



Different adaptability of the brown planthopper, *Nilaparvata lugens* (Stål), to gradual and abrupt increases in atmospheric CO₂

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Abstract

Increasing atmospheric CO₂ concentrations affect the performances of herbivores. Most previous studies have focused on the effects of abrupt increases in CO₂ concentration on herbivore performance, but knowledge about the response of herbivores to gradual increases in CO₂ is lacking. We tested the hypothesis that herbivores will show different responses to abrupt and gradual CO₂ increases. We measured the performance of the brown planthopper (BPH) (*Nilaparvata lugens* (Stål)) reared on rice for 15 successive generations under three CO₂ levels: ambient CO₂ (375 µl/L), a gradual increase in CO₂ (25 µl/L increase per generation, 390–750 µl/L), and an abrupt increase in CO₂ (750 µl/L). During the first generation, the female and male longevities were affected by both the gradual and abrupt increases in CO₂, and the fecundity and net reproductive rate (R_0) of the BPH in the abruptly increased CO₂ treatment were significantly lower than those in the other two treatments; there were no significant differences in the intrinsic rate of increase (r) and the finite rate of increase (λ) among the three CO₂ treatments. After 14 generations, female longevity was significantly prolonged in treatments with both gradual and abrupt CO₂ increases. The fecundity of the BPHs reared in the gradual CO₂ treatment was significantly higher than that in the other two CO₂ treatments. According to the population parameters (r , λ , and R_0) and population projection, under a gradual increase in CO₂, the BPH population size was higher than that under an abrupt CO₂ increase. We concluded that the BPH abundance will increase under a gradual CO₂ increase and consequently result in an increase in rice yield loss.

Keywords *Nilaparvata lugens* · Elevated CO₂ · Gradual CO₂ increase · Abrupt CO₂ increase · Age-stage, two-sex life table · Multiple generations

Key messages

- Herbivores will show different responses to abrupt and gradual increases in CO₂ concentration. However, little is known about the impacts of gradually increasing CO₂ on herbivores.
- We determined the short-term and long-term effects of gradual and abrupt increases in CO₂ concentrations on the developmental time, fecundity, and population growth of the BPH.
- Our results show that the effect of elevated CO₂ on BPH population growth will decrease over multiple generations, and gradually increased CO₂ promoted BPH adaptation to CO₂-enriched conditions.
- Knowledge of herbivore responses to gradually and abruptly increased CO₂ improves our ability to predict the population dynamics of pest in future CO₂-enriched conditions.

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Introduction

The mean global atmospheric carbon dioxide (CO₂) concentration is continuing to increase primarily due to human activities; the ambient CO₂ concentration has increased to over 400 µl/L today from 280 µl/L at the beginning of the industrial revolution and is expected to reach 750 µl/L by 2100 (IPCC 2014). It has been suggested that increased CO₂ concentrations change the morphological, physiological, and biochemical traits of plants, and these changes are expected to alter herbivore performance (Guo et al. 2013; Landosky and Karowe 2014; Dai et al. 2018; Sun et al. 2018; Yan et al. 2020). The quality and quantity of food supply can directly affect the performance of all organisms (Bestete et al. 2016; Sun et al. 2019). After analyzing 122 studies, Robinson et al. (2012) concluded that elevated CO₂ increased the relative consumption rate of arthropods (+14%) but reduced the relative growth rate (−4.5%) as well as the pupal and adult weights (−5.5%). Elevated CO₂ also decreased fecundity in Coleoptera, Lepidoptera, and Orthoptera (−13%, −13%, and −34%, respectively) and increased fecundity in Homoptera (+8.5%). Survival and abundance also significantly increased in Homoptera (+16% and +22%, respectively) but decreased in Lepidoptera (−7% and −65%, respectively).

Earlier studies have focused mainly on the short-term responses of herbivores to CO₂ enrichment (Ferreira et al. 2013; Hentley et al. 2014; Jiang et al. 2018). Moreover, few of these experiments have spanned more than three generations, and the long-term effects of elevated CO₂ levels on herbivorous populations remain unknown. As Carroll et al. (2007) pointed out, ecologically significant evolutionary change occurring over tens of generations or fewer is widely documented in nature.

Most studies have focused on differences in herbivore responses to ambient CO₂ or abrupt increases in CO₂ concentrations (Liu et al. 2017; Qian et al. 2018). Although abrupt CO₂ increases did occur during deglaciation events (Marcott et al. 2014), the global atmospheric CO₂ concentration is generally experiencing a gradual rather than an abrupt increase. Herbivore performances are affected by CO₂ concentration (Fu et al. 2016), but whether an abrupt increase in CO₂ causes responses similar to those driven by the gradual increase observed since the onset of the industrial revolution is unknown. Moreover, the ecological effects of elevated CO₂ on host plants may further indirectly influence the responses of herbivores (Shi et al. 2019). Klironomos et al. (2005) pointed out that researchers might overestimate the community response to elevated CO₂, and they showed that the abrupt increase in CO₂ resulted in a significant change in mycorrhizal diversity and functioning in the first generation but little change in subsequent generations. Therefore, the effects of both abrupt and gradual increases in CO₂ deserve further investigation.

In this study, we used a sap feeding fulgoroid, the brown planthopper (BPH) *Nilaparvata lugens* (Stål), as a model. The BPH, which causes substantial crop yield losses, is a primary phloem-sucking pest in rice (Zhang et al. 2018). Although several studies have investigated BPH responses to increasing CO₂ concentrations (Wen et al. 2019; Wang et al. 2020), a comparative study of BPH responses to gradual versus abrupt increases in CO₂ is still lacking. We hypothesized that the responses of the BPH to a gradual and an abrupt increase in CO₂ will be different and that the effect of elevated CO₂ on BPH population growth will decrease over multiple generations. In this study, BPHs were subjected to ambient, gradual, or abrupt CO₂ concentration treatments over fifteen generations. To obtain a comprehensive understanding, we collected data on the BPH developmental time, growth rate, and fecundity and analyzed these data by using an age-stage, two-sex life table. Furthermore, the population growth rate was projected for 60 days. This information will contribute novel insight into the effects of gradual and abrupt increases in CO₂ on pest populations.

