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Preference and performance of the rice leaf folder, *Cnaphalocrocis medinalis*, in relation to rice developmental stage

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Abstract

The relationship between oviposition preference and offspring performance is critical to an understanding of the interaction between herbivores and host plants. Although the topic has been addressed widely in plant species-herbivore systems, it has rarely been investigated in plant stage-herbivore systems. In this study, we evaluated oviposition preference and offspring performance of the rice leaf folder (RLF), *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae), on rice plants at the seedling (SS), tillering (TS), and booting (BS) stages. In preference assays, females deposited more eggs on TS and BS than on SS plants in cage tests, and preferred TS and BS odors over SS odors in Y-tube olfactometer tests. Offspring performance was affected by plant stage. The RLF offspring performed well when the larvae fed on BS leaves, as indicated by the highest larval survival and pupation rate and the greatest adult longevity. RLF offspring performed also well when the larvae fed on TS leaves, where fecundity was the highest. The high RLF offspring performance on TS and BS plants coincided with high larval consumption of TS and BS leaf mass relative to SS leaf mass. Our findings confirm the prediction of the preference–performance hypothesis. The results explain the pest damage patterns in mixed croppings of one- and two-season rice and are of significance for management of the pest through synchronization of rice planting.

Introduction

Host plant selection is governed by an array of complex factors and is central to the interaction between herbivores and their host plants. The preference–performance hypothesis (PPH), also known as the 'mother knows best' hypothesis or the optimal oviposition theory, hypothesizes that a female will prefer those hosts for oviposition on which her offspring perform best (Awmack & Leather, 2002; Scheirs & De Bruyn, 2002; Gripenberg et al., 2010; Rigsby et al., 2014; Wist & Evenden, 2016; Altesor & González, 2018; Zhang et al., 2019). In most cases, especially for lepidopteran insects in which offspring possess limited mobility, the 'wise' selection of host plants by the mother can ensure fitness of their offspring (Gripenberg et al., 2010; Zhang et al., 2012; Du et al., 2016; Zhang et al., 2019). Although there are cases where female choice and offspring performance do not match (Jallow & Zalucki, 2003; Jiao et al., 2012, 2017; Piyasaengthong et al., 2016; Liao & Chen, 2017), the results of most studies clearly support the PPH: offspring perform better on preferred plant types, and females deposit more eggs on those plant types conducive to their offspring performance (Gripenberg et al., 2010; Zhang et al., 2012; Du et al., 2016; de la Masselière et al., 2017; Altesor & González, 2018; Baleba et al., 2019; Zhang et al., 2019). Nevertheless, the strength of the relationship between female preference and offspring performance varies among insect groups with different dietary ranges and requirements (de la Masselière

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et al., 2017). In particular, females prefer 'high quality' plants more strongly in oligophagous than in polyphagous insects (Gripenberg et al., 2010; Birke & Aluja, 2017).

Whereas there has been a tremendous body of literature investigating the preference–performance relationship, prior investigations have focused almost exclusively on preference and performance of insects in the context of different plant species for polyphagous insects or different plant genotypes for oligophagous and monophagous insects (Li & Liu, 2015; de la Masselière et al., 2017; García-Coapio et al., 2017; Liao & Chen, 2017). The different developmental stages of a plant are characterized by varying architectural, morphological, anatomical, and biochemical features, which can affect the interaction between oviposition preference of a mother and her offspring's performance (Hoffman & Rao, 2010, 2011). However, the PPH relationship in plant stage-herbivore systems is less often addressed, even though different stages of a plant species do co-exist in natural and agricultural habitats.

Numerous studies have documented herbivorous insect responses to host plant stages, either of adults or of immatures. However, only a few studies have linked adult preference with offspring performance in response to plant stages. The cereal leaf beetle *Oulema melanopus* (L.) deposits more eggs on young leaves of oat plants that are of low nitrogen content and tender, whereas the newly hatched larvae often feed on leaves usually avoided as oviposition sites, indicating the lack of a (positive) correlation between host suitability and ovipositional preference (Hoffman & Rao, 2011). On the contrary, oviposition preference for old leaves was reported in *Trichoplusia ni* (Hübner) (García-Coapio et al., 2017). In the butterfly *Pieris brassicae* (L.), Fei et al. (2017) found no correlation between *P. brassicae* preference and performance on three age classes of black mustard plants (*Brassica nigra* L.), and only a weak correlation in mustard plants (*Sinapis arvensis* L.).

