Effects of elevated carbon dioxide and temperature on rice brown planthopper, *Nilaparvata lugens* (Stål) populations in India

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Two populations of the brown planthopper (BPH), *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) were collected from two hotspot locations of India – Ludhiana (Punjab) in the north and West Godavari (Andhra Pradesh) in the south, and their biological parameters were studied under ambient conditions. Results showed that the above two populations were notably different in three out of five biological parameters recorded. The response of these two populations to climate variables, viz. elevated temperature and increased levels of CO_2 was assessed. These conditions prolonged the nymphal duration (14.2 days) and lowered female longevity (9.6 days), fecundity (155.5 eggs/♀) and nymphal feeding rate (14.3 mm^2) compared to ambient CO_2 and temperature across the populations. Honeydew excretion by adults was significantly higher at elevated CO_2 than at ambient level. At elevated CO_2 and higher temperature, the Ludhiana population recorded significantly longer nymphal duration (15.9 days) and decreased amount of honeydew excretion by nymphs (13.8 mm^2) compared to the parameters recorded at elevated CO_2 and ambient temperature (12.8 days and 32.8 mm^2 respectively). In contrast, West Godavari population recorded significantly reduced female longevity and fecundity under elevated CO_2 and higher temperature. Elevated CO_2 per se did not adversely affect BPH biology across populations but with the concomitant increase in temperature, populations showed varying response. Location-specific mitigation strategies for management of hoppers will be required to address the varying responses of populations to climate variables.

Keywords: Climate variables, fecundity, honeydew excretion, *Nilaparvata lugens*, nymphal duration.

GLOBAL climate change is a reality now. The global average temperature which has at present increased by 0.6°C is projected to further increase by 1.4–7.5°C; whereas the elevated atmospheric CO_2 level at 380 ppm presently is expected to reach 560 ppm by the end of the 21st century[1]. It is also predicted that temperature increase of about 2–3°C would result in 5–10% yield loss in rice crop, if no proper counter measures are adopted between 2030 and 2050 (ref. 2). Climate change is expected to have major impacts on crop pests directly as well as indirectly through their host plants[3]. Many species of herbivorous insects tend to show altered behaviour under CO_2 enrichment and have been studied extensively[4–8]. The consequences differ among species and include retarded growth rate, increased nymphal development time, higher mortality rates[9,10], accelerated development of eggs and larvae, and delayed emergence of adults[11]. The brown planthopper (BPH), *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) is one of the most serious pests of rice in both temperate and tropical regions of East and South Asia, and has reached outbreak levels over the past few years[12]. It is known for its seasonal migration and *r* strategy pattern of life. It directly damages the plant by sucking phloem sap, causing hopper burn, and also by transmitting viral diseases[13]. It has emerged as the major pest of rice in India only after 1971, with cultivation of short-statured, high-yielding and nitrogen-responsive varieties. Widespread outbreaks of brown planthopper causing heavy yield losses were observed in recent years[14,15]. In 2005–06, more than 485,000 ha of rice in southern Vietnam was severely affected by viral diseases spread by BPH, resulting in losses valued at US $120 million[16]. The planthopper populations from different countries and areas within countries differ in their responses to rice varieties with the same resistance genes[17,18]. Similar differences may be reflected in their response to climate change. There is scant information available on the impact of elevated CO_2 and temperature individually and in combination on BPH, and the variations in response of populations from different geographical regions. Hence, the present study was envisaged to assess the interactive effects of elevated CO_2 and temperature on BPH populations collected from two different geographical regions of India, which are hotspots for the outbreak of this insect pest.

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Materials and methods

CO_2 chambers

A specially designed, closed, climate-controlled chamber was constructed with a total dimension of 10′ × 8′ × 10′. It had three chambers, each of dimension 2.5′ × 8′. The chambers were maintained at three levels of CO_2 concentration and temperature combination, continuously, at the ICAR-Indian Institute of Rice Research (IIRR), Hyderabad (lat. 17°10″N, long. 78°E, altitude 542 m above msl) as follows: (1) Ambient CO_2@ 380 ± 25 ppm and ambient temperature (aCO_2 + aT), (2) Elevated CO_2@550 ± 25 ppm and ambient temperature (eCO_2 + aT), and (3) Elevated CO_2@550 ± 25 ppm and elevated temperature (eCO_2 + eT).

