will enhance the fertility of spikelets. In this experiment, the N3 treatment helped rice plant to produce higher number of fertile grains upto iCO_2 but not eCO_2 (Table 1). It implied that iCO_2 and N3 synergistically helped in increasing spikelets number as well as improving fertility of grains. Though, higher number of spikelets plant^{-1} was recorded under eCO_2, but the dose of N applied in this experiment could not meet up the demand of rice plant under raising CO_2 condition. This finding implies that higher amount of N fertilizer may be needed for rice in order to get more fertile grains panicle^{-1} under eCO_2 condition.

Growth and yield of rice

Growth parameters such as plant height, SDM and RDM were significantly influenced by the interaction of CO_2 and N application (Figure 3). Rice produced taller plants under aCO_2, iCO_2 and eCO_2 condition under both N2 and N3 conditions. Irrespective of N treatments, rice plants produced higher amount of SDM under eCO_2 condition (Figure 3). Significantly the highest SDM production was recorded from eCO_2 with N1 (46.08 g plant^{-1}). Though, SDM production under aCO_2 was numerically higher than OF, but they were not statistically different in all N treatments. The root DM of rice plant also increased gradually from OF to eCO_2 as well as N1 to N3 (Figure 3). The similar trend was also obtained in case of N2 and N3 treatments. The grain yield of rice varied significantly due to interaction of time of N application under eCO_2 (Figure 3). Rice plant produced higher grain yield at iCO_2 condition with N3 treatment. In N3 treatment, rice grown under iCO_2 produced 36.83 g grain plant^{-1}, which was 19.38, 14.74 and 29.68 % higher than that of OF, aCO_2 and eCO_2 conditions, respectively. Similarly, in both N1 and N2 treatments, significantly higher grain yield also recoded from iCO_2 as compared to other environmental conditions. However, rice grain yield obtained from iCO_2 and eCO_2 condition were statistically similar in N2 treatment. Similarly, in both N1 and N2 treatments, significantly higher grain yield also recoded from eCO_2 as compared to other environmental conditions. The highest grain was observed under eCO_2 with N3 treatment due to production maximum number of productive panicles hill^{-1} and a greater number of grains panicle^{-1}. The eCO_2 enhanced plant height of rice (Figure 3) in all N treatments. In N1 treatment, plant height increased by 37, 40 and 44 % in aCO_2, iCO_2 and eCO_2 condition, respectively compared to that under OF condition. The trend of plant height increment is also true for N2 and N3. The result is in agreement with the findings of Haque et al. (2005). Elevated CO_2 increased the Pn rate of rice (Figure 1) and the high Pn rate might have contributed to production of taller plants under such condition. Similar results also reported by Satapathy et al. (2015) who stated that the increased biomass under eCO_2 condition was due to increasing LAI and tiller production.

The taller plant resulting more DM accumulation in rice plants grown under eCO_2 condition is due to increased Pn and net assimilation capacity by promotion of carboxylation (Long et al., 2006). Wang et al. (2020) and Ainsworth and Long (2004) showed that eCO_2 increased rice yield by increasing the numbers of tillers and productive panicles m^{-2} and DM production. Elevated CO_2 induced increase in biomass was also observed in mungbean (Chowdhury et al., 2005) and rice (Razzaque et al., 2009). As both SDM and RDM increased proportionately under eCO_2 condition and N3 treatment, it might be led to shoot: root ratio unchanged. Razzaque et al. (2009) also reported similar results under eCO_2. Thus, increase in root dry weight under eCO_2 and N3 treatments had a great impact on nutrient acquisition, growth and productivity of rice. It well known that photosynthesis and carbon accumulation in plant roots increase as atmospheric CO_2 rises, leading to an increase in root mass (Satapathy et al., 2015). Kimball et al. (2002) also reported an increase of 47 % in root biomass of plants grown under eCO_2. Enriched CO_2 up to 500 ppm with N3 increased panicles hill^{-1} and filled grains panicle^{-1} significantly compared to other treatments combination (Figures 3 and 4). Pn, root and SDM production was higher, thus increased yield was expected under eCO_2 condition along with N3. Many earlier studies reported that crops produced under eCO_2 condition produced higher yield (Wang et al., 2020; Ainsworth and Long, 2004; Kim et al., 2001; Kim et al., 2003; Razzaque et al., 2009). The effect of CO_2 enrichment on rice yield has been verified by numerous controlled-environment experiments, showing a yield increase of 5 - 51 % depending on rice varieties, planting regions and climate conditions (Yang et al., 2006; Liu et al., 2008; Hasegawa et al., 2013; Cai et al., 2016). The increase in yield under eCO_2 is primarily attributed to increases in panicle number, spikelet number, percent filled grains or 1000- grain weight (Yang et al., 2006; Roy et al., 2012; Hasegawa et al., 2013; Cai et al., 2016).