Materials and methods

Experimental design and brown planthopper rearing

The BPH colony was originally established in August 2012 and has been maintained since then in the Insect Ecology Laboratory, Huazhong Agricultural of University, Wuhan, Hubei Province, China. The BPHs were reared on susceptible rice (Taichung Native 1 (TN1)) and kept in a CO₂ chamber with a closed system (PRX-450D-30; Haishu Safe Apparatus, Ningbo, China) at 28 ± 0.5 °C, 70 ± 5% relative humidity (RH), and a 16:8 (L:D) h photoperiod. Three CO₂ concentration levels were applied: (1) a constant atmospheric CO₂ level of 375 µl/L ('ambient'); (2) gradually increasing CO₂ levels (from 390 µl/L to 750 µl/L), with a 25 µl/L increase at the beginning of each generation ('gradual'); and (3) an abrupt increase in ambient CO₂ to 750 µl/L ('abrupt'). Four CO₂ growth chambers were used to establish the ambient, gradual, and abrupt CO₂ treatments; two growth chambers were needed for the treatment with gradually increasing CO₂ levels due to the overlapping BPH generation traits. The infrared automatic control system in the chambers was used to monitor and adjust the CO₂ concentrations every 20 min. The CO₂ concentrations were also observed and recorded at 18:30 daily, and no significant variations were found. During the experiment, the four growth chambers were swapped every month, and the locations of the subjects (BPHs) were changed every day to equalize the possible biases due to the chamber-specific growth conditions. Chen et al. (2005) described the detailed automatic

control system and the specifications for the type of growth chamber used in this study. The TN1 rice was grown in the respective CO₂ treatments using Kimura B nutrient solution (Liang et al. 2006).

Eighty newborn BPH nymphs were selected randomly for each CO₂ treatment. The newborn nymphs were transferred individually to a three-leaf rice seedling in a glass tube (height: 18 cm, diameter: 1.8 cm) covered with nylon net to prevent escape. The developmental time and survival of the individuals were recorded daily. The rice and nutrient solution were replaced as necessary (approximately every 2–3 days). The mass rearing colonies were cultured in plots (diameter: 12 cm, height: 15 cm), with 15 plots per CO₂ treatment. After the adults emerged, they were sexed and paired in glass cages (height: 45 cm, diameter: 28 cm) and supplied with five seedlings of three-leaf rice. If the sex ratio of the BPH population was not 1:1 or an individual died early during the study, the individual was replaced with another BPH from the mass rearing colony reared in the same CO₂ treatment. The pairs were moved to fresh rice after 3 days. The newborn nymphs were counted daily and then removed and placed in the mass rearing colony to establish the next generation. Only hatched eggs were included in the calculation of age-specific fecundity (Mou et al. 2015). The longevity, survivorship, and reproduction of the adults were recorded daily until the death of all the individuals. The BPHs were continuously exposed to three CO₂ levels over 15 generations.

Life table data analysis

The raw life table data for all individuals from the egg stage through the adult stage were analyzed based on the age-stage, two-sex life table theory (Chi and Liu 1985) using the method described in detail by Chi (1988). We used the raw life table data to calculate the age-stage-specific survival rate (*s_{xj}*) (where *x*=age and *j*=stage), determining that a newborn individual will survive to age *x* and stage *j*, the age-specific survival rate (*l_x*), the age-stage fecundity (*f_{xj}*), the age-specific fecundity (*m_x*), the age-stage life expectancy (*e_{xj}*), the total pre-oviposition period (TPOP) (from birth to the first oviposition), and the adult pre-oviposition period (APOP) (from adult emergence to the first oviposition). According to the age-stage, two-sex life table (Chi and Liu 1985), *l_x* is calculated as:

$$l_x = \sum_{j=1}^{\beta} s_{xj} \tag{1}$$

where *β* is the number of stages. In addition, *m_x* is calculated as:

$$m_x = \frac{\sum_{j=1}^{\beta} s_{xj} f_{xj}}{\sum_{j=1}^{\beta} s_{xj}} \tag{2}$$

The population parameters, including the net reproductive rate (*R₀*), the intrinsic rate of increase (*r*), the finite rate of increase (*λ*), and the mean generation time (*T*), were calculated accordingly. *R₀* is calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{3}$$

The intrinsic rate of increase (*r*) was estimated using the iterative bisection method from the Euler–Lotka formula with age indexed from zero (Goodman 1982) as:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{4}$$

λ is calculated as *λ* = *e^r*. The mean generation time (*T*) is calculated as:

$$T = \frac{\ln R_0}{r} \tag{5}$$

The age-stage life expectancy (*e_{xj}*) is defined as the total time that an individual of age *x* and stage *j* is expected to live and is calculated according to the procedures described in Chi and Su (2006):

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{\beta} s'_{iy} \tag{6}$$

where *s'_{iy}* is the probability that an individual of age *x* and stage *j* will survive to age *i* and stage *y* and is calculated by assuming *s'_{xj}* = 1. The life table data were analyzed using the computer program TWSEX-MSChart (Chi 2019a), available at <http://140.120.197.173/Ecology/Download/TWSEX-X-MSChart.rar>. The variances and standard errors of the developmental time, adult longevity, fecundity, and population parameters were calculated using a bootstrap method with 100,000 resamplings (Akköprü et al. 2015). A paired bootstrap test was used to compare differences among the three CO₂ treatments at the 5% significance level. The bootstrap method and paired bootstrap test are embedded in the TWSEX-MSChart computer program. We fitted the age-specific survival curve (*l_x*) of different treatments to the cumulative Weibull distribution (Johnson et al. 1970; Pinder et al. 1978) using the following formula:

$$s_x = \exp \left[-\left(\frac{x}{b} \right)^c \right] \tag{7}$$

where *b* is the scale parameter, *c* is the shape parameter, and *s_x* is the expected survival rate to age *x*.

Population growth rate projection

The age-stage, two-sex life table data for the BPHs were used to project the population growth rates for 60 days using the TIMING-MSChart (Chi 2019b) computer program, which is available for download at the same website as TWSEX-MSChart. The method was described in detail by Chi (1990) and Akca et al. (2015). For comparative purposes, the initial population sizes were set as 10 newborn eggs in all CO₂ treatments.

