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Effects of Priming Rice Seeds with Decoyinine on Fitness Traits and Virus Transmission Ability of the Small Brown Planthopper, *Laodelphax striatellus*

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Abstract: *Laodelphax striatellus* is a notorious sap-feeding insect that also serves as a vector of rice stripe virus (RSV) and is responsible for a significant decline in rice yield. Pesticide application remains a crucial strategy for controlling insect pests. In recent years, the utilization of biopesticides has gained attention due to their eco-friendliness and suitability for controlling insect pests and pathogens in agriculture. The present study aimed to evaluate the potential efficacy of a microbial pesticide, decoyinine (DCY), as a seed priming agent in rice against SBPH's biology, feeding behavior, and RSV transmission ability in the laboratory. Here, we revealed that the body weight of females and males and honeydew extraction of RSV-virulent SBPH were (22.50%, 25.0%, and 23.25%, respectively) significantly lower than non-virulent SBPH. Meanwhile, the fecundity of RSV-virulent SBPH females was significantly higher (8.24%) than non-virulent SBPH. However, nymphal survival and RSV transmission (horizontal and vertical) were found to be non-significantly affected by DCY application. Furthermore, DCY-primed rice seedlings significantly prolonged the time period and frequency of the electrical penetration graph (EPG) feeding waveforms (np, N2, and N3), and also reduced the time period of the waveform (N4-b) for both RSV-virulent and non-virulent SBPH strains with reduced RSV inoculation. The recent study provides new insights for DCY application in rice against SBPH by reducing fecundity, body weight, and honeydew contents, which might contribute to modern integrated pest management.

Keywords: small brown planthopper (SBPH); decoyinine (DCY); electrical penetration graph (EPG); fecundity; RSV transmission



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1. Introduction

Rice, *Oryza sativa* L., is the most important crop in Asia and is a staple food for half of the world's population [1]. Many biotic and abiotic factors challenge rice production, and the first major challenge is insect pests [2]. The small brown planthopper (SBPH), *Laodelphax striatellus* Fallén (Hemiptera; Delphacidae), is one of rice's most important insect pests in Asia. SBPH extracts rice phloem sap with a piercing-sucking stylet and serves as a rice stripe virus (RSV) vector, which may result in a significant yield decline [3]. The majority of plant viruses that cause diseases in crops rely on biotic vectors for transmission and survival [1]. RSV is the most crucial virus in rice, causing serious diseases in rice fields in China [4,5]. RSV is a tenuivirus [3], which is transmitted by SBPH in a persistent, circulative, and propagative manner [6]. RSV usually causes chlorotic or necrotic stripes on newly developed leaves, then premature wilting and stunting, and sometimes resulting in total crop loss [7–9]. RSV can be transmitted by SBPH from mother to offspring [10]. The rice

stripe disease caused by RSV damaged over 1,571,000 hectares in 2004, accounting for 80% of the rice fields and a 30–40% yield loss in China [6]. Viral diseases have been economically destructive in rice-growing areas in China for decades [11]. Rapid virus diagnosis in a vector is important for viral disease forecast and control. Several approaches have been developed for the detection of RNA viruses in their insect vectors, including biological inoculation of virus into a non-infected plant [12,13], direct observation using electron microscopes [3,14], antibody-based serological method, and other molecular detection methods [15].

The population dynamics of SBPH are influenced by numerous factors, including crop rotation, agroecological changes, and pesticide use [16–19]. Injudicious pesticide application to manage insect pests in recent years has resulted in the development of resistance in insects [20]. It also leads to the eradication of the biological agents of these insect pests and has a detrimental effect on both humans and the environment [21]. Pesticide application at sub-lethal doses encourages SBPH resurgence. Furthermore, pesticides are exposed to various environmental factors, which aid pesticide degradation [22]. A prior study investigated whether carbendazim and chlorpyrifos applications enhanced the SBPH population in wheat and rice fields [23,24]. In these circumstances, a substitute strategy for pest management is required [20]. Microbial pesticide application is one of the most appropriate and environmentally friendly approaches in the management of insect pests in agriculture [25,26]. Additionally, it has no adverse effects on crops, and a small amount of these pesticides is also effective against insect pests [27,28].