Fully automatic control and monitoring system with CO_2 sensors, programmable logic controller (PLC), and supervisory control and data acquisition (SCADA) programme to monitor the desired CO_2 level within the chambers, was established in an anteroom and the climate variables as listed above were maintained throughout the study period. CO_2, temperature and humidity were recorded continuously during the experiment. Temperatures were 31°C/26°C for day/night cycle; relative humidity was 70–80% for ambient temperature and 60–70% for elevated temperature (34°C/29°C).

Insect material

BPH populations were collected from two different states of the country. One population was collected from Ludhiana, Punjab, falling under hot, semi-arid climatic conditions representing northwest India, where rice crop is grown only during June to November (wet season). The second population was collected from West Godavari district, Andhra Pradesh, which falls under hot, sub-humid to semi-arid conditions, where rice is grown in two seasons (dry and wet). The populations were individually reared on young rice seedlings of susceptible cultivar TN1, using modified Japanese method[19,20], in flexi cages to avoid mating and intermingling of the two populations in a greenhouse at IIRR.

Biological parameters

Baseline biological data of populations: The biological parameters such as nymphal survival, nymphal duration, longevity and fecundity of the two populations were studied in the laboratory under ambient conditions. Newly emerged first instar nymphs were used for this experiment. A single 45-day-old rice plant (cv. TN1) was taken in a glass test tube (25 × 200 mm dia) containing Hoagland's nutrition medium up to 5 cm depth and 20 nymphs were released into it. When the plants showed yellowing due to feeding, they were replaced with plants of the same age. The level of Hoagland solution was maintained by topping regularly. Observations were recorded on various biological parameters.

Nymphal duration: Five pairs of adults from each population were collected from the stock culture and reared in CO_2 chambers designated as (F_0) generation. Subsequently, the newly hatched nymphs of F_1 generation were transferred singly on 30-day-old TN1 plants placed in Hoagland solution inside a glass test tube (25 × 200 mm). Forty replications were maintained in each chamber. The rice seedlings were replaced every alternate day. Nymphal duration was calculated from the day of hatching up to adult emergence.

Fecundity and longevity of adults: One pair of newly emerged adults of F_1 generation was released on potted plants of TN1 (45-day-old) covered with a mylar cage. Every third day, adults were transferred to fresh 45-day-old TN1 plants until the death of adults. Observations were also recorded on nymphal hatching every day until no nymphal hatching was observed for four consecutive days. Survival of the male and female hoppers was recorded, and longevity was calculated as the period from emergence to death.

Honeydew excretion test: Feeding behaviour of the two populations at three different treatments was estimated by honeydew excretion of third instar nymphs and newly emerged brachypterous females, individually, according to protocol[21]. Five third instar nymphs or a one-day-old brachypterous female starved for 2 h, were released on 30-day-old rice seedlings (cv. TN1) at the three-leaf stage. Each treatment was replicated thrice and the area of honeydew excretion was measured from the scanned image of the filter paper using Image J software.

Data analysis

Data collected for each variable were analysed using the software General Linear Model (GLM) SYSTAT 12 (Systat software Inc., Chicago, IL, USA) with CO_2 concentration and temperature included as factors. Datasets were transformed where necessary to satisfy assumptions of normality and homogeneity of variances. Where a significant interaction between the two factors occurred in the GLM analysis, a post-hoc comparison of means was carried out. For datasets with homogenous variances, LSD test was used. When heteroskedasticity occurred that could not be removed through data transformation, the Games and Howell method was used to compare means.