Grain quality

Amylose percentage was found higher at iCO_2 concentration followed by eCO_2 concentration and OF condition in all N treatments (Figure 4). The aCO_2 showed the lowest percentage of amylose irrespective of N treatments. Protein percentage was found lower under eCO_2 concentration but higher in OF condition in all N treatments. The aCO_2 with N2 showed the lowest percentage of amylose. Protein percentage was found lowest at eCO_2 with N1 and the highest amount of protein percentage was found in OF condition with N3. The reduction in N and crude protein content in maize has been reported under eCO_2 condition (Abebe et al., 2016). However, protein content at iCO_2 slightly increased with N2 treatment. Moreover, the percentage of the both characters decreased under aCO_2 condition. Amylose content determines the cooking and eating quality of rice. Khanam et al. (2004) reported that eCO_2 adversely affect the amylose content of rice.

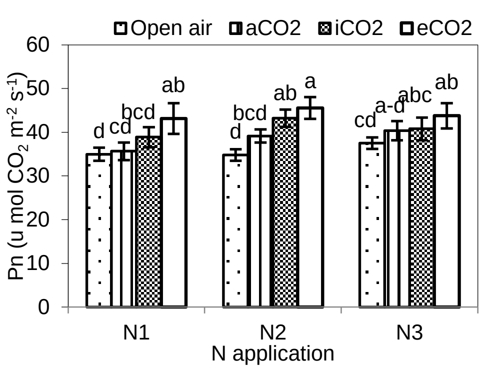
Nutrient acquisition and translocation in grain

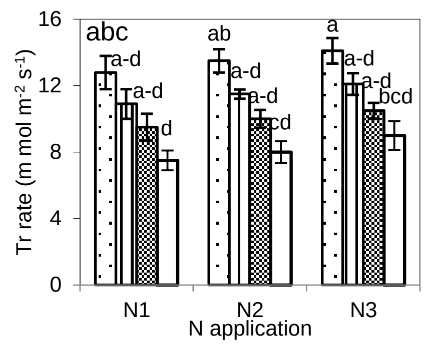
Significantly higher amount of N was accumulated by the plants in straw at iCO_2 condition in N3 followed by N2 and N1 (Table 2). Under iCO_2 condition, rice grain, straw and plant accumulated 0.49, 0.33 and 0.82 g N plant^{-1} in N2, while 0.50, 0.33 and 0.83 g N plant^{-1} in N3 treatment, respectively. The NTC in OF rice ranged from 2.14 to 2.69, while it was 1.25 to 1.49 in iCO_2 and 1.22 to 1.39 in eCO_2 conditions across N treatments (Table 2). However, rice plant absorbed numerically higher amount P in all N treatments at iCO_2 condition followed by aCO_2. The accumulation of P in rice grain ranged from 0.14 to 0.15 g plant^{-1} under iCO_2, while 0.10 to 0.12 g plant^{-1} under aCO_2 condition in N1 to N3 treatments (Table 3). The PTC was higher in iCO_2 (1.48 to 1.65) followed by OF condition (1.23 to 1.53). The accumulation of K was higher in straw at OF condition and the lowest at eCO_2 in all N treatments. The accumulation of K was higher in straw than

Table 1. Effect of elevated CO_2 and N fertilization on grain production of rice.

