

Plant chemicals affect trade-offs between adult preference and larval performance of the rice water weevil, *Lissorhoptrus oryzophilus*

Qiyun Wang

Henan University College of Life Science

Wei Huang

Wuhan Botanical Garden

Jialiang Zhang

Wuhan Botanical Garden

Dingli Wang

Henan University of Science and Technology

Wandong Yin (✉ wojiaowandong1@163.com)

Henan University College of Life Science <https://orcid.org/0000-0002-3418-2477>

Jianqing Ding

Henan University College of Life Science

Research Article

Keywords: plant volatiles, plant defence, host plant selection, adult performance, offspring performance, *Lissorhoptrus oryzophilus*

Posted Date: March 23rd, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-222227/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

Herbivores use plant chemicals for host-plant selection to maximize their own and/or offspring performance. Since host plants that are optimal for mother and offspring are often different and spatially/temporally separated, how plant chemicals affect trade-offs between adult preference and larval performance remains unclear. We found that adults of the rice water weevil (*Lissorhoptrus oryzophilus*), one of the most important pests on rice in the world, preferred volatiles from barnyard grass over rice, tended to feed and oviposit on barnyard grass compared with rice. In contrast, larvae performed better on rice roots than on barnyard grass roots. Chemical analysis further show that rice roots had higher nitrogen and soluble sugar but lower lignin and cellhouse contents than barnyard grass. Together, these results suggest that volatile, nutritive and defensive chemicals could jointly determine trade-offs of the adult preference and larval performance on these two hosts. As developing chemical-based technology is one of the main approaches for control of pest insects, our findings may also contribute to the future efforts for management of the rice water weevil.

Key Message

- This study aimed to explore how volatile, nutritive and defensive chemicals affect adult preference and larval performance of rice water weevils on barnyard grass and rice.
- Adults preferred barnyard grass over rice for feeding and oviposition. Y-tube tests on adult behaviours and analysis of volatiles indicate that chemicals emitted by barnyard grass might attract more adults than those of rice.
- Larvae developed better on rice than on barnyard grass. Rice roots had higher nitrogen and soluble sugar but lower lignin and cellhouse contents than barnyard grass.

Introduction

Insect host selection behaviour and performance are affected by plant primary and secondary metabolites (Awmack and Leather 2002; Jakobs and Müller 2019; Wang et al. 2020). When insects locate and select potential host plants, volatile secondary metabolites emitted by plants can function as long-distance cues (Allmann et al. 2013; Dahlin et al. 2014; Liu et al. 2020). For example, plum psyllid (*Cacopsylla pruni*) can use plant volatiles to locate their favorable food resources from a distance (Gallinger et al. 2019). When insects come into contact with plants, nutritive and defensive metabolites can determine host plant suitability and subsequently affect their survival, growth, and reproduction (Gonçalves-Alvim et al. 2004; Michael 2018; Brzozowski et al. 2020). Therefore, simultaneously assessing the roles of plant volatiles, nutritive and defensive chemicals in determining the relationship between insect host selection and their performance is of the utmost importance to better understanding the underlying mechanism of host plant selection. This knowledge may also contribute to the development of environmentally sustainable integrated pest management strategies, such as breeding high resistant

cultivars, developing push-pull technologies and volatile-based traps, given plant primary and secondary metabolites can significantly affect pest insect preference and performance.

Many previous studies have reported the relationships between insect adult preference (e.g., feeding and oviposition) and larval performance (e.g., growth development) (Wiklund 1975; Jaenike 1978; Fox 1993; Gripenberg et al. 2010). According to the preference–performance hypothesis (or the mother knows best hypothesis) (Jaenike 1978), female adults are expected to optimize their fitness by laying eggs on the host plants on which their offspring will perform best. Findings from many previous studies supported this theory (e.g., Heisswolf et al. 2005; Zhang et al. 2012), however, some other studies also found that host plants preferred by parental adults for oviposition might not be the best hosts for development of their offspring larvae (Scheirs et al. 2000; Scheirs et al. 2004; Jiao et al. 2012; Smith et al. 2018). These adult-larva conflicts, or trade-offs between adult preference and larval performance may be attributed to a lot of factors (Wiklund 1975; Fox 1993; Van Nouhuys et al. 2003; Merwin et al. 2020), such as variation in host suitability. For example, insect adults and larvae often feed on different plant tissues (leaves vs. roots) and these tissues are often spatially and temporally separated (Krebs and Davies 1997; Clark et al. 2011; Lee et al. 2016), different chemicals in leaves and roots may then differently affect adult preference and larval performance (Huang et al. 2013). Therefore, understanding chemical-mediated host plant selection in the context of trade-offs between adult preference and larval performance may help us to better understand the ultimate and proximate reasons for insect host plant selection and development.

Plant species differ in volatile, nutritive, and defensive chemicals, thus differently affecting insects and their interactions with host plants (Mattson 1980; Bezemer and van Dam 2005; Aartsma et al. 2019). Different plants emit variable chemicals that attract different insects or different numbers of individuals. It is also well-known that high contents of nitrogen, or low carbon/nitrogen in plants may favour insect development as of more proteins, while high content of lignin and celluloses can inhibit insect digestion (Awmack and Leather 2002; Kitajima et al. 2012; Armani et al. 2020). Moreover, flavonoids and oxalate are often considered defensive chemicals in some crops, such as rice (Yoshihara et al. 1980; Nenaah 2013; Dai et al. 2019), and contents of these chemicals may differ between host species. Therefore, variations of these volatile, nutritive, and defensive chemicals in host plant species may determine the difference of adult host location behaviours, oviposition, and larval development, leading to potential trade-offs between adult preference and larval performance. Tests on this prediction is critical in understanding of the chemical-mediated insect host plant selection and performance.

Here, we report how host plant chemicals affect adult location behaviours and larval performance of the rice water weevil (abbreviated RWW), *Lissorhoptrus oryzophilus* (Coleoptera: Curculionidae). RWW is one of the most destructive pests on rice (*Oryza sativa* L.) in the world (Saito et al. 2005; Aghaee and Godfrey 2014). In many introduced ranges such as China, RWW undergoes parthenogenetic reproduction without mating and there has been no males invaded. Adults primarily feed on leaves and lay eggs on submerged areas of the leaf sheaths, and their larvae develop in the plant roots (Stout et al. 2002; Aghaee and Godfrey 2014). Larvae pupate on roots. *L. oryzophilus* has a wide range of host plants, including rice and barnyard grass (*Echinochloa crusgalli* L.). The insect occurs one generation per year in central China

where we conducted our study. Previous studies have found that females performed better on barnyard grass, while their larvae survived better on rice (Tindall and Stout 2003). However, it remains unknown that how host plant volatiles, nutrients and defensive compounds affect host selection and performance when the optimal adult and offspring plants are different.

In this study, we focus on the roles of chemicals in host selection and performance in *L. oryzaophilus* with rice (*O. sativa*) and barnyard grass (*E. crusgalli*). Specifically, we first compared the responses of *L. oryzaophilus* adult females to volatiles from rice and barnyard grass in a Y-tube olfactometer. We also measured volatiles from rice and barnyard grass to compare the volatile composition difference. We then determined the feeding and oviposition preferences of *L. oryzaophilus* adult females between rice and barnyard grass, as well as larval performance (i.e., weight) on these two hosts. Finally, we analysed the nutritional and defensive compounds in the roots of rice and barnyard grass to examine their effects on larval performance.

