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Impact of elevated CO_2 on *Oryza sativa* phenology and brown planthopper, *Nilaparvata lugens* (Hemiptera: Delphacidae) population

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The impact of elevated CO_2 (570 ± 25 ppm) on brown planthopper, *Nilaparvata lugens* (Stål) and Pusa Basmati 1401 rice in comparison to ambient CO_2 was studied in open top chambers (OTCs) during the rainy seasons of 2013 and 2014. Crop canopy circumference was higher (13.1–16.8 cm) under elevated CO_2 when compared to ambient CO_2 (10.3–13.1 cm) during different rice phenological stages indicating the positive influence of elevated CO_2. In addition, elevated CO_2 exhibited a positive effect on rice plants through increase in tiller number (17.6%), reproductive tiller

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number (16.2%), number of seeds/panicle (15.1%) and thousand grains weight (10.8%) that resulted in higher grain yield (15%) when compared to ambient CO_2. Elevated CO_2 also exhibited a positive effect on brown planthopper population through increase in fecundity (29% and 31.6%) which resulted in a significant increase in its population to 150.3 ± 16.4 and 97.7 ± 8.7 hoppers/hill at peak incidence during 2013 and 2014 respectively, when compared to the corresponding 49.1 ± 9.3 and 43.7 ± 7.0 hoppers/hill under ambient CO_2. Moreover, brown planthopper females excreted more honeydew (68.2% and 72.3%) under elevated CO_2 over ambient CO_2 during both years. However, elevated CO_2 caused reduction in the longevity of females (23.9–27.4%) during both years and male longevity (24.1%) during 2013. Despite the positive effect, rice crops suffered higher yield loss under elevated CO_2 (29.9–34.9%) due to increased brown planthopper infestation coupled with higher sucking rate due to reduced nitrogen level under elevated CO_2 compared to ambient CO_2 (17–23.1%) during 2013 and 2014.

Keywords: Brown planthopper, climate change, elevated CO_2, hopper burn, Poaceae, yield loss.

BEING a staple food, rice is cultivated mainly in developing countries and directly influences the economy and nutrition of millions of people in Asia and Africa. To meet the country's stated goal of ensuring food for all, farmers have to use farm inputs in an efficient and sustainable manner to increase productivity per unit area. Burgeoning population along with changing dietary habits have increased the global demand for food. Hence, the global food production has to be increased by 40% by 2030 and 70% by 2050 (ref. 1). India has the largest acreage under rice (43.94 m ha) with a production of about 106.65 mt and productivity of 3.01 t/ha (ref. 2). However, rice productivity in India (3.1 t/ha) is still lower than those of China (6.5 t/ha) and Indonesia[3] (4.9 t/ha)[3]. Intensive and extensive cultivation systems, especially monoculture of rice have increased problems in rice cultivation including incidence of insect pests, diseases and weeds[4]. During the last three decades, after the green revolution, a paradigm shift has occurred in the insect pest complex in rice ecosystems[5,6]. In recent years, especially in northern states of India, brown planthopper (BPH), *Nilaparvata lugens* (Stål) has gained importance and has the potential to pose a serious threat to rice production[3,7]. At higher population densities, hopper burn is observed, which may cause up to 70% of yield loss[3]. Planthopper also acts as a vector for viruses such as rice ragged stunt virus and rice grassy stunt virus.

Atmospheric CO_2 increased from 280 ppm in pre-industrial times to 400 ppm at present and will reach 550 ppm by 2050 (ref. 8). In the absence of strict controls on emission, atmospheric CO_2 is likely to reach 730–1020 ppm by 2100 (ref. 9). Under such conditions, 30% decrease in crop yield is likely to be expected even in regions accounting for direct positive physiological effects of increased CO_2 on crop plants[9,10]. Also, 15% decrease in irrigated rice yields in developing countries and 12% increase in the price of rice are anticipated as a result of climate change by 2050 (ref. 11).

Insects are affected by climate change due to their ectothermic nature and sensitivity to temperature[12]. Climate change affects insects directly by affecting their physiology and behaviour[13] and indirectly via host plants, natural enemies and other competitors[14,15]. Under elevated CO_2, carbon in plant tissues is relatively more. The corresponding increase in the C : N ratio causes reduction in plant protein concentration thereby lowering the availability of nutrients to herbivores[16,17]. Besides, the size of the plant canopy may also influence pest populations, especially those of sucking pests such as rice planthoppers, through changes in micro-environment.

Earlier studies have been challenged to visualize the expected consequences of rising atmospheric CO_2 concentrations and other associated environmental changes on biotic systems. So far studies on plant responses to climate change have been extensive and have narrated the positive effect of elevated CO_2 on the yield in rice and other crops[18–21]. However, insect herbivore responses towards climate change have been less studied. Understanding the effect of climate change on the major economic insect pest, brown planthopper in the rice ecosystem will help understand their population fluctuation in a changing environment, which will in turn help manage the pests effectively.

Experiments on the effect of elevated CO_2 on crop phenology and brown planthopper population compared to ambient CO_2 were undertaken on rice (*Oryza sativa* L; variety Pusa Basmati 1401) in open top chambers (OTCs) during the rainy seasons (June–October) of 2013 and 2014 at the Indian Agricultural Research Institute, New Delhi (28°38′N, 77°09′E and 228.61 m). The experimental site was classified as semi-arid type with hot and dry summer and cold winter with annual rainfall of 708.7 mm (mainly from the south west monsoon – 80%). The average temperature during rainy season was 29°C. During the experimental period mean daily evaporation was about 4.8 and 5.9 mm d^{-1} during 2013 and 2014 respectively. The rainfall was measured by a FRP (Fibre Reinforced Plastic) rain gauge in the university meteorological observatory. Through the study period, crops (mainly in the vegetative period) received a net rainfall of 109 and 92 mm, in 2013 and 2014 respectively. The soil of the experimental site belongs to Holambi series, typical Indo-Gangetic alluvium (typic Haplustept family).

