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Effects of elevated CO₂ and temperature on survival and wing dimorphism of two species of rice planthoppers (Hemiptera: Delphacidae) under interaction

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Abstract

BACKGROUND: Anthropogenic climate change (ACC) may have significant impacts on insect herbivore communities including pests. Two of the most important climate-change related factors are increased atmospheric concentrations of carbon dioxide (CO₂), and increasing mean global temperature. Although increasing attention is being paid to the biological and ecological effects of ACC, important processes such as interspecific interaction between insect herbivores have been little explored. Here, in a field experiment using the FACE (free-air CO₂ enrichment) system, we investigated the effect of elevated CO₂ and temperature on survival and wing dimorphism of two species of rice planthoppers, *Laodelphax striatellus* and *Nilaparvata lugens* under interaction.

RESULTS: The two species were grouped into five treatments of relative density (0/50, 13/37, 25/25, and 37/13, 50/0), each of which was allocated to one of a factorial combination of two CO₂ concentrations and two temperature treatments (elevated and ambient levels). Our results revealed that climatic treatment has no effects on survivorship of interspecific competing planthoppers. However, climatic treatment affected wing-form of planthoppers under interspecific interaction. For females of *N. lugens*, in the 37/13 ratio, proportion macropterous form was lower under elevated CO₂ + temperature than under the ambient environment or than under elevated temperature. For females of *L. striatellus*, proportion macropterous form did not differ among climatic treatments at each ratio treatment.

CONCLUSION: These findings illustrate that climate change-related factors, by affecting the macropetry of interspecific competing planthoppers, may influence planthopper fitness. We provide new information that could assist with forecasting outbreaks of these migratory pests.

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Keywords: anthropogenic climate change; global warming; FACE system; interspecific interaction; planthoppers; migratory pests

1 INTRODUCTION

Empirical evidence suggests that the planet's air and surface mean temperatures have been increasing since the Industrial Revolution.¹ There is a strong scientific consensus that most of the recent increasing mean global temperature is explained by rising atmospheric concentrations of carbon dioxide (CO₂) and other greenhouse gases (GHGs).² Air and surface temperatures across the biosphere are predicted to increase by ~2–4 °C with a doubling of the current atmospheric CO₂ concentration by the year 2100 unless measures are taken to drastically reduce GHG emissions.¹ The Paris Agreement (2015) suggests that the average temperature of the planet is going to rise at least 1.5 °C above pre-industrial levels by 2040 and perhaps earlier.³ This rate of warming is unprecedented in hundreds of thousands, or perhaps even millions of years.

Most phytophagous organisms in terrestrial ecosystems are insects, both in absolute numbers and in the number of species.⁴

Interspecific interaction among phytophagous insects sharing the same food plant is widespread when resources are limiting.^{5–7} The effect of climate change on interspecific interaction can be direct, via affecting their physiology,^{8–10} behavior,⁹ and phenology,^{11,12} or indirect, through climate-induced changes in the quality of their food resources.^{13,14} The responses of insects in interspecific interaction to anthropogenic climate change (ACC) are likely to

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be both complex and variable, which may largely depend on life histories and traits of the insects.^{15–18}

Life histories and trait expression of planthoppers (Hemiptera: Delphacidae) have been well studied over the last several decades.^{19–22} One typical life history trait of planthoppers is wing dimorphism. Studies show that both winged (macropterous) and flightless (brachypterous) adults with reduced wings can exist in the same population.^{22–24} Since migratory (macropterous) and sedentary (brachypterous) individuals can be identified easily, planthoppers are excellent organisms for understanding the evolutionary basis of this trait. Moreover, as they are often abundant and ubiquitous, they are model organisms for studies of insect population dynamics and life history evolution.^{21,25} Wing dimorphism of planthoppers is determined by a developmental switch, which responds to the local environment, such as population density, host plant nutrition, temperature, and photoperiod.^{26–29} Among the identified factors affecting wing dimorphism, population density is by far the most influential one.³⁰ The production of macroptery is density-dependent, which is highly variable among species and is often escalated with nutritional inadequacy of host plants.³⁰

More than one species of planthopper sometimes cohabits on the same individual host plant. The outcome of their interactions is determined by the suitability of the host environment for each interacting species.³¹ With increasing population densities, they may compete for limited food resources. When the population reaches the threshold density that triggers the production of macroptery, one species could effectively influence the dispersal capability of the other by triggering the production of macropterous forms.³⁰ Matsumura and Suzuki²⁴ found that the effect of interspecific crowding on macropterous forms was as significant as that of intraspecific crowding. However, the effects of interspecific interaction of planthoppers have rarely been addressed in previous studies.