Materials And Methods

Plants and insects

We used the rice variety Shenliangyou 3117 for this experiment. This variety is widely grown in the Yangtze River basin. Rice seeds were purchased from Hubei Seed (Wuhan, Hubei Province, China). The barnyard grass seeds were collected from a rice field (Shenliangyou 3117) near Wuhan city, Hubei province, China (31°54' N, 115°24' E). The seeds were sown in seedling trays with 72 plugs filled with commercial nutrition soil for germination. After 10 days, similar-sized seedlings were individually transplanted into plastic pots (25 cm height and 20 cm diameter) with a substrate of standard paddy soil and arranged in an outdoor common garden. Potted plants at the early tillering stage (32-36 cm height) were used for following experiments. To prevent herbivore damage, each pot was enclosed by a small nylon screen cage (60 × 60 × 60 cm). The RWWs for this study were collected from the same rice field mentioned above and were reared on potted rice seedlings (Shenliangyou 3117) in an insectary at 32 ± 1 °C, 70% relative humidity and 16:8 h photoperiod.

Adult feeding and oviposition preferences

To determine RWW adult preference in feeding and oviposition between rice and barnyard grass, we conducted two choice experiments in the summer of 2019 at Wuhan Botanical Garden, Chinese Academy of Science, Wuhan city, Hubei Province, China (30°32' N, 114°25' E). The choice arena was set up as follows. Two potted plants, one of each species (i.e., rice and barnyard grass), were carefully placed into basins (28 cm in height and 48 cm in diameter). Each basin was then filled with water until the water depth inside the basin was approximately 8 cm above the soil surface. To prevent the weevils from escaping, each basin was covered with a large screen cage (100 × 100 × 100 cm).

In the feeding preference experiment, we released five RWW adults into each cage and allowed them to feed for 10 days. Then, we collected all the leaves of both plant species to measure total area and damaged areas of each leaf using a Vernier calliper (0.02 mm accuracy). This experiment was repeated 24 times.

In the oviposition preference experiment, we released six RWW adults into each cage for oviposition. After 5 days, we removed all adults and counted the number of eggs on each plant according to the method described in Stout et al. (2002). After cleaning the plants with running water, whole plants were placed in 95% alcohol for bleaching. The number of eggs on each plant was counted under a dissecting microscope. This experiment was repeated 15 times.

Y-tube olfactometer assays

To test the effect of volatile on adult preference, we carried out a choice experiment using a Y-tube olfactometer. The experimental setup and parameter settings are based on those in our previous work (Sun et al. 2019). Briefly, the Y-shaped glass tube consisted of a base tube (12 cm length and 2 cm diameter) and two 12-cm branching arms. The angle between the two arms was 90°. Each arm of the Y-tube was connected through Teflon tubing to a glass cylindrical container (90 cm height and 22 cm diameter) with the odour source. The Y-tube was placed horizontally during the experiments. The experiments were conducted under dark conditions in a climate-controlled room (28 °C and 70% relative humidity) to ensure air purity and exclude light effects.

RWW adults were starved for 24 h before the choice experiment, and only healthy and active adults were used. For each test, an adult was released into the downwind arm of the Y-tube and given 2 min to make a choice. A positive choice was recorded when the adult entered the right or left arm of the olfactometer and remained there for at least 10 s. If the adult failed to make a choice within 2 min, it was removed from the Y-tube and excluded from the statistical analyses. To avoid positional effects, we alternated between stimuli in each Y-tube arm for every test. The Y-tube olfactometer was also cleaned with alcohol between tests. Each adult was tested only once. In total, 60 female adults were recorded in this experiment.

Volatile collection and identification

To examine whether there is a difference in volatile composition and determine which active compounds RWW adults might use to locate their preferred host plant, we collected and then identified volatiles from the two host plants. Dynamic headspace methods were used to collect the volatiles as described by Turlings et al. (1998). Individual plants were bagged with polyethylene oven bags (406 × 444 mm; Reynolds, Richmond, VA, USA). Volatile collection lasted for 24 h and was replicated 10 times for each plant species. We also carried out the same procedure with empty oven bags (N = 10) to obtain negative

controls. After collection, the volatiles were eluted from the adsorbent (80/100 mesh Porapak Q adsorbent, Sigma, USA) with 1.5 mL of dichloromethane (Sigma-Aldrich) for gas chromatography-mass spectrometry (GC-MS) analyses.

We conducted volatile analyses using a GC-MS system (GC-2010 Plus; Shimadzu Inc., Japan) equipped with a fused silica capillary column (Rxi-5 MS; Shimadzu Inc., Japan) according to Sun et al. (2019). We used the NIST08 MS spectral library database to identify the plant volatiles. We obtained the percentage of each compound by integrating their peak areas. We confirmed the identities of the compounds using chromatographic comparisons with commercial standards (Sigma, USA). We used principal component analysis (PCA) to analyse these data.

Adult oviposition in no-choice test

To examine how a single host plant affected RWW oviposition, we conducted a test on the insect fecundity in a no-choice test. We reared and observed the weevils from individual flooded pots (25 cm height and 20 cm diameter) that each contained a plant. A single female adult from the colony was introduced to each pot. To confine the adult to the plant, the plant in the pot was sealed with a nylon bag. The cylindrical nylon bag (30 cm diameter, 100 cm height) was made of white netting (0.02 mm mesh size) and secured with a string. Every 4 days, we collected the plant from each pot, counted the number of eggs on the plant, and transferred the adult to a new potted plant of the same species. The experiment was terminated after 12 days. During the experiments, if an adult weevil could not be found on a test plant, that replicate was removed, and a new replicate was established to ensure that 20 similar-sized adults would be tested for each plant species. The experiment was conducted in an insectary ($32 \pm 1^\circ\text{C}$, 70% relative humidity and 16:8 h photoperiod).

Larval performance tests

To examine the effects of host plants on the growth of RWW larvae, we conducted a larval performance test with rice and barnyard grass in an insectary ($32 \pm 1^\circ\text{C}$, 70% relative humidity and 16:8 h photoperiod). A female adult was transferred to each pot ($n=15$ for each species of rice and barnyard grass) and allowed to lay eggs for 1 day. The pot was covered with a cylinder (15 cm diameter and 50 cm height) with one end inserted into the soil to confine the weevil. One day later, the adult weevil was removed. Twenty-five days later, we carefully uprooted the plants from the pots and searched for larvae on the roots. Each larva was weighed using an electronic balance (Sartorius BS 110 S, Germany). In total, 23 and 21 larvae were examined on rice and barnyard grass, respectively.

Leaf and root chemicals

To determine primary and secondary chemicals in leaves and roots, we harvested plant materials to make measurement of total nitrogen, carbon, soluble sugars and flavonoids, oxalates, lignin and cellulose. The leaves and roots of the potted plants at the tillering stage were separately collected. Each pot contained 3-5 healthy individual plants, and 8 pots were used for each plant species, resulting in 8 leaf samples and 8 root samples for each plant species. The samples were first divided into two parts before being weighed. One part of each sample was immediately frozen in liquid nitrogen and stored at -80°C until the oxalate content analysis. The other part of each sample was oven-dried at 105°C for 30 min and then oven-dried at 65°C for 48 h for analysis of N, soluble sugar, soluble protein, cellulose, lignin and flavonoid contents.

The oxalate concentration of each sample was analysed by high-performance liquid chromatography (HPLC) according to Libert (1981) and Xu et al. (2006). The concentrations of flavonoid, soluble sugar, soluble protein, cellulose and lignin were analysed with an ultraviolet and visible spectrophotometer (UVS) (Thermo Scientific GENESYS 10S, Waltham, MA, USA). The flavonoid concentrations were analysed as described by published methods (Sun et al. 2016). The soluble protein and soluble sugar were determined as described by Bradford (1976) and Elleuch (2007), respectively. The plant cellulose and lignin contents in dry tissue were determined by the methods of Updegraff (1969) and Morrison (1972), respectively. The total nitrogen content of each sample were measured using an elemental autoanalyser (Vario MAX CN, Germany).