Rice (*Oryza sativa* L., Poaceae) is the second-most widely cultivated food crop grown worldwide and serves as a staple food for more than half of the world's population (Yuan, 2014). In recent years, cultivation systems in major rice-producing areas in China have undergone significant changes, characterized by reduction of two-season (early- and late-season) rice acreage, and increase of one-season (middle-season) rice acreage and mixed croppings of one- and two-season rice (Jiang et al., 2019).

The rice leaf folder (RLF), *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae), is a migratory insect pest that poses a major threat to rice crops throughout Asia. Annual occurrence of RLF in China follows its migration with southwestern monsoons from the Sino-India peninsula in the spring (Heong, 1993). Rice leaf folders damage rice crops during their larval stage by folding one or more leaf blades longitudinally with silk strands and feeding on mesophyll tissue inside the folded leaf/leaves, thus disturbing photosynthesis and growth, and ultimately reducing rice yield (Gangwar, 2015). In China, since 2003, the pest has reduced annual rice yields by 760 million kg (Han et al., 2015). This serious occurrence of RLF has been attributed to susceptible varieties, injudicious use of chemical insecticides, and climate change (Gangwar, 2015; Xu et al., 2017). However, the increase of mixed croppings of one- and two-season rice may have also added to its pest status, in that mixed croppings provide RLF with an undisrupted sympatric food source that can ensure the insect's high performance (Behera et al., 2013).

Keeping in mind the new situation of rice cultivation, the present study was conducted with the aim to clarify whether RLF females are able to distinguish between rice plants of different stages and if the mothers' preference increases the performance of their offspring. Our specific objectives were to: (1) evaluate oviposition preference for rice plants of different stages, (2) assess the performance of RLF offspring developing on rice leaves of different stages, and (3) determine the association between offspring performance and host selection by adult females.

Materials and methods

Plants and insects

Rice plants were grown in a greenhouse at the Guilin Experiment Station for Crop Pests (25°36′00″N and 110°41′24″E), Ministry of Agriculture and Rural Affairs, China, at 23–33 °C, 70–90% r.h., and ambient illumination. Germinated rice seeds (Taichung Native 1, TN1) were planted in nursery substrate (pH neutral, >50% organic content; Shandong Jinrun Bio, Jinan, China) in 8-l PVC pots in the greenhouse. Rice plants at seedling stage (10 days, SS), tillering stage (45–55 days, TS), and booting stage (75–85 days, BS) were obtained by staggered timing of seeding. To prevent herbivore damage, plants were kept in cylindrical insect-proof cages within the greenhouse. Watering was administered as necessary. Pesticides were not used throughout the experiment. Rice leaf folders used in the experiments originated from sweeping catches during immigration periods in the experimental station. The collected RLF adults were reared for oviposition in cages with tillering rice plants and a cotton ball soaked with 20% honey solution, with 40 females per cage. The plants in the oviposition cage were replaced every 24 h and the eggs on the plants were allowed to develop in separate rearing cages until pupation. Pupae were collected daily from the rearing cages and, to synchronize adult emergence, the pupae collected early were stored at a relatively low temperature (18–20 °C) for 3 days and then mixed with the late-collected pupae.

Preference of RLF female adults

Preference of RLF female adults was measured in both cage tests and Y-tube olfactometer tests. Potted plants were thinned at 5-day seedling stage to 10 plants per pot. For the cage tests, three potted plants from each of the three stages (SS, TS, and BS) were arranged alternatively and at equal distances from each other in a circle of 90 cm diameter within a cage (1.2 m diameter, 1 m high). At around 17:00 hours, 30 pairs of RLF adults (96 h old) were introduced into the center of the cage and left to select and oviposit on the plants for 72 h. Eggs on each plant were then counted. Prior to the cage tests, the pot openings were covered with plastic film to prevent the test insects from drowning and to avoid the influence of mud odor on the insects' orientation behavior. The tests were repeated 9× in the greenhouse; between repetitions, the relative positions of plants were rotated to avoid any position effects.