Among the four OTCs, two were allocated to elevated condition, in which 570 ± 25 ppm CO_2 was maintained from 9 : 30 a.m. to 4 : 30 p.m. from rice transplanting to harvest. The other two OTCs under ambient CO_2 were without an external supply of CO_2. One OTC had plants

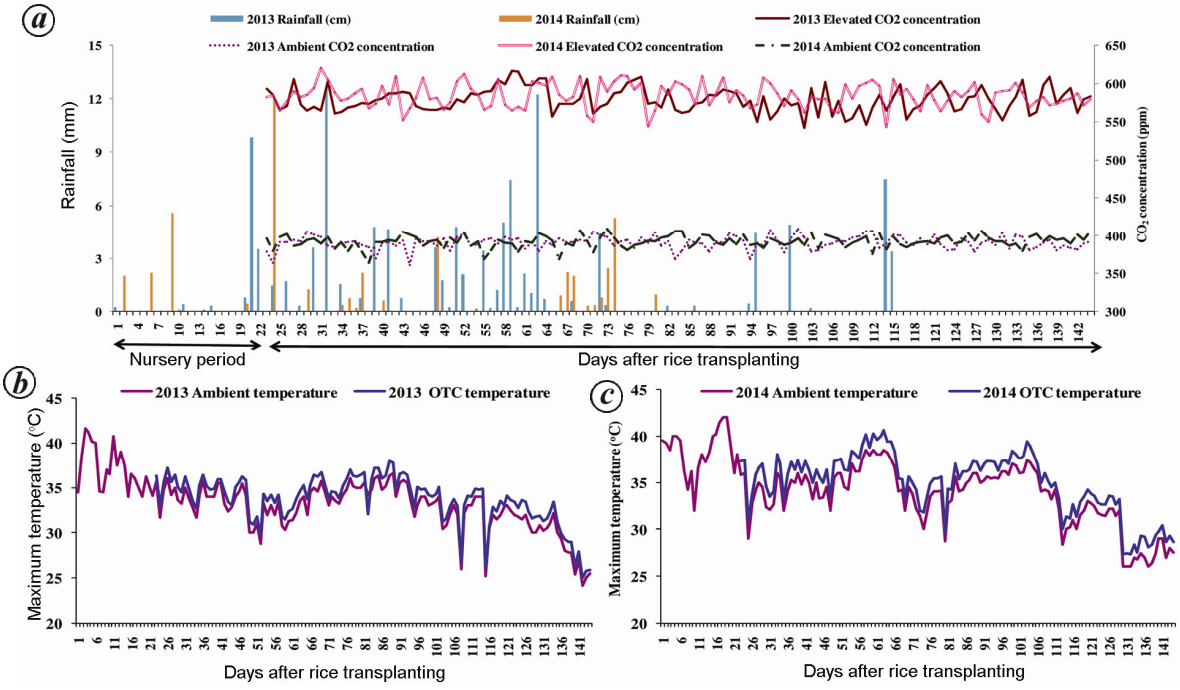

Figure 1. ***a***, Rainfall and CO_2 concentration under ambient and elevated CO_2 OTCs during the rice growing season of 2013 and 2014. ***b*** and ***c***, Daily maximum temperature in the ambient and elevated CO_2 OTCs during the rice growing season of 2013 and 2014.

with brown planthopper infestation under elevated and ambient CO_2 conditions; while in the other uninfested crop was maintained. Since plants use CO_2 for photosynthesis during the day time (presence of light) only, CO_2 concentration was maintained during the day. In the absence of light, plants do not respond to elevated CO_2 as photosynthesis does not occur during night time. This also helped in saving the cost of the experiment by reducing the consumption of CO_2 gas. The height and diameter of the OTC were 2.5 and 3.0 m respectively. The OTC's daily temperature (maximum and minimum) and relative humidity were also recorded during the study period with the help of sensors (Model TRH 511, Ambetronics, Switzerland) fitted in the middle of each OTC and data logger (Model TC 800D, Ambetronics, Switzerland). The season-long daytime average CO_2 in the ambient and elevated OTCs were 390 ppm and 578 ppm in 2013, and 392 ppm and 584 ppm in 2014 respectively (Figure 1). Rice nursery was raised in wet nursery beds following recommended agronomic practices. Transplanting was done manually with 15 cm spacing between plants and 20 cm between rows in the OTCs with two 22-day-old seedlings on 15 July and 20 July during rainy seasons of 2013 and 2014. All the post-transplanting agronomic practices except plant protection were followed according to the recommended package and practices for rainy season paddy crop cultivation.

Initial population of healthy unparasitized adult females/nymphs was collected from IARI farm and maintained in the glass house at 28 ± 2°C and 65 ± 5% relative humidity (RH). These laboratory reared insects were used for further experiments. Fifteen plants were selected in each of the OTCs under elevated and ambient CO_2 wherein each OTC represented one treatment and each plant was designed as one replication and thus 15 replications were followed. After 10 days of crop exposure to elevated CO_2, five pairs of fully matured gravid brachypterous females and winged males of the *N. lugens* were released in each selected plant under elevated and ambient CO_2 conditions[22,23]. Weekly observations on the number of nymphs, males, brachypterous (wingless) females and macropterous (winged) females were recorded.