Statistical analyses

Data analyses were performed with R (v3.6.3). All data were tested for normality using the Shapiro-Wilk test before being compared. For the Y-tube olfactory assay, the proportions of RWW female adults on rice and barnyard grass were compared using Wilcoxon's signed rank test, as the data were not normally distributed even after being transformed. To test for the feeding and oviposition preferences of RWW female adults, the leaf area removed (cm^2) and the number of eggs between rice and barnyard grass were separately compared using the paired samples t -test. The volatile compounds identified (peak areas corrected by dry plant weight in grams) from rice and barnyard grass were analysed by a principal component analysis (PCA) to detect the differences between rice and barnyard grass volatiles. The PCA was conducted using the function `prcomp` in R, and further screened by partial least squares discriminant analysis (PLS-DA). We compared the 12-day fecundity of RWW female adults feeding on rice leaves or barnyard grass leaves using the independent samples t -test. We also compared the larval weights feeding on rice roots or barnyard grass roots using the Mann-Whitney U test, as the data were not normally distributed even after being transformed. The differences in nitrogen, C: N ratio, soluble sugar, soluble protein, cellulose, lignin, flavonoid and oxalate contents in roots and leaves of rice and barnyard grass were separately compared by using the independent samples t -test. Data analyses were performed with R (v3.6.3) using the `mixOmics` and `RVAideMemoire` packages.

Results

Adult feeding and oviposition preferences

In the two-way feeding choice experiments (Fig. 1a), the leaf area removed by *L. oryzaophilus* females was significantly larger for barnyard grass than for rice ($t_{45.84} = 3.98$, d.f. = 1, $p < 0.001$). Similarly, in the two-way oviposition choice experiments (Fig. 1b), *L. oryzaophilus* females laid significantly more eggs on barnyard grass than on rice ($t_{14.00} = 5.61$, d.f. = 1, $p < 0.001$).

Y-tube olfactometer assays and volatile identification

L. oryzaophilus females showed a stronger preference for the volatiles from barnyard grass (*E. crusgalli*) than for those from rice (*O. sativa*) ($V = 4.99$, $p < 0.001$; Fig. 2a). In total, 105 volatile compounds were identified from barnyard grass and rice via GC-MS (electronic supplementary material, Table S1). The PCA plot indicated that the volatile compositions of rice and barnyard grass were significantly different (Fig. 2b). Twelve compounds were primarily responsible for the difference in volatile composition between rice and barnyard grass (electronic supplementary material, Table S1).

Adult oviposition and larval performance in no-choice tests

The adult oviposition and larval growth of *L. oryzaophilus* on rice and barnyard grass differed significantly (Fig. 3). *L. oryzaophilus* females reared on barnyard grass laid $50.50 (\pm 1.22 \text{ s.e.})$ eggs within 12 days, which was significantly higher than the number of eggs laid by *L. oryzaophilus* females reared on rice ($38.85 \pm 1.01 \text{ s.e.}$) ($t_{36.74} = 7.40$, d.f. = 1, $p < 0.001$; Fig. 3a). In terms of larval performance, *L. oryzaophilus* larvae were significantly heavier on rice than barnyard grass ($W = 2.93$, $p < 0.01$; Fig. 3b).

Leaf and root chemicals

There were significant differences in the nutrient and defensive chemicals in the leaves of rice and barnyard grass (Fig. 4a-d). Nitrogen contents were significantly higher in the rice leaves than in the barnyard grass leaves ($t_{13.77} = 9.08$, d.f. = 1, $p < 0.001$; Fig. 4a), and the leaf C:N ratio ($t_{11.56} = -13.70$, d.f. = 1, $p < 0.001$; Fig. 4d) were significantly higher in the barnyard grass than in the rice. Compared to the barnyard grass, leaf soluble protein ($t_{13.50} = 2.39$, d.f. = 1, $p < 0.05$; Fig. 4b) and soluble sugar ($t_{13.58} = 23.42$, d.f. = 1, $p < 0.001$; Fig. 4c) contents in rice were significantly higher.

In terms of leaf defences, the rice leaves had significantly higher flavonoid content ($t_{13.99} = 17.29$, d.f. = 1, $p < 0.001$; Fig. 4e) and oxalate content ($t_{10.63} = 2.42$, d.f. = 1, $p < 0.05$; Fig. 4f) than the barnyard grass leaves. However, there was no significant difference in the cellulose ($t_{7.96} = -1.05$, d.f. = 1, $p > 0.05$; Fig. 4g) and lignin ($t_{13.85} = -0.83$, d.f. = 1, $p > 0.05$; Fig. 4h) contents between rice and barnyard grass leaves.

Similarly, root nutrient and root defensive contents also differed significantly between rice and barnyard grass (Fig. 5a-h). The nitrogen contents in rice roots were significantly higher than those in barnyard

grass roots ($t_{13.29} = 5.55$, d.f. = 1, $p < 0.001$; Fig. 5a). The root C:N ratio ($t_{13.78} = -14.22$, d.f. = 1, $p < 0.001$; Fig. 5d) in barnyard grass were also significantly higher than those in rice. However, the rice roots had significantly higher soluble protein ($t_{13.97} = 2.31$, d.f. = 1, $p < 0.05$; Fig. 5b) content and soluble sugar ($t_{12.51} = 8.07$, d.f. = 1, $p < 0.001$; Fig. 5c) content than the barnyard grass roots.

The oxalate content ($t_{13.73} = 2.36$, d.f. = 1, $p < 0.05$; Fig. 5f) and flavonoid content ($t_{11.95} = 9.15$, d.f. = 1, $p < 0.001$; Fig. 5e) were significantly higher in rice roots than in barnyard grass roots. Additionally, the contents of cellulose ($t_{10.26} = -4.09$, d.f. = 1, $p = 0.001$; Fig. 5g) and lignin ($t_{13.20} = -3.38$, d.f. = 1, $p \leq 0.01$; Fig. 5h) were significantly higher in barnyard grass roots than those in rice roots.

Discussion

In this study, we found RWW adults preferred barnyard grass over rice for feeding and oviposition while their larvae developed better on rice than on barnyard grass which are in line with previous studies (Tindall and Stout 2003). Our Y-tube tests on adult behaviours and analysis of volatile chemicals indicate that chemicals emitted by barnyard grass might attract more adults than those of rice. Moreover, our analyses of nutritive and defensive chemicals show rice roots had higher nitrogen and soluble sugar but lower lignin and cellulose contents than barnyard grass, being more suitable host for larvae. Therefore, our study provides evidence showing chemicals affect trade-offs of RWW adult preference and larval performance on these two hosts, which is critical in understanding of the ecological interactions of this global pest insect and its important crop host.

In general, herbivorous insect adults use chemical cues to choose suitable host plants for feeding and oviposition (Trona et al. 2013; Knolhoff and Heckel 2014; Webster and Cardé 2016; Berteaux et al. 2020). Our olfactometer assays showed that RWW adults had a stronger preference for the volatiles from barnyard grass than for those from rice. Through volatile analysis, we further found that the types and contents of volatile compounds differed considerably between rice and barnyard grass. This suggests that RWW adults can distinguish differences in the quality and/or quantity of volatile compounds between barnyard grass and rice and that they rely on volatile cues to locate host plants. In the choice bioassay, we also found that RWW adults preferred to feed and lay their eggs on barnyard grass over rice. Our adult performance tests on oviposition showed the same results (Fig. 3a), further confirming that barnyard grass is better host for adults than rice. Together, in this study volatile cues may provide RWW adults with reliable and easily assessed information to use to select high-quality host plants.