Growing conditions	N application	Total spikelets [no. hill^{-1}]	Grain fertility [%]	1000-grain weight [g]
Open field	N1	1716 d	75 a-d	20.32
	N2	1876 bcd	78 a	20.46
	N3	1974 a-d	75 abc	22.18
aCO_2	N1	1690 d	72 bcd	20.39
	N2	1824 bcd	76 ab	20.31
	N3	1755 cd	70 d	22.23
iCO_2	N1	2220 a-d	74 a-d	21.74
	N2	2265 abc	76 ab	22.02
	N3	2355 ab	76 ab	21.71
eCO_2	N1	2432 a	70 d	21.71
	N2	2432 a	73 a-d	22.77
	N3	2499 a	70 cd	22.87
CV [%]		10.1	5.6	3.4

eCO_2, iCO_2 and aCO_2 indicate 500, 450 and 400 ppm CO_2, respectively, N1 = 1/3rd of N at ET + 1/3rd at AT + 1/3rd before PI, N2 = 1/3rd of N at ET + 1/3rd before PI + 1/3rd at BS, and N3 = 1/3rd of N at ET + 1/3 N before PI + 1/3rd at FS.





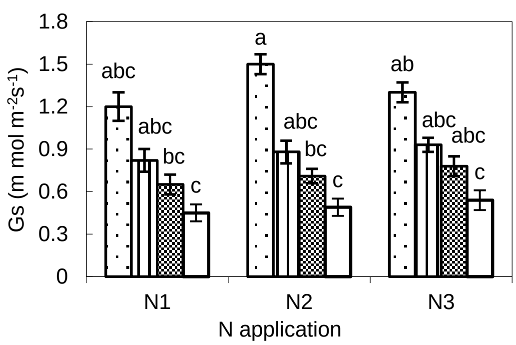
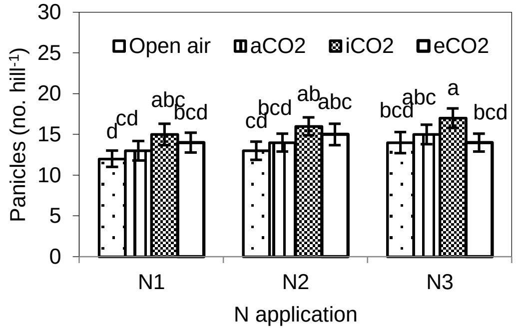


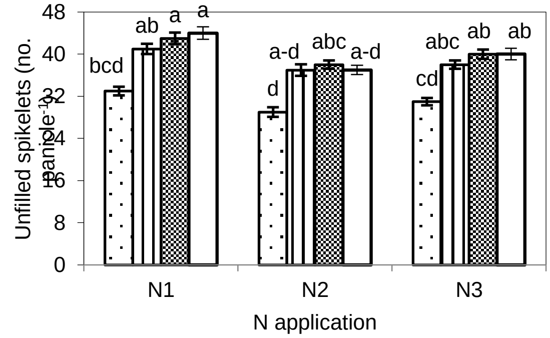
Figure 1. Photosynthetic traits of rice as affected by N fertilization under elevated CO_2 at FS. eCO_2, iCO_2 and aCO_2 indicate 500, 450 and 400 ppm CO_2, respectively, N1 = 1/3rd of N at ET + 1/3rd at AT + 1/3rd before PI, N2 = 1/3rd of N at ET + 1/3rd before PI + 1/3rd at BS, and N3 = 1/3rd of N at ET + 1/3 N before PI + 1/3rd at FS.

Table 2. Nitrogen acquisition and translocation in rice grain as affected by N fertilization under elevated CO_2.