For assessing the *N. lugens* fecundity, one pair of freshly emerged *N. lugens* adults (brachypterous female and winged male) was confined to 40-day old potted rice seedlings for mating and oviposition under elevated and ambient CO_2 conditions with 10 replications. After 5 days, leaf sheaths were dissected and eggs were counted under a binocular microscope. Nymphal development was studied by releasing 10 newly emerged first instar *N. lugens* nymphs on 40-day-old potted rice plants covered with a mylar film cage under both CO_2 conditions. Observations on nymphal moulting were recorded at daily intervals until adult emergence. At each observation, the numbers in each nymphal instar were recorded. The presence of exuviae was considered as an indicator of moulting. The newly emerged adults (brachypterous female and winged male) were maintained under both CO_2 conditions until their death to record adult longevity.

Honeydew excretion by newly emerged females of *N. lugens* was estimated through graphical method[24,25]. Methods to determine sucking rate *via* honeydew excretion

have been discussed in detail[22]. In brief, five one-day-old brachypterous *N. lugens* females that were starved for 3 h, were released in each pot inside the cup and allowed to feed on seedling bases for 24 h. Honeydew droplets excreted by the females were deposited on filter papers causing colour change from yellowish orange to blue. The areas of blue rimmed spots that appeared on the filter paper as a result of honeydew excretion were measured graphically. The *N. lugens* sucking rate was then estimated based on average area (mm^2) of excreted honeydew.

Observations on plant parameters, viz. number of tillers, reproductive tillers, circumference of the hill, number of seeds/panicles, 1000-seed weight and yield were recorded for both the infested and uninfested plants in the four OTCs. The plants were harvested in the first week and second week of November during 2013 and 2014 respectively. After threshing, grains were oven dried to measure the 1000-seed weight and grain yield. Plant yields of uninfested (UI) and infested (I) plants under elevated CO_2 as well as ambient CO_2 were compared to determine the effect of elevated CO_2 on the extent of yield loss (yield loss = {yield (UI) – yield (I)/yield (UI)} × 100) due to brown planthopper. The N content in rice plant was determined by the improved Kieldahl method[22]. Similarly, total soluble sugar was measured by anthrone method[23]. Statistical analyses were performed using SAS Software, Version 9.3. Repeated measure ANOVA was used to analyse the interactive effect of CO_2 concentration and exposure duration on brown planthopper population[23,26], while the effect of CO_2 on plant parameters was analysed through *t*-test and statistical significance was compared based on confidence intervals, i.e. $P < 0.05$.

During both the years, fecundity of brachypterous females differed significantly on rice plants grown under elevated CO_2 when compared to those grown under ambient CO_2 ($t = 2.1$, $P < 0.05$) (Figure 2). Elevated CO_2 thus stimulated fecundity of brown planthopper by 29% and 31.6% more when compared to ambient CO_2 during the first and second years respectively. The study revealed that the population of brown planthopper in both the years was significantly higher under elevated CO_2 than ambient CO_2. During the first year, the peak pest population was observed during the 5th week after adult release (WAR) under elevated CO_2 as well as ambient CO_2. Besides the first population peak, a second peak was again witnessed in the 8th WAR. During the first three weeks, total population of brown planthopper under both conditions did not differ significantly; however, higher brown planthopper population was recorded during the 4th WAR onwards under elevated CO_2 ($F = 70.2$, $P < 0.0001$) (Table 1). In the second year of study, the peak pest population was recorded during the 3rd WAR under both elevated and ambient CO_2 conditions. The brown planthopper population under elevated CO_2 was significantly higher than ambient CO_2 during 3rd–6th WAR ($F = 38.4$, $P < 0.0001$) (Table 2). The peak brown planthopper population thus occurred earlier during the second year of the study compared to the first year. However, only one peak of the brown planthopper population was observed during the second year indicating that only one generation of the pest developed during this year unlike the first year when two generations occurred.

Nymphal population of the brown planthopper was significantly higher under elevated CO_2 than ambient condition during both the years. Maximum population of the brown planthopper nymphs was recorded during the 5th week in the first year and 3rd week in the second year of adult release (Table 3). Hence nymphal population followed a similar trend as that of the total brown planthopper population. It thus appears that significantly higher fecundity under elevated CO_2 resulted in more nymphal population during both the years. During both years, significantly more number of brachypterous females was observed under elevated CO_2 over ambient CO_2 (Table 3). The peak brachypterous female population under elevated CO_2 was observed during the 5th WAR in the 1st year and 3rd WAR in the 2nd year, while it occurred during the 5th WAR under ambient CO_2 during both the years. However, during the first year a second peak appeared in the 7th WAR under elevated CO_2 and in the 8th WAR in ambient CO_2, indicating that females appeared one week earlier under elevated CO_2 (Table 4). On the other hand, male population significantly differed under elevated and ambient CO_2 with peak population levels having developed during the 5th WAR in the first year (Table 3). However, in the second year male population did not differ significantly between the two CO_2 conditions. It is thus evident that elevated CO_2 appreciably influenced the brachypterous female than male population.