Results

BPH developmental time, survival, adult longevity, and fecundity

The developmental times differed with the elevated CO₂ levels. The developmental time of the egg stage in the abrupt CO₂ treatment was significantly longer than that in the other two CO₂ treatments (Table 1) over the course of the

experiment. The results indicated the absence of short-term effects of elevated CO₂ (gradual and abrupt changes in CO₂) on nymphal development time, with the exception of the first instar. Although the developmental times in both the fourth and fifth instars were significantly decreased under gradual CO₂ enrichment compared to those under the ambient CO₂ treatment during the last (15th) generation, no significant differences were found in the second to fifth instars between the first and last generations. However, significant differences were observed in the total pre-adult duration. The shortest pre-adult duration (17.20 days) was observed in the treatment with a gradual increase in CO₂. No significant differences in TPOP and APOP were observed among the three CO₂ treatments during the first generation. After 14 generations, however, the total pre-oviposition period (TPOP) of the BPHs in the treatment with a gradual CO₂ increase was significantly shorter than that in the ambient and abrupt CO₂ treatments. Additionally, both female and male adult longevity were significantly shortened by elevated CO₂ (gradual and abrupt) in the first generation. However, in the last generation, the females reared in the treatment with gradual CO₂ changes

Table 1 Mean (\pm SE) developmental time, survival, adult longevity, and fecundity of BPHs under three CO₂ treatments in generation 1 and generation 15

Parameters	CO ₂ concentration (Generation 1)			CO ₂ concentration (Generation 15)		
	Ambient	Gradual	Abrupt	Ambient	Gradual	Abrupt
Egg (day)	6.71 \pm 0.05bA (80)	6.69 \pm 0.08bA (80)	7.19 \pm 0.11aA (80)	6.25 \pm 0.06bB (80)	6.00 \pm 0.06cB (80)	6.56 \pm 0.07aB (80)
First instar (day)	3.01 \pm 0.03bA (79)	3.29 \pm 0.05aA (80)	3.00 \pm 0.03bA (78)	2.01 \pm 0.05cB (80)	2.19 \pm 0.05bB (80)	2.50 \pm 0.06aB (80)
Second instar (day)	2.04 \pm 0.04aA (79)	2.00 \pm 0.03aA (77)	2.01 \pm 0.03aA (76)	1.99 \pm 0.04aA (80)	1.94 \pm 0.03aA (80)	1.95 \pm 0.03aA (80)
Third instar (day)	2.14 \pm 0.06aA (77)	2.05 \pm 0.04aA (75)	2.04 \pm 0.05aA (71)	1.99 \pm 0.03aB (78)	1.98 \pm 0.04abA (80)	2.14 \pm 0.08aA (77)
Fourth instar (day)	2.05 \pm 0.05aB (76)	2.07 \pm 0.04aA (72)	2.01 \pm 0.06aB (69)	2.42 \pm 0.07bA (76)	2.03 \pm 0.03cA (79)	3.01 \pm 0.09aA (75)
Fifth instar (day)	3.26 \pm 0.06aA (72)	3.14 \pm 0.07aA (65)	3.18 \pm 0.06aA (67)	3.30 \pm 0.07aA (73)	3.09 \pm 0.04bA (78)	3.12 \pm 0.04bA (74)
Total pre-adult (day)	19.29 \pm 0.12abA (72)	19.41 \pm 0.14aA (65)	19.03 \pm 0.10bA (67)	17.90 \pm 0.12bB (73)	17.20 \pm 0.07cB (78)	19.24 \pm 0.12aA (74)
TPOP (day)	21.88 \pm 0.19aA (34)	22.42 \pm 0.21aA (33)	21.92 \pm 0.28aA (36)	20.49 \pm 0.19bB (37)	19.53 \pm 0.14cB (47)	21.51 \pm 0.20aB (35)
APOP (day)	2.59 \pm 0.10aA (34)	2.67 \pm 0.11aA (33)	2.64 \pm 0.24aA (36)	2.43 \pm 0.08aB (37)	2.38 \pm 0.09aB (47)	2.40 \pm 0.10aB (35)
Female longevity (day)	16.05 \pm 0.98aA (37)	13.08 \pm 0.95bB (36)	12.75 \pm 0.68bB (36)	13.71 \pm 0.85bA (38)	17.96 \pm 0.87aA (48)	15.40 \pm 0.88bA (35)
Male longevity (day)	21.51 \pm 1.16aA (35)	17.07 \pm 1.59bA (29)	17.19 \pm 1.61bA (31)	17.80 \pm 1.36aB (35)	17.17 \pm 1.4aA (30)	19.92 \pm 1.25aA (39)
Pre-adult survival rate	0.900 \pm 0.001aA (80)	0.812 \pm 0.002aB (80)	0.837 \pm 0.002aA (80)	0.912 \pm 0.001aA (80)	0.975 \pm 0.001aA (80)	0.925 \pm 0.0001aA (80)
Fecundity (eggs/female)	130.55 \pm 16.85aB (37)	149.90 \pm 18.75aB (36)	83.99 \pm 11.85bB (36)	210.18 \pm 15.85bA (38)	258.49 \pm 17.96aA (48)	204.03 \pm 16.43bA (35)

The standard errors (SE) were calculated using 100,000 bootstrap resamplings

Different lowercase letters indicate significant differences among the three CO₂ treatments within the same generation, while different uppercase letters indicate significant differences between generation 1 and 15 using a paired bootstrap test at a 5% significance level. The numbers in parentheses are the numbers of individuals at that specific stage