Growing conditions	N application	Grain N content [g plant^{-1}]	Straw N content [g plant^{-1}]	Total N content [g plant^{-1}]	NTC
Open field	N1	0.36 cd	0.17 e	0.52 f	2.14
	N2	0.38 bcd	0.18 de	0.56 f	2.15
	N3	0.47 a	0.18 de	0.65 cd	2.69
aCO_2	N1	0.38 bcd	0.19 de	0.56 ed	2.03
	N2	0.46 ab	0.25 bcd	0.71 bc	1.85
	N3	0.44 abc	0.24 bcd	0.68 cd	1.80
iCO_2	N1	0.42 abc	0.33 a	0.75 b	1.25
	N2	0.49 a	0.33 a	0.81 a	1.49
	N3	0.50 a	0.33 a	0.83 a	1.49
eCO_2	N1	0.32 d	0.26 bc	0.58 ef	1.22
	N2	0.44 abc	0.31 ab	0.75 b	1.39
	N3	0.36 cd	0.26 bc	0.62 de	1.37
CV [%]		5.3	9.3	7.9	

eCO_2, iCO_2 and aCO_2 indicate 500, 450 and 400 ppm CO_2, respectively, N1 = 1/3rd of N at ET + 1/3rd at AT + 1/3rd before PI, N2 = 1/3rd of N at ET + 1/3rd before PI + 1/3rd at BS, and N3 = 1/3rd of N at ET + 1/3 N before PI + 1/3rd at FS. NTC = Nitrogen translocation coefficient.





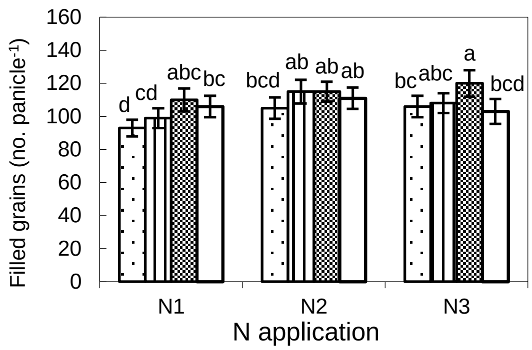


Figure 2. Number of panicles and grains of rice as affected by N fertilization under elevated CO_2. eCO_2, iCO_2 and aCO_2 indicate 500, 450 and 400 ppm CO_2, respectively, N1 = 1/3rd of N at ET + 1/3rd at AT + 1/3rd before PI, N2 = 1/3rd of N at ET + 1/3rd before PI + 1/3rd at BS, and N3 = 1/3rd of N at ET + 1/3 N before PI + 1/3rd at FS.

Table 3. Phosphorus acquisition and translocation in rice grain as affected by N fertilization under elevated CO_2.

Growing conditions	N application	Grain P content [g plant^{-1}]	Straw P content [g plant^{-1}]	Total P content [g plant^{-1}]	PTC
Open field	N1	0.10	0.08	0.18	1.23
	N2	0.10	0.07	0.17	1.33
	N3	0.11	0.07	0.19	1.53
aCO_2	N1	0.12	0.11	0.22	1.09
	N2	0.11	0.11	0.22	0.99
	N3	0.10	0.11	0.21	0.90
iCO_2	N1	0.14	0.10	0.24	1.48
	N2	0.15	0.09	0.24	1.65
	N3	0.15	0.10	0.24	1.56
eCO_2	N1	0.12	0.09	0.22	1.27
	N2	0.13	0.10	0.23	1.41
	N3	0.10	0.10	0.20	1.05
CV [%]		7.6	12.1	11.3	

eCO_2, iCO_2 and aCO_2 indicate 500, 450 and 400 ppm CO_2, respectively, N1 = 1/3rd of N at ET + 1/3rd at AT + 1/3rd before PI, N2 = 1/3rd of N at ET + 1/3rd before PI + 1/3rd at BS, and N3 = 1/3rd of N at ET + 1/3 N before PI + 1/3rd at FS. PTC = Phosphorus translocation coefficient.

Table 4. Potassium acquisition and translocation in rice grain as affected by N fertilization under elevated CO_2.