Results

Baseline biological data of populations

The two populations showed significant differences for various biological parameters. Lower nymphal survival

Table 1. Biological parameters of two populations of brown planthopper, *Nilaparvata lugens*

Parameters	West Godavari (mean ± SE)	Ludhiana (mean ± SE)	*t* value (d*f*)	*P*-value
Nymphal survival (%)	48.5 ± 1.5	90.0 ± 0.5	5.36 (18)	0.000
Nymphal developmental duration (days)				
Brachypterous (male + female)	13.6 ± 0.2	19.9 ± 0.5	8.42 (104)	0.000
Macropterous (male + female)	12.9 ± 0.2	18.2 ± 1.0	5.26 (25)	0.000
Female (brachypterous + macropterous)	13.5 ± 0.3	20.8 ± 1.3	7.39 (64)	0.000
Male (brachypterous + macropterous)	13.3 ± 0.3	18.1 ± 1.2	6.77 (66)	0.000
Brachypterous – female	13.6 ± 0.3	21.0 ± 1.3	7.00 (60)	0.000
Brachypterous – male	13.5 ± 0.3	17.8 ± 1.2	4.59 (42)	0.000
Macropterous – male	12.9 ± 0.2	18.6 ± 1.1	5.32 (22)	0.000
Adult longevity (days)				
Brachypterous – female	15.8 ± 0.7	12.5 ± 0.9	–2.35 (13)	0.030
Brachypterous – male	10.0 ± 1.0	6.1 ± 0.6	–2.90 (8)	0.020
Macropterous – male	6.6 ± 0.8	7.5 ± 0.6	0.83 (9)	0.428
Fecundity (no. of eggs laid/female)				
Brachypterous – female	62.5 ± 7.5	116.4 ± 9.2	–4.40 (11)	0.001

(48.5%) was observed in the West Godavari population compared to the Ludhiana population (90%; Table 1). The latter showed prolonged nymphal duration in brachypterous female and male, and macropterous male compared to West Godavari population. Irrespective of wing morphs, female and male hoppers took longer to develop in the Ludhiana population (Table 1). Similar trend was observed in brachypterous and macropterous forms, irrespective of gender. The development of macropterous female forms was very low in the study as food was not a constraint. The longevity of brachypterous female and male was significantly higher in the West Godavari population. On the other hand, fecundity was higher in the Ludhiana population (116 eggs/♀) compared to the West Godavari population (62.5 eggs/♀).

Nymphal development

Nymphal duration did not differ significantly in the West Godavari population among the treatments. In the Ludhiana population it was significantly prolonged in eCO_2 + eT (15.9 days) compared to other treatments. Across treatments, nymphal duration was highest in eCO_2 + eT (14.2 days). Across populations, the population from West Godavari had lesser developmental duration (12.8 days) than that from Ludhiana (13.8 days; Figure 1 and Table 2).

Longevity of adults

In the West Godavari population, female longevity did not differ significantly among the CO_2 treatments (Figure 2 *a* and Table 2). On the other hand, female longevity in the Ludhiana population was significantly less in eCO_2 + eT (10.4 days) than in aCO_2 + aT (15.0 days). Across treatments, female longevity was significantly reduced at eCO_2 + eT (9.6 days) compared to other treatments. Across populations, female longevity was significantly higher in the Ludhiana population (12.3 days) than the West Godavari population (10.3 days). However, male longevity did not differ significantly across treatments and populations (Figure 2 *b* and Table 2).

Fecundity of female adults

Fecundity increased in the West Godavari population at eCO_2 + aT (275.5 eggs/♀) compared to eCO_2 + eT (134.2 eggs/♀) and aCO_2 + aT (113.2 eggs/♀), whereas it was not significantly different in the Ludhiana population. Across treatments, fecundity was significantly higher at eCO_2 + aT (251.3 eggs/♀) compared to eCO_2 + eT (155.5 eggs/♀) and aCO_2 + aT (188.3 eggs/♀). However, across populations, the two did not differ significantly (Figure 3 and Table 2).

Feeding assessed by honeydew excretion

Honeydew excretion by third instar nymphs of the West Godavari population was on par in all the treatments. The Ludhiana population showed significant differences between eCO_2 treatments: lower amount of honeydew was excreted by third instar nymphs at eCO_2 + eT (13.8 mm^2) compared to eCO_2 + aT (32.8 mm^2). Similarly, across treatments, significantly lower amount of honeydew was excreted at eCO_2 + eT (14.3 mm^2) compared to eCO_2 + aT (29.6 mm^2) and aCO_2 + aT (21.8 mm^2), though difference among the populations was not significant (Figure 4 *a* and Table 2).