Similarly, we also found that the nitrogen and soluble sugar content were lower in barnyard grass leaves than in rice leaves. We are unclear how such differences are related to the high RWW fecundity on barnyard grass leaves. However, we found that the flavonoid and oxalate contents were lower in barnyard grass leaves, and the lignin and cellulose contents were similar between two host plants. Previous studies reported that flavonoids could negatively affect food consumption and utilization by adult insects (Nenaah 2013), thus high flavonoid in barnyard grass leaves might have negative impact on RWW fecundity in our study. Similarly, oxalate and its calcium salts are widely existing in plants and often deter

insect herbivory (Franceschi and Nakata 2005), thus rice varieties with high rich oxalate could have high resistance to insect herbivory (Yoshihara et al. 1980). Overall, in this study, the low defensive compounds such as flavonoid and oxalate in barnyard grass leaves might explain the better adult performance on this host.

In contrast to adults, larval performance was better on rice than on barnyard grass in this study. Abundant evidence has shown that high nitrogen contents contribute to the enhancement of herbivore performance (Atijegbe et al. 2020; Eberl et al. 2020). Consistently, our results showed that the nitrogen and soluble sugar content were higher in rice roots than in barnyard grass roots, suggesting that rice roots would provide more nutrients to larvae than barnyard grass. Moreover, the low lignin and cellulose in rice roots might facilitate food digestion in the larvae, thus also improving their performance. In addition, in this study, flavonoid and oxalate in roots appear to have less effects on RWW larvae than the effect of those chemicals in leaves on adults. Due to their limited mobility and food exploration ability, larvae likely have a stronger ability to detoxify plant defences than adults (Mason et al. 2019). We also acknowledge that some other chemicals such as lipids which were not measured in this study might affect RWW growth in this study. Finally, as RWW laid more eggs on barnyard grass, competition between larvae for food and space could potentially have affected their development. Future work is needed to explicitly reveal how these factors differently affect larval developments on the two host plants.

Adults often choose high-quality host plants for maximizing their offspring performance (Minkenberg and Ottenheim 1990; Thompson and Pellmyr 1991; Gripenberg et al. 2010; Heisswolf et al. 2005). Our findings of the trade-offs between adult preference and larval performance on barnyard grass and rice are inconsistent with the “mother knows best” theory (Scheirs et al. 2000; Mayhew 2001). Previous studies show that genetic correlations, natal-habitat experience, natural host plant range and maternal effects can affect adult preference and offspring performance, leading to their trade-offs (Wiklund 1975; Fox 1993; Merwin et al. 2020). For RWW, such trade-offs on barnyard grass and rice were reported in several previous studies and the maternal effects were likely small (Tindall and Stout 2003; Tindall et al. 2004). In our study, the differences in volatile, nutritive and defensive compounds between the two hosts could largely explain differences in the adult preference and larval performance. However, some other ecological and evolutionary factors may also affect the adult host selection and larval performance. RWW is native to North America where barnyard grass is its one of the ancestral host (Webb 1914; Lange and Grigarick 1959), however, rice, which is native to Asia, is a relatively novel host of this insect. Therefore, lack of long-term co-evolution with rice may affect the adult host selection, even if rice is more nutritive and less defended than its ancestral host barnyard grass. In addition, since adult host selection is often affected by natural enemies, different predators or parasitoids associated with the two hosts and their field habitats may also determine adult behaviours. In this regard, future work is needed to reveal how evolution history and natural enemies affect the adult host selection and larval performance. Moreover, in this study, our data could not show the linkages between the adult feeding and larval development, which may be mediated by the volatile cues and/or the herbivory-induced resistance that may vary between adults and larvae, future experiments focusing on these issues may also assist to explicitly unveil mechanisms behind these complex interactions.

In conclusion, this study shows chemicals determine the trade-offs of RWW adult preference and larval performance on barnyard grass and rice. Our findings highlight the importance of considering plant nutrients, defences and volatiles for better understanding the relationship between adult selection and offspring performance. Since RWW has become one of the most important invasive pests worldwide affecting rice production, our findings may also be useful in future efforts around integrated pest management. Our results on rice root chemicals will facilitate future selection and breeding for rice cultivars with high chemical resistance to belowground pests such as RWW larvae. Moreover, because RWW adults showed a strong tendency for volatiles of barnyard grass, it may be possible to use barnyard grass as a bait plant growing nearby rice to attract adults. We identified 12 volatile compounds that were responsible for the differences between the volatile compositions of rice and barnyard grass, further research is also needed to identify the specific volatile compounds used for host selection by RWW adults. This will be a basis for further development of volatile-based trap to manipulate the pest populations in the field.

Declarations

Author's contributions JD and WY conceived the idea and designed the experiments, QW conducted the experiments and analysed the data. JD and WY, WH drafted the manuscript. All authors revised and approved the manuscript.

Acknowledgements We are grateful to Jialiang Zhang and Chujun Zhang for their help with the collection of the field populations and Dingli Wang for their assistance with the bioassays.

Funding We gratefully acknowledge funding support from Henan University.

Compliance with ethical standards

Conflict of interests We have no competing interests.

References

Aartsma Y, Leroy B, van der Werf W, Dicke M, Poelman EH, Bianchi FJJA (2019) Intraspecific variation in herbivore-induced plant volatiles influences the spatial range of plant-parasitoid interactions. *Oikos* 128:77–86

Aghaee MA, Godfrey LD (2014) A century of rice water weevil (Coleoptera: Curculionidae): a history of research and management with an emphasis on the United States. *J Integr Pest Manag* 5:1–14

Allmann S, Späthe A, Bisch-Knaden S, Kallenbach M, Reinecke A, Sachse S, Baldwin IT, Hansson BS (2013) Feeding-induced rearrangement of green leaf volatiles reduces moth oviposition. *eLife* 2:e00421

Armani M, Goodale UM, Charles-Dominique T, Barton KE, Yao X, Tomlinson KW (2020) Structural defence is coupled with the leaf economic spectrum across saplings of spiny species. *Oikos* 129:740–752

- Atijegbe SR, Mansfield S, Ferguson CM, Worner SP, Rostás M (2020) Host range expansion of an endemic insect herbivore is associated with high nitrogen and low fibre content in exotic pasture plants. *J Chem Ecol* 46:544–556
- Awmack CS, Leather SR (2002) Host plant quality and fecundity in herbivorous insects. *Annu Rev Entomol* 47:817–844
- Bertea CM, Casacci LP, Bonelli S, Zampollo A, Barbero F (2020) Chemical, physiological and molecular responses of host plants to Lepidopteran egg-laying. *Front Plant Sci* 10:1768
- Bezemer TM, van Dam NM (2005) Linking aboveground and belowground interactions via induced plant defenses. *Trends Evol* 20:617–624
- Bradford MM (1976) A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Anal Biochem* 72:248–254
- Brzozowski LJ, Gore MA, Agrawal AA, Mazourek M (2020) Divergence of defensive cucurbitacins in independent *Cucurbita pepo* domestication events leads to differences in specialist herbivore preference. *Plant Cell Environ* 40:31–39
- Clark KE, Hartley SE, Johnson SN (2011) Does mother know best? The preference-performance hypothesis and parent-offspring conflict in aboveground-belowground herbivore life cycles. *Ecol Entomol* 36:117–124
- Dahlin I, Vucetic A, Ninkovic V (2014) Changed host plant volatile emissions induced by chemical interaction between unattacked plants reduce aphid plant acceptance with intermorph variation. *J Pest Sci* 88:249–257
- Dai Z, Tan J, Zhou C, Yang X, Yang F, Zhang S, Sun S, Miao X, Shi Z (2019) The OsmiR396-OsGRF8-OsF3H-flavonoid pathway mediates resistance to the brown planthopper in rice (*Oryza sativa*). *Plant Biotechnol J* 17:1657–1669
- Eberl F, Fernandez de Bobadilla M, Reichelt M, Hammerbacher A, Gershenzon J, Unsicker SB (2020) Herbivory meets fungivory: insect herbivores feed on plant pathogenic fungi for their own benefit. *Ecol Lett* 23:1073–1084
- Elleuch M, Besbes S, Roiseux O, Blecker C, and Attia H (2007) Quality characteristics of sesame seeds and by-products. *Food Chem* 103:641-650
- Fox CW (1993) A quantitative genetic analysis of oviposition preference and larval performance on two hosts in the bruchid beetle, *Callosobruchus maculatus*. *Evolution* 47:166–175
- Franceschi VR, Nakata PA (2005) Calcium oxalate in plants: formation and function. *Annu Rev Plant Biol* 56:41–71