Decoyinine (DCY; $C_{11}H_{13}N_5O_4$) is a hexose analog nucleoside antibiotic, isolated from *Streptomyces hygroscopicus* var. *decoyicus* [29]. DCY is quite similar in structure to Angustmycin A, a particular inhibitor of guanosine monophosphate (GMP) synthase, which can prevent the alteration of xanthosine monophosphate (XMP) to GMP and intrude with pyrophosphokinase activity [30–33]. DCY has the ability to initiate *Bacillus subtilis* sporulation by fractional inhibition of GMP synthesis [34,35]. Additionally, it can also stop *B. subtilis* cell wall turnover and cellular autolysis [36]. Along with inhibiting tumorigenicity in immune-compromised mice, DCY is also effective in inhibiting melanoma cell invasion in the laboratory [37]. Earlier research on DCY primarily focused on its antimicrobial, antitumor, and nucleoside antibiotic properties. DCY is termed Lingfasu (LFS) or Wugufengsu (WGF) in China and is mostly applied in agronomy and botany [38,39]. A study revealed that LFS can induce auxin and cytokinin activities, which in turn stimulate plant tissue regeneration [38]. Furthermore, WGF can also enhance maize and rice yields [39]. A rice variety, “Baixiang 139” treated with DCY (50 mg L^{-1}) enhanced the germination rate, germination potential, seedling base width, number of roots, root length, plant height, bud length, leaf age, dry matter, and fresh weight accumulation [39]. Our prior study revealed that DCY has reduced the fecundity of *L. striatellus* and also altered the response of a few physiological indices of rice against SBPH [40].

DCY priming of TN1 rice seeds showed greater resistance against BPH in terms of low fecundity, declining net reproductive rate (R_0), reduced intrinsic rate of natural increase (r_m), low finite capacity of increase (λ), and reduced population size as compared with untreated rice. DCY application also reduced the ovary development and the expression level of vitellogenin (*NIVg*) in BPH. Furthermore, DCY application reduces the oviposition and feeding preference of BPH in rice. The frequency and time period of np, N2, and N3 of BPH were dramatically increased on DCY treated rice as compared with control rice plants, while the time period of N4-b waveforms was shortened [41]. The physio-biochemical study of DCY-treated rice fed with PBH revealed that plant defense-related enzymes and chemical activities, such as superoxide dismutase (SOD), catalase (CAT), glutathione S transferase (GST), peroxidase (POD), polyphenol oxidase (PPO), free amino acids, callose, and hydrogen peroxide (H_2O_2), were enhanced, while the concentration of malondialdehyde (MDA) was significantly decreased in DCY-treated rice upon BPH feeding. The transcriptomic analysis showed that the resistance-related WRKY genes were upregulated in DCY-treated rice upon BPH feeding [42].

A prior study evaluated that DCY seed priming of different rice varieties significantly affects fecundity, oviposition period, adult longevity, net reproductive rate (R_0), finite rate of increase (λ), intrinsic rate of increase (r_m), doubling time (DT), and population size of BPH on DCY-treated rice varieties as compared with their respective control plants. Similarly, the body weight and honeydew excretions of BPH on DCY-treated rice varieties were also significantly lowered as compared with their corresponding control plants. Furthermore, the feeding and oviposition preferences of BPH were also reduced on DCY-treated rice varieties as compared with respective control rice plants. The results of the two-way ANOVA also showed that the effects of DCY treatment, rice variety, and interactions between DCY treatment and rice variety led to significant variations in the biological parameters, honeydew excretions, and BPH weights. Additionally, BPHs showed less preference for the DCY-treated rice plants for feeding and oviposition [43]. The feeding of the two-spotted spider mite (TSSM), *Tetranychus urticae*, on their host Lima bean, *Phaseolus lunatus*, was studied via metabolomics and transcriptomics approaches. Transcriptomics analysis of TSSMs showed that several genes were overexpressed, especially Guanosine Monophosphate Synthetase (GMPS), which is mainly involved in guanine production. It was discovered that DCY is a potential GMPS inhibitor and acts as noval aciricide to decline TSSM infestation in beans. Metabolomics analysis of TSSM confirmed the existence of different chlorophyll pigments and their degradation products in TSSM and its excreta. [44].

No prior study has been conducted to determine the extensive impact of decoyinine (DCY) on RSV-virulent and non-virulent SBPH in rice. Here, we hypothesized that seed priming with DCY in rice could suppress the infestation of SBPH by altering the fecundity, feeding behavior, and transmission capacity. The current study evaluated the impacts of DCY on RSV-virulent and non-virulent SBPH's fecundity, feeding behavior, and RSV transmission ability in rice.