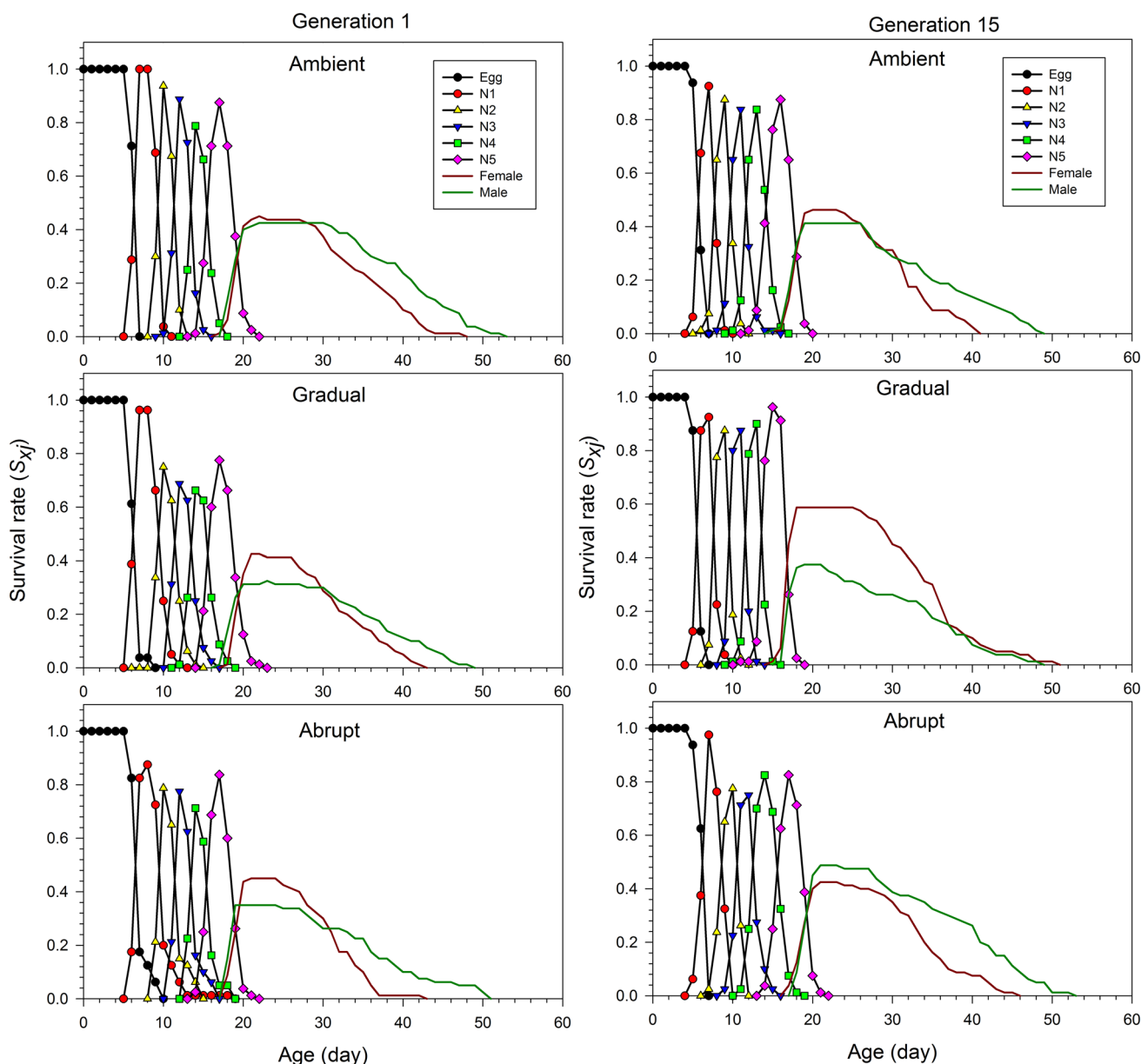


Fig. 1 Age-stage-specific survival rates (s_{xj}) of brown planthoppers reared on rice in generation 1 and generation 15 in ambient, gradual, and abrupt CO_2 treatments

survived longer than those reared in the treatment with ambient CO_2 conditions. The age-stage survival rates (s_{xj}) of the BPHs are plotted in Fig. 1. The survival rates, stage differentiation, and variable developmental times can be observed. The pre-adult survival rates and female adult longevity varied across CO_2 treatments and tended to increase in the gradual CO_2 treatment in the last generation. Moreover, the proportion of females was higher than that of males ($P=0.0427$) in the treatment with gradual CO_2 changes, while the proportion of females was not significantly different from that of males in the abrupt CO_2 treatment ($P=0.6420$). The fecundity was lowest in the abrupt CO_2 treatment group during the first

generation, while there was no difference in fecundity among the individuals in the ambient and gradual CO_2 treatments. By the end of the study, the fecundity of the BPHs reared in the gradual CO_2 treatment was significantly higher than that in the other two CO_2 treatments (Table 1). Differences in daily fecundity between the CO_2 treatments were observed in the age-specific daily fecundities (m_x) (Fig. 2); during the first generation, the peak of m_x was 5.94 eggs (at an age of 24 days), 9.17 eggs (at 23 days), and 6.55 eggs (at 23 days) for the ambient, gradual, and abrupt CO_2 groups, respectively. At the end of the experiment, the fecundity of the BPHs in