Longevity of brachypterous females was significantly reduced under elevated CO_2 when compared to ambient

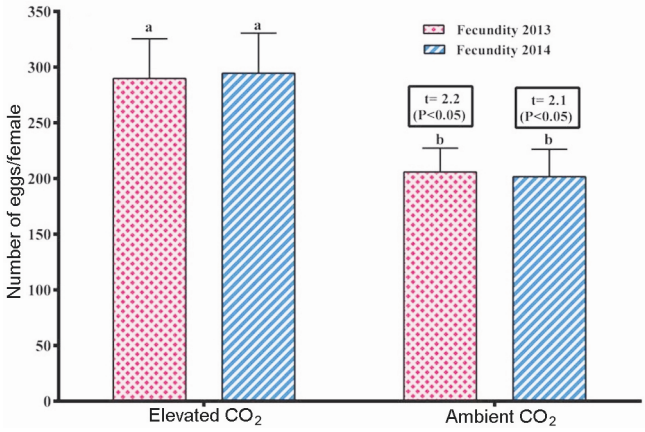

Figure 2. Fecundity of brown planthopper females under elevated and ambient CO_2 (bars with same superscript do not differ significantly).

Table 1. Brown planthopper population/hill (nymphs, males and females) in open-top chambers during 2013

	Brown planthopper population* (nymphs + males + females)								
	Weeks after adult release								
Treatment	1	2	3	4	5	6	7	8	9
Elevated CO_2	4.1 ± 1.0 (0.4 ± 0.1)^{k}	13.1 ± 2.2 (1.0 ± 0.1)^{hi}	32.9 ± 3.1 (1.5 ± 0.1)^{def}	73.1 ± 8.4 (1.8 ± 0.1)^{cd}	150.3 ± 16.4 (2.1 ± 0.1)^{a}	67.9 ± 11.5 (1.7 ± 0.1)^{ab}	71.3 ± 5.2 (1.8 ± 0.03)^{bc}	114.5 ± 21.0 (2.0 ± 0.1)^{bc}	23.7 ± 4.9 (1.3 ± 0.1)^{fgh}
Ambient CO_2	3.7 ± 0.8 (0.4 ± 0.1)^{k}	8.0 ± 1.1 (0.9 ± 0.1)^{ij}	16.7 ± 2.3 (1.2 ± 0.1)^{gh}	40.4 ± 5.4 (1.6 ± 0.1)^{fg}	49.1 ± 9.3 (1.6 ± 0.1)^{cd}	29.8 ± 7.1 (1.3 ± 0.03)^{cd}	24.4 ± 3.3 (1.3 ± 0.1)^{efg}	46.1 ± 8.2 (1.6 ± 0.1)^{de}	11.1 ± 2.6 (0.8 ± 0.2)^{j}

Treatment, $F = (70.2)$, LSD = (0.08), d$f = 1$, $P < 0.0001$; Week, $F = (61.0)$, LSD = (0.17), d$f = 8$, $P < 0.0001$; Interaction (treatment × week), $F = (2.2)$, LSD = (0.24), d$f = 8$, $P < 0.05$. Planthopper counts with same superscripts do not differ significantly. *Mean of fifteen replications. Data in parentheses are log(x + 0.5) transformed values.

Table 2. Brown planthopper population/hill (nymphs, males and females) in open-top chambers during 2014

	Brown planthopper population* (nymphs + males + females)					
	Weeks after adult release					
Treatment	1	2	3	4	5	6
Elevated CO_2	3.0 ± 1.6 (0.7 ± 0.13)^{d}	24.3 ± 4.0 (1.3 ± 0.08)^{c}	97.7 ± 8.7 (2.0 ± 0.04)^{a}	48.7 ± 5.0 (1.7 ± 0.05)^{b}	45.7 ± 5.4 (1.6 ± 0.05)^{b}	17.9 ± 3.2 (1.1 ± 0.12)^{c}
Ambient CO_2	2.5 ± 2.0 (0.7 ± 0.18)^{d}	24.8 ± 4.3 (1.3 ± 0.07)^{c}	43.7 ± 7.0 (1.6 ± 0.06)^{b}	22.0 ± 3.1 (1.3 ± 06)^{c}	13.0 ± 1.8 (1.1 ± 0.07)^{c}	5.2 ± 1.5 (0.5 ± 0.13)^{d}

Treatment, $F = (38.4)$, LSD = (0.11), d$f = 1$, $P < 0.0001$; Week, $F = (39.7)$, LSD = (0.18), d$f = 5$, $P < 0.0001$. Interaction (treatment × week), $F = (3.8)$, LSD = (0.26), d$f = 5$, $P < 0.01$. Planthopper counts with same superscripts do not differ significantly. *Mean of fifteen replications. Data in parentheses are log(x + 0.5) transformed values.

CO_2 during both the years (Table 4). Females lived 4.0 ($t = 1.5$; $P = 0.01$) and 3.4 ($t = 3.6$; $P = 0.002$) days less under elevated CO_2 compared to ambient CO_2 during the first and second year of the study respectively. Elevated CO_2 thus reduced female life span by 27.4% in the first year and 23.9% in the second year. In the case of males, longevity was significantly reduced ($t = 2.8$; $P = 0.02$) by 2.8 days (24.1%) during the first year under elevated CO_2. However, during the second year, the male developmental period did not significantly differ between the two CO_2 conditions. Similarly, nymphal developmental duration did not differ significantly under elevated CO_2 and ambient CO_2 during both the years (Table 4). Nevertheless, total developmental period (1st instar to adult) was significantly shorter under elevated CO_2 in both the years compared to ambient CO_2. Elevated CO_2 thus reduced brown planthopper lifespan by 4.6 days (15.4%) ($t = 4.0$; $p = 0.001$) and 2.6 days (9.4%) ($t = 2.2$; $P = 0.04$) in the first and second year of the study respectively. The amount of honeydew excreted revealed the quantum of feeding by the brachypterous females and was found to have significantly increased under elevated CO_2 condition (Figure 3). It was found to be 68.2% ($t = 3.4$, $P = 0.003$) and 72.3% higher ($t = 3.9$, $P = 0.001$) in the first and second year respectively, under elevated CO_2 when compared to ambient CO_2.

