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Research Paper

Rice brown planthopper, *Nilaparvata lugens* (Stål) feeding behavior in relation to elevated CO₂ and temperature

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ABSTRACT

Feeding behavior of brown planthopper, *Nilaparvata lugens* (Stål) populations collected from different geographical regions Ludhiana, Nalgonda and West Godavari at three generations 1, 5 and 10 fed on rice plants grown under different CO₂ and temperature levels 1) Ambient CO₂@ 380±25ppm + ambient temperature (aCO₂+aT), 2) Elevated CO₂@500±25ppm + ambient temperature (eCO₂+aT) and 3) Elevated CO₂@500±25ppm + elevated temperature (eCO₂+eT) in closed CO₂ chambers was studied. Elevated CO₂ + elevated temperature increased feeding rate of BPH nymphs while BPH adults showed declined feeding rate. BPH nymphal feeding rate increased with progressive generations while it decreased in BPH adults. Ludhiana adult BPH population showed higher honeydew excretion compared to West Godavari and Nalgonda populations. CO₂ + temperature levels at progressive generations have varying effects on adults and nymphs of three BPH populations. Biochemical composition of rice plants grown under different CO₂ levels revealed increased rate of soluble sugars, phenols and decreased rate of reducing sugars, soluble proteins, free amino acids, nitrogen, potassium, phosphorous in elevated CO₂ + elevated temperature levels compared to ambient conditions. Increased feeding rate of BPH under elevated CO₂ levels may be to compensate changes in host plant quality *i.e.*, high soluble sugars and low nitrogen.

Keywords: Elevated CO₂ and temperature, honeydew excretion, *Nilaparvata lugens*, feeding behavior, Brown planthopper populations.

The current atmospheric CO₂ concentration is at an average of approximately 421.37 parts per million (ppm). According to Prather *et al.*, (2001), CO₂ concentration is predicted to rise to 550 µl l⁻¹ by 2050. Rice (*Oryza sativa* L.) is one of the most important staple food crops in Asia and the world. The brown planthopper (BPH), *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) is one of the most serious insect pests of rice and has become problematic over the past few years (Vailla *et al.*, 2017) which 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 such as rice grassy stunt and rice ragged stunt (JhansiLakshmi *et al.*, 2019). It causes yield losses as high as 60% under epidemic conditions. In India, during *kharif*, 2017, several rice fields were damaged due to BPH attack. Rising temperatures and humidity were also favourable for BPH outbreaks.

Doubling of air CO₂ concentration results in an increase

of vegetative growth of rice plants and faster biomass accumulation (Raj *et al.*, 2016). Elevated CO₂ treatment results in lower nitrogen, protein and total amino acid content and increased carbohydrate concentration in the C3 plants like rice due to accumulation of non-structural carbohydrates compared to ambient CO₂ treatment. Changes in N and carbohydrate levels correlate with the performance of insects, altering their fecundity, population size, food consumption and development time and increased Carbon to Nitrogen ratio results in negative impacts on phloem feeding insects (Stiling and Cornelissen 2007). To meet the amino acid requirement, phloem feeders increase ingestion of assimilates from the phloem, leading to an increase in crop damage (Sun *et al.*, 2009). Temperature directly affects the insects, while CO₂ affects them through host plants. Temperature influences insect behaviour, distribution, development, survival, and reproduction. Rise of CO₂ and temperature directly affects the food grain production and

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indirectly affects through its effect on crop pests. Under elevated CO₂ (570-700 ppm) and elevated temperature (3°C higher) BPH had shorter nymphal duration, lower female longevity and higher fecundity (36.1%) without effecting honeydew excretion of adults (Shi *et al.*, 2014). The information available on interactive effects of elevated CO₂ and temperature on the biology of different BPH populations collected from different ecosystems is scanty. In this study, effect of different levels of CO₂ and temperature on feeding of three complete generations of three BPH populations reared on rice plants in three CO₂×temperature combinations, along with biochemical changes in the rice plant were observed.