- Gallinger J, Jarausch B, Jarausch W, Gross J (2019) Host plant preferences and detection of host plant volatiles of the migrating psyllid species *Cacopsylla pruni*, the vector of European Stone Fruit Yellows. *J Pest Sci* 93:461–475
- Gonçalves-Alvim SJ, Collevatti RG, Fernandes GW (2004) Effects of genetic variability and habitat of *Qualea Parviflora* (Vochysiaceae) on herbivory by free-feeding and gall-forming insects. *Ann Bot* 94:259–268
- Gripenberg S, Mayhew PJ, Parnell M, Roslin T (2010) A meta-analysis of preference-performance relationships in phytophagous insects. *Ecol Lett* 13:383–393
- Heisswolf A, Obermaier E, Poethke HJ (2005) Selection of large host plants for oviposition by a monophagous leaf beetle: nutritional quality or enemy-free space? *Ecol Entomol* 30:299–306
- Huang W, Siemann E, Yang X, Wheeler GS, Ding J (2013) Facilitation and inhibition: changes in plant nitrogen and secondary metabolites mediate interactions between above-ground and below-ground herbivores. *Proc R Soc B* 280:20131318
- Jaenike J (1978) On optimal oviposition behavior in phytophagous insects. *Theor Popul Biol* 14:350–356
- Jakobs R, Müller C (2019) Volatile, stored and phloem exudate-located compounds represent different appearance levels affecting aphid niche choice. *Phytochemistry* 159:1–10
- Jiao X, Xie W, Wang S, Wu Q, Zhou L, Pan H, Liu B, Zhang Y (2012) Host preference and nymph performance of B and Q putative species of *Bemisia tabaci* on three host plants. *J Pest Sci* 85:423–430
- Kitajima K, Llorens AM, Stefanescu C, Timchenko MV, Lucas PW, Wright SJ (2012) How cellulose-based leaf toughness and lamina density contribute to long leaf lifespans of shade-tolerant species. *New Phytol* 195:640–652
- Knolhoff LM, Heckel DG (2014) Behavioral assays for studies of host plant choice and adaptation in herbivorous insects. *Annu Rev Entomol* 59:263–278
- Krebs JR, Davies NB (1997) Behavioural ecology. Blackwell Science.
- Lange WH, Grigarick AA (1959) Rice water weevil: Beetle pest in rice growing areas of southern states discovered in California. *Calif Agr* 13:10–11
- Lee G, Joo Y, Diezel C, Lee EJ, Baldwin IT, Kim SG (2016) *Trichobaris* weevils distinguish amongst toxic host plants by sensing volatiles that do not affect larval performance. *Mol Ecol* 25:3509–3519
- Libert B (1981) Rapid determination of oxalate acid by reverse-phase high performance liquid chromatography. *J Chromatogr* 210:540–543

- Liu Z, Zhang C, Ma L, Sun X, Ding J (2020) Elevated temperature decreases preferences of native herbivores to an invasive plant. *Entomol Gen* (accepted)
- Mattson WJ (1980) Herbivory in relation to plant nitrogen content. *Annu Rev Ecol Syst* 11:119–161
- Mayhew PJ (2001) Herbivore host choice and optimal bad motherhood. *Trends Ecol Evol* 16:165–167
- Mason CJ, Long DC, Lindroth RL, Hoover K (2019) Divergent host plant utilization by adults and offspring is related to intra-plant variation in chemical defenses. *J Anim Ecol* 88:1789–1798
- Merwin AC, Inouye BD, Underwood N (2020) Natal-habitat experience mediates the relationship between insect and hostplant densities. *Oecologia* 193:261–271
- Michael W (2018) Plant secondary metabolites modulate insect behavior-steps toward addiction? *Front Physiol* 9:364
- Minkenberg OPJM, Ottenheim JJGW (1990) Effect of leaf nitrogen content of tomato plants on preference and performance of a leafmining fly. *Oecologia* 83:291–298
- Morrison IM (1972) A semi-micro method for the determination of lignin and its use in predicting the digestibility of forage crops. *J Sci Food Agric* 23:455–463
- Nenaah GE (2013) Potential of using flavonoids, latex and extracts from *Calotropis procera* (Ait.) as grain protectants against two coleopteran pests of stored rice. *Ind Crop Prod* 45:327–334
- Prudic KL, Oliver JC, Bowers MD (2005) Soil nutrient effects on oviposition preference, larval performance, and chemical defence of a specialist insect herbivore. *Oecologia* 143:578–587
- Saito T, Hirai K, Way MO (2005) The rice water weevil, *Lissorhoptus oryzophilus* Kuschel (Coleoptera: Curculionidae). *Appl Entomol Zool* 40:31–39
- Scheirs J, Bruyn LD, Verhagen R (2000) Optimization of adult performance determines host choice in a grass miner. *Proc R Soc B* 267:2065–2069
- Scheirs J, Zoebisch TG, Schuster DJ, De Bruyn L (2004) Optimal foraging shapes host preference of a polyphagous leafminer. *Ecol Entomol* 29:375–379
- Schaffner U (2001) Host range testing of insects for biological weed control: how can it be better interpreted? *BioScience* 51:951–959
- Shikano I, Akhtar Y, Isman MB (2010) Relationship between adult and larval host plant selection and larval performance in the generalist moth, *Trichoplusia ni*. *Arthropod-Plant Inte* 4:197–205
- Smith GP, Johnson CA, Davidowitz G, Bronstein JL (2018) Linkages between nectaring and oviposition preferences of *Manduca Sexta* on two co-blooming *Datura* species in the Sonoran Desert. *Ecol Entomol*

- Stout MJ, Rita Riggio M, Zou L, Roberts R (2002) Flooding influences ovipositional and feeding behavior of the rice water weevil (Coleoptera: Curculionidae). *J Econ Entomol* 95:715–721
- Sun X, Siemann E, Liu Z, Wang Q, Wang D, Huang W, Zhang C, Ding J (2019) Root feeding larvae increase their performance by inducing leaf volatiles that attract aboveground conspecific adults. *J Ecol* 107:2713–2723
- Sun Y, Xia XL, Jiang JF, Chen SM, Chen FD, Lv GS (2016) Salicylic acid-induced changes in physiological parameters and genes of the flavonoid biosynthesis pathway in *Artemisia vulgaris* and *Dendranthema nankingense* during aphid feeding. *Genet Mol Res* 15:1–15
- Thompson JN, Pellmyr O (1991) Evolution of oviposition behavior and host preference in Lepidoptera. *Annu Rev Entomol* 36:65–89
- Tindall KV, Stout MJ (2003) Use of common weeds of rice as hosts for the rice water weevil (Coleoptera: Curculionidae). *Environ Entomol* 32:1227–1233
- Tindall KV, Stout MJ, Williams BJ (2004) Effects of the presence of barnyardgrass on rice water weevil (Coleoptera: Curculionidae) and rice stink bug (Hemiptera: Pentatomidae) populations on rice. *Environ Entomol* 33:720–726
- Trona F, Anfora G, Balkenius A, Bengtsson M, Tasin M, Knight A, Janz N, Witzgall P, Ignell R (2013) Neural coding merges sex and habitat chemosensory signals in an insect herbivore. *Proc R Soc B* 280:20130267
- Turlings TC, Bernasconi M, Bertossa R, Bigler F, Caloz G, Dorn S (1998) The induction of volatile emissions in maize by three herbivore species with different feeding habits: possible consequences for their natural enemies. *Biol Control* 11:122–129
- Updegraff DM (1969) Semimicro determination of cellulose in biological materials. *Anal. Biochem* 32:420–424
- Van Nouhuys S, Singer MC, Nieminen M (2003) Spatial and temporal patterns of caterpillar performance and the suitability of two host plant species. *Ecol Entomol* 28:193–202
- Webb JL (1914) Notes on the rice water-weevil (*Lissorhoptrus simplex* Say). *J Econ Entomol* 7:432–438
- Webster B, Cardé RT (2016) Use of habitat odour by host-seeking insects. *Biol Rev* 92:1241–1249
- Wiklund C (1975) The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. *Oecologia* 18:185–197
- Wang D, Zhou L, Wang Q, Ding J (2020) Plant chemistry determines host preference and performance of an invasive insect. *Front Plant Sci* 11:594663