In the Y-tube olfactometer tests, four treatments, i.e., rice plants of the three stages (potted plants) and a blank control (pot with mud only), were included, which resulted in six pairs of comparisons. The Y-tube olfactometer was modified from Takemoto & Takabayashi (2015). Briefly, the Y-tube olfactometer consisted of a Y-shaped glass tube, with a stem and two arms each measuring 20 cm long and 3 cm inner diameter. The arms were angled at 75°. Inside each of the arms, a 50-ml centrifuge tube cut open at the tip was embedded so that the opening (1 cm diameter) was 4 cm away from the junction between the stem and arms. This design allows the adult females to make a selection between the two arms while preventing them from returning to the stem once they have entered the centrifuge tube. Odors from the two odor source jars were pumped (QC-1B air pump; Beijing Municipal Institute of Labor Protection, Beijing, China) through the arms into the stem after being cleaned and humidified through bottles containing active carbon and distilled water, respectively. Air flow was controlled at 300 ml per min by an inline flowmeter (LZB-3WB; Changzhou Kede Thermo-Engineering Meter, Changzhou, China) at each of the arms. The odor source glass jars (23 cm diameter, 70 cm high) each with one pot of plants or mud covered by film at the opening were placed on the ground while the other parts of the system were placed on a table. Vaseline was used to seal the jar. All the parts in the system were connected using Teflon tubing. Before each bioassay, the pumps were turned on and ran for 8 h to remove any residual air inside the system. Six gravid females (96 h old) were introduced into the inlet of the stem at 19:00 hours and the opening of the stem was sealed with a perforated silica gel stopper. The Y-tube olfactometer was then covered with a red cloth and all illumination was turned off. Numbers of females in the stem and the two arms were recorded at 06:00 hours the next morning. Those females that entered the centrifuge tubes were considered to have made a choice. The bioassay was repeated 10× for each pair of comparisons. Between repetitions of the same pair of comparison, the position of the odor source jars was rotated. After each repetition, eggs in the arms were removed, and the inner sides of the Y-tube olfactometer and the jars were cleaned using absolute ethanol and dried at 80 °C. The tests were performed in a room at 27 ± 3 °C and 80 ± 5% r.h.

Performance of RLF offspring

The performance of RLF offspring on SS, TS, and BS rice plants was tested using the leaf segment method described by Han et al. (2015). Rice leaf folder larvae can develop to the fifth instar and pupate when they are fed rice leaves from the vegetative stage until the panicle formation stage, regardless of the variety and position of leaves (Miyashita & Kawanishi, 2003). Therefore, all vigorous leaves collected from plants of a stage were mixed to feed RLF larvae. Leaf segments (each from a different leaf, 6 cm long) were placed adjacent to one another, eight segments per dish, on the bottom of a Petri dish (9 cm diameter, 1.5 cm high) into which a thin layer of 1% agar had been poured to maintain moisture. Thereafter, one newly hatched RLF larva was transferred onto the leaf segments in the Petri dish in a climate chamber at 27 ± 1 °C, 80 ± 5% r.h., and L16:D8 photoperiod. The leaf segments were replaced on alternative days until pupation. Daily observations were made to record larval survival and date of pupation. Once pupation had occurred, pupae were weighed individually using an electronic balance (Model AL 240-IC; Metter, Shanghai, China) to the nearest 0.1 mg. A total of 300 insects, evenly divided in 10 groups, were observed for each rice stage. Larval duration was calculated individually for all the insects, and larval survival rate (no. mature larvae × 100/no. newly hatched larvae) and pupation rate (no. pupae × 100/no. mature larvae) were calculated for each group.

Pupae obtained from a rice stage treatment were transferred individually to glass tubes lined with 1% agar and observed daily for emergence. Ten groups of 10–20 pupae were observed for each rice stage. Pupal duration was calculated individually for all the pupae, and emergence rate (no. adults emerged × 100/total no. pupae) was calculated for each group.

Adults that emerged on the same day from a rice stage treatment were paired in a cage (30 cm diameter, 70 cm high) with one pot containing a plant of the originating rice stage. Upon death of the adults, eggs on the plant were counted and adult longevity was calculated. For each rice stage treatment, 45 pairs of adults were tested.

Food utilization efficiency of RLF third instars

Food utilization efficiency of RLF larvae may vary according to plant developmental stages. This was tested in the third instars using the leaf segment method (Han et al., 2015). After being weighed, eight leaf segments were lined on the bottom of a Petri dish covered with a thin layer of 1% agar. A newly molted third instar (<24 h), starved for 6 h and weighed, was transferred onto the leaf segments in the Petri dishes. The insect was left to feed for 72 h in the climate chamber. It was then starved for another 6 h to allow all the feces to be evacuated and weighed again. Thereafter the insect was dried at 80 °C for 72 h and weighed. The remaining leaf segments were cleared of feces and then dried at 80 °C for 72 h and weighed. Feces was collected, dried, and weighed. Forty third instars randomly selected from a homogeneous cohort were tested for each rice stage.