MATERIALS AND METHODS

Insect populations

BPH populations were collected from three different regions of the country *viz.*, Ludhiana (Punjab state-North West India) with hot semi-arid climate where rice crop is grown only during May to September (Wet season); West Godavari District (Andhra Pradesh state) with hot sub-humid to semi-arid climate and Nalgonda district (Telangana state- Deccan Plateau) with hot semi-arid climate in South India where rice is grown in two seasons (Dry and Wet). From Ludhiana, BPH populations were collected from Shergarh, Chuharpur, Machhiwara, GarhiTarkhana, Ramgarh and Samrala; from West Godavari district, the BPH populations were collected from Tanuku, Penumantra, Iragavaram, Poduru and Achanta; from Nalgonda district, the BPH populations were collected from Tipparthi, Peddavoora, Nidamanur, Tripuraram, Miryalaguda and Huzurnagar. The populations were separately reared on young rice seedlings (cvTN1) using modified Japanese method (Sunil *et al.*, 2018) in flexi cages to avoid mating and intermixing of the three populations in the CO₂ chambers at ICAR-Indian Institute of Rice Research, Hyderabad, India.

CO₂ chambers

A specially designed closed climate controlled chamber was constructed at ICAR-Indian Institute of Rice Research, Hyderabad (Latitude-17°10' N, Longitude-78°E, Altitude -542m) with a total dimension of 10'x8'x10'. It had three chambers each of 2.5'x 8'. The chambers were maintained at three levels of CO₂ concentration and temperature combinations continuously as given below

1. Ambient CO₂@ 380±25ppm + ambient temperature (aCO₂+aT),
2. Elevated CO₂@500±25ppm + ambient temperature (eCO₂+aT) and
3. Elevated CO₂@500±25ppm + elevated temperature (eCO₂+eT).

The aforesaid climate variables were maintained throughout the study through fully automatic control and monitoring system with CO₂ sensors, PLC and SCADA programme for PC within the chambers in an anteroom. The CO₂ levels, temperature and humidity were recorded continuously during the experiment. A temperature of 26-30°C and relative humidity of 70-80% was

recorded in ambient temperature chambers and 29-33°C and relative humidity of 60-70% was recorded in elevated temperature chambers. The BPH populations were reared for 10 generations in the CO₂ chambers and the feeding studies were conducted in 1st, 5th and 10th generations. The susceptible rice variety TN1 was grown for 30 days in CO₂ chambers and used for honeydew excretion test. The amount of honeydew excreted by the adults and nymphs of BPH on rice plants exposed to different CO₂ and temperature levels in 1, 5 and 10 generations was measured by following methodology described by Nanthakumar *et al.*, (2012). Whatman No.1 filter paper was dipped in bromocresol green solution in ethanol and allowed to dry for one hour and dipped again till the filter paper turned yellowish orange. The treated paper was then placed on the wooden plank with a central hole kept at the base of 30-days old plant and a single stem was inserted into the hole of the plastic cup placed over the filter paper. Five 1day old brachypterous female adults pre-starved for 1 hour were released into the plastic cup and the hole was closed with cotton and the experiment was repeated with 3rd instar nymphs. The BPH adults and nymphs were allowed to feed for 24 hours on the rice stem. The honeydew droplets excreted by the BPH when come in contact with bromocresol green turn into blue spots. The area of blue spots on filter paper was measured by using ImageJ software and the data was analyzed by Factorial Completely Randomized Design.

Estimation of plant nutrients

TN1 rice seedlings were grown in plastic pots in CO₂ chambers for 30 days and the leaf sheaths were sampled after 30 days and samples were dried at 32°C in a hot-air oven for 24-48 hours and powdered using pestle and mortar. The powdered samples were sieved through a 100 mesh screen and stored in the sealed containers at 4°C, for estimation of biochemical constituents. The total soluble proteins, soluble sugars, reducing sugars and total free amino acid content in the samples were estimated by the standard procedures suggested by Bradford (1976). Nitrogen, potassium and phosphorous were estimated by using micro Kjeldahl distillation method (Yoshida *et al.*, 1976).

Statistical analysis

The effect of CO₂ levels, generations and populations on honeydew excretion was statistically analyzed by three 3³ factorial ANOVA.