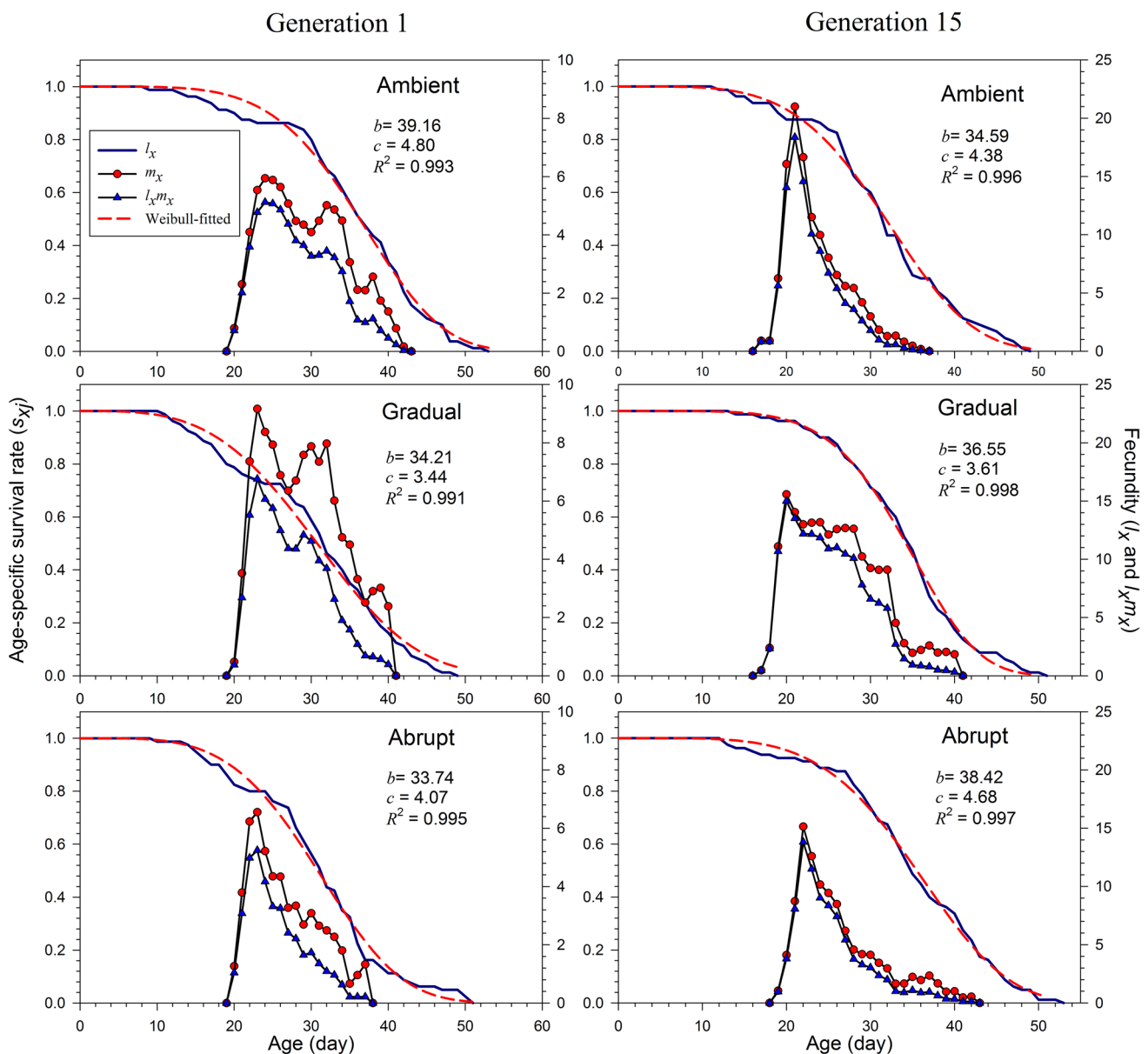


Fig. 2 Age-specific survival rate (l_x) (left y-axis), fecundity (m_x) (right y-axis), net maternity ($l_x m_x$) (right y-axis), and fitted Weibull survival rate (left y-axis) (dashed lines, with parameters b and c of

Eq. (7) and the coefficient of determination (R^2)) of brown planthoppers reared on rice in generation 1 and generation 15 in ambient, gradual, and abrupt CO₂ treatments

all the treatments was significantly higher than that in the F1 generation. In the 15th generation, although the BPHs showed a higher female age-specific daily fecundity peak in the ambient CO₂ treatment ($m_{21} = 20.99$ eggs) than in the gradual CO₂ ($m_{20} = 15.58$ eggs) and abrupt CO₂ ($m_{22} = 15.13$ eggs) treatments, the lifelong fecundity of the BPHs in the ambient CO₂ treatment was 210.18 eggs, which was significantly less than that in the gradual CO₂ treatment (258.49 eggs). All the age-specific survival rates (l_x) could be fitted well to the Weibull distribution with high coefficient of determination ($R^2 > 0.99$).

Population parameters

The differences in the population parameters among the three CO₂ treatments varied over time (Table 2). No significant differences in the intrinsic rate of increase (r) or the finite rate of increase (λ) were observed in the first generation among the three CO₂ treatments. However, the r and λ in the fifteenth generation of the BPHs in the ambient and gradual CO₂ treatments were significantly higher than those in the abrupt CO₂ treatment. After 14 generations of growth,

Table 2 Means (\pm SE) of the BPH population parameters under the three CO₂ treatments in generation 1 and generation 15

Parameters	CO ₂ concentration (Generation 1)			CO ₂ concentration (Generation 15)		
	Ambient	Gradual	Abrupt	Ambient	Gradual	Abrupt
Intrinsic rate of increase (r) (day ⁻¹)	0.1481 \pm 0.0065aB	0.1551 \pm 0.0068aB	0.1416 \pm 0.0068aB	0.1986 \pm 0.0066aA	0.2076 \pm 0.0052aA	0.1791 \pm 0.0063bA
Finite rate of increase (λ) (day ⁻¹)	1.1597 \pm 0.0075aB	1.1678 \pm 0.0080aB	1.1521 \pm 0.0079aB	1.2197 \pm 0.0081aA	1.2307 \pm 0.0063aA	1.1961 \pm 0.0075bA
Net reproductive rate (R_0) (offspring/individual)	60.4 \pm 10.6abB	67.5 \pm 11.7aB	37.8 \pm 7.0bB	99.8 \pm 13.9bA	155.1 \pm 17.7aA	89.3 \pm 13.4bA
Mean generation time (T) (day)	27.7 \pm 0.4aA	27.1 \pm 0.3aA	25.645 \pm 0.4bA	23.2 \pm 0.3cB	24.3 \pm 0.2bB	25.1 \pm 0.3aA

The standard errors (SE) were calculated using 100,000 bootstrap resamplings

Different lowercase letters indicate significant differences among the three CO₂ treatments within the same generation, while different uppercase letters indicate significant differences between generation 1 and 15 using a paired bootstrap test at a 5% significance level

the net reproductive rate (R_0) of the BPHs in the gradual CO₂ treatment was significantly higher than that in the other two CO₂ treatments. In contrast to the last generation, no significant differences in the mean generation times (T) were observed in the first generation between the ambient and gradual CO₂ treatments.

Life expectancy

The life expectancies (e_{xj}) of the BPHs are shown in Fig. 3. The e_{xj} value shows the length of time that individuals at age x and stage j are expected to live. The life expectancy of an egg in the ambient CO₂ treatment was 35.8 days during the first generation, which was higher than that of the BPH eggs reared in the gradual and abrupt CO₂ treatments (both 30.7 days). However, in the last generation, the life expectancies of newly laid eggs in both the gradual CO₂ (34.4 days) and abrupt CO₂ (35.4 days) treatments were higher than that in the ambient CO₂ treatment (32.0 days).

Growth projection

The population stage size and growth rates of the BPHs reared on rice under the three CO₂ treatments are presented in Figs. 4 and 5, respectively. Our results showed that the BPH population growth rate in the abrupt CO₂ group was lower than that in the gradual and ambient CO₂ groups during the last generation (Fig. 5); moreover, using the reference day (i.e., the 50th day; vertical dashed lines in Fig. 5), the emergence of the different stages in the ambient and gradual CO₂ treatments was clearly earlier than that in the abrupt CO₂ treatment compared with the first generation.

Discussion

Most previous studies tested the effects of abruptly elevated CO₂ on herbivores using CO₂ concentrations ranging from 550 to 800 μ L (Liu et al. 2017; Qian et al. 2018; Boullis et al. 2018). In our previous study (Wen et al. 2019), we reported that an abrupt increase in CO₂ (550 μ L) could enhance the adaption of BPHs, with higher development rates, fecundities, and population parameters than those of BPHs exposed to abrupt increases in CO₂ (750 μ L).

In this study, we provided the first experimental data regarding gradual and abrupt increases in atmospheric CO₂ on BPH life history traits. Our results demonstrated that the BPH populations reared under gradual and abrupt increases in CO₂ levels differed from one another in developmental times, fecundity, and population growth.