In the present study, uninfested plants exposed to elevated CO_2 had significantly higher number of tillers ($t = 2.9$, $P = 0.009$), reproductive tillers ($t = 2.6$, $P = 0.02$), 1000-grain weight ($t = 0.9$, $P = 0.05$) and yield ($t = 2.2$, $p = 0.04$). Elevated CO_2 thus increased tillers (19.7%), reproductive tillers (17.8%), seeds/panicle (16.3%) and 1000-grain weight (9.0%). This resulted in an overall increase in grain yield by 15% under elevated CO_2 when compared to ambient CO_2 during the first year (Table 5). In the second year, a similar fertilization effect was observed in uninfested plants grown under elevated CO_2 condition with increase in tiller number (15.4%), reproductive tillers (14.6%), seeds/panicle (13.8%), 1000-grain weight (12.2%) and yield (15.2%) (Table 5). There was significant difference in the uninfested plants canopy circumference of the two CO_2 treatments at different crop growth stage during both the years. During 2013 under elevated CO_2, higher canopy circumferences of 13.9, 16.3 and 13.2 cm were recorded during vegetative (45–50 DAS), flowering (85–90 DAS) and post-flowering (115–120 DAS) phases respectively, compared to 10.16, 12.52 and 10.08 cm, at the respective stages under ambient CO_2 (Figure 4). Similar results for canopy circumferences were obtained during vegetative, flowering and post-flowering period during 2014. The canopy circumferences at vegetative, flowering and post-flowering period were 15.8, 17.2 and 12.7 cm respectively, under elevated CO_2 compared to 12.8, 13.6 and 10.4 cm under ambient CO_2 respectively (Figure 4). The nitrogen level was significantly lower under elevated CO_2 when

Table 3. Mean number of brown planthopper developmental stage at peak and during the entire season in open-top chambers*

	Nymphs/hill				Brachypterous female/hill					Males/hill			
	2013		2014		2013			2014		2013		2014	
Treatment	Peak	Season	Peak	Season	Peak 1	Peak 2	Season	Peak	Season	Peak	Season	Peak	Season
Elevated CO_2	115.8 ± 16.6 (2.0 ± 0.1)[a]	45.0 ± 4.3 (1.3 ± 0.1)[a]	88.1 ± 8.6 (1.9 ± 0.1)[a]	34.0 ± 3.5 (1.3 ± 0.1)[a]	17.5 ± 2.3 (1.2 ± 0.1)[a]	16.1 ± 1.9 (1.2 ± 0.1)[a]	8.2 ± 0.7 (0.6 ± 0.1)[a]	6.3 ± 1.3 (0.6 ± 0.01)[a]	3.3 ± 0.5 (0.3 ± 0.1)[a]	21.8 ± 2.7 (1.3 ± 0.1)[a]	8.0 ± 1.0 (0.5 ± 0.1)[a]	4.8 ± 1.1 (0.4 ± 0.3)[a]	2.4 ± 0.2 (0.2 ± 0.1)[a]
Ambient CO_2	25.0 ± 7.6 (1.0 ± 0.1)[b]	17.8 ± 1.5 (0.9 ± 0.1)[b]	37.8 ± 7.2 (1.5 ± 0.1)[b]	16.4 ± 1.9 (0.9 ± 0.1)[b]	6.9 ± 1.1 (0.7 ± 0.1)[b]	10.4 ± 2.2 (0.9 ± 0.1)[b]	3.9 ± 0.4 (0.3 ± 0.1)[b]	2.5 ± 0.8 (0.2 ± 0.01)[b]	1.2 ± 0.2 (0.01 ± 0.0)[b]	13.7 ± 1.7 (1.1 ± 0.1)[b]	3.7 ± 0.3 (0.2 ± 0.1)[b]	3.7 ± 1.0 (0.3 ± 0.3)[a]	2.0 ± 0.3 (0.1 ± 0.1)[a]

*Mean of fifteen replications. Data in parentheses are $\log(x + 0.5)$ transformed values. Values with same superscripts in the same column do not differ significantly.

Table 4. Different developmental stages of brown planthopper under elevated and ambient CO_2 condition