RESULTS AND DISCUSSION

Honeydew excretion at different CO₂ levels

Honeydew excretion (feeding rate) of brown planthopper adults was highest at elevated CO₂ levels with increasing temperature (eCO₂+eT) (188.8 mm²) compared to that of eCO₂+aT (138.6 mm²) and aCO₂+aT (123.4 mm²). Brown planthopper nymphs excreted highest honeydew at elevated CO₂ levels with increasing temperature (eCO₂+eT) (57.4 mm²) compared to that of eCO₂+aT (47.8 mm²) and aCO₂+aT (24.7 mm²). Brown planthopper adults excreted more honeydew compared to nymphs (Table 1).

Table 1: Honeydew excretion (mm²) of female adults and 3rd instar nymphs of BPH populations, at CO₂ levels and progressive generations

Populations/CO ₂ levels/ generations	Honeydew excretion (mm ²) (Mean ± SE)	
	Adults	3 rd instar nymphs
BPH Populations		
West Godavari BPH	140.9±14.0 ^b	44.9±6.2
Ludhiana BPH	177.9±19.4 ^a	38.6±4.5
Nalgonda BPH	131.9±15.0 ^b	46.3±6.2
S.Em (±)	8.84	3.42
C.V. (%)	21.63	29.0
CD (0.05)	17.73	NS
CO ₂ levels		
eCO ₂ +aT	138.6±17.1 ^b	47.8±5.0 ^b
eCO ₂ +eT	188.8±14.4 ^a	57.4±6.9 ^a
aCO ₂ +aT	123.4±16.0 ^b	24.7±1.9 ^c
S.Em (±)	8.84	3.42
C.V. (%)	21.63	29.0
CD (0.05)	17.73	6.85
Generations		
1	237.3±10.9 ^a	24.5±1.7 ^c
5	101.5±14.0 ^b	43.0±3.6 ^b
10	112.0±9.4 ^b	62.4±7.4 ^a
S.Em (±)	8.84	3.42
C.V. (%)	21.63	29.0
CD (0.05)	17.73	6.85

eCO₂+aT- elevated CO₂ & ambient temperature; eCO₂+eT- elevated CO₂ & elevated temperature; aCO₂+aT- ambient CO₂ & ambient temperature;

Means in a column followed by same letter are not significantly different from each other

Honeydew excretion of different BPH populations

Among the BPH populations, adult honeydew excretion was more in Ludhiana BPH population (177.9 mm²) compared to that of West Godavari (140.9 mm²) and Nalgonda BPH populations (131.9 mm²). In 3rd instar nymphs, honeydew excretion was highest in Nalgonda BPH population (46.3 mm²) compared to West Godavari (44.9 mm²) and Ludhiana (38.6 mm²) brown planthopper populations but there was no significant difference in the honeydew excretion in these three populations (Table 1).

Honeydew excretion in different generations

The adult honeydew excretion decreased with advanced generations whereas in 3rd instar nymphs, the honeydew excretion was increased with the increasing generations (Table 1). At all the CO₂ levels, the honeydew excretion of brown planthopper adults was highest in the 1st generation (237.4 mm²) and it decreased in the 5th generation (101.5 mm²) and again increased in 10th generation

(112.0 mm²). In brown planthopper nymphs, the honeydew excretion at all CO₂ levels increased with increasing generations viz., 24.5 mm² in 1st generation; 43.0 mm² in 5th generation and 62.3 mm² in 10th generation (Table 1).

Honeydew excretion of adults decreased at all CO₂ levels with increase in number of (progressive) generations but in 3rd instar nymphs increased rate of honeydew excretion was noticed at all CO₂ levels with advanced generations (Table 2). The interaction of BPH populations and CO₂ levels revealed higher feeding rate of adults and nymphs at eCO₂+eT followed by eCO₂+aT. However, lower honeydew excretion was noticed in aCO₂+aT level. The feeding rate of BPH populations was significantly reduced in adults in advanced generations but the feeding rate increased in 3rd instar nymphs (Table 3).

The three BPH populations exhibited varying correlations with different generations and CO₂ levels. In West Godavari BPH population, adult honeydew excretion was negatively correlated with generations and positively correlated with CO₂ levels (r=-0.54 and 0.99 respectively). In 3rd instar nymphs, honeydew excretion was positively correlated with generations (r= 0.64) and CO₂ levels (r= 0.99). In Ludhiana BPH population, adult and 3rd instar nymphal honeydew excretion was positively correlated with CO₂ levels (r=0.96 and 0.99 respectively) and negatively correlated with generations (r=-0.60 and -0.46 respectively). In Nalgonda BPH population, adult honeydew excretion was significantly and negatively correlated with generations (r=-0.69) but positive correlation was there with CO₂ levels (r=0.314). In 3rd instar nymphs, honeydew excretion was positively correlated with generations (r= 0.51) and CO₂ levels (r= 0.89) (Table 6).