Studies have shown that ACC is having significant impacts on the biology and ecology of planthoppers.^{32,33} Climate change can directly alter planthopper migration, population size, geographical range, potential overwintering boundary and mate location.^{33–37} It has been well acknowledged that climate change is one of the factors causing disruption in population dynamics of rice planthoppers.^{32–39} Several studies have shown that elevated temperatures or CO₂ may enhance the population size, and accelerate outbreaks of planthoppers.^{32,35,38,39} However, how planthoppers in interspecific interaction respond to warming and enhanced CO₂ concentrations has not been explored. Moreover, most studies focusing on the effect of ACC on planthoppers were carried out in either glasshouses or controlled-environment chambers where conditions are simulated. Few studies have examined the climate change effects using FACE (free-air CO₂ enrichment) system under field conditions including elevated air temperature. Using FACE system is more preferable because the response of planthoppers to elevated CO₂ and temperature under such experimental conditions in FACE system would be more realistic. The FACE approach provides effective experimental control over climatic factors (e.g. CO₂, temperature) without causing appreciable changes in other environmental variables, while avoiding artifacts with chamber walls.⁴⁰

In this study we examined the effect of ACC (temperature and CO₂) on survival and wing dimorphism of two planthoppers either alone or under interspecific interaction in a FACE system. The small brown planthopper, *Laodelphax striatellus* (Fallén), and the

brown planthopper *Nilaparvata lugens* (Stål.) (Hemiptera: Delphacidae) are two major pests across much of Asia.^{41–43} They can seriously damage rice under favorable conditions for their population development.^{44,45} These two species occur simultaneously in rice fields following colonization by macropterous immigrants in China.^{43,46–48} In addition, warming in the climate since the 1960s has been demonstrated in China.⁴⁹ For better forecasting the population dynamics of these two planthoppers, it is important to understanding the role of current and future climate change-related factors on their biology and under interspecific interaction.

The main aim of this study is to determine whether or to what extent climate change affects the wing form and survival rate of *L. striatellus* and *N. lugens* with or without interspecific interaction at different initial relative densities under two CO₂ and two temperature combination treatments in the FACE system. We discuss our results in the context of ACC as an influential factor on the outcome of interspecific interaction among planthoppers. We also speculate on how this translates into management of these injurious pests.

2 MATERIALS AND METHODS

2.1 FACE system

The field FACE system was established in Kangbo village (31° 30' N, 120° 33' E), Guli Township, Changshu city in the province of Jiangsu, China, with a total area of 1300 m². The site, located in the center of the Taihu Lake basin, has been used for cultivation for 50 years. It has a subtropical monsoon climate with a mean annual temperature of 16 °C, precipitation of 1100 to 1200 mm during 2004–2013, annual sunshine duration of over 2000 h, and annual frost-free period of more than 230 days.

The FACE system contained 12 octagonal plots each of 50 m² laid out with a distance of 90 m between each other (Fig. 1). The atmospheric CO₂ enrichment to 500 µL/L was made by pumping CO₂ gas through pipelines from a liquid CO₂ supplier (Fig. 1). Sixteen Li-820 CO₂ sensors (Li-COR Inc., Lincoln, NE, USA) per plot were arranged evenly 1.5 m above the ground to control the CO₂ concentration in real time by automatically adjusting to wind direction and velocity. The warming treatment was imposed to the inner circle of 25 m² canopy area by 2 °C above ambient temperature using 12 infrared heaters (2000 W, 240 V, 1.65 m long × 0.14 m wide; HS-2420, Kalglo Electronics Co., Inc., Bethlehem, PA, USA). The elevated temperature was recorded by six infrared thermometers (Model SI-121, Apogee Instruments Inc, Logan, UT, USA) scattered above the rice canopy.