Xu H-W, Ji X-M, He Z-H, Shi W-P, Zhu G-H, Niu J-K, Li B-S, Peng X-X (2006) Oxalate accumulation and regulation is independent of glycolate oxidase in rice leaves. *J Exp Bot* 57:1899–1908

Yoshihara T, Sogawa K, Pathak MD, Juliano BO, Sakamura S (1980) Oxalic acid as a sucking inhibitor of the brown planthopper in rice (Delphacidae, Homoptera). *Entomol Exp Appl* 27:149–155

Zhang PJ, Lu YB, Zalucki MP, Liu SS (2012) Relationship between adult oviposition preference and larval performance of the diamondback moth, *Plutella xylostella*. *J Pest Sci* 85:247–252

Figures

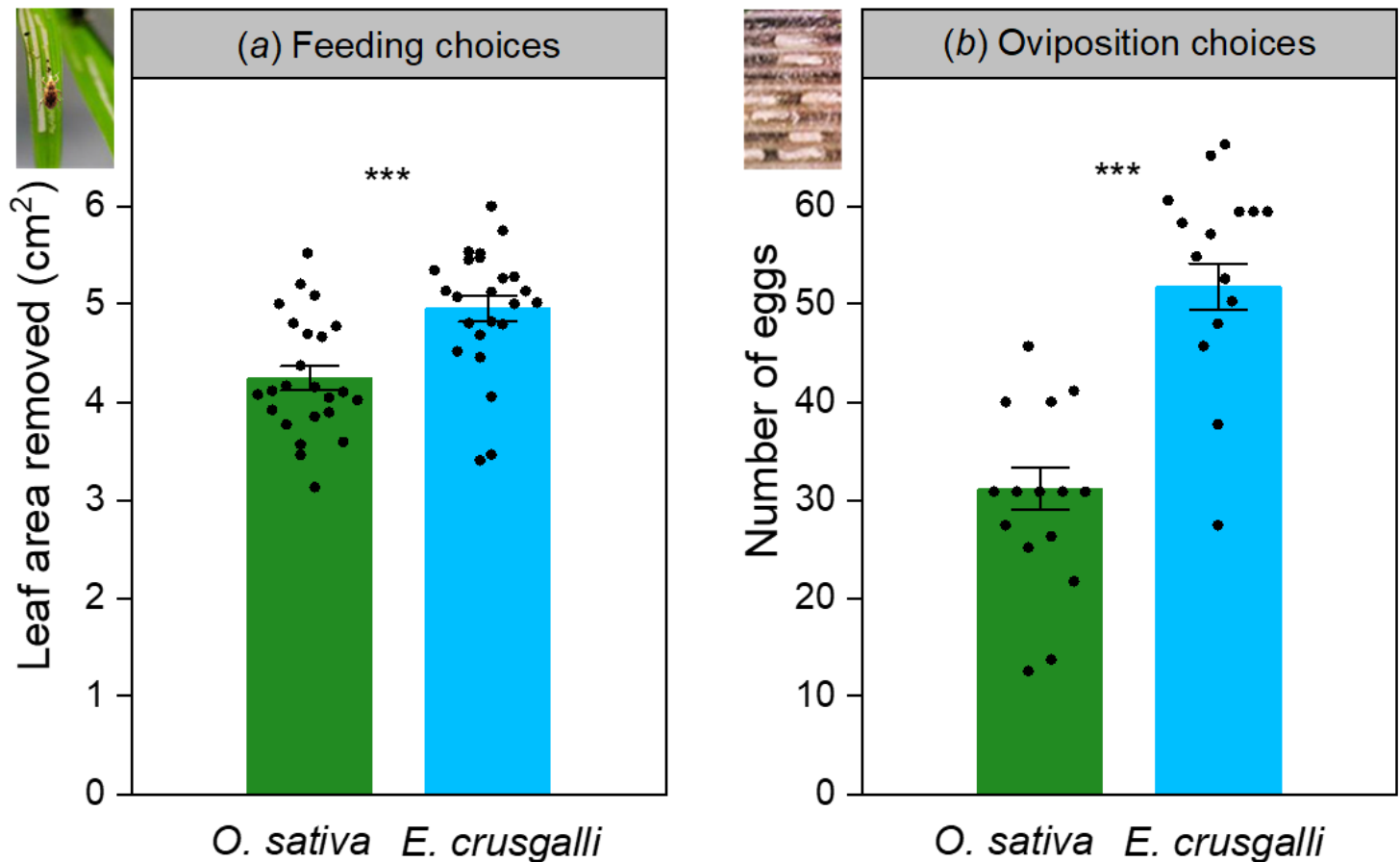


Figure 1

Feeding and oviposition preferences. (a) Leaf area removed per plant (means \pm se) by *L. oryophilus* female adults from rice (*O. sativa*) and barnyard grass (*E. crusgalli*) in the two-way feeding choice experiments (*** $p < 0.001$, paired samples t-test). (b) Number of eggs (means \pm se) laid by *L. oryophilus* female adults on rice (*O. sativa*) and barnyard grass (*E. crusgalli*) in the two-way oviposition choice experiments (*** $p < 0.001$, paired samples t-test). Each solid dot represents one replicate.