A life table can provide the most comprehensive description of the developmental time, survival, and fecundity of a pest population in response to diverse ecological conditions. In the present study, we opted to use a two-sex, age-stage life table to analyze the raw data rather than the traditional female age-specific life table, primarily because the traditional female-based, age-specific life table ignores stage differentiation and the male component of the population being studied (Chi and Liu 1985; Chi 1988; Mou et al. 2015; Huang et al. 2018). In general, different developmental stages and ages of herbivores have variable susceptibilities to different stimuli. Stage differentiation of insects is critical for understanding insect population ecology and scheduling pest management against a specific stage of a pest (Chen et al. 2018). Thus, the prediction of population growth using

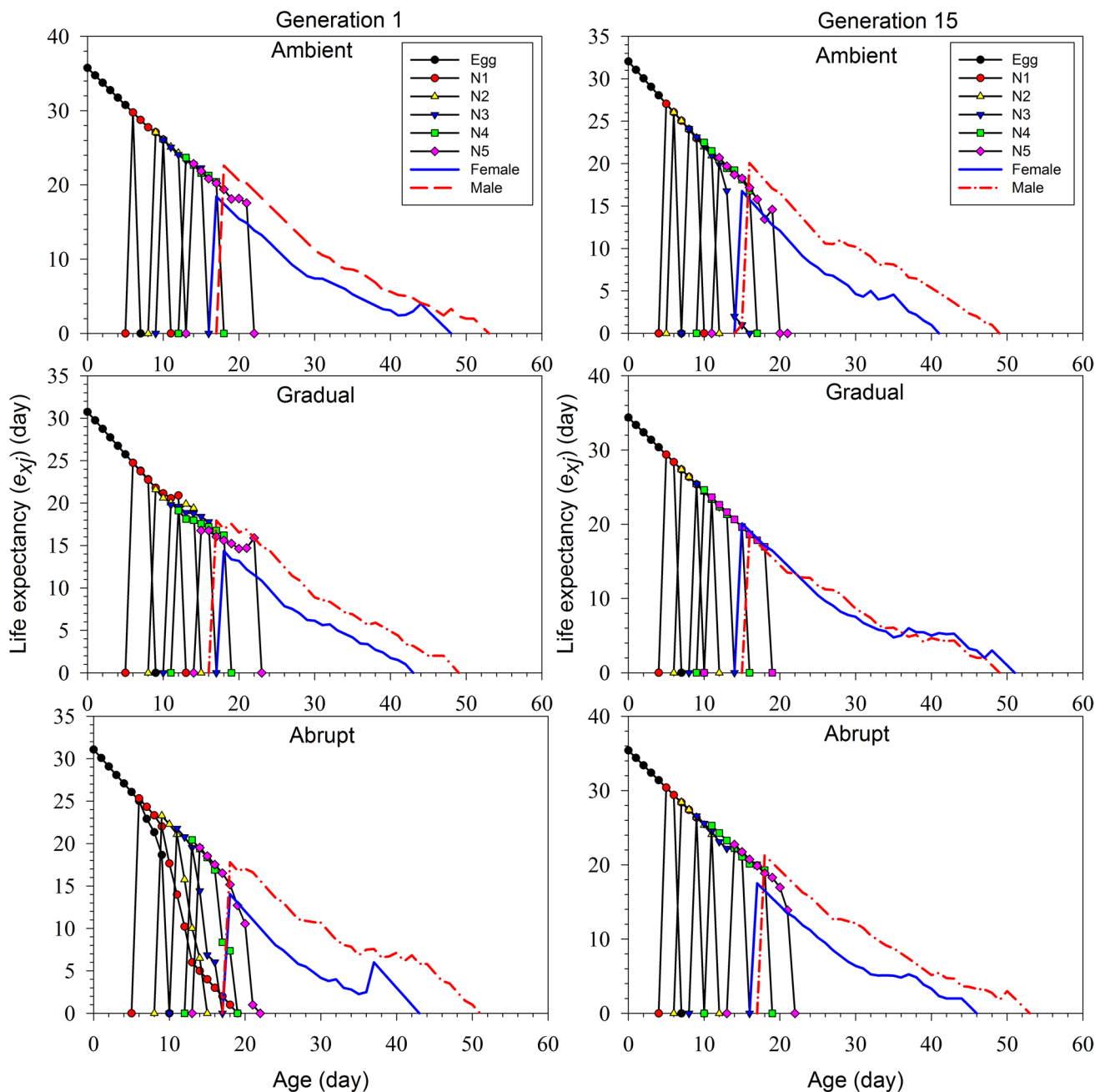


Fig. 3 Age-stage-specific life expectancy (e_{xj}) of brown planthoppers reared on rice in generation 1 and generation 15 in ambient, gradual, and abrupt CO_2 treatments

age-stage, two-sex life tables offers valuable information for the evaluation of the effect of variable environmental factors. In this study, every developmental stage, from the egg to the adult stage, was analyzed and compared to the results of previous studies involving a single stage. There were obvious overlaps between the stages in the current study (Figs. 1, 4). The male population was included in the current study because differences in longevity and survival are known to exist between females and males

(Tuan et al. 2016). In addition, a bootstrap technique was employed to estimate the variance and standard errors of the developmental time, survival rate, fecundity, and population parameters. Akca et al. (2015) used longevity and fecundity data to examine the quantitative differences in their results when using a generalized statistical method compared to a bootstrap method and suggested that bootstrap techniques should be used to obtain representative variances and standard errors. Using a bootstrap method