2.2 Plant and insect

The rice variety 'Changyou 5' was used in the experiments. Seeds were sowed in plastic pots (7 cm diameter × 5 cm height) in a glasshouse at 26 ± 1 °C, relative humidity (r.h.) 60–70%, and 16 h light (L)/8 h dark (D). Seedlings were manually transferred into the field at the height of ca. 15 cm on August 5, 2013.

The small brown planthopper, *L. striatellus* (Fallén), and the brown planthopper, *N. lugens* (Stål), were originally collected from rice fields on the Jiangpu farm of Nanjing Agriculture University, Nanjing city. The planthoppers used in the experiments were reared on rice seedlings in incubator (26 ± 1 °C, r.h. 60–70%, and 16 h L/8 h D) in the laboratory for three generations.

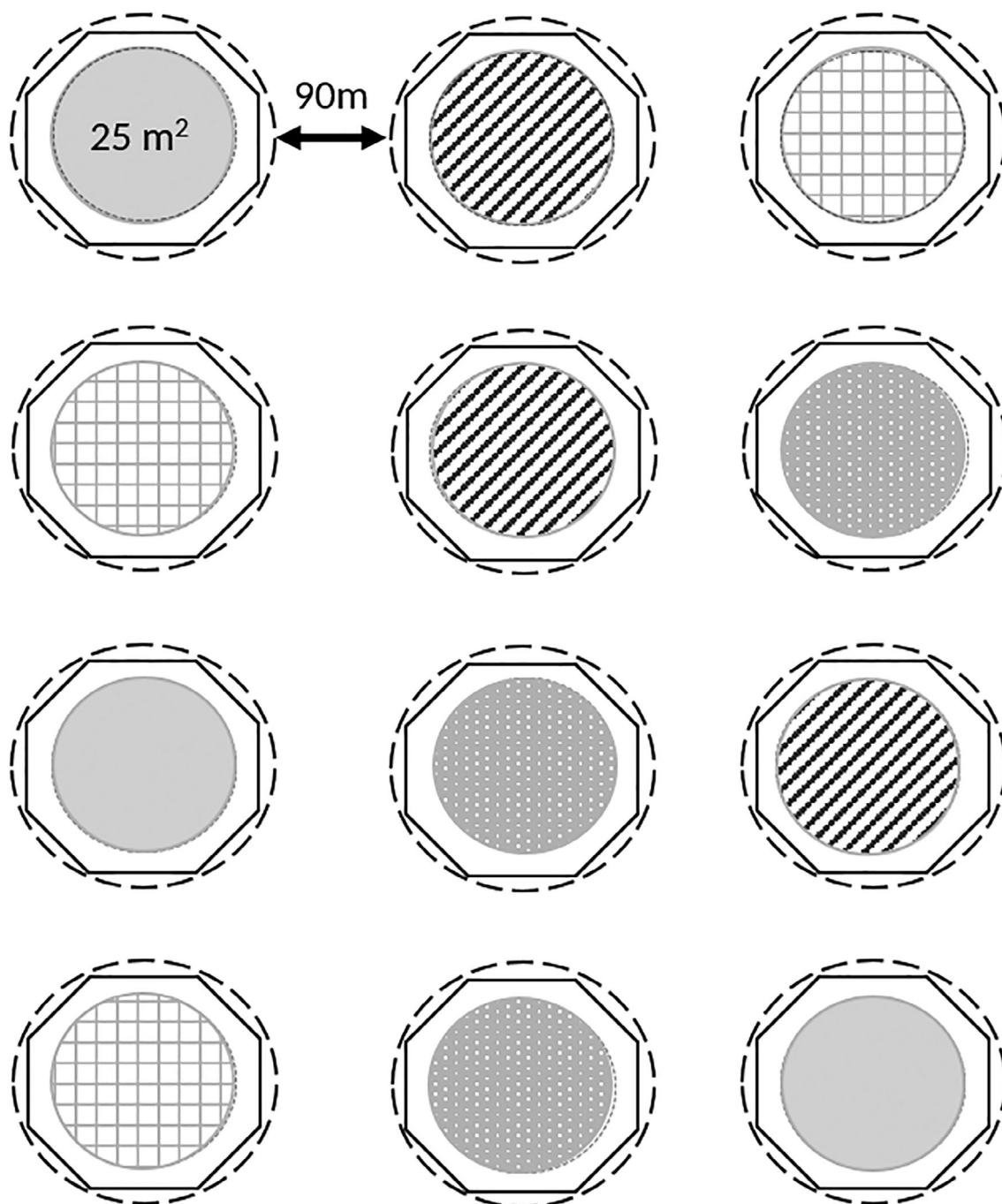


Figure 1. The position of 12 octagonal plots in the experimental field, where the distance between plots is 90 m. The inner circle (25 m²) is the experimental area where both CO₂ and temperature treatments were applied, by dark fill representing the ambient levels, oblique lines the elevated CO₂, grids the elevated temperature, and dark fill with scattered light dots the elevated temperature and CO₂.

2.3 Experimental set-up

A factorial combination of two CO₂ (ambient, 500 µL/L) and two temperatures (ambient, +2 °C) treatments, each of three replicates, was randomly allocated to 12 octagonal plots. In each plot, five organza cages (16 cm diameter × 75 cm height), each covering a cluster of rice seedlings, were set up at an equal distance between each other around the center. After transferring the rice into the field for 15 days (August 19, 2013), the cage was cleared using the insect suction apparatus VORTIS^R, it was introduced

with the second instar planthoppers. Each of these cages were allocated randomly with one of five two-species ratios in a total of 50 (0/50, 13/37, 25/25, 37/13, 50/0). Insects were consistently checked over the following 19 days (from August 19 to September 7, 2013) to record the number of emerged adults. These were collected to record the survival rate (the proportion of nymphs developed into adults out of total number of those initially transferred), and the number of macropterous forms in male and female insects of both species.

2.4 Statistical analysis