	Duration of development (days ± SE)					
	Rainy season 2013			Rainy season 2014		
Developmental stage	Elevated CO_2	Ambient CO_2	*t* statistics	Elevated CO_2	Ambient CO_2	*t* statistics
I instar nymph	3.4 ± 0.21	3.8 ± 0.15	$t = 1.5^{NS}$	3.7 ± 0.15	3.6 ± 0.21	$t = 0.2^{NS}$
II instar nymph	3.2 ± 0.20	3.6 ± 0.22	$t = 1.5^{NS}$	3.5 ± 0.17	3.4 ± 0.20	$t = 0.4^{NS}$
III instar nymph	3.0 ± 0.16	3.1 ± 0.12	$t = 0.8^{NS}$	3.0 ± 0.14	3.1 ± 0.19	$t = 0.4^{NS}$
IV instar nymph	2.5 ± 0.15	2.7 ± 0.22	$t = 0.6^{NS}$	2.6 ± 0.24	2.4 ± 0.20	$t = 0.6^{NS}$
V instar nymph	3.3 ± 0.17	3.2 ± 0.19	$t = 0.4^{NS}$	3.0 ± 0.16	3.0 ± 0.26	$t = 0.2^{NS}$
Total nymphal period	15.3 ± 0.46	16.4 ± 0.43	$t = 1.7^{NS}$	15.6 ± 0.40	15.4 ± 0.54	$t = 0.3^{NS}$
Female longevity	10.6 ± 1.09	14.6 ± 0.90	$t = 1.5$ ($P = 0.01$)	10.8 ± 0.66	14.2 ± 0.68	$t = 3.6$ ($P = 0.002$)
Male longevity	8.8 ± 1.03	11.8 ± 0.65	$t = 2.8$ ($P = 0.02$)	9.1 ± 0.66	11.4 ± 1.13	$t = 1.8^{NS}$
Adult longevity	9.7 ± 0.68	13.2 ± 0.47	$t = 4.2$ ($P = 0.001$)	10.0 ± 0.52	12.8 ± 0.67	$t = 3.4$ ($P = 0.004$)
I instar nymph to adult	25.0 ± 0.85	29.6 ± 0.78	$t = 4.0$ ($P = 0.001$)	25.6 ± 0.84	28.2 ± 0.88	$t = 2.2$ ($P = 0.04$)

NS, Non-significant.

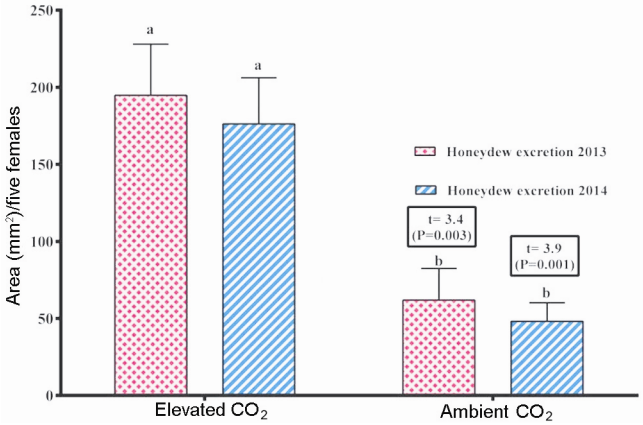

Figure 3. Honeydew excretion of brown planthopper females under elevated and ambient CO_2 (bars with same superscript do not differ significantly).

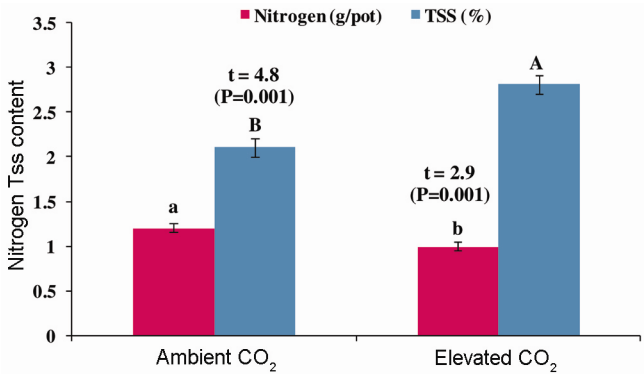

Figure 5. Nitrogen and total soluble sugars (mean ± SE) of Pusa basmati 1401 under elevated and ambient CO_2 (bars with same superscript do not differ significantly).

compared to ambient condition and for total soluble sugars (TSS) the results were vice-versa. Despite the positive effect of elevated CO_2 on rice crop, the brown planthopper infestation under elevated CO_2 reduced the yield by 38.5% and 29.9% during 2013 and 2014 respectively (Table 5). The corresponding yield reduction due to brown planthopper infestation under ambient CO_2 was 23.1% and 17.0% during the two years.

In the present study, elevated CO_2 stimulated brown planthopper multiplication and pest population more than doubled when compared to ambient CO_2 despite hardly any difference in the pest incidence during the initial three weeks under both the CO_2 conditions. The increase in the brown planthopper population could mainly be attributed to its increased fecundity and increased number of brachypterous females, probably due to more congenial micro-climate under dense canopy induced by elevated CO_2 along with changes in the TSS and nitrogen level. It has been found earlier that brown planthopper[23,27], wheat aphid, *Sitobion avenae*[28], potato aphid, *Macrosiphum euphorbiae*[29], western corn rootworm, *Diabrotica virgifera*[30] and pea aphid, *Acyrthosiphon pisum*[31] populations significantly increased under elevated CO_2 when compared to ambient CO_2. Likewise, soybean aphid, *Aphis glycines* populations under elevated CO_2 were significantly greater after the first week of incidence and attained twice the size compared to ambient CO_2 (refs 30, 32). Similarly, combined effects of both elevated temperature and CO_2 altered the pest biology via plant phenology and aggravated the damage by potato aphid, *M. euphorbiae* and corn leaf aphid, *Rhopalosiphum maidis* (Fitch) on their host plants[33,34].