Food utilization parameters expressed on a dry weight basis were calculated for each rice stage treatment as described by Han et al. (2015). To estimate dry weight of leaves of different rice stages and the third instars before the feeding tests, conversion coefficients between fresh and dry weight were established for leaves and larvae as described by Waldbauer (1968) and Han et al. (2015). The parameters included food consumption (FC) = E/T (mg/day), relative consumption rate (RCR) = E/(T × A) (mg/mg/day), relative growth rate (RGR) = P/(T × A) (mg/mg/day), approximate digestibility (AD) = 100 × (E−F)/E (%), efficiency of conversion of ingested food (ECI) = 100 × (P/E) (%), and efficiency of conversion of digested food (ECD) = 100 × P/(E−F) (%), where A = average of initial and final larval dry weights (mg), E = dry weight of ingested food (mg), F = dry weight of feces produced (mg), P = gain in larval dry weight (mg), and T = duration of feeding period (days).

RLF oviposition and damage in field plots

Field plots were set up at the experiment station in 2017 and 2018 for investigation of RLF oviposition and damage in relation to rice plant stages. The plots were planted with either early- and late-season rice or middle-season rice, where the late-season rice was transplanted at 5 days after harvest of the early-season rice. The plots – at four per treatment, each 150 m^2 (10 × 15 m) – were arranged alternatively according to treatment and managed conventionally without pesticide application. Transplanting was on 4 May, 9 June, and 30 July in 2017 and on 10 May, 9 June and 28 July in 2018 for early, middle, and late-season rice, respectively. Numbers of RLF eggs and RLF-damaged and total leaves were scouted in four consecutive hills per sample point at 10 sample points per plot, where one sample point was randomly selected from a row out of every four rows in a plot. The final numbers of RLF eggs per plot were based on 100 hills, and leaf folding (%) per plot was calculated from the number of damaged and total leaves.

Data analysis

Statistical analyses were performed using IBM-SPSS v.23.0. for Windows. Independent-sample t-tests were used to compare the preference of RLF female adults in the Y-tube olfactometer tests. Other data were subjected to ANOVA, followed by Tukey's honestly significant difference (HSD) test to separate means between treatments. Percentage data were arcsine $\sqrt{x}$-transformed and homogeneity of variance of all data was tested using Levene's statistic before ANOVA.

Results

Preference of RLF female adults

In the cage tests, oviposition on rice plants differed among stages ($F_{2,24}$ = 40.267, P<0.001). More eggs were deposited on TS (21-fold) and BS (18.2-fold) rice plants than on SS plants (Figure 1). In Y-tube olfactometer tests, RLF females oriented more to the arm with rice odors vs. the arm without rice plants (CK) (t≤−7.055, d.f. = 18, P<0.001; Figure 2). When given choices between rice plants of different stages, the females preferred TS (t = −2.204, d.f. = 18, P = 0.04) and BS (t = −7.778, d.f. = 18, P<0.001) over SS plants, whereas they showed

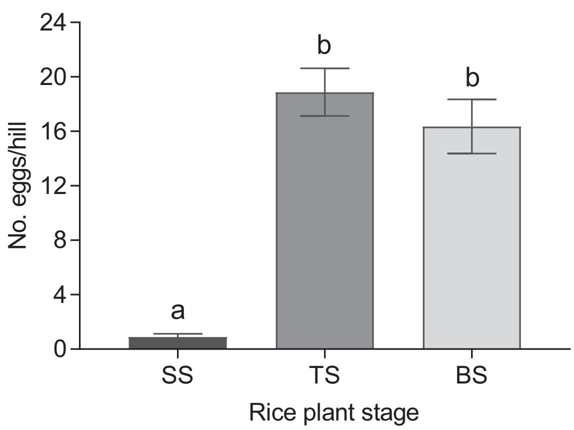

Figure 1 Mean (± SE) oviposition (no. eggs per hill) of *Cnaphalocrocis medinalis* female adults on rice plants of seedling stage (SS), tillering stage (TS) or booting stage (BS) in cage tests. Means capped with a different letter are significantly different (Tukey's HSD test: P<0.05).