2. Materials and Methods

2.1. Rice, Insects, and DCY Treatments

A susceptible rice variety, Wuyujing-3, was grown [18]. Seeds were supplied by the China National Rice Research Institute, Hangzhou, China. A microbial antibiotic, DCY, was obtained from Shanghai Macklin Biochemical Co., Ltd., Shanghai, China. Seeds were treated with different DCY water solutions (0, 25, 50, and 100 mg DCY L⁻¹) for 24 h at 28 °C, then transferred to plastic trays, covered with a wet towel, and kept in dark conditions for a further 24 h to sprout, following the same procedure as Sun (2020) and Ma et al. (2022) [39,41]. Sprouted paddy seeds were sown in plastic cups (depth/height: 18 cm; diameter: 8 cm), which contained nutritional soil (Jiangsu Xingnong Substrate Technology Co., Ltd., Zhenjiang, Jiangsu, China). Cups with paddy saplings were covered with nylon mesh using rubber binds to avoid pre-insect infestation. Cups were kept in an artificial growth chamber (27 ± 1 °C, 70–80% R.H., and 14:10 h light:dark [L:D]). Both the RSV-virulent and non-virulent SBPH populations were reared on various DCY-primed paddy saplings (7 ± 3 days old) as stock populations for subsequent experiments [40,45]. The virulence of SBPH was tested by the dot immune binding assay (DIBA) technique [45–47]. Paddy saplings were replaced every 10–14 days to guarantee adequate food for SBPH [40,45].

2.2. DCY Effects on SBPH Body Weight

To calculate the body weight of SBPH adults, newly hatched 1st-instar SBPH nymphs were captured via aspirator from cultured stock populations (RSV-virulent and non-virulent) of each treatment and transferred into cups with corresponding DCY-treated rice saplings (7 ± 3 days old). Cups were covered with nylon mesh using rubber binds to avoid insect escape; nymphs were kept alive until they molted into adults. The body weight of newly hatched twenty males and females (2 days old) from each treatment of both populations was measured using a microelectric balance (AUY120, capacity/readability 120 g; 0.1 mg; Shimadzu Corporation, Kyoto, Japan) [48].

2.3. DCY Effects on SBPH Honeydew

The honeydew secreted by adult female SBPH was collected using the Parafilm[®] sachet technique [49]. Parafilm pouches (wt. of pouch = W_0) were independently weighed via microelectric balance (as previously described) prior to being stitched to paddy sapling (10 ± 3 days old) stems. SBPH female adults (2 days old) were unfed for 2 h, a solely starved SBPH female was placed in each pouch and allowed to feed. SBPH were sucked individually via aspirator from each pouch after 72 h of feeding, and the pouch with honeydew was discretely weighted by microelectric balance (wt. of pouch + honeydew = W_1). The amount of honeydew is calculated as ($W_1 - W_0$). For each treatment of both SBPH populations, twenty females were taken for observation [50].

2.4. DCY Effects on SBPH Fecundity

To investigate the fecundity rate of RSV-virulent and non-virulent SBPH females, they were evaluated on DCY-treated rice saplings (7 ± 3 days old). A newly emerged male and female (a mating pair/replication) from both populations (RSV-virulent and non-virulent) were captured and then transferred into test tubes having the corresponding DCY-primed paddy saplings. Test tubes with paddy saplings were kept in an artificial growth chamber and covered with cotton swabs to avoid insects' escape. Females were individually aspirated after a two-day interval and then shifted to subsequent DCY-primed fresh saplings in test tubes. Rice seedlings were dissected via a needle under a microscope to observe the fecundity until the SBPH female's death. Each treatment was replicated 20 times in the experiment, following the same procedure as Wang et al. (2008b) [51].

2.5. DCY Effects on SBPH Survival

To further investigate the survival of RSV-virulent and non-virulent SBPH nymphs, the 3rd-instar SBPH nymphs were captured from both stock populations and transferred into plastic cups (18 cm depth/height, 8 cm diameter), which contained DCY-treated rice saplings (7 ± 3 days old). Further, the cups were filled up to 5 cm high at the bottom with nutritional soil and kept in an artificial growth chamber. Cups were also covered with nylon mesh using rubber binds to avoid insects' escape, as described by Shah et al. (2022) [40]. The viability of SBPH nymphs was observed after 72 h, and the data were converted into a percentage. Each treatment was replicated 25 times. A replication consists of ten 3rd-instar SBPH nymphs in a single cup.