In the present study higher fecundity of brown planthopper under elevated CO_2 (Figure 2) ultimately resulted in increased brown planthopper population compared to ambient CO_2. The BPH exposed to elevated CO_2 had higher consumption rate which ultimately contributed to more fecundity. Similar response by brown planthopper females towards elevated CO_2 was reported earlier[23,35]. Increased fecundity under elevated CO_2 has also been reported earlier in other species of Homoptera such as peach aphid, *Myzus persicae*[36] (Sulzer); grain aphid, *S. avenae*[28]; cotton aphid, *Aphis gossypii*[37]; birch aphid, *Euceraphis betulae*[38]; and corn leaf aphid, *R. maidis*[35] whereas decrease in fecundity was observed in case of woolly beech aphid, *Phyllaphis fagi*[39] and pea aphid, *A. pisum*[40]. Changes in the population dynamics of insect pests is a complex issue. The possible reason for two generations observed in 2013 was that both maximum and minimum temperature was slightly lower (about 3°C) when compared to 2014 (Figure 1); likewise rainfall was more and later part of crop growth (90–100 days) also received rainfall, which contributed to the required RH for BPH multiplication. All these factors contributed to second generation emergence in the first year. However, in the second year higher temperatures coupled with less rainfall did not favour emergence of the second generation.

Elevated CO_2 significantly reduced the pest developmental period from first instar nymph to adult emergence and subsequently adult longevity of both brachypterous female and male. This was possibly due to greater effort by the insects to derive required amount of nitrogen under higher carbon to nitrogen (C : N) ratio under elevated CO_2. To complete the lifecycle an insect requires a certain amount of temperature over a period of time (degree days). In the present study an average 1–1.5°C increase under elevated condition might speed up the BPH growth (Table 4) and development. Brown planthopper female longevity was considerably lower in elevated CO_2 when compared to ambient CO_2 (ref. 35). The female exposed to elevated condition had more sucking rate (consumption rate) that was clearly quantified by the excretion of honeydew. An earlier study clearly indicated that herbivore consumption rates and development time increased under elevated CO_2 when compared to ambient CO_2 conditions[41], whereas relative growth rate

Table 5. Rice growth and yield parameters under elevated and ambient CO_2 condition

	Rainy season 2013						Rainy season 2014					
	Uninfested			Infested			Uninfested			Infested		
Parameters	ECO_2	ACO_2	*t* Statistics	ECO_2	ACO_2	*t* Statistics	ECO_2	ACO_2	*t* Statistics	ECO_2	ACO_2	*t* Statistics
No. of tillers/hill	29.5 ± 1.62	23.7 ± 1.15	$t = 2.9$ ($P = 0.009$)	30.2 ± 2.09	25.2 ± 2.52	$t = 1.5^{NS}$	31.1 ± 1.53	26.3 ± 1.49	$t = 2.3$ ($P = 0.04$)	27.8 ± 2.61	25.0 ± 2.15	$t = 0.8^{NS}$
No. reproductive tillers/hill	25.3 ± 1.32	20.8 ± 1.06	$t = 2.6$ ($P = 0.02$)	25.4 ± 1.86	21.1 ± 2.06	$t = 1.6^{NS}$	26.8 ± 2.22	22.9 ± 1.99	$t = 1.6^{NS}$	24.2 ± 2.84	21.9 ± 1.83	$t = 0.7^{NS}$
Seeds/panicles	94.3 ± 7.22	78.9 ± 8.96	$t = 1.3^{NS}$	85.6 ± 9.13	73.7 ± 6.75	$t = 1.0^{NS}$	86.3 ± 7.67	74.4 ± 8.16	$t = 1.1^{NS}$	80.4 ± 10.19	70.5 ± 7.19	$t = 0.8^{NS}$
1000 seed weight (g)	22.7 ± 0.84	20.6 ± 0.44	$t = 0.9$ ($P < 0.05$)	16.6 ± 2.07	17.2 ± 1.53	$t = 0.2^{NS}$	22.6 ± 1.07	19.8 ± 0.44	$t = 2.4$ ($P = 0.03$)	17.7 ± 1.01	18.4 ± 0.94	$t = 0.5^{NS}$
Yield (g)	32.1 ± 1.62	27.3 ± 1.15	$t = 2.2$ ($P = 0.04$)	19.8 ± 4.21	21.0 ± 2.55	$t = 0.5^{NS}$	37.6 ± 2.05	31.9 ± 1.68	$t = 2.4$ ($P < 0.05$)	26.4 ± 4.91	27.3 ± 4.13	$t = 0.4^{NS}$
Yield loss (%)	–	–		38.3	23.1		–	–		29.8	14.4	

ECO_2, Elevated CO_2; ACO_2, Ambient CO_2; NS, Non-significant.