Growing conditions	N application	Grain K content [g plant^{-1}]	Straw K content [g plant^{-1}]	Total K content [g plant^{-1}]	KTC
Open field	N1	0.09 cd	0.42 cd	0.51 bc	0.22
	N2	0.08 d	0.42 cd	0.51 bc	0.20
	N3	0.09 cd	0.49 bc	0.57 bc	0.19
aCO_2	N1	0.17 ab	0.49 bc	0.66 ab	0.34
	N2	0.14 a-d	0.49 bc	0.63 ab	0.28
	N3	0.11 bcd	0.48 bc	0.60 bc	0.23
iCO_2	N1	0.17 ab	0.40 cd	0.57 bc	0.41
	N2	0.19 a	0.29 d	0.48 c	0.66
	N3	0.19 a	0.41 cd	0.60 bc	0.47
eCO_2	N1	0.15 abc	0.63 ab	0.77 a	0.23
	N2	0.14 a-d	0.64 ab	0.78 a	0.22
	N3	0.13 a-d	0.66 a	0.79 a	0.20
CV [%]		10.5	11.7	12.2	

eCO_2, iCO_2 and aCO_2 indicate 500, 450 and 400 ppm CO_2, respectively, N1 = 1/3rd of N at ET + 1/3rd at AT + 1/3rd before PI, N2 = 1/3rd of N at ET + 1/3rd before PI + 1/3rd at BS, and N3 = 1/3rd of N at ET + 1/3 N before PI + 1/3rd at FS. KTC = Potassium translocation coefficient.

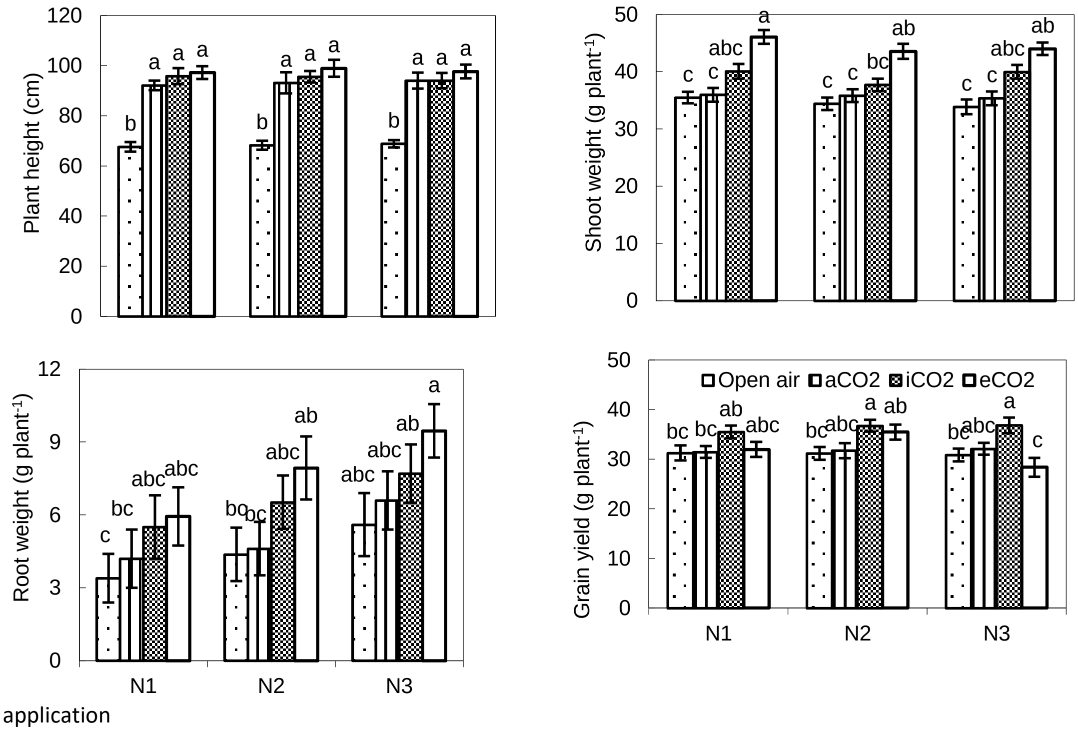


Figure 3. Growth and yield of rice as affected by N fertilization under elevated CO_2.
eCO_2, iCO_2 and aCO_2 indicate 500, 450 and 400 ppm CO_2, respectively, N1 = 1/3rd of N at ET + 1/3rd at AT + 1/3rd before PI, N2 = 1/3rd of N at ET + 1/3rd before PI + 1/3rd at BS, and N3 = 1/3rd of N at ET + 1/3 N before PI + 1/3rd at FS.