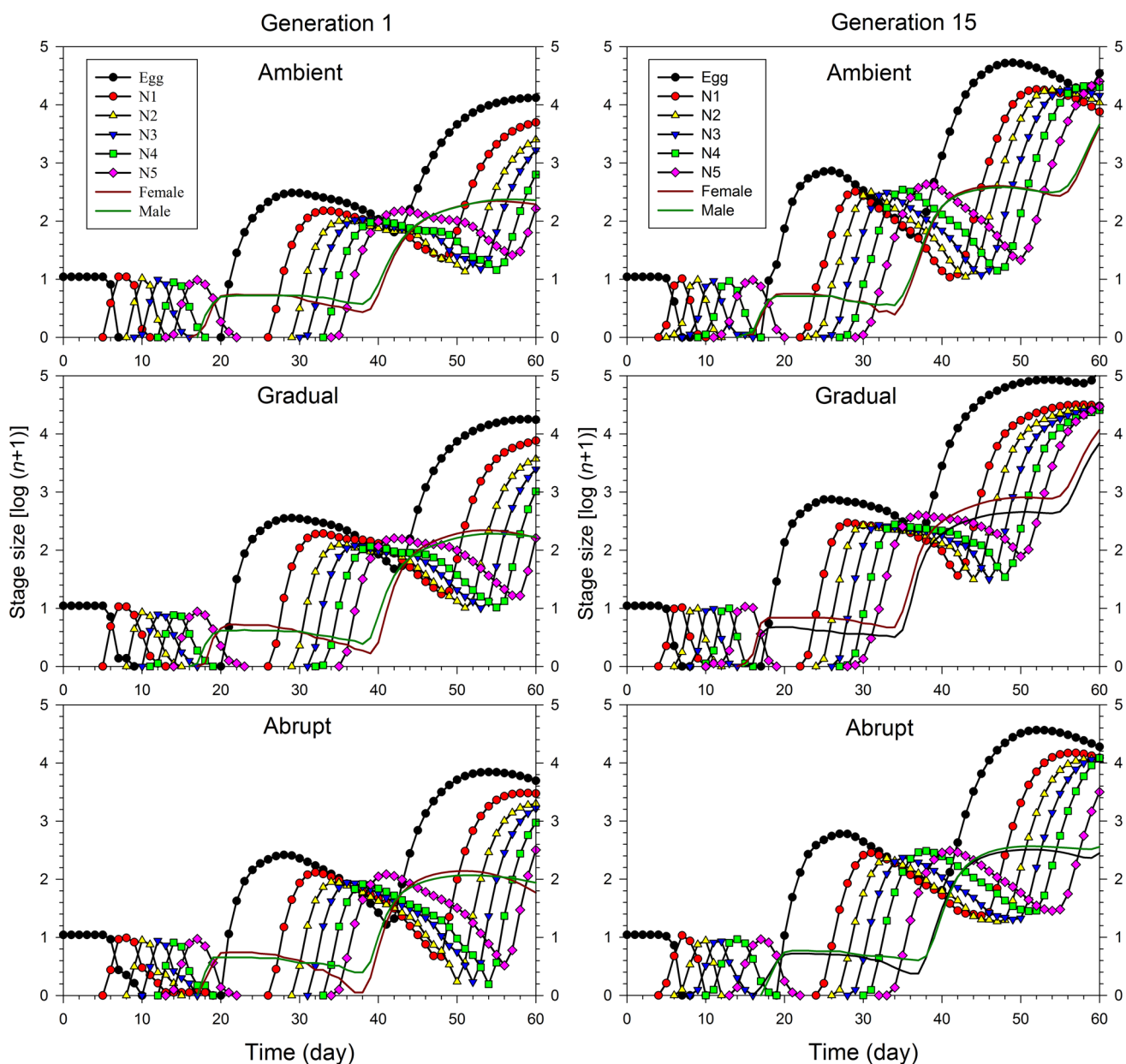


Fig. 4 Simulated population growth of brown planthoppers reared on rice from an initial population size of 10 eggs in generation 1 and generation 15 in ambient, gradual, and abrupt CO_2 treatments

in our study has produced a more realistic insight into how the BPH population responds to increasing CO_2 concentrations. In this study, because the pre-adult mortalities were low in all the treatments, curves of age-specific survival rates (l_x) fit well to the Weibull distribution, with a high coefficient of determination (R^2). However, as Tuan et al. (2016) demonstrated, when there is a higher mortality in specific life stages, the fitted Weibull distribution is inaccurate in describing the survival curve, and the application of the Weibull distribution should be carried out with caution.

In the first generation, no significance was observed in the nymphal developmental time, with the exception of the first instar nymphs in the abrupt CO_2 treatment (Table 1), which reflected that young nymphs were more sensitive to an incrementally increased CO_2 . However, after fourteen generations, the pre-adult developmental time of the BPH in the gradual CO_2 treatment was significantly shortened, which is in contrast to the results of the abrupt CO_2 treatment. The gradual and abrupt CO_2 increases were detrimental to the female and male longevity in the first generation. In the 15th generation, the longevity of the females reared in the gradual