2.6. DCY Effects on Seedling Mortality Fed with SBPH

To study the effects of DCY on seedling mortality against SBPH (virulent and non-virulent) infestation, seeds were treated with different DCY water solutions (0, 25, 50, and $100 \text{ mg DCY L}^{-1}$) for 24 h at 28°C , transferred to plastic trays, covered with a wet towel, and kept in dark conditions for 24 h to sprout. About 20 sprouted seeds were sown in an individual disposable plastic cup (height/depth = 7 cm; diameter = 5 cm), which contained nutritional soil. Cups with seedlings were kept in an artificial growth chamber. One-week-old rice seedlings were infested with 2nd and 3rd-instar SBPH nymphs at 10 insects per seedling [52]. Seedling mortality was recorded after 7 days post-infestation (dpi). Each treatment was replicated five times. A cup having 20 seedlings was considered a replicate.

2.7. DCY Effects on RSV Transmission

2.7.1. DCY Effects on Horizontal RSV Transmission Rates by SBPH

i. RSV acquisition/development (Transfer of RSV from infected rice to SBPH)

To study the effects of DCY on the RSV acquisition/development ability of SBPH, different DCY-treated healthy rice saplings (7 ± 3 days old) in test tubes were incubated with RSV-virulent SBPH to get RSV-infected rice seedlings. Seedlings were kept in a growth chamber until rice stripe symptoms were noticed. Fifty non-virulent SBPH (3rd-instar) nymphs were starved for 5 h and then shifted into test tubes containing RSV-infected paddy saplings that had formerly been primed with different DCY treatments. The SBPH

nymphs were aspirated after a 72 h acquisition period, then transferred to freshly primed DCY saplings for a further one-week feeding period to assist the development of RSV in SBPH. To check the RSV transmission, the nymphs were merely subjected to the DIBA (dot immune binding assay) technique [53]. The acquisition rate is determined as the ratio of the total number of virulent SBPH to the total number of tested SBPH. Each treatment consisted of 50 replications, and each replication included a single non-virulent nymph in each test tube.

ii. RSV inoculation (Transfer of RSV from virulent SBPH to healthy rice)

To study the effects of DCY on the RSV inoculation ability of SBPH, a freshly hatched SBPH female from the virulent population and a recently developed SBPH male from the non-virulent population were trapped in test tubes with paddy saplings that had previously been primed with different DCY treatments. The males were removed from each tube after a 48 h mating period, and the mated females were kept on the rice seedlings for oviposition until their deaths. For each treatment, fifty SBPH replicates (mating pairs) were arranged. A putatively virulent SBPH of the coming generation was added to test tubes containing healthy rice seedlings to assist RSV transmission. The nymphs were independently checked for RSV after 48 h feeding on paddy through the DIBA technique [53]. Non-virulent nymphs were excluded, and only virulent nymphs were regarded as authentic individuals. In order to facilitate the development of RSV, the test seedlings were kept in a growth chamber for around 15 days. The seedlings were individually subjected to the DIBA technique to confirm RSV transmission. The inoculation rate is determined as the ratio of the total number of virulent seedlings to the total number of virulent SBPH. Each treatment consisted of 30 replications, and each replication included a single virulent nymph in each test tube.

2.7.2. DCY Effects on Vertical RSV Transmission Rates by SBPH

To study the effects of DCY on the RSV vertical ability of SBPH, a freshly hatched SBPH female from the virulent population and a recently developed SBPH male from the non-virulent population were trapped in test tubes with paddy saplings that had previously been primed with different DCY treatments. The males were removed from each tube after a 48 h mating period, and the mated females were kept on the rice seedlings for oviposition until their deaths. For each treatment, fifty SBPH replicates (mating pairs) were arranged. The dead females were independently checked for RSV after feeding on paddy through the DIBA technique [12,53]. Non-virulent females were excluded, and only virulent females were regarded as authentic individuals. The paddy seedlings fed by virulent SBPH females were kept in a growth chamber until the eggs hatched. The newly born nymphs were transferred within 24 h after hatching to new test tubes, which contained fresh, non-infectious paddy saplings that had previously been primed with different DCY treatments. The nymphs were raised on those seedlings until their 3rd-instar stage of development. The nymphs were then independently checked for RSV through the DIBA technique [53]. The vertical transmission rate is determined as the ratio of virulent nymphs produced by a single SBPH female to the total number of nymphs produced by the same SBPH female. A replication is comprised of a single virulently fertilized SBPH female (e.g., mother). There were 96 replications of each treatment.