A generalized liner mixed effects model (binomial error distribution and logit link function) was used to analyze the probability of survival or macropterous form production as a function of climatic and starting relative density treatment factors; field plot was entered as random effects variable to control for non-independence among relative densities in one plot. Overdispersion was taken into account where appropriate via empirical estimation of scaling parameters. The likelihood ratio test was run to determine the effect of model terms. For macropterous form production, the study in the agricultural field has shown significant difference between sexes in how wing-form responds to crowding; the production of macropterous females is density-dependent, but males often emerge macropterous regardless of rearing density in some planthoppers species.²⁷ We thus first analyzed the data from female and male separately. Then we combined the data from female and male together and included sex as another fixed explanatory variable based on the previous model to analyze the differences of wing polymorphism between male and female planthoppers. When detecting a significant interaction effect, Tukey *post hoc* comparisons were made to make pairwise contrasts between treatments of one factor at individual levels of another one. Data analyses were performed with R version 3.4.4 software.⁵⁰

3 RESULTS

3.1 Survival

Different climatic factors did not have a significant effect on the probability of survival of either of the two competing planthopper species in variable species ratios (interaction among climatic factors-relative density-planthopper species: $\chi^2 = 10.78$, $df = 9$, $P = 0.29$, Fig. 2). For both *N. lugens* and *L. striatellus*, no statistically significant difference was observed in survivorship in the different treatments (climatic factors-planthopper species: $\chi^2 = 2.37$, $df = 3$, $P = 0.50$; climatic factors-relative density: $\chi^2 = 10.49$, $df = 9$,

$P = 0.31$; relative density-planthopper species: $\chi^2 = 0.74$, $df = 3$, $P = 0.86$; climatic factors: $\chi^2 = 11.19$, $df = 3$, $P = 0.11$; relative density: $\chi^2 = 7.43$, $df = 3$, $P = 0.06$; planthopper species: $\chi^2 = 8.19$, $df = 1$, $P = 0.004$; Fig. 2).