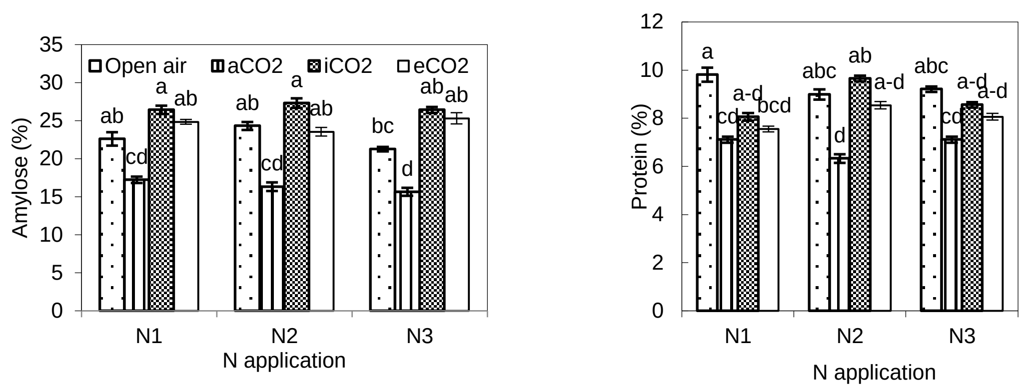


Figure 4. Grain quality properties of rice as affected by N fertilization under elevated CO_2.
eCO_2, iCO_2 and aCO_2 indicate 500, 450 and 400 ppm CO_2, respectively, N1 = 1/3rd of N at ET + 1/3rd at AT + 1/3rd before PI, N2 = 1/3rd of N at ET + 1/3rd before PI + 1/3rd at BS, and N3 = 1/3rd of N at ET + 1/3 N before PI + 1/3rd at FS.

grain in all growing conditions. Therefore, the KTC was lower than 1.0. The translocation of N was significantly higher in OF condition, though P and K was significantly higher in iCO_2 in N2. Higher grain as well as biomass yield under high CO_2 treatment has resulted in higher N uptake of the crop. Earlier workers also reported that in rice crop total N uptake for the whole plant get increased under eCO_2 condition (Yang et al., 2007). Wang et al. (2020) speculate that increased temperature and eCO_2 promote N uptake by the root and translocation from the root to the leaf blades and ultimately influence leaf biochemical properties. In this experiment, the results demonstrated that the amount of N accumulation in rice grain was significantly higher at higher level of CO_2 with N3 (application up to flowering stage) compared to N1 (application up to PI stage) (Table 2). The results also indicated that amount of N in rice straw was half as compared to grain at OF in all N treatments. Similarly, concentration of P and K in grain and straw was also higher under eCO_2 compared to OF condition (Tables 3 to 4). Similar trend was also observed in case of total nutrient acquisition by rice plant. Increased growth of crops under eCO_2 condition will require higher nutrient uptake and assimilation. Numerous studies suggested that nitrogen could be a key factor in regulating the response of ecosystem to eCO_2 (Reich et al., 2006). Lenka and Lal (2012) reported that eCO_2 condition increases recalcitrant carbon fractions in plant biomass causing progressive decline in availability of soil N which necessitates application of supplemental N. Moreover, maximum amount of K accumulated in shoot translocated to grain at iCO_2 condition in all N treatments.

Materials and methods

Experimental site

An experiment was conducted inside OTC at Bangabandhu Sheikh Mujibur Rahman Agricultural University (24.09° N latitude and 90.26° E latitude), Bangladesh in aman, 2017. Aman is one of the major rice growing seasons in Bangladesh. The OTCs (area 9 m^2) were constructed with iron frame that installed on the ground according to Uprety (1998).