Honeydew excreted by the brachypterous females showed significant differences in the West Godavari population; the feeding under eCO_2 treatments was on par,

Table 2. Summary of GLM analysis (ANOVA) results on the effect of elevated CO_2 and temperature on *N. lugens*

Measurements	Treatments	*F*-value (d*f*)	*P*-value
Nymphal duration	West Godavari population – CO_2 and temperature	5.43(2)	0.01
	Ludhiana population – CO_2 and temperature	35.01(2)	0.00
	CO_2 and temperature (across treatments)	13.85(2)	0.00
	Population	5.46(1)	0.00
Longevity – female	West Godavari population – CO_2 and temperature	2.98(2)	0.06
	Ludhiana population – CO_2 and temperature	3.30(2)	0.04
	CO_2 and temperature (across treatments)	4.11(2)	0.02
	Population	4.89(1)	0.03
Longevity – male	West Godavari population – CO_2 and temperature	2.16(2)	0.13
	Ludhiana population – CO_2 and temperature	0.88(2)	0.42
	CO_2 and temperature (across treatments)	0.07(2)	0.93
	Population	3.67(1)	0.06
Fecundity	West Godavari population – CO_2 and temperature	16.71(2)	0.00
	Ludhiana population – CO_2 and temperature	2.53(2)	0.10
	CO_2 and temperature (Across treatments)	3.23(2)	0.03
	Population	0.71(1)	0.40
Honeydew excretion by third instar	West Godavari population – CO_2 and temperature	2.17(2)	0.15
	Ludhiana population – CO_2 and temperature	4.07(2)	0.04
	CO_2 and temperature (across treatments)	6.58(2)	0.01
	Population	0.09(1)	0.76
Honeydew excretion by female adults	West Godavari population – CO_2 and temperature	9.82(2)	0.01
	Ludhiana population – CO_2 and temperature	3.59(2)	0.09
	CO_2 and temperature (across treatments)	3.40(2)	0.05
	Population	7.98(1)	0.01

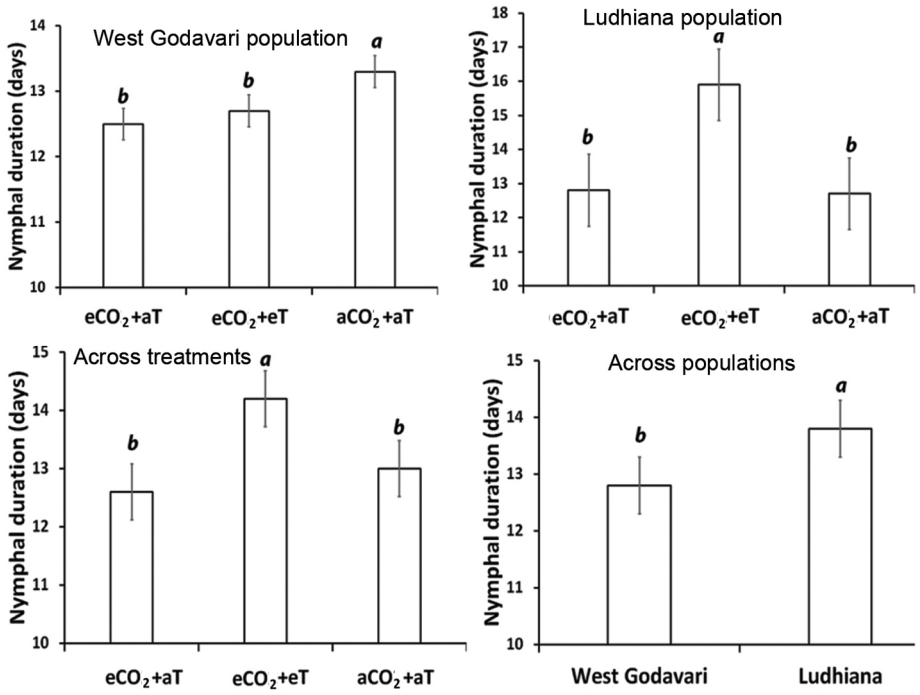

Figure 1. Nymphal duration: Effects of CO_2 concentration and temperature on nymphal duration of the brown planthopper, *Nilaparvata lugens* in TN1 variety. $n = 40$ replications for each treatment; aCO_2 + aT, Ambient CO_2 and ambient temperature; eCO_2 + aT, Elevated CO_2 and ambient temperature; eCO_2 + eT, Elevated CO_2 and elevated temperature. Different letters on the bars in a panel denote significant difference (LSD test, $P = 0.05$).