2.8. DCY Effects on SBPH Feeding Behavior

The feeding behavior of RSV-virulent and non-virulent SBPH females was studied for eight consecutive hours on DCY-treated and untreated rice seedlings (20 days old) via a Giga-8 (DC-EPG) amplifier device enclosed in a Faraday cage (Wageningen Agricultural University, Wageningen, The Netherlands). Rice saplings were grown in cups (height = 7 cm; diameter = 5 cm), which contained nutritional soil (Jiangsu Xingnong Substrate Technology Co., Ltd., Zhenjiang, Jiangsu, China). The experiment was executed in a quiet room with a controlled environment. Initially, SBPH females (2 days old) were captured from both stock populations (virulent and non-virulent RSV) and starved for 2 h. Prior to EPG execution, a few prerequisites are required, i.e., construction of insect

electrodes, wire attachment with insect body via silver glue (wiring), insect plant contact, and adjustment of EPG amplifier were arranged [54]. A total of 10–15 individual recordings were observed for RSV-virulent and non-virulent SBPH fed on control and DCY-50-treated rice saplings. A software program, PROBE 3.0, was used to analyze EPG recordings (Wageningen Agricultural University, Wageningen, The Netherlands). In addition to the seven waveforms identified previously, the EPG waveforms detected from SBPH were categorized into non-penetration, np; initial penetration, N1; salivation and stylet movement, N2; extracellular activity adjacent to the phloem, N3; intracellular activity in the phloem, N4-a; phloem sap ingestion, N4-b; and activity in the xylem, N5. The SBPH captured from stock populations used in the EPG was again subjected to the DIBA assay to confirm its validity. The valid EPG recordings of the tested SBPH were included in the respective insect population in their final analysis.

2.9. Statistical Analysis

A two-way analysis of variance (ANOVA) was conducted for the biological parameters of SBPH and seedling mortality. Multiple comparisons of means were conducted based on Tukey's Honestly Significant Difference (HSD) test. RSV transmission rates by SBPH exposed to DCY treatments were analyzed by one-way ANOVA. Means comparisons were evaluated by the Chi-squared (χ^2) test (Yang et al. 2017) [55]. A one-way ANOVA was applied to analyze the feeding differences of SBPH, and a Tukey's HSD test was done for mean differences [41]. A computer software, SPSS Inc., Chicago, IL, USA (SPSS 16.0) was applied for all the statistical analyses.

3. Results

3.1. Body Weight of Different Populations of SBPH on DCY-Treated Rice

The body weight of both SBPH female populations (RSV-virulent and non-virulent) was studied in response to DCY treatment (Figure 1 and Table S1). ANOVA showed that SBPH, DCY treatments, and interactions significantly influenced SBPH females' body weight (Table 1). The body weights of RSV-virulent and non-virulent SBPH females were significantly altered with DCY application ($F = 29.059$, $df = 1$, $p < 0.001$). Among DCY treatments, significant variations in SBPH females' body weight were also observed ($F = 89.749$, $df = 3$, $p < 0.001$), whereas the interaction between SBPH females and DCY treatments was significantly altered as well ($F = 3.241$, $df = 3$, $p = 0.024$) (Table S1).

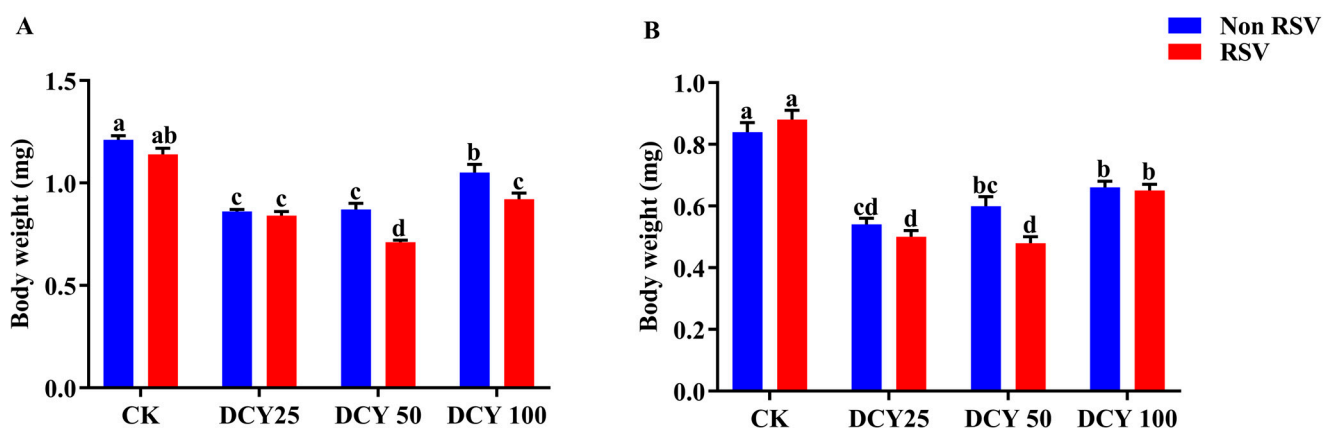


Figure 1. Body weight of different populations of SBPH on DCY-treated rice. Significant differences between treatments are indicated by different letters ($p < 0.05$, Tukey's HSD test). (A) Female; and (B) Male.