3.2 Wing dimorphism

The probability of female macropterous morph production was affected by interaction among planthopper species, relative density, and climatic factors ($\chi^2 = 24.10$, $df = 9$, $P < 0.001$, Fig. 3). For *N. lugens*, in the 50/0 ratio treatment, the proportion of macropterous forms found was lower under ambient conditions than under the elevated CO₂ + temperature or under the elevated CO₂ treatments (Tukey multiple comparison tests: CK versus CO₂ + T: $P = 0.021$; CK versus CO₂: $P < 0.001$; Fig. 3(a)). When the ratio was 37/13, the proportion of the macropterous form was lower under elevated CO₂ + temperature than under the ambient environment or under elevated temperature (Tukey multiple comparison tests: CO₂ + T versus CK: $P = 0.029$; CO₂ + T versus T: $P = 0.019$; Fig. 3(b)). For *L. striatellus*, the proportion of the macropterous form did not differ among climatic treatments at each ratio treatment (Fig. 3).

The probability of male macropterous morph production was affected by three-way interaction among planthopper species, relative density, and climatic factors ($\chi^2 = 19.11$, $df = 9$, $P = 0.024$, Fig. 4). For *N. lugens*, in the 37/13 ratio treatment, the proportion of the macropterous form was higher under the ambient environment than under the other climatic treatments (higher temperature, enhanced CO₂). For *L. striatellus*, there was no significant difference in the proportion of the macropterous form among the various climatic treatments in each species ratio (Fig. 4).

The proportion of macropterous forms of female and male responded differently to climatic factors in variable relative densities (sex: $\chi^2 = 27.02$, $df = 1$, $P < 0.001$), which was affected by planthopper species, relative density, climatic factors (interaction

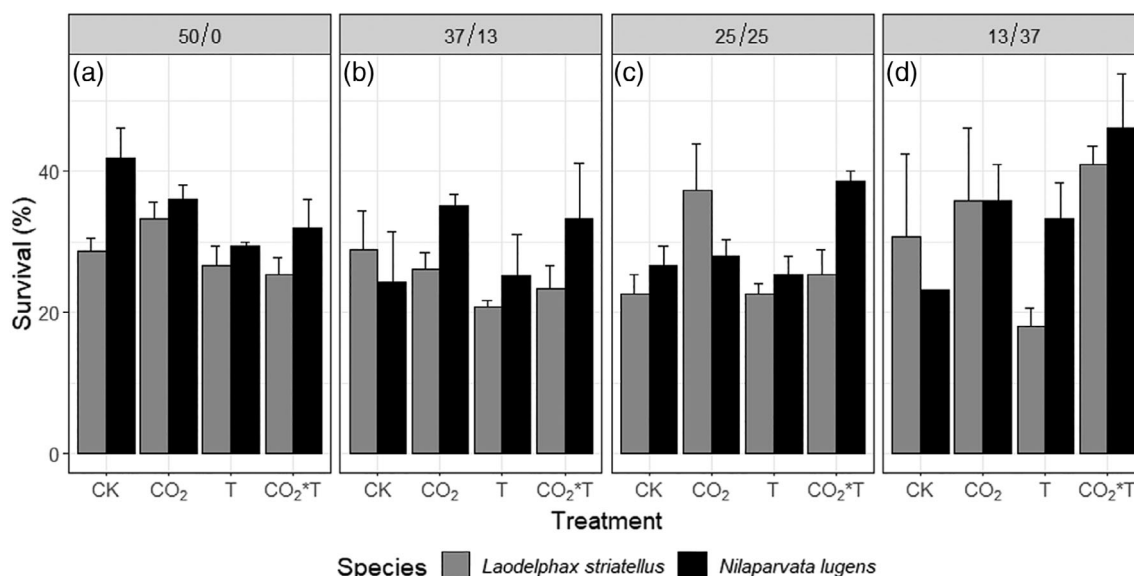


Figure 2. Effects of climatic treatment (CK, CO₂, T, CO₂ × T) under each relative density (50/0, 37/13, 25/25, 13/37) (a, b, c, d) on survival rate (mean ± SE) of nymphs of *Nilaparvata lugens* (black bars) and *Laodelphax striatellus* (gray bars). CK represents ambient temperature and CO₂, CO₂ represents the treatment of elevated CO₂, T represents the treatment of elevated temperature, and CO₂ × T represents the treatment of elevated temperature and CO₂. Bars present the means + standard error.