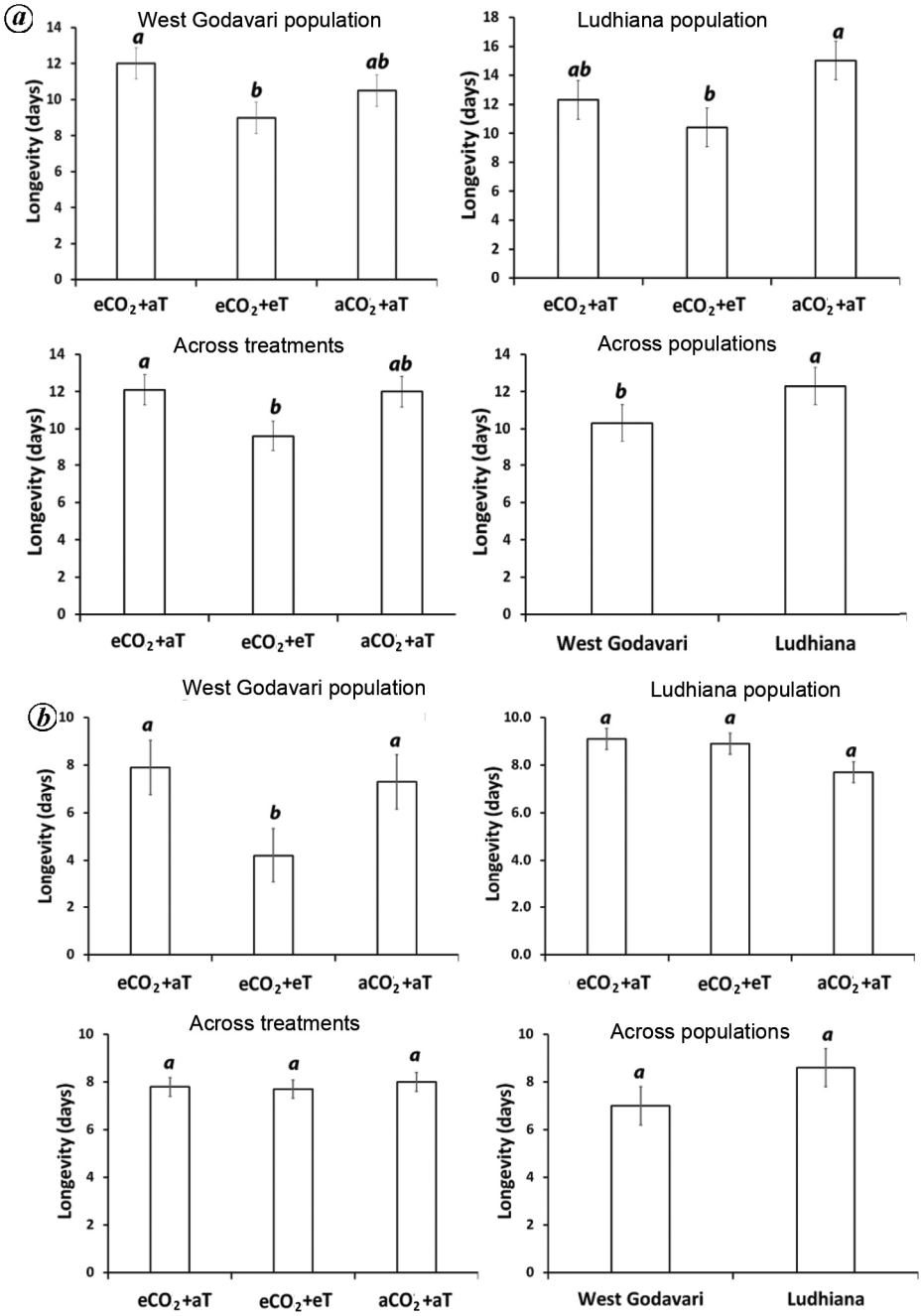

Figure 2. ***a***, Female longevity: Effects of CO_2 concentration and temperature on female longevity of *N. lugens* in TN1 variety. n = 10–12 for each treatment; ***b***, Male Longevity: Effects of CO_2 concentration and temperature on male longevity of *N. lugens* in TN1 variety. n = 10–12 for each treatment.