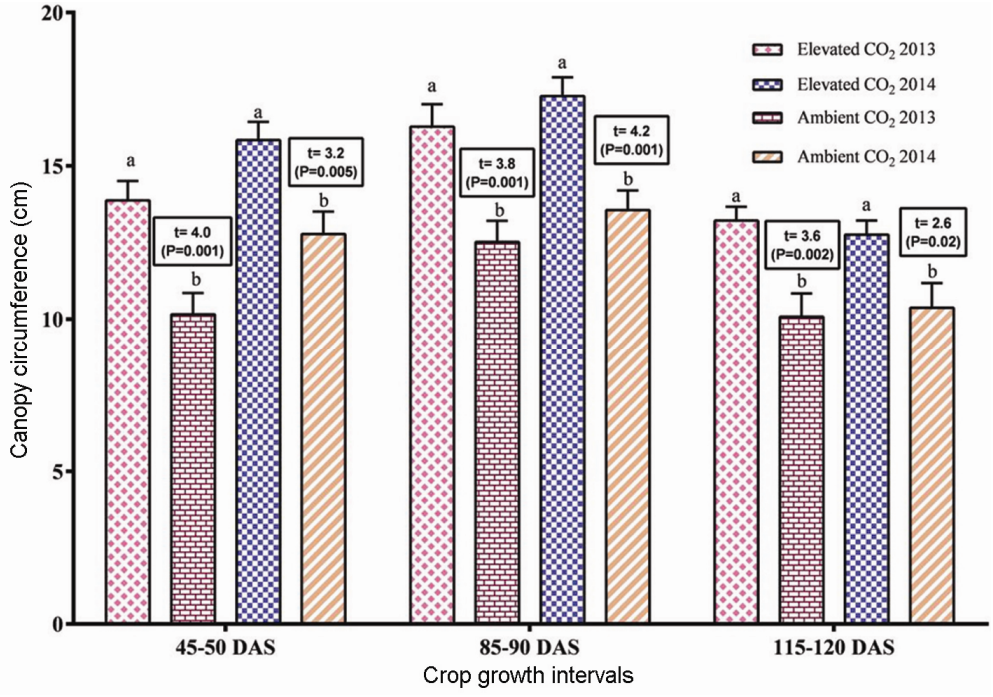

Figure 4. Canopy circumferences (mean ± SE) of Pusa Basmati 1401 under elevated and ambient CO_2 (bars with same superscript do not differ significantly).

and pupal weight decreased[41]. Combination of elevated CO_2 and temperature significantly reduced the nymphal and adult developmental period of corn leaf aphid, *R. maidis*[34] and yellow sugarcane aphid, *Sipha flava*[42].

In the present study, elevated CO_2 effected 15% increase in tiller number that eventually improved the plant density and growth, which in turn manifested as a significant increase in canopy size (Figure 4), providing a congenial micro-environment for brown planthopper multiplication. Earlier, plants exposed to elevated CO_2 showed enhanced photosynthetic rate and lower respiration that was attributed to the doubling of the tillers[18–21]. Besides, elevated CO_2 also resulted in higher number of brachypterous females (Table 3) that produced more eggs resulting in enhanced brown planthopper population. Plants grown under elevated CO_2 experienced constant increase in leaf temperature by 0.2°C and 0.5°C (ref. 43) and decreased stomatal conductance that led to increase in canopy temperature[44]. Earlier higher brown planthopper population in closer spacing was observed compared to wider spacing. It was also reported earlier that dense growth of rice plants with increased canopy size, coupled with higher canopy temperature under elevated CO_2 created warm and humid micro-climate, which proved congenial for the brown planthopper, thereby increasing its population[27].

Sap feeders excrete 40% of the sucked assimilates as honeydew and quantification of honeydew was directly related to the sucking rate[45,46]. The present study revealed significantly higher honeydew excretion by brown planthopper (Figure 3) in elevated CO_2 than ambient CO_2. This might be because the insects had to suck more assimilates to draw requisite amount of nitrogen for their nourishment under higher C : N ratio under elevated CO_2. Earlier studies also observed increased sucking rate by brown planthopper under elevated CO_2 (refs 23, 35). When compared to ambient CO_2, more honeydew excretion under elevated CO_2 clearly indicated higher sucking rate of the pest which was eventually exhibited by severe hopper burn under elevated CO_2.

Nitrogen (N) is essential for insects to grow and produce more number of eggs as studied in various groups of insects such as Orthoptera, Homoptera, Lepidoptera, Hymenoptera and Coleoptera. Under elevated CO_2, nutritional status of host plants might deteriorate leading to dilution of N (ref. 47), thus forcing brown planthopper to enhance its feeding to counter the nitrogen deficit in their phloem sap. Similarly increased consumption of insects feeding on the plants grown under elevated CO_2 has also been reported earlier[23,24,36,48–50]. In addition, phloem feeders such as *A. pisum* could keenly trigger the host plant and its bacteriocytes to enhance the amino acid metabolism in favour of its population growth under elevated CO_2 (ref. 51).

The present study evinced the positive effect of elevated CO_2 on rice plant that resulted in an increase in canopy size, 1000-grain weight and yield. However, elevated CO_2 also increased brown planthopper population via higher fecundity and higher sucking rate that caused greater yield loss relative to ambient CO_2. Higher damage

caused by brown planthopper under elevated CO_2 was evident in the form of severe hopper burn when compared to ambient CO_2. It has been found earlier that increase in atmospheric CO_2 has a significant impact on C_3 plants such as rice due to changes in photosynthetic carbon assimilation pattern that leads to increase in biomass and productivity[18–21]. It has also been opined that rising concentration of CO_2 improves plant growth but may simultaneously cause damage due to phytophagous insects. Rising atmospheric CO_2 at the projected level would thus definitely hinder rice production.

It is thus evident that the brown planthopper population was enhanced under elevated CO_2 that consequently reduced the rice yield. Due to shorter life span, high reproductive potential and physiological sensitivity, insects are more readily amenable to changing climatic conditions. Climate change thus has a paramount impact on the distribution pattern and abundance of insects. The present study revealed that elevated CO_2 stimulated brown planthopper population by increasing fecundity and creating more congenial micro-climate through dense plant growth. Higher brown planthopper population coupled with its increased sap sucking rate under elevated CO_2, resulted in more yield loss compared to ambient CO_2. Crop losses due to brown planthopper may thus aggravate under changing climate conditions. Further, the interactive effect of elevated CO_2 and temperature provides a realistic insight into plant–insect interactions under changing climate, which will be studied in the near future.

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