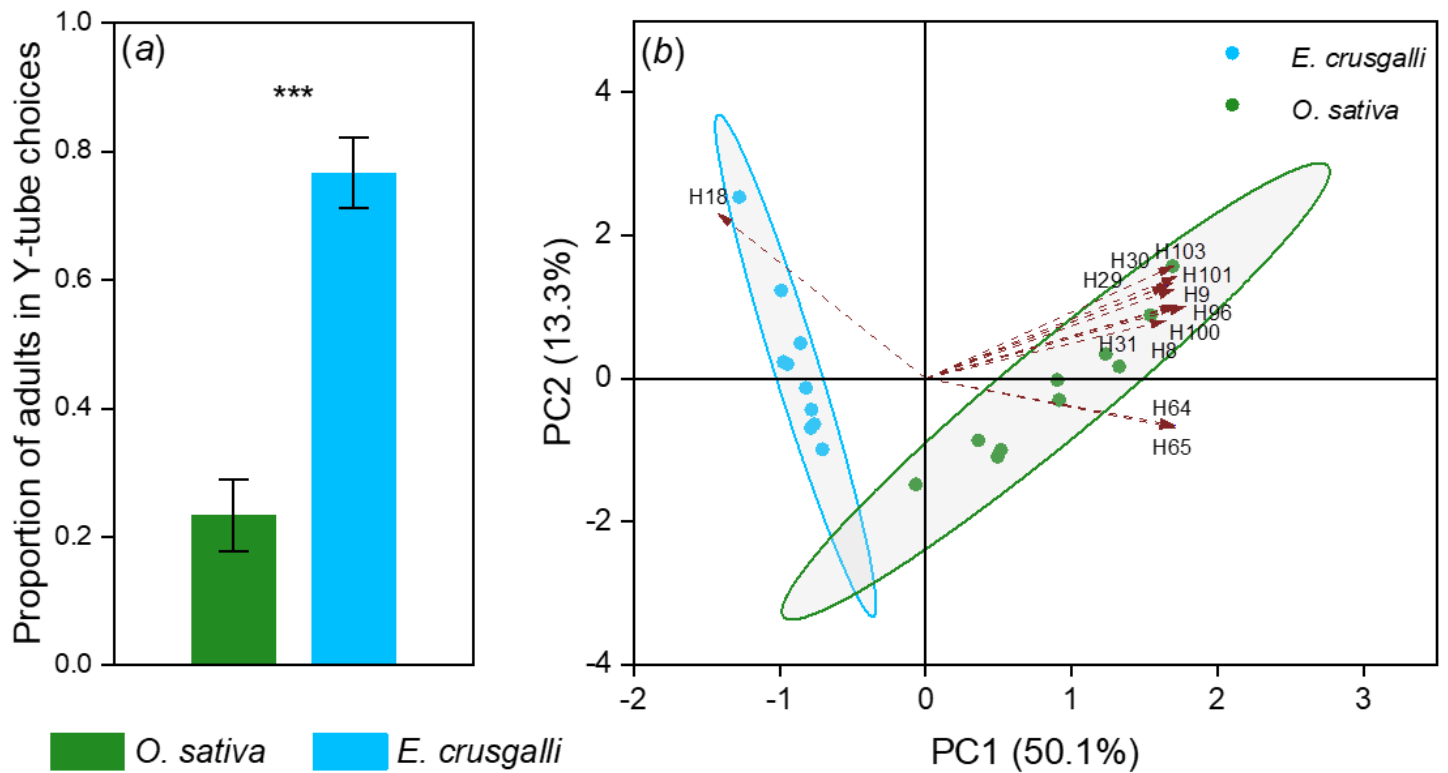


Figure 2

Olfactory preferences (a) of *L. oryzoophilus* female adults for host plant volatiles between rice (*O. sativa*) and barnyard grass (*E. crusgalli*) in the pairwise Y-tube olfactometer assays (***) $p < 0.001$, Wilcoxon's signed rank test). Principal component analysis (b) of volatiles emitted from rice and barnyard grass. The length and direction of the arrows indicate the relative contribution and correlation of each volatile compound, respectively. The ellipses represent 95% confidence intervals, in which one point denotes one sample ($n = 10$ for each plant species). Principal components 1 and 2 explained 50.1% and 13.3% of the variance, respectively.

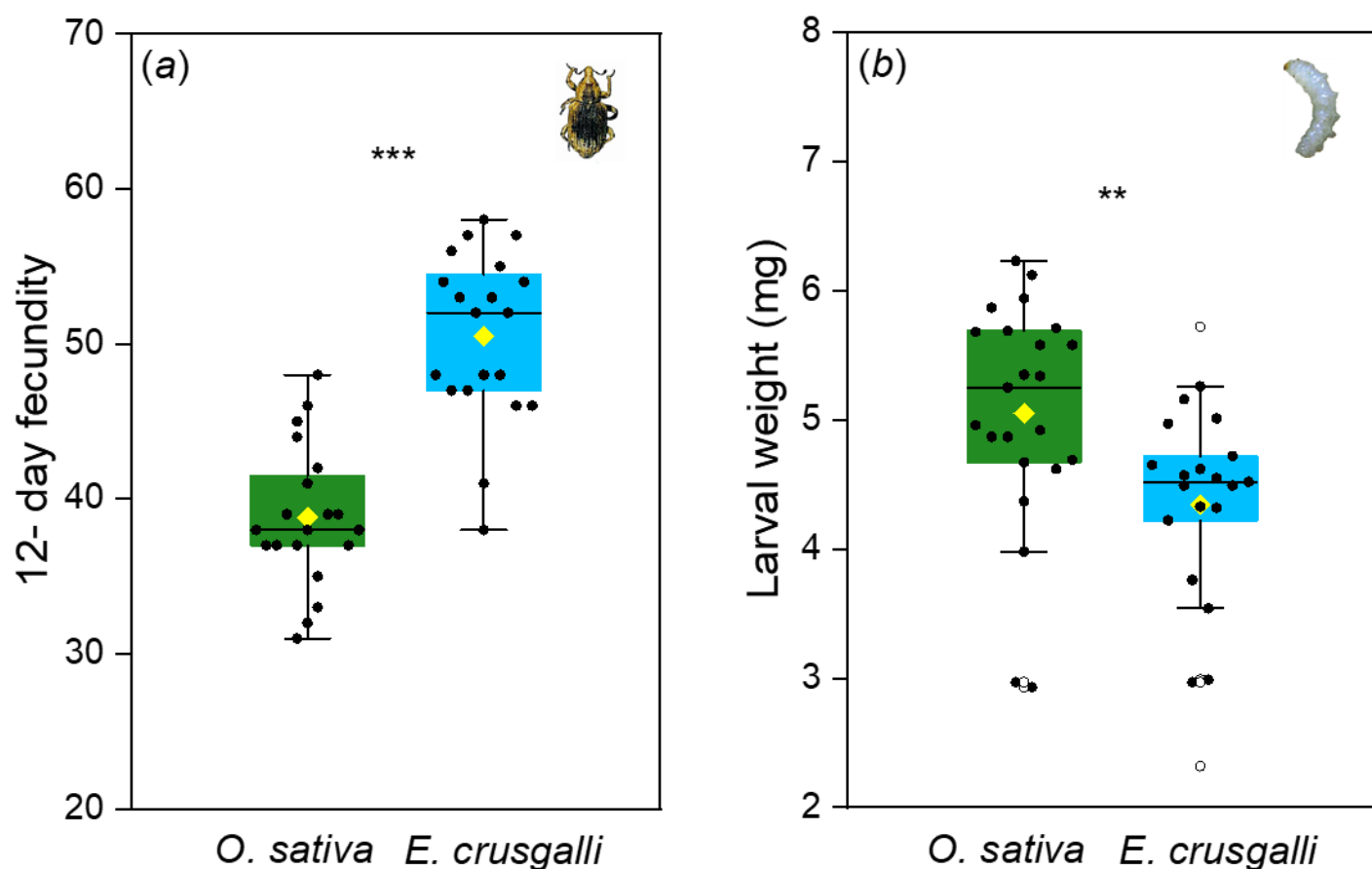


Figure 3

Adult and offspring performance. (a) Twelve-day fecundity of *L. oryophilus* female adults on rice (*O. sativa*) and barnyard grass (*E. crusgalli*) (*** p < 0.001, independent samples t-test). (b) *L. oryophilus* larval weight (mg) on rice (*O. sativa*) and barnyard grass (*E. crusgalli*) (** p < 0.01, Mann-Whitney U test). Boxes represent inter-quartile ranges, the centerline inside the boxes represents the median value, the yellow diamond in the middle of box plot represents the mean value, and the tails represent the non-outlier range and the empty dots represent outlier values. Each solid dot represents one replicate.