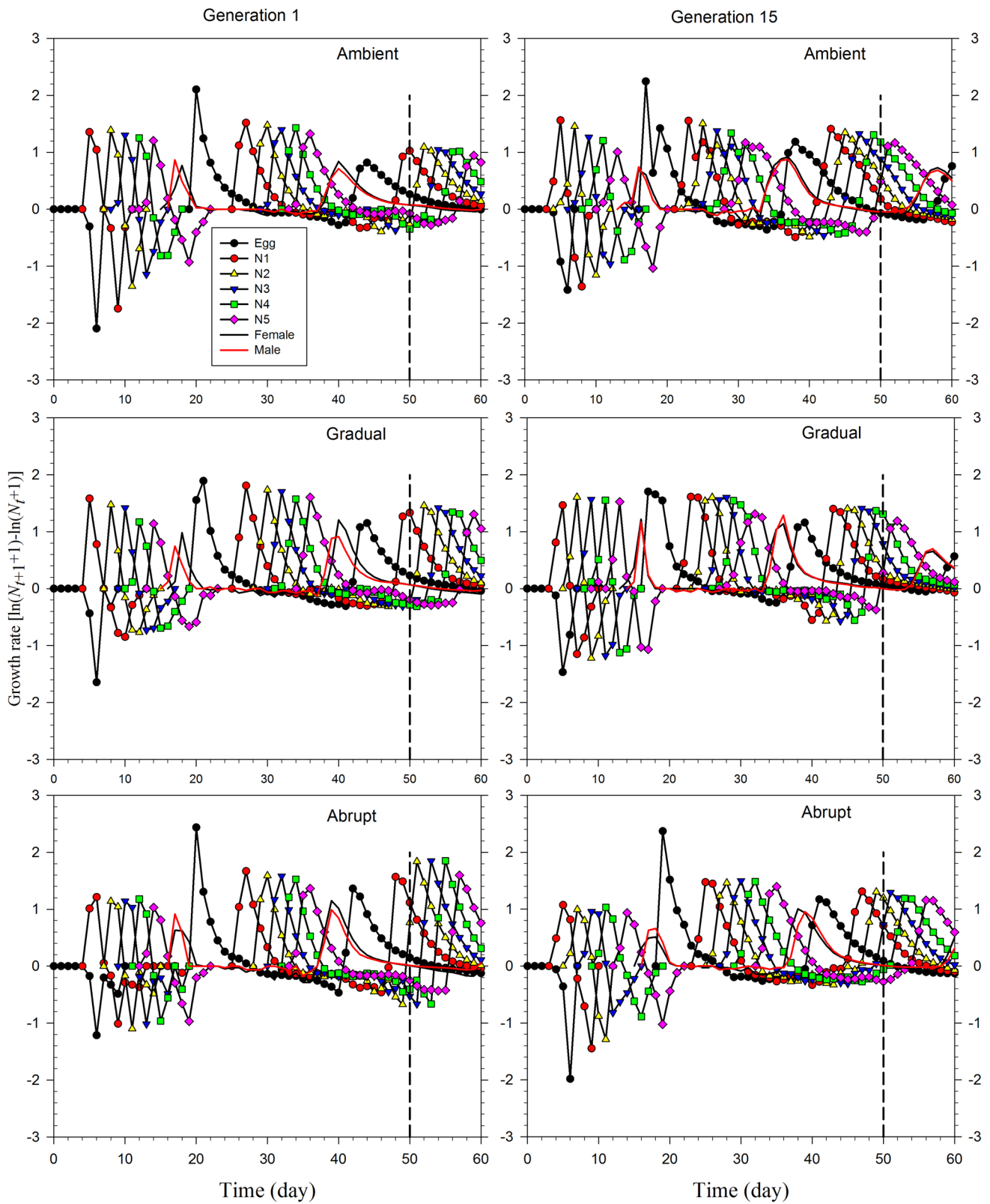


Fig. 5 Stage-specific growth rate of brown planthoppers reared on rice from an initial population size of 10 eggs in generation 1 and generation 15 in ambient, gradual, and abrupt CO₂ treatments. The dashed lines mark the 50th day

CO₂ treatment was, however, significantly longer than that in the other two CO₂ treatments, and there was no significant difference among the ambient CO₂ and abrupt CO₂ treatments. According to Eq. (3), the net reproductive rate (R_0) takes both the survival rate and fecundity into account. The R_0 in the treatment with an abrupt CO₂ increase was significantly reduced compared to that in the gradual CO₂ treatment due to the lower fecundity of the BPHs in the abrupt CO₂ treatment in the first generation. Our results showed that the R_0 of the BPHs reared in the gradual CO₂ treatment was significantly higher than those reared in the ambient and abrupt CO₂ treatments in generation 15. All of these data demonstrated that the effect of elevated CO₂ on BPH population growth would be decreased over multiple generations. BPHs could adapt both gradual and abrupt increase of CO₂; however, gradually increasing the CO₂ allowed the BPHs to rapidly adapt to the enriched CO₂ conditions. The shortened pre-adult duration and total pre-oviposition period (TPOP) and higher fecundity in the gradually increasing CO₂ treatment resulted in higher population parameters (r and λ). Consequently, the BPH population grew faster than those in the abrupt CO₂ treatment. These results are inconsistent with Lewontin's important finding that "One day saved in development is worth a doubling of fecundity" (Lewontin 1965), i.e., the intrinsic rate of increase will significantly increase when the first reproductive age occurs earlier. Therefore, our results illustrated that the number of annual generations of the BPH may increase under gradually increasing CO₂, indicating that the BPH will be able to cause substantial crop damage in the future. Therefore, the effects of increased CO₂ on herbivores may be underestimated based on the results of studies using abrupt CO₂ increases.

In the present study, the long-term effects of abrupt and gradual increases in CO₂ on BPH were examined, which can help us better understand the effects of elevated CO₂ on herbivores. Reich et al. (2018) reported an unexpected reversal to a much more positive response to elevated CO₂ by C₄ than by C₃ grasses based on a long-term (20-year) experiment. This finding shows that even the best-supported short-term response to global change might not predict long-term results. In natural ecosystems, herbivores will also experience elevated CO₂ over multiple generations. Thus, the long-term effect of elevated CO₂ on pest populations may provide important demographic data for pest management in the future.

Earlier studies tested the effects of CO₂ enrichment on BPHs based on abrupt increases in CO₂. Shi et al. (2014) reported similar results, i.e., significantly lower female longevity but higher fecundity when BPHs were reared under elevated CO₂ (700 µl/L) for one generation. In contrast to Shi et al. (2014), our results demonstrated long-term effects (15 generations). The population size of BPHs in transgenic Bt rice (TT51) and non-transgenic rice (MH63) at the

tillering stage treated with 40 µl/L triazophos in elevated CO₂ (750 µl/L) conditions was significantly higher than that in ambient CO₂ conditions (Ge et al. 2015). This finding is different from our results, which may be due to the use of triazophos. Chang et al. (2011) noted that elevated CO₂ (750 µl/L) significantly enhanced the brachypterous and macropterous subpopulations and the total population. BPHs at different stages may respond differently to CO₂ enrichment. Because only fourth–fifth instars and adults were used in the study by Chang et al. (2011), their data could not represent the effect of CO₂ enrichment over a whole generation. In addition, in this study, we began with 80 hatched eggs, and all the life table parameters were recorded over the entire life span of the BPHs; moreover, an age-stage, two-sex life table was used in this study. Therefore, the data covered survival, development, and fecundity, and the analysis was more comprehensive. Prasannakumar et al. (2012) tested the effect of elevated CO₂ (570 µl/L) on a BPH population and found no significant difference in the BPH population between elevated CO₂ and ambient CO₂ up to the fourth week after adult release; however, the BPH population was significantly higher under elevated CO₂ after 8 weeks in 2010 and 6 weeks in 2011. This finding is consistent with our previous study (Wen et al. 2019). In this study, we obtained a comprehensive description of the effect of elevated CO₂ on BPHs based on life table theory. Other studies have found that herbivores respond differently to moderately elevated CO₂ (e.g., 550 µl/L) and abruptly increased CO₂ (e.g., 750 µl/L) (Xie et al. 2015; Shi et al. 2019).

In conclusion, our results indicated that the BPHs responded differently to gradual and abrupt CO₂ increases on both short- and long-term time scales. Both gradual and abrupt increases in CO₂ will increase BPH fecundity; however, a gradual increase in CO₂ will result in higher BPH fitness than an abrupt increase in CO₂. Our study demonstrated that it is vital to collect life table data at elevated CO₂ concentrations for a comprehensive understanding of the effects of CO₂ on pest populations and for predictive pest management.

Author contributions

GW, JZ, WH, and HH conceived and designed the research; JL, JZ, and CW conducted the experiments; JL, HC, and GW analyzed the data and wrote the manuscript. All the authors read and approved the publication.

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Compliance with ethical standards

Conflict of interest All authors declare no conflicts of interest.

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