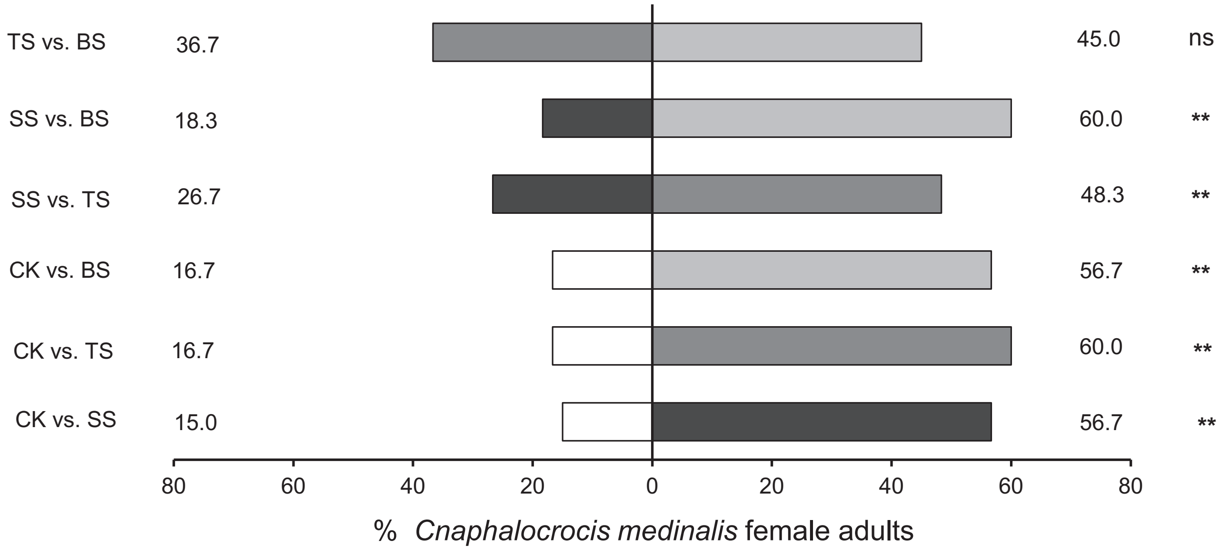

Figure 2 Preference of *Cnaphalocrocis medinalis* female adults for rice plants of seedling stage (SS), tillering stage (TS) or booting stage (BS) in Y-tube olfactometer tests. CK, control without rice plant. Asterisks indicate significant difference between treatments (Independent-samples t-tests: P<0.01; ns, P>0.05).

no preference between TS and BS plants ($t = -1.197$, d.f. = 18, $P = 0.25$; Figure 2).

Performance of RLF offspring

Rice stage effects were not observed in larval duration, pupal duration, and pupal weight ($F_{2,359} \leq 1.888$, $P \geq 0.15$) in the larvae feeding on leaves of different stage plants (Table 1), but they were evident in adult longevity ($F_{2,360} = 72.135$, $P<0.001$) and fecundity ($F_{2,132} = 97.746$, $P<0.001$). Adults from the BS treatment lived the longest, followed by those from the TS treatment (Table 1). Fecundity (no. eggs per offspring female) was 110.7 and 98.3% higher in the TS and BS treatments than in the SS treatment, respectively (Table 1). Rice stage effects were also observed in larval survival rate ($F_{2,27} = 7.585$, $P = 0.002$) and pupation rate ($F_{2,27} = 3.717$, $P = 0.04$) (Table 1). Larvae in the TS treatment exhibited 12.7 and 19.3% lower survival than those in the SS and BS treatments, respectively. Pupation rate was highest in the BS treatment, reaching up to 91.8%. Adult emergence rate did not differ between the treatments ($F_{2,27} = 0.352$, $P = 0.71$; Table 1).

Food utilization efficiency of RLF third instars

Food consumption (FC) of the third instars increased with increasing plant age ($F_{2,117} = 3.626$, $P = 0.03$; Figure 3A). Food consumption was higher, by 18.8 and 25.0%, in the TS and BS treatments than in the SS treatment, respectively. Approximate digestibility (AD) also responded to the plant stage treatment ($F_{2,117} = 8.172$, $P<0.001$; Figure 3B); but, in contrast to FC, AD decreased with the progress of plant stages. Efficiency of conversion of ingested food (ECI) was different among the treatments ($F_{2,117} = 3.138$, $P = 0.047$; Figure 3C) and was higher (by 40.5%) in the SS than in the TS treatment. Relative consumption rate (RCR) ($F_{2,117} = 2.314$, $P = 0.10$;

Table 1 Mean (± SE) performance parameters of *Cnaphalocrocis medinalis* offspring developing on leaves from rice plants of different stages

Rice stage	Larval duration (days)	Pupal duration (days)	Pupal weight (mg)	Adult longevity (days)	Fecundity (eggs/female)	Larval survival rate (%)	Pupation rate (%)	Emergence rate (%)
Seedling	16.2 ± 0.07a	6.0 ± 0.62a	14.1 ± 0.26a	6.3 ± 0.11a	23.3 ± 2.00a	51.2 ± 1.87b	82.8 ± 1.79a	89.5 ± 3.10a
Tillering	16.1 ± 0.10a	6.2 ± 0.58a	14.3 ± 0.32a	7.5 ± 0.09b	49.1 ± 1.30b	44.7 ± 1.87a	89.0 ± 2.93ab	92.6 ± 2.63a
Booting	16.1 ± 0.10a	6.1 ± 0.47a	14.2 ± 0.17a	7.9 ± 0.17c	46.2 ± 1.50b	55.4 ± 2.18b	91.8 ± 1.92b	90.5 ± 2.35a

Means within a column followed by different letters are significantly different (Tukey's HSD test: P<0.05).