In general, DCY decreased the body weight of both RSV-virulent and non-virulent SBPH female populations fed on rice seedlings. In comparison, among both populations, the body weight of non-virulent SBPH was significantly higher than that of RSV-virulent SBPH. Furthermore, in the DCY treatments, the body weight of both SBPH female popula-

tions (RSV-virulent and non-virulent) was lowered as compared with the control. Among DCY treatments and SBPH populations (interaction), the virulent SBPH females fed on DCY 50 body weight (0.71 mg) as compared with non-virulent SBPH females fed on DCY 50 treated rice body weight (0.87 mg), which is significantly (22.5%) lower than non-virulent SBPH (Figure 1A).

Table 1. RSV inoculation rate of SBPH fed on DCY-treated rice.

| DCY | Concentration (mg L ⁻¹) | No. of Valid Insects | No. of Plants Acquiring RSV | Virus Transmission Rate (%) | Chi-Square (χ^2) Test |
|-----|-------------------------------------|----------------------|-----------------------------|-----------------------------|------------------------------|
| | 0 | 30 | 6 | 20.00 | $\chi^2 = 4.40$ |
| | 25 | 30 | 3 | 10.00 | $df = 3$ |
| | 50 | 30 | 3 | 10.00 | $p = 0.22$ |
| | 100 | 30 | 1 | 3.33 | |

The body weight of both SBPH male populations (RSV-virulent and non-virulent) was studied in response to DCY treatments (Figure 1 and Table S1). ANOVA showed that SBPH, DCY treatments, and interactions significantly influenced SBPH males' body weight (Table 1). The body weights of RSV-virulent and non-virulent SBPH males were significantly altered with DCY application ($F = 4.079$, $df = 1$, $p = 0.045$). Among DCY treatments, significant variations in SBPH males' body weight were also observed ($F = 102.471$, $df = 3$, $p < 0.001$); whereas the interaction between SBPH males and DCY treatments was significantly altered as well ($F = 4.671$, $df = 3$, $p = 0.004$) (Table S1).

In general, DCY decreased the body weight of both virulent and non-virulent SBPH male populations fed on rice seedlings. In comparison, among both populations, the body weight of virulent SBPH was significantly lower than non-virulent SBPH. Furthermore, in the DCY treatments, the body weight of both SBPH male populations (RSV-virulent and non-virulent) was lowered as compared with the control. Among DCY treatments and SBPH populations (interaction), the RSV-virulent SBPH males fed on DCY 50 body weight (0.48 mg) as compared with non-virulent SBPH males fed on DCY 50 treated rice body weight (0.60 mg), which is significantly (25.0%) lower than non-virulent SBPH (Figure 1B).

3.2. Effects of DCY on SBPH Fecundity

The fecundity of both SBPH female populations (virulent and non-virulent) was studied in response to DCY treatments (Figure 2 and Table S1). ANOVA showed that SBPH, DCY treatments, and interactions significantly influenced SBPH fecundity (Table S1). The number of eggs laid by RSV-virulent and non-virulent SBPH females significantly changed with DCY application ($F = 338.901$, $df = 1$, $p < 0.001$). In DCY treatments, significant variations in SBPH females' fecundity were also observed ($F = 476.185$, $df = 3$, $p < 0.001$), whereas the interaction between SBPH females and DCY treatments was significantly altered as well ($F = 37.557$, $df = 3$, $p < 0.001$) (Table S1).

In general, DCY decreased the fecundity of both virulent and non-virulent SBPH female populations fed on rice seedlings. In comparison, among both populations, the fecundity of non-virulent SBPH was significantly lower than that of virulent SBPH. Furthermore, in the DCY treatments, the fecundity of both SBPH female populations (virulent and non-virulent) was lowered as compared with the control. Among DCY treatments and SBPH populations (interaction), the non-virulent SBPH females fed on DCY 50 produced (95.15 eggs female⁻¹) as compared with virulent SBPH females fed on DCY 50 treated rice who produced (103.70 eggs female⁻¹), which is 8.24 % lower than virulent SBPH (Figure 2).