but lower amount of honeydew was excreted by adults under aCO_2 + aT (166.3 mm^2) compared to other treatments (Figure 4 *b*). In the Ludhiana population, though higher amount of honeydew was excreted by female adults under eCO_2 + aT (323.0 mm^2), it was not statistically significant. Across treatments, honeydew excretion was significantly higher under eCO_2 + aT (284.0 mm^2) compared to aCO_2 + aT (206.9 mm^2), but temperature fluctuations did not have a significant influence. Across populations, higher amount of honeydew excretion was noticed in the Ludhiana population (274.4 mm^2) than in the West Godavari population (213.3 mm^2; Figure 4 *b* and Table 2).

Discussion

Climate change is associated with warming, elevated CO_2 and regionally changing precipitation[22]. Temperature directly influences the survival, development and abundance of insects. Insects inhabiting colder climates with

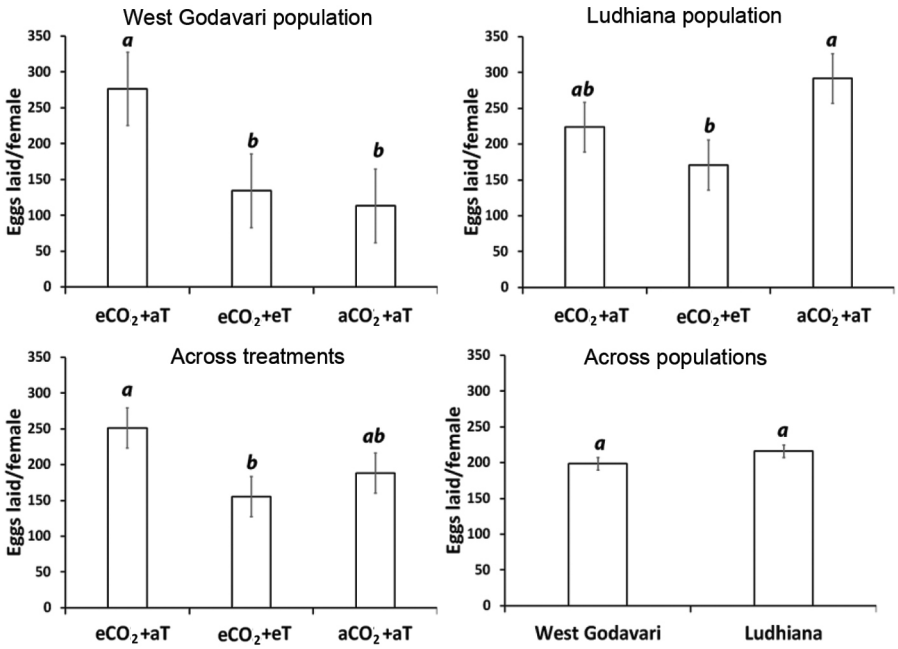

Figure 3. Fecundity of female adults: Effects of CO_2 concentration and temperature on fecundity of *N. lugens* in TN1 variety. n = 5–10 for each treatment.

marked seasons have better tolerance to thermal extremes. Global warming may benefit such insects which are currently exposed to cooler temperatures that are lesser than their optima[22]. Insects inhabiting the tropical regions are already living at environmental temperatures close to their optimum and any further increase may have adverse effects.

Environmental heterogeneity affects the phenotypic expressions of insects[23]. Similarly, biological evidence suggests that rice planthoppers show significant geographic structure[19]. The present study also indicates that geographical variations exist in planthoppers with respect to biological parameters, viz. survival, developmental period, longevity, fecundity and wing morphs.

When geographical variations exist in populations without climate stress, the response to climatic variables may also differ. The results of this study show that elevated temperature with increased levels of CO_2 significantly affect the biological parameters of BPH. It prolongs the nymphal duration and lowers longevity, fecundity and nymphal feeding rate. When the temperatures are lower than or above the optimum range, biological functions like feeding, rate of development and longevity are lowered while nymphal duration is prolonged in BPH[24]. Our results are in line with earlier findings[25] that the duration of nymphal growth was shorter at a mean temperature of 30°C, and prolonged with increased temperature. Other studies have reported that temperature between 25°C and 30°C is optimal for egg and nymphal development of BPH[26–30], whereas temperature above 30°C is unfavourable for insect survival[27,28,30,31].