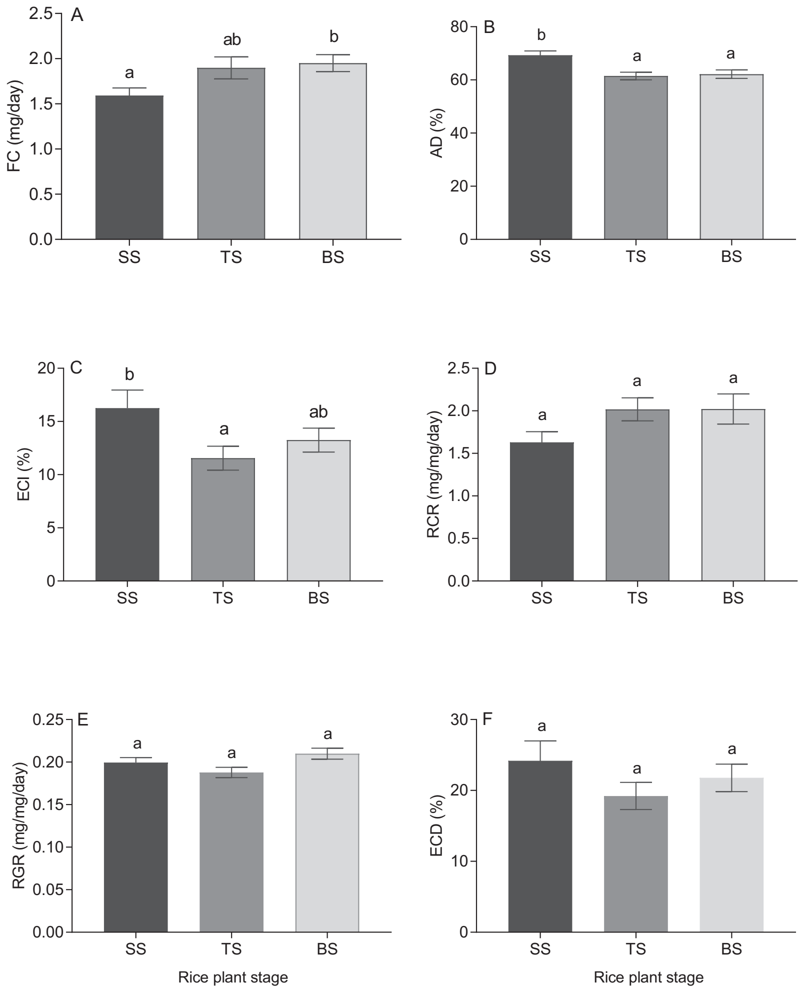

Figure 3 Mean (± SE) food utilization efficiency parameters in third instar *Cnaphalocrocis medinalis* feeding on leaves from rice plants of seedling stage (SS), tillering stage (TS) or booting stage (BS): (A) food consumption (FC), (B) approximate digestibility (AD), (C) efficiency of conversion of ingested food (ECI), (D) relative consumption rate (RCR), (E) relative growth rate (RGR), and (F) efficiency of conversion of digested food (ECD). Means within a panel capped with different letters are significantly different (Tukey's HSD test: P<0.05).

Figure 3D), relative growth rate (RGR) ($F_{2,117} = 3.056$, $P = 0.051$; Figure 3E), and efficiency of conversion of digested food (ECD) ($F_{2,117} = 1.239$, $P = 0.29$; Figure 3F) all did not differ among the treatments.

RLF oviposition and damage in field plots

Due to low RLF occurrence during the late season, the number of eggs and leaf folding (%) per plot were not compared between the middle- and the late-season rice. Between the early- and the middle-season rice, on 17 and 30 June 2017 and 16 June 2018, RLF females preferred the early- (at the booting stage) over the middle- (at tillering stage) season rice for oviposition (Table 2) when plants of the two-season rice plants co-existed in between the field plots. On 3 July 2018, the pest population was low and the difference in number of eggs between rice stages was not evident. It is not surprising that the difference in % folded leaves between rice stages followed the same pattern as number of eggs, higher in the early-season (booting stage) than in the middle-season (tillering stage) rice (Table 2).