The interaction of BPH populations at different CO₂ levels with increasing generations revealed that honeydew excretion of adults was significantly decreased with increasing generations and elevated CO₂ levels. On the other hand, honeydew excretion of 3rd instar nymphs increased at elevated CO₂ levels compared to that of ambient CO₂ level (aCO₂+aT) (Table 3).

Biochemical composition of plants grown at different CO₂ levels

30 days old TN1 rice plants grown under different CO₂ levels showed increased rate of soluble sugars (10.53mg/g), total phenols (0.07 mg/g) and decreased rate of reducing sugars (1.19 mg/g), total soluble proteins (1.19 mg/g), total free amino acids (42.73 mg/g), nitrogen (1.08%), phosphorous (0.15%) and potassium (1.19%) in elevated CO₂ and temperature conditions (eCO₂+eT) compared to those grown in elevated CO₂ and ambient temperature (eCO₂+aT) (8.92 mg/g, 0.06 mg/g, 1.50 mg/g, 1.46 mg/g, 81.56 mg/g, 2.11%, 0.29% and 1.31% respectively) and in ambient CO₂ and ambient temperature (aCO₂+aT) (8.20 mg/g, 0.06 mg/g, 2.16 mg/g, 3.03 mg/g, 121.11 mg/g, 2.33%, 0.22% and 1.38% respectively) (Table 4).

Correlation between CO₂ levels and biochemical components indicates that reducing sugars (r=-0.987), soluble proteins (r=-.775) and free amino acids (r=-0.504) were negatively correlated with increased CO₂ levels whereas total sugars (r=0.292)

Table 2: Honeydew excretion (mm²) of adults and 3rd instar nymphs of BPH populations at different CO₂ levels and progressive generations

CO ₂ levels	Honeydew excretion (mm ²) (Mean ± SE)					
	Adults			3 rd instar nymphs		
	Generations					
	1	5	10	1	5	10
eCO ₂ +aT	237.6±26.7 ^a	73.2±6.4 ^{ef}	105.1±13.6 ^d	31.5±3.6 ^{de}	41.0±6.5 ^d	70.9±9.2 ^b
eCO ₂ +eT	248.5±10.2 ^a	176.4±27.7 ^b	141.5±19.8 ^e	19.6±1.9 ^f	55.2±6.1 ^c	97.3±6.7 ^a
aCO ₂ +aT	226.0±17.4 ^a	54.8±5.4 ^f	89.4±10.5 ^e	22.3±1.5 ^{ef}	32.9±4.0 ^{de}	18.8±2.3 ^f
S.Em (±)		15.32			5.92	
C.V. (%)		21.63			29.0	
CD (0.05)		30.71			11.86	
BPH Populations	CO ₂ levels					
	eCO ₂ +aT	eCO ₂ +eT	aCO ₂ +aT	eCO ₂ +aT	eCO ₂ +eT	aCO ₂ +aT
West Godavari	149.4±26.6 ^c	180.4±19.0 ^b	93.0±19.0 ^d	48.5±10.0 ^b	61.3±13.7 ^a	24.9±2.2 ^c
Ludhiana	162.8±41.5 ^{bc}	231.8±21.1 ^a	139.1±30.1 ^c	36.0±4.7 ^c	54.9±10.6 ^{ab}	25.0±2.9 ^c
Nalgonda	103.7±12.7 ^d	154.2±28.5 ^{bc}	138.0±32.4 ^e	58.9±9.5 ^{ab}	55.9±12.8 ^{ab}	24.1±4.9 ^c
S.Em (±)		15.32			5.92	
C.V. (%)		21.63			29.0	
CD (0.05)		30.71			11.86	
BPH Populations	Generations					
	1	5	10	1	5	10
West Godavari	213.3±13.8	89.8±15.5	119.7±21.4	22.4±1.6 ^d	39.7±4.5 ^{bc}	72.7±13.8 ^a
Ludhiana	274.4±16.2	131.3±37.7	128.0±14.9	22.6±3.8 ^d	44.4±8.0 ^b	48.9±8.5 ^b
Nalgonda	224.4±20.8	83.3±9.0	88.2±8.7	28.4±3.0 ^{cd}	45.0±6.4 ^b	65.5±15.3 ^a
S.Em (±)		15.32			5.92	
C.V. (%)		21.63			29.0	
CD (0.05)		NS			11.86	