Female longevity was significantly reduced under elevated CO_2 and elevated temperature in the Ludhiana population. A similar trend was observed in the West Godavari population, though not statistically significant. However, male longevity did not show any significant difference in both populations. The yellow sugarcane aphid, *Sipha flava* (Forbes) showed shorter longevity at elevated CO_2 (500 ppm) and elevated temperature (28°C), than at the same CO_2 conditions but lower fluctuating temperatures[32]. The female longevity of *S. flava* was also found to be shorter at elevated CO_2 (700 ppm) and elevated temperature (28°C) than ambient CO_2 and temperature[32].

We observed that the fecundity of BPH increased at elevated CO_2 levels, elevated temperature decreased the fecundity of BPH across treatments. The number of eggs laid by BPH was found to be lower at higher temperature regimes of 34°C and 36°C and that these increased temperatures were not suitable for egg-laying and development of BPH[33]. The number of eggs laid by BPH decreased rapidly as the temperature increased[34]. However, in contrast, it was reported that fecundity was higher at elevated temperature with elevated CO_2 than at ambient temperature with ambient CO_2 (ref. 35). The experiment was however conducted in a temperate region which has been hypothesized to benefit insects that are exposed to cooler temperatures[36]. The elevated temperature in the present study, being in a tropical region, was a +3°C increase from 31°C/26°C to 34°C/29°C (day/night cycle), which might have lead to decreased egg-laying capacity of BPH. Further, it was observed that fecundity