Discussion

The relationships between herbivorous insects and their host plants are profoundly impacted by herbivore behaviors that govern acceptance of plants for oviposition and subsequent feeding of the neonates (Schoonhoven et al., 2005). Herbivores usually prefer host plant species that maximize their offspring fitness, and avoid those hosts that lower their fitness (Piyasaengthong et al., 2016; Fei et al., 2017). The mechanism for these choices is described by various hypotheses, which link adult oviposition preference to offspring performance (Scheirs & De Bruyn, 2002; Gripenberg et al., 2010). The PPH predicts maximum oviposition on plants that provide for optimal larval success (Jaenike, 1978; Gripenberg et al., 2010).

Table 2 Mean (± SE) number of *Cnaphalocrocis medinalis* eggs per 100 hills of plants and percentage of folded leaves in field plots of early-season rice (ESR) and middle-season rice (MSR) plants of different developmental stages

Year	Date	Rice stage	No. eggs	% folded leaves
2017	17 June	Booting-ESR	61.3 ± 11.79b	1.8 ± 0.55b
		Tillering-MSR	0.0 ± 0.00a	0.0 ± 0.00a
	30 June	Booting-ESR	13.8 ± 4.27b	18.1 ± 5.73b
		Tillering-MSR	2.5 ± 1.44a	0.6 ± 0.08a
2018	16 June	Booting-ESR	18.1 ± 2.77b	2.1 ± 0.09b
		Tillering-MSR	0.0 ± 0.00a	0.0 ± 0.00a
	3 July	Booting-ESR	1.3 ± 1.25a	3.1 ± 0.27b
		Tillering-MSR	0.6 ± 0.63a	0.2 ± 0.05a

Means within a date and within a column followed by different letters are significantly different (Tukey's HSD test: $P<0.05$).

The PPH has been investigated mostly in plant species-herbivore systems (Wist & Evenden, 2016; Liao & Chen, 2017; García-Coapio et al., 2017), whereas it has been addressed in only a few cases in plant stage-herbivore systems. Varying effects of host stage on herbivore performance have been reported. The larvae of *P. brassicae* feeding on young cabbage plants developed fastest and the resulting pupae weighed the most (Fei et al., 2017). Piyasaengthong et al. (2016) revealed that the small tea tortrix *Adoxophyes honmai* Yasuda neonates performed better on young than on old leaves, whereas the adult female preferred to oviposit on old leaves. In the current study, we found that RLF offspring performed well when the larvae fed on leaves of TS and BS plants, as indicated by the highest fecundity on TS leaves or by the highest larval survival and pupation rate and the greatest adult longevity on BS leaves. These results generally agree with a previous report (Dan & Chen, 1990), in which larval survival rate, pupal weight, and adult longevity and fecundity were highest in RLF larvae feeding on leaves of TS and BS plants. It is worth of mentioning that, although offspring larval survival rate was marginally lower (by 12.7%) on TS than on SS, fecundity was much higher (by 110.7%) on TS than on SS. The quality of host plants affects the insects' behavior and physiology at the population and ecosystem levels (Scriber & Slansky, 1981). The varying RLF offspring performance on leaves of different stage plants may occur as a result of differences in larval food utilization efficiency and nutritional levels of the leaves. Our results showed that third instars consumed most leaf mass when feeding on BS leaves. Previous studies reveal that abundance of chemical compounds in leaves changes with rice growth stage (Sun et al., 2013); particularly, nitrogen content is highest in leaves of TS and BS plants (Chang et al., 2018). The high nitrogen nutritional level of TS and BS leaves coupled with increased consumption of these leaves by RLF larvae may have contributed to their high performance. Although secondary metabolites in rice change radically during development (Sriseadka et al., 2006), it is not certain how the secondary metabolites change in leaves during rice plant development; further studies are needed to measure the changes for interpreting the interaction between leaf-feeding herbivores and host plants.