eCO₂+aT- elevated CO₂ & ambient temperature; eCO₂+eT- elevated CO₂ & elevated temperature; aCO₂+aT- ambient CO₂ & ambient temperature; Means in a column followed by same letter are not significantly different from each other

Table 3: Honeydew excretion (mm²) of female adults and 3rd instar nymphs of brown planthopper at different CO₂ levels in progressive generations

BPH Populations & CO ₂ levels	Honeydew excretion (mm ²) (Mean ± SE)					
	Generations					
	Adults			3 rd instar nymphs		
	1	5	10	1	5	10
West Godavari BPH- eCO ₂ +aT	244.9±7.9 ^b	74.9±12.9 ^{hi}	128.3±26.8 ^{def}	26.3±3.1 ^{ij}	32.0±3.1 ^{hij}	87.3±6.5 ^{bc}
West Godavari - eCO ₂ +eT	228.5±21.8 ^b	147.0±8.2 ^{cd}	165.7±44.5 ^e	18.4±1.1 ^{ij}	56.2±4.8 ^{efg}	109.3±11.3 ^a
West Godavari - aCO ₂ +aT	166.3±3.0 ^c	47.6±3.0 ⁱ	65.1±14.2 ^{ghi}	22.4±1.8 ^{ij}	31.0±0.9 ^{hij}	21.3±4.8 ^{ij}
Ludhiana BPH- eCO ₂ +aT	323.0±18.7 ^a	59.9±4.1 ^{hi}	105.4±23.7 ^{defgh}	32.8±8.7 ^{hij}	27.9±5.7 ^{hij}	47.3±7.4 ^{fgh}
Ludhiana- eCO ₂ +eT	252.8±16.9 ^b	277.5±29.3 ^{ab}	165.1±26.5 ^{defg}	13.8±0.9 ^j	73.3±7.1 ^{cde}	77.5±4.8 ^{cd}
Ludhiana- aCO ₂ +aT	247.4±27.1 ^b	56.5±12.4 ^{hi}	113.4±19.0 ^{defg}	21.2±1.5 ^{ij}	31.9±7.4 ^{hij}	21.9±2.4 ^{ij}
Nalgonda BPH- eCO ₂ +aT	144.7±11.6 ^{cd}	84.9±12.5 ^{fghi}	81.4±19.4 ^{fghi}	35.5±6.8 ^{hi}	63.1±9.6 ^{def}	78.2±21.7 ^{cd}
Nalgonda- eCO ₂ +eT	264.2±12.3 ^b	104.7±12.8 ^{def}	93.6±18.1 ^{efghi}	26.5±1.2 ^{ij}	36.2±4.9 ^{ghi}	105.1±9.4 ^{ab}
Nalgonda- aCO ₂ +aT	264.2±12.3 ^b	60.3±12.1 ^{ghi}	89.5±12.9 ^{fghi}	23.0±4.6 ^{ij}	35.8±11.2 ^{ghi}	13.2±2.9 ^j
S.Em (±)		26.53			10.25	
C.V. (%)		21.63			29.0	
CD (0.05)		53.20			20.55	

*Significant at 0.05; eCO₂+aT- elevated CO₂ & ambient temperature; eCO₂+eT- elevated CO₂ & elevated temperature; aCO₂+aT- ambient CO₂ & ambient temperature. Means in a column followed by same letter are not significantly different from each other

Table 4: Biochemical composition of 30 days old TN1 plants grown in different CO₂ levels