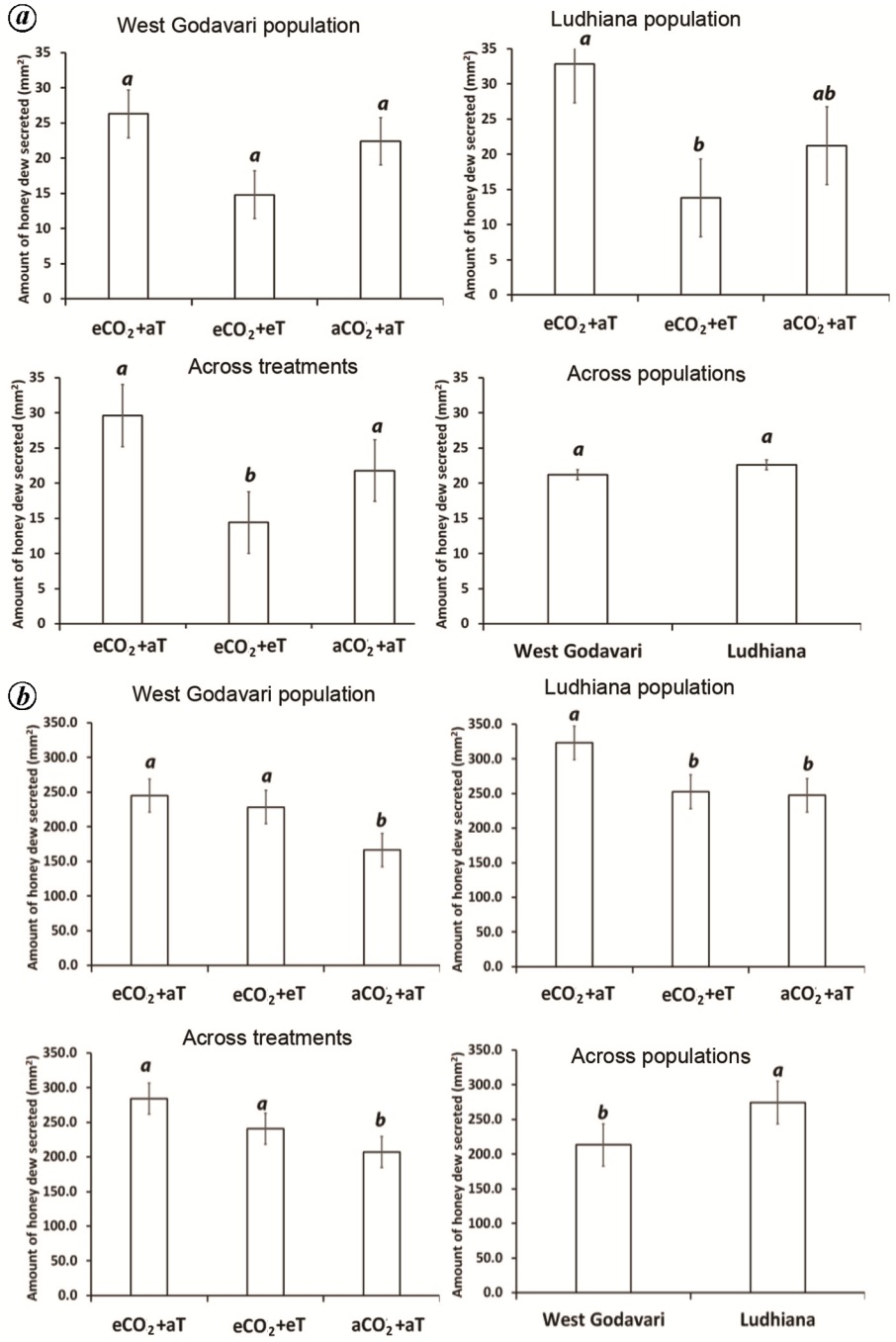

Figure 4. ***a***, Honeydew excretion by third instar nymphs: Effects of CO_2 concentration and temperature on honeydew excretion in 24 h per five third instar nymphs of *N. lugens* in TN1 variety. $n = 5$ for each treatment; ***b***, Honeydew excretion by brachypterous female adults: Effects of CO_2 concentration and temperature on honeydew excretion in 24 h per five brachypterous females of *N. lugens* in TN1 variety. $n = 5$ for each treatment.

of BPH showed varying results between populations with respect to elevated temperature and CO_2. Population from the West Godavari which is a coastal region, showed decreased rate of fecundity at elevated temperature and elevated CO_2, whereas the Ludhiana population exposed to distinct hot and cooler climes, was not influenced by elevated temperature and elevated CO_2. The optimum temperature for survival and reproduction varies between insect species and populations of each species[22]. The results of the present study indicate that the feeding rate of third instar nymphs is more influenced by the combined effect of elevated CO_2 and temperature in both populations, which is in accordance with earlier reports[5,8] that elevated temperature may directly reduce feeding in

insects or the reduced water content in stem parts and altered osmotic potential in the phloem sap may reduce the feeding rate. In case of adults, elevated CO_2 increased feeding in both the populations, while temperature did not have a significant impact. On the other hand, an earlier study had shown that high temperature exposure reduced feeding activity and honeydew production in both life stages (nymphs and adults) of *N. lugens*[37]. This clearly indicates that insects from tropical and temperate regions exposed to different temperature regimes will show varied responses to climate change.

The average temperature range prevailing at Ludhiana is wider with a minimum being 9.5°C and maximum of 35.3°C, whereas the temperature range in West Godavari is narrower with a minimum of 25.3°C and maximum of 31.8°C (mean of two years 2013–14). Across all the parameters, The Ludhiana population responded positively to climate change with prolonged nymphal duration, higher longevity of females and higher feeding rate. The results of this study indicate that the population exposed to a greater temperature range, i.e. lower/higher temperatures may be positively impacted.

The present study reveals that elevated CO_2 (550 ppm) with elevated temperature (+3°C) significantly increases nymphal duration but reduces female longevity, fecundity and amount of honeydew excreted by nymphs of BPH in comparison with those noted at elevated CO_2 and ambient temperature across the two populations studied. However, at elevated CO_2 and ambient temperature, significantly higher amounts of honeydew excretion by adults compared with those at ambient CO_2 and ambient temperature have been recorded. Performance of BPH populations from Ludhiana and West Godavari was notably different in three out of five parameters recorded, indicating that the populations have a differential response to environmental changes. Future studies should focus more on the responses of biotypes and populations to projected changes in the environment, and formulate risk management strategies specific to each region.

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