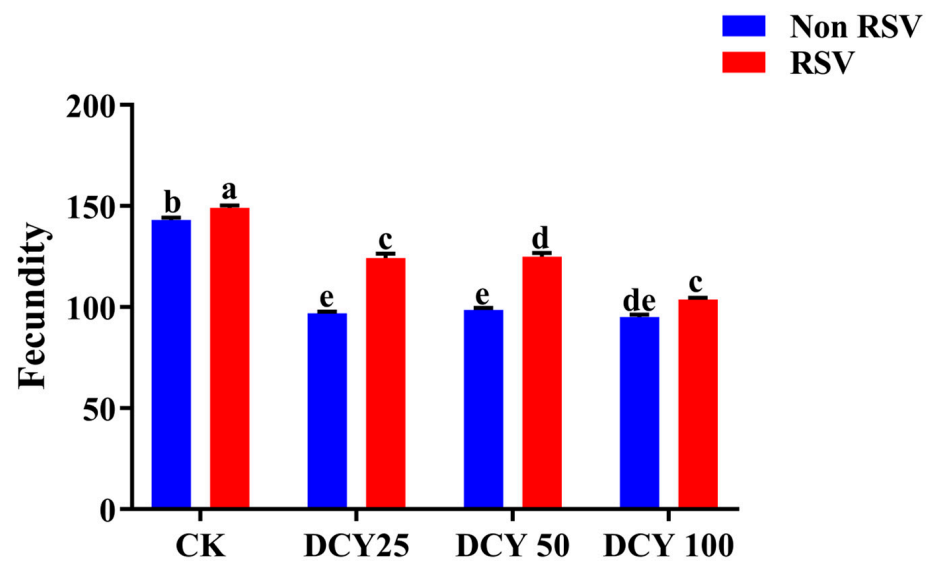


Figure 2. The number of eggs laid by SBPH females exposed to DCY gradient concentrations. Vertical columns represent means \pm S.E, and columns labeled with different letters indicate significant differences between treatments ($p < 0.05$, Tukey's HSD test).

3.3. Nymphal Survival of Different Populations of SBPH on DCY-Treated Rice

The nymphal survival of both SBPH female populations (virulent and non-virulent) was studied in response to DCY treatments (Figure 3 and Table S1). ANOVA showed that nymphal survival in SBPH is significantly influenced (Table S1). The nymphal survival of RSV-virulent and non-virulent SBPH was significantly changed with DCY application ($F = 27.797$, $df = 1$, $p < 0.001$). Nymphal survival for different DCY treatments and interactions was recorded as non-significant (Table S1).

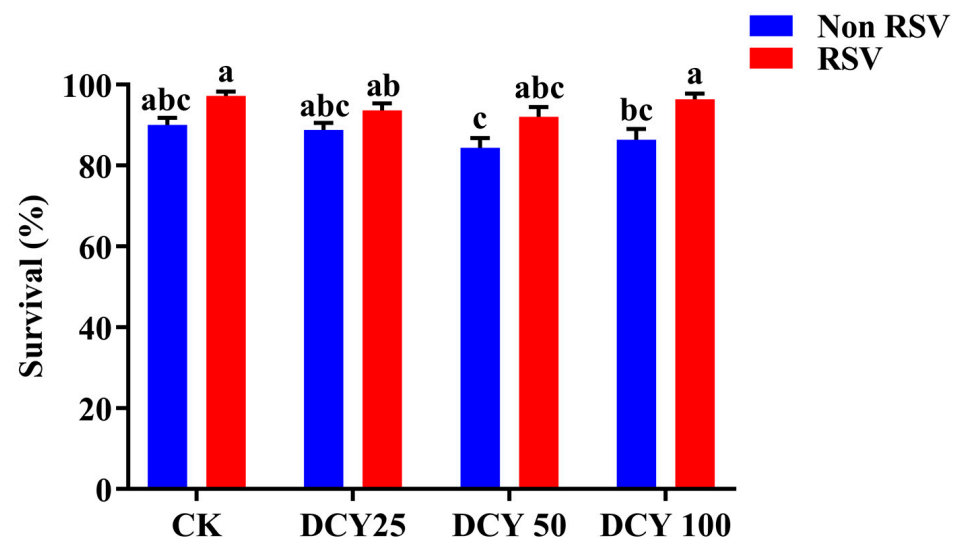


Figure 3. Nymphal survival of different populations of SBPH on DCY-treated rice. Significant differences between treatments are indicated by different letters ($p < 0.05$, Tukey's HSD test).