In the present study, RLF females preferred TS and BS plants over SS plants for oviposition in the cage tests and oriented more to TS and BS plant odors than to SS plant odors in the Y-tube olfactometer tests. These findings are similar to the cage test results in a previous study (Dan & Chen, 1990). Oviposition preference of phytophagous insects may be affected by such factors as the presence of natural enemies (de Silva et al., 2011), host plant species (Knolhoff & Heckel, 2014), leaf age (Rodrigues & Moreira, 1999; Bittencourt-Rodrigues & Zucoloto, 2005; Thomas et al., 2012; Piyasaengthong et al., 2016), morphological characteristics (García-Coapio et al., 2017), and volatiles (Knolhoff & Heckel, 2014). The results of our cage tests and Y-tube olfactometer tests indicate that plant volatiles may play an important role in the selection of plants for oviposition in RLF. Volatiles from TS and BS plants appear more attractive to RLF females. A previous study showed that headspaces of SS, TS, and BS plants of a rice variety Minghui 63 were of the same chemical composition qualitatively, but showed varying concentrations of specific compounds between rice stages (Sun et al., 2013). Further studies are needed to identify specific differences in the relative composition of compounds in odors that elicit RLF female preference among rice plant stages. Once alighting on the plants, females further evaluate the plants using tactile and other cues for oviposition suitability (Hoffman & Rao, 2011). The higher number of eggs deposited on TS and BS plants than on SS plants in the cage tests indicates that leaves of TS and BS plants are more suitable for oviposition than leaves of SS plants.

When considered together, RLF maternal preference for and offspring performance on rice plants of different stages are closely aligned, which is consistent with the PPH (Levins & Macarthur, 1969; Jaenike, 1978; Valladares & Lawton, 1991; Gripenberg et al., 2010; Rigsby et al., 2014; Birke & Aluja, 2017). Rice leaf folder females select TS and BS rice plants for oviposition that are conducive to the development of their offspring. Similar positive coupling between preference and performance have been reported in multiple plant species-herbivore systems (Zhang et al., 2012; Du et al., 2016; Fei et al., 2017). With different stages of a plant species or leaf ages, there are also reports, albeit fewer, supporting the PPH. The caterpillars of *Ascia monuste* Godart feeding on young leaves of *Brassica oleracea* L. showed higher performance than those feeding on old leaves, which matches with adult females' oviposition preference for young leaves (Bittencourt-Rodrigues & Zucoloto, 2005). The larvae of *Ophraella communa* LeSage prefer feeding on vegetative plants of *Ambrosia artemisiifolia* L., on which adult females prefer for oviposition (Wang et al., 2011). Nevertheless, there are also cases in which oviposition preference and offspring performance do not match (Jallow & Zalucki, 2003; Jiao et al., 2012; Li & Liu, 2015; Piyasaengthong et al., 2016; Jiao et al., 2017). Specifically, for RLF, no significant correlation between offspring performance and oviposition preference for rice genotypes was found (Liao & Chen, 2017), whereas for rice and non-rice graminaceous plants, a strong preference and performance correlation was reported (Zhang et al., 2019). Therefore, the preference and performance relationship in herbivorous insects may be case-specific, depending on the host plant species/genotype, the herbivorous insect, and/or the plant stage. As shown by the analysis by Gripenberg et al. (2010), several ecological and/or life-history factors can modify the strength of the preference and performance relationship, which may include diet specialization of the herbivore, temporal variation in host plant quality, offspring mobility, egg distribution, importance of larval food resource on adult fitness, and inter- or intraspecific plants (Gripenberg et al., 2010). The facts of limited mobility in neonate RLF larvae, RLF adult fitness depending heavily on larval feeding, and temporal difference in nitrogen content between rice stages (Chang et al., 2018) drive to the 'wise' selection by the RLF mothers when confronted by rice plants of different stages, i.e., selecting TS and BS plants that are conducive to their offspring performance for oviposition.

The current results are meaningful in explaining patterns of RLF damage in the field. Currently, in the major rice-producing areas in southern China, early-, middle-, and late-season rice are often intercropped. Rice leaf folder immigration peaks during mid-May and late June (Jiang et al., 2011), coinciding with the tillering stage of early-season rice and the seedling stage of middle-season rice. Our laboratory test results predict that immigrant RLF adults will mostly select the early-season rice for oviposition, which matches with our field plot results and also explains the heavy RLF infestation and damage in early-season rice during late May and mid-June (Jiang et al., 2011). During the middle rice producing season, the mostly locally produced RLF adult populations (Jiang et al., 2011), based on the results of this study, would select the middle-season rice for oviposition, corresponding to a second slight damage peak in the middle-season rice during mid- and late July (Jiang et al., 2011), which is not evident in the current field plot experiment because of low RLF occurrence. In light of the current findings, synchronizing rice planting, either double-season or single-season rice, instead of intercropping double- and single-season rice in an area, can be expected to lessen RLF infestation in the early- and middle-season rice, and will reduce RLF damage and pesticide application for RLF control.

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