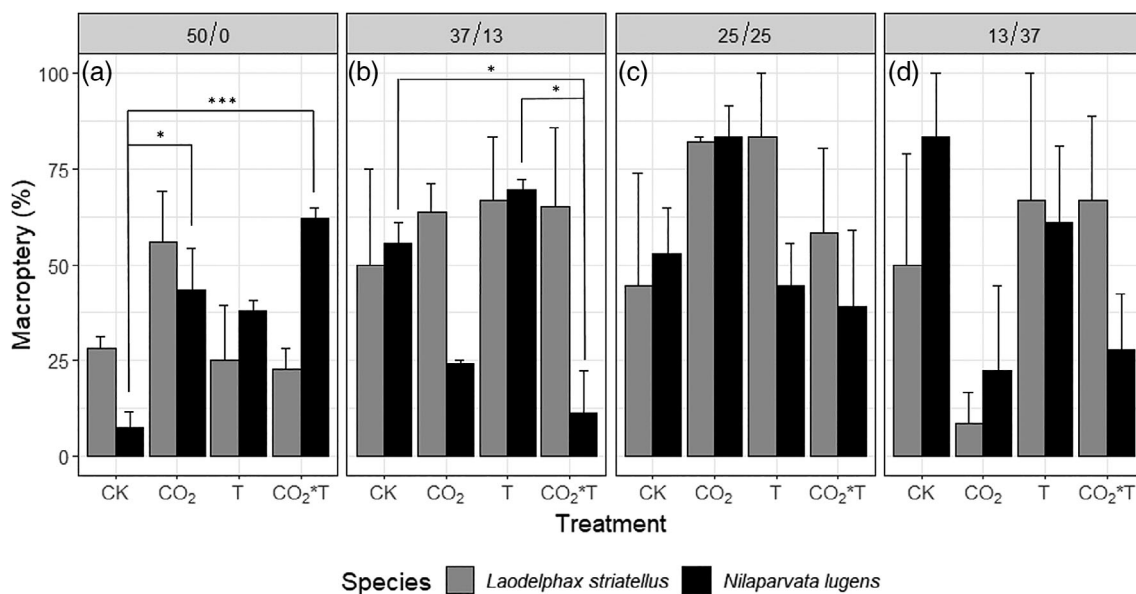


Figure 3. Effects of climatic treatment (CK, CO₂, T, CO₂ × T) under each relative density (50/0, 37/13, 25/25, 13/37) (a, b, c, d) on macroptery (%) in female adults of *Nilaparvata lugens* (black bars) and *Laodelphax striatellus* (gray bars). Line with asterisk refers significant differences in macroptery (%) across different climate treatments. CK represents ambient temperature and CO₂, T represents the treatment of elevated temperature, and CO₂ × T represents the treatment of elevated temperature and CO₂. Bars present the means + standard error. *P < 0.05, **P < 0.01, ***P < 0.001.