Treatments and design

For growing rice plants, 96 pots (24 cm in diameter and 27 cm in height) were filled up with wet soil (13 kg). Physic-chemical properties of initial soil were determined during pot preparation. BU dhan1, was used as planting material. Thirty-day old seedlings were transplanted on 03 August 2017. Transplanting was done by hand with two seedlings hill^{-1} pot^{-1}. After potting, urea, TSP, MoP, gypsum, $ZnSO_4$ were added @ 1.27, 0.715, 0.32, 0.13, 0.026 g pot^{-1}, respectively. All the fertilizers except N were applied before transplanting of rice seedlings. A randomized complete block design with eight replications was used for the experimentation. The treatments comprised of two factors. Factor A: (growing conditions) OTC with eCO_2 (500 ppm) (eCO_2), 450 ppm CO_2 (iCO_2), ambient CO_2 (aCO_2) and OF (380 ppm). Factor B: (timing of N application) N1 = 1/3rd N at ET + 1/3rd at AT + 1/3rd before PI stage PI, N2 = 1/3rd N at ET + 1/3rd before PI + 1/3rd at BS and N2 = 1/3rd N at ET + 1/3rd before PI + 1/3rd at FS.

Gas supply

The CO_2 gas was supplied to the OTC chambers from CO_2 gas cylinder using a blower from 7 DAT to physiological maturity of rice. A portable Pn system (model: LICOR 6200, Lincoln, Nebraska) was used to determine the CO_2 concentration inside the OTC regularly. In eCO_2 treatment, the CO_2 concentration fluctuated from 490 to 510 ppm while it was 440 to 460 ppm in case of iCO_2. A floodwater depth of 2 - 3 cm was maintained in each pot until a week before maturity of the crop. Other intercultural operations were done uniformly in each pot to ensure normal growth of the crop.

Data collection

The Pn, Tr and Gs were determined during full flowering. A portable Pn system (LICOR 6400) was used to record Pn, Tr and Gs. The Pn, Tr and Gs were taken in a clear sunny day from the uppermost fully expanded leaf of the main shoot at flowering stages of the crop during 11:30 am to 12:00 pm. Plant height, number of effective tillers hill^{-1}, filled and unfilled grains panicle^{-1}, grain size, grain yield, SDM and RDM were taken at harvest. Plant height was measured using a meter scale considering base (soil level) to the top of the plant. The numbers of panicle bearing tillers (effective tillers) of each replicated hills were counted and the mean was calculated. At harvest, the total spikelets of each hill were separated; filled as well as unfilled grains were counted manually. The filled grains were considered as fertile, while unfilled grains as sterile grains. The total grain of each hill was weight and recorded as grain yield g hill^{-1} at 14 % moisture content.

The SDM and RDM were recorded at maturity stage. Grain amylose and protein content as were measured after harvesting of the crop. Protein content in rice samples were determined by macro Kjeldahl procedures. Grain and straw nutrient uptake as well as nutrient transfer coefficients were estimated using the following formula:

Grain nutrient uptake (g plant^{-1}) = Grain yield (g plant^{-1}) × grain nutrient concentration

Straw nutrient uptake (g plant^{-1}) = Straw yield (g plant^{-1}) × straw nutrient concentration

Aboveground nutrient uptake (g plant^{-1}) = Grain + Straw nutrient uptake (g plant^{-1})

$$\text{Nutrient transfer coefficient} = \frac{\text{Nutrient accumulation in grain}}{\text{Nutrient accumulation in straw}}$$

Higher transfer coefficient of nutrient indicates relatively poor retention in straw or greater efficiency of plants to transfer nutrients from straw to grain, and low transfer coefficient depicts the low nutrients absorption by grain (Alloway and Ayres, 1997).

Statistical analysis

Data gathered on different parameters were statistically analyzed using computer software package CropStat, version 7.2. Analysis of variance of the data was calculated and the significance of the factor was tested at the 5 % level of probability. Treatment means were separated with DMRT at 5 % level of probability.

Conclusions

The results of this study revealed that the elevated CO_2 with N application upto flowering stage favored Pn, more SDM and RDM, higher number of spikelets, heavier grain and greater accumulation of nutrient in plants, resulting higher grain yield. To maintain this production, it is likely that rice crops growing under elevated eCO_2 will need a greater amount of N after PI stage. Therefore, rescheduling of N with higher amount for rice will be need to maintain the extra dry matter production and filling spikelets produced under the elevated CO_2 condition.

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