CO ₂ level	Biochemical parameters							
	Soluble sugars (mg/g)	Reducing sugars (mg/g)	Phenols (mg/g)	Soluble proteins (mg/g)	Free amino acids (mg/g)	Nitrogen (%)	Phosphorous (%)	Potassium (%)
eCO ₂ +aT	8.92±0.25 ^b	1.50±0.04 ^b	0.06±0.0 ^b	1.46±0.02 ^b	81.56±0.50 ^b	2.11±0.05 ^b	0.29±0.02 ^a	1.31±0.02 ^a
eCO ₂ +eT	10.53±0.03 ^a	1.19±0.02 ^c	0.07±0.0 ^a	1.19±0.02 ^b	42.73±0.59 ^c	1.08±0.02 ^c	0.15±0.02 ^b	1.19±0.04 ^b
aCO ₂ +aT	8.20±0.12 ^c	2.16±0.08 ^a	0.04±0.0 ^c	3.03±0.19 ^a	121.11±1.09 ^a	2.33±0.02 ^a	0.22±0.03 ^{ab}	1.38±0.03 ^a
S.Em	0.2	0.03	0.01	0.15	1.1	0.02	0.032	0.04
CD 0.05	0.6	0.08	0.01	0.40	2.70	0.06	0.08	0.1

Table 5: Correlation between CO₂ levels and biochemical content of 30 days old rice plant

Biochemical component	Correlation Coefficient (r)
Soluble sugars	0.292 ^{NS}
Reducing sugars	-0.987* ^{0.1}
Soluble Proteins	-0.775 ^{NS}
Free amino acids	-0.504 ^{NS}
Total Phenols	0.451 ^{NS}
Nitrogen	-0.125 ^{NS}
Phosphorous	-0.456 ^{NS}
Potassium	-0.302 ^{NS}

Significant at $p < 0.1$

lower honeydew excretion. In the brown planthopper nymphs also, reduced feeding and honeydew excretion was noticed and negative correlation was observed with increased levels of reducing sugars ($r=-0.999$), proteins ($r=-0.98$), free amino acids ($r=-0.97$), Nitrogen ($r=-0.82$), Phosphorous ($r=-0.28$) and potassium ($r=-0.92$) (Table 6).

In our study, it was observed that 30 days old rice plants grown under elevated CO₂ levels had higher sugars, higher phenols, lower reducing sugars, proteins, free amino acids, nitrogen, phosphorus and potassium content. Nitrogen limiting rice plants grown under elevated CO₂ accumulates more carbohydrates, produce more phenolic based compounds and low total soluble proteins, total amino acids (Rashid *et al.*, 2017). Lower concentrations of N,

Table 6: Correlation between honeydew and CO₂ levels, generations and biochemical components

Biochemical component	Honeydew excretion of Correlation Coefficient (r) between biochemical components and honeydew excretion					
	WG Nymphs	WG adults	Nalgonda Nymphs	Nalgonda adults	Ludhiana nymphs	Ludhiana adults
CO ₂ level	0.99* ^{0.1}	0.99* ^{0.1}	0.89 ^{NS}	0.31 ^{NS}	0.99 ^{NS}	0.96 ^{NS}
Generations	0.64* ^{0.1}	-0.54* ^{0.1}	0.51 ^{NS}	-0.69* ^{0.1}	-0.46 ^{NS}	-0.60* ^{0.1}
Sugars	-0.51 ^{NS}	0.47 ^{NS}	-0.02 ^{NS}	0.18 ^{NS}	-0.18 ^{NS}	-0.27 ^{NS}
Reducing sugars	-0.28 ^{NS}	-0.86 ^{NS}	-0.49 ^{NS}	0.78 ^{NS}	-0.65 ^{NS}	-0.37 ^{NS}
Proteins	0.04 ^{NS}	-0.81 ^{NS}	-0.36 ^{NS}	0.33 ^{NS}	-0.40 ^{NS}	-0.02 ^{NS}
Free amino acids	0.36 ^{NS}	-0.64 ^{NS}	-0.16 ^{NS}	0.01 ^{NS}	-0.05 ^{NS}	0.27 ^{NS}
Phenols	-0.24 ^{NS}	0.64 ^{NS}	0.04 ^{NS}	-0.05 ^{NS}	-0.01 ^{NS}	-0.19 ^{NS}
Nitrogen	0.59 ^{NS}	-0.38 ^{NS}	0.11 ^{NS}	-0.39 ^{NS}	0.26 ^{NS}	0.54 ^{NS}
Phosphorous	0.42 ^{NS}	0.05 ^{NS}	0.38 ^{NS}	-0.75 ^{NS}	0.45 ^{NS}	0.73 ^{NS}
Potassium	0.27 ^{NS}	-0.43 ^{NS}	-0.26 ^{NS}	-0.22 ^{NS}	-0.04 ^{NS}	0.39 ^{NS}