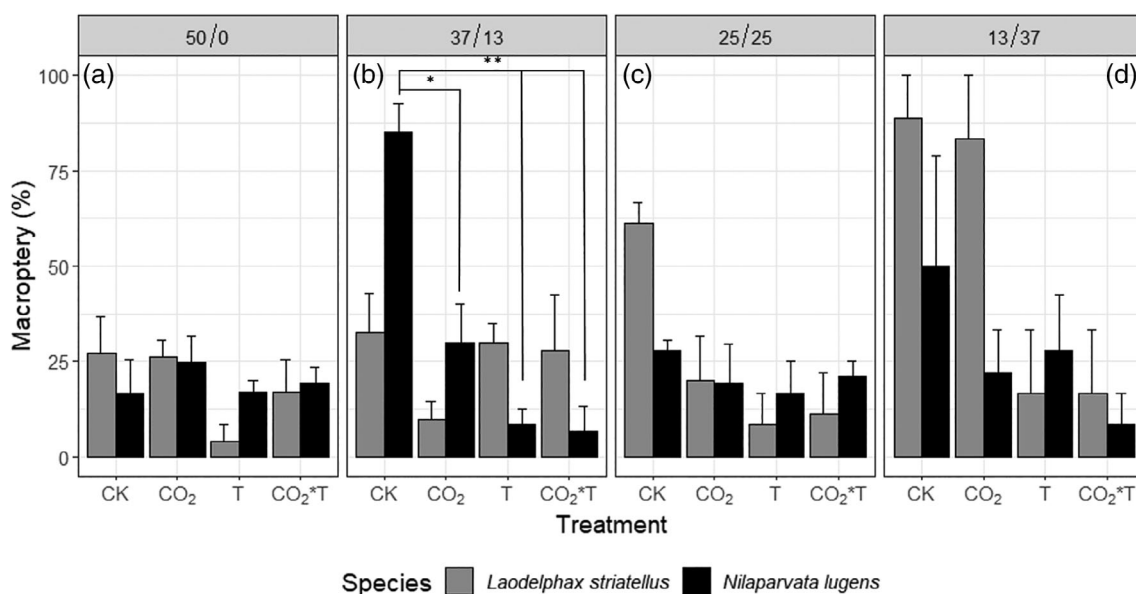


Figure 4. Effects of climatic treatment (CK, CO₂, T, CO₂ × T) under each relative density (50/0, 37/13, 25/25, 13/37) (a, b, c, d) on macroptery (%) in male adult of *Nilaparvata lugens* (black bars) and *Laodelphax striatellus* (gray bars). Line with asterisk refers significant differences in macroptery (%) across different climate treatments. CK represents ambient temperature and CO₂, T represents the treatment of elevated temperature, and CO₂ × T represents the treatment of elevated temperature and CO₂. Bars present the means + standard error. *P < 0.05, **P < 0.01, ***P < 0.001.

among climatic factors–relative density–planthopper species–sex: $\chi^2 = 20.10$, $df = 9$, $P = 0.017$).

4 DISCUSSION

The results of this study show that climatic treatment – ambient or elevated temperature and CO₂ – had no significant effects on the survival of planthoppers (either alone or in interspecific

interaction). By contrast, our results reveal that the effects of elevated temperature and CO₂ on wing form of male and female planthoppers was highly species-dependent and context-dependent (= density). In *N. lugens*, the production of macropterous individuals varied considerably depending on climatic treatment, with the frequency of the macropterous form in males and females dependent on the relative density of *N. lugens* in the presence (or absence) of *L. striatellus*. However, we do not wish to

overstate the significance of these results, since similar variation in survival is non-significant. Nevertheless, the absence of effects of temperature and/or CO₂ on survival and wing form in some density treatments is also important because it shows that these insects are potentially resilient or physiologically 'buffered' to changes in abiotic conditions attendant with ACC.

Planthoppers possess stylets as mouthparts that pierce the leaf integument to feed on phloem.^{26,51} Perhaps this mode of feeding makes these insects less susceptible to abiotic factors that might be more clearly demonstrated in the behavior, morphology and development of chewing insects (e.g. caterpillars, beetle larvae, etc.) that consume whole leaf tissues. It must be borne in mind that temperature and especially CO₂ change plant quality by causing water stress and/or altering leaf allelochemistry.^{52–54} Despite that, other factors may have reduced the sensitivity of planthoppers to climatic factors under interspecific interaction. For example, the relative insect density in our experiment may not have been crowded enough (e.g. did not reach a critical threshold) to trigger climatic effects on survivorship under interspecific interaction. However, other climatic variables may also affect a range of other traits in planthoppers alone or under interspecific interaction that were not studied here, including development time, adult longevity, female fecundity and population dynamic, all of which need to be further investigated.