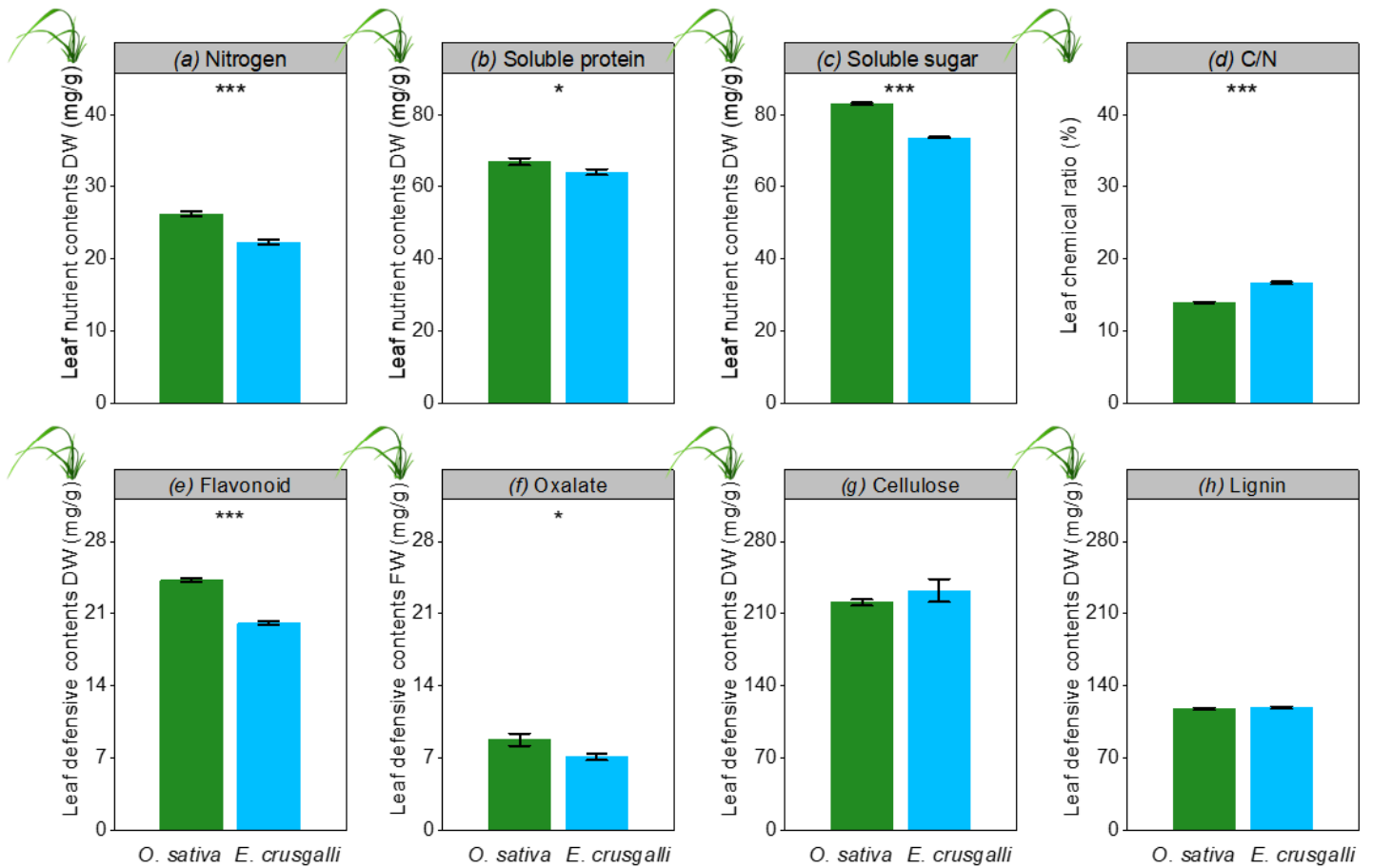


Figure 4

Difference in leaf nutrients and defensive chemicals among rice (*O. sativa*) and barnyard grass (*E. crusgalli*). Nitrogen content (a); soluble protein (b); soluble sugar (c); C: N (d); flavonoid (e); oxalate (f); cellulose (g); lignin (h). (* p < 0.05, *** p ≤ 0.001; independent samples t-test).

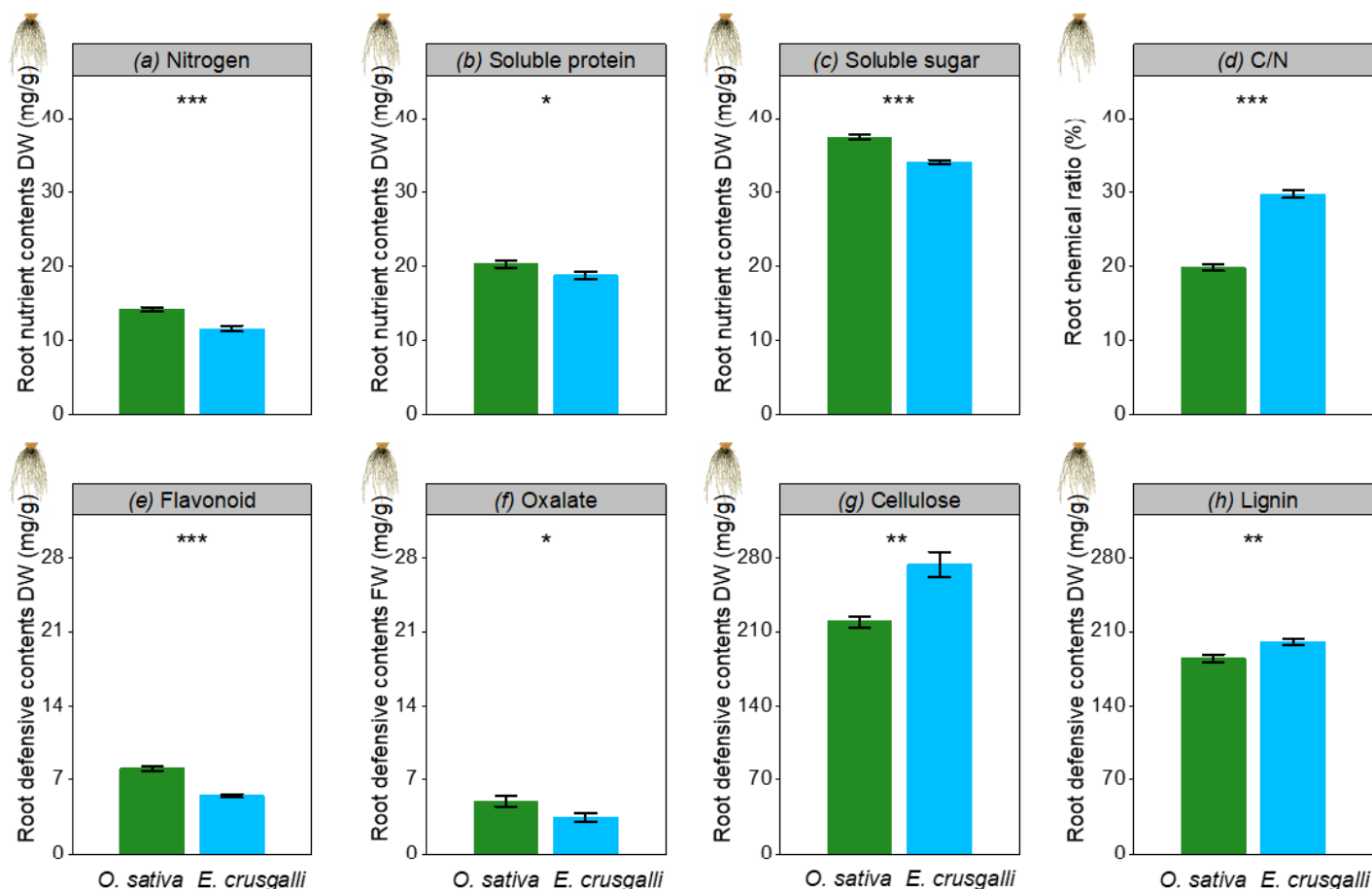


Figure 5

Root chemical analysis. Mean (± se) nutrients (a-d) and defensive chemicals (e-h) nitrogen, soluble protein, soluble sugar, C: N, flavonoid, oxalate, cellulose and lignin contents in rice (*O. sativa*) and barnyard grass (*E. crusgalli*). (* $p < 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$; independent samples t-test).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [ElectronicsupplementarymaterialtableS1.docx](#)