• Significant at $p < 0.1$

and total phenols (0.451) were positively correlated with increased CO₂ levels. Nitrogen ($r=-0.125$), Potassium ($r=-0.301$) and Phosphorous content ($r=-0.456$) contents decreased with increasing CO₂ levels (Table 5).

Correlation between honeydew excretion and biochemical composition of rice plants

The honeydew excretion of brown planthopper adults and nymphs increased when the sugar levels ($r=0.99$ and $r=0.89$ respectively) and phenols ($r=0.88$ and $r=0.99$ respectively) in the rice plants were more. The increased levels of reducing sugars ($r=-0.87$), proteins ($r=-0.77$), free amino acids ($r=-0.95$), Nitrogen ($r=-0.99$), Phosphorous ($r=-0.73$) and potassium ($r=-0.9$) have negative impact on the feeding of brown planthopper adults and resulted in

P and K were observed in rice plants grown at elevated CO₂ which may be due to dilution of N due to extra carbohydrates (Seneweera, 2011). In our present study, it was observed that when BPH was continuously exposed to different levels of CO₂, the feeding rate of nymphs was increased than that of adults. Elevated CO₂ levels with increasing temperature had accelerated the feeding rate of brown planthopper nymphs and adults than ambient CO₂ and temperature.

Under elevated CO₂ levels, carbon to nitrogen ratio is increased in the phloem sap resulting in diminished nutritive value of host plants and it negatively affects the phloem feeding insects due to limitations in nitrogen supply (Stiling and Cornelissen 2007). Therefore, in order to meet the amino acid requirement, phloem feeders increase ingestion of assimilates from the phloem, leading

to an increase in crop damage (Sun *et al.*, 2009). Changes in N and carbohydrate levels correlate with the performance of insects, altering their fecundity, population size, food consumption and development time. Shi *et al.*, (2014) also observed increased sap sucking by BPH under elevated CO₂ conditions.

Among the BPH populations, adult honeydew excretion was more in Ludhiana BPH population compared to that of West Godavari and Nalgonda BPH populations. In 3rd instar nymphs, honeydew excretion was highest in Nalgonda BPH population compared to West Godavari and Ludhiana brown planthopper populations. Honeydew excretion of adults decreased at all CO₂ levels with increase in number of (progressive) generations but in West Godavari BPH, adult feeding rate was not affected. However, 3rd instar nymphs positively responded to elevated CO₂ levels over generations but ambient CO₂ had not influenced the feeding rate of nymphs in all BPH populations over successive generations. Srinivasa Rao *et al.*, (2014) observed that *Spodoptera litura* larvae fed with peanut foliage exposed to eCO₂ exhibited increased consumption by 29-35% over the four generations. The average temperature range prevailing in Ludhiana is wider with minimum temperature of 9.5°C and maximum of 35.3°C while the temperature range in West Godavari and Nalgonda region is narrower with minimum temperature of 25.3°C and a maximum of 31.8°C over years. Ludhiana population responded positively to elevated CO₂ levels with higher feeding rate. The results of the present study indicated that populations brought from areas with a greater temperature range *i.e.* lower/higher temperatures are positively affected. Flynn *et al.*, (2006) reported that the responses of aphid populations to elevated CO₂ were highly species-specific. Neumeister, 2010 reported that the optimum temperature for surviving and reproduction varies between insect species and even different populations of each species.

CONCLUSIONS

The present study revealed significant effects of elevated CO₂ + elevated temperature on biochemical composition of rice plants *viz.*, soluble sugars, free amino acids, soluble proteins and nitrogen in rice plants. Feeding measured as honeydew excretion of brown planthopper nymphs was high under elevated CO₂ with increased temperature over successive generations. Ludhiana adult brown planthopper population showed higher feeding rate under elevated CO₂ and temperature conditions compared to other two BPH populations.

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