In planthoppers, polymorphic life histories, including wing form, confer metabolic and fitness-related costs and benefits.^{55,56} Wing-form in planthoppers is determined by a developmental switch that occurs in response to a range of environmental cues. It is also associated with habitat suitability, stability, and availability.²⁶ Seasonal changes in the host plant could affect wing dimorphism for planthoppers because planthoppers need to locate suitable host plants, whose growing time and location determines the wing form of planthoppers.²⁷ Hu *et al.*⁴³ also found that the spatiotemporal dynamics and migration patterns of brown planthoppers have dramatically changed in the lower-middle reaches of the Yangtze River, because double-cropping rice has been greatly reduced whereas single-cropping rice has been rapidly increasing since 1997. Among all the identified environmental factors affecting wing-form in planthoppers, population density is the most influential one for most species.²⁶ The production of migratory planthopper forms is positively density-dependent, which is highly variable between sexes and populations of the same species and among different species.²⁷ The effects of population density on behavior is not only affected by intraspecific interactions, but also by interspecific interactions.¹⁸ Even though interspecific interaction could also trigger the production of migratory forms, few studies have directly addressed the role of interspecific interaction. Denno and Roderick²² found that the interspecific crowding between *Prokelisi marginata* and *P. dolus* acted as a powerful stimulus in triggering the production of migratory forms. Matsuura and Suzuki²⁴ reared *Sogatella furcifera* and *N. lugens* at different densities in pure and mixed species cultures in laboratory tube cages. They found that interspecific effects on macroptery were stronger than intraspecific effects for *N. lugens*, whereas interspecific effects on macroptery were weaker than intraspecific impacts for *S. furcifera*. In our study, we found that there was no consistent pattern of interspecific interaction that triggers macroptery in climatic treatments. This is probably because experimental densities are not high enough and thus fall below a critical threshold where the planthoppers are less sensitive to abiotic factors.

Based on our results and the complex interplay between abiotic factors and biotic responses, it is difficult to predict how the

dispersal and migration pattern of these two planthoppers will be affected by climate change in the future. One of the major problems with conducting these types of experiments in FACE is the duration over which they are performed (e.g. usually over the short-term) and the fact that weather (and temperature) is highly stochastic whereas CO₂ is highly deterministic and is increasing only gradually over time. Of particular interest is how these insects will respond to ACC-related conditions, such as intense heat waves, sudden sharp downpours or rapid shifts in temperature and precipitation. Moreover, one must question the ecophysiological realism of exposing insects to unnaturally high concentrations of CO₂ that will not occur for perhaps several decades. Despite these constraints, we feel that our study sheds some light on the non-linearity of these responses and encourages the setting up of longer term studies.

Thus far, most existing studies on the impact of ACC-related factors on planthoppers have been conducted in glasshouses or climate chambers, which is less realistic than the FACE system used here. Furthermore, most studies on the effects of ACC on planthoppers have only focused on the population dynamic of single species, whereas far fewer studies have explored interspecific interaction between two planthoppers. Importantly, several planthopper species coexist in Chinese rice fields, including *L. striatellus* and *N. lugens*. Interspecific interactions, in response to climate change, may also influence planthopper population dynamics in addition to morphological traits. By triggering the production of macropterous forms, each species effectively influenced the dispersal capability of the other, which may have important implications on demographic parameters as well as on their status as pests.

In summary, our study reveals that climatic treatment (ambient versus elevated temperature and CO₂) generated variable effects on life-history traits in one planthopper species but not on another under intraspecific and interspecific crowding. However, there was no consistent pattern of these treatments on planthopper wing-form. As a result, it is difficult to predict the population dynamics of migratory insects in response to changes in abiotic conditions associated with ACC. To better understand these underlying mechanisms and to incorporate these mechanisms into integrated pest management strategies, it is important to examine longer-term interspecific interactions among migratory pests in more details, such as adult longevity and female fecundity, and with broadly overlapping niches in the context of climate change.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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