In general, DCY decreased the nymphal survival of both virulent and non-virulent SBPH female populations fed on rice seedlings. In comparison, among both populations, the nymphal survival of non-virulent SBPH was significantly lower than that of virulent SBPH. Furthermore, in the DCY treatments, the nymphal survival of both SBPH female populations (virulent and non-virulent) was non-significantly lowered as compared with their corresponding control. Among DCY treatments and SBPH populations (interaction), the non-virulent SBPH females fed on DCY 100 nymphal survival had a lower survival

rate (86.40%) as compared with virulent SBPH females fed on DCY 100 treated rice nymph survival (96.40%), which was higher (10.37%) than non-virulent SBPH (Figure 3).

3.4. Mortality of Rice Seedlings Fed with Different Populations of SBPH

The seedling mortality of rice fed with SBPH populations (virulent and non-virulent) was studied in response to DCY application (Figure 4). ANOVA revealed that SBPH feeding does not significantly affect seedling mortality ($F = 1.66$, $df = 1$, $p = 0.267$) (Figure S1). Seedling mortality among the treatments was found to be significantly different ($F = 98.35$, $df = 3$, $p < 0.0001$), while the interaction was recorded as non-significant ($F = 0.290$, $df = 3$, $p = 0.83$).

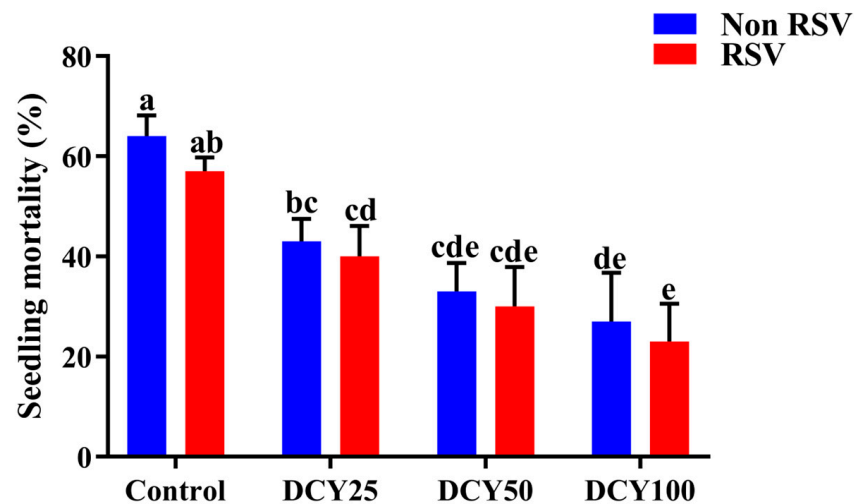


Figure 4. Mortality of DCY-treated rice seedlings fed with different populations of SBPH. Significant differences between treatments are indicated by the letters (a, b, c, d, and e) ($p < 0.05$, Tukey's HSD test).

In general, DCY decreased the seedling mortality of rice fed with both virulent and non-virulent SBPH populations. In comparison, among both populations, the seedling mortality of rice fed by virulent SBPH was non-significantly lower than that of non-virulent SBPH. Furthermore, in the DCY treatments, the seedling mortality of rice fed with both SBPH females populations (virulent and non-virulent) was significantly lower as compared with the control. Among DCY treatments and SBPH populations (interaction), the seedling mortality in DCY 100 (23%) fed by virulent SBPH was compared with the seedling mortality in DCY 100 (27%) fed with non-virulent SBPH, which is 17.4% lower (Figure 4).

3.5. Effects of DCY on SBPH Feeding Behavior

The feeding behavior of SBPH females (RSV-virulent and non-virulent) on differently treated rice seedlings via EPG recordings is shown in Figure 5. We observed the total time period and frequency of seven different waveforms (i.e., np, N1, N2, N3, N4-a, N4-b, and N5) of RSV-virulent and non-virulent SBPH females on rice seedlings (Control and DCY 50) for an 8 h successive feeding.

The time periods of np, N2, and N3 waveforms of non-virulent SBPH female adults on seedlings grown from DCY50-pretreated seeds were significantly higher than the untreated rice seedlings ($df = 1$, $F = 12.10$, $p = 0.002$ for np; $df = 1$, $F = 60.30$, $p < 0.001$ for N2; $df = 1$, $F = 12.50$, $p = 0.002$ for N3, Figure 5A). Although the time period of the N4-b waveform of non-virulent SBPH on DCY 50 treated seedlings was 122.55% lower than control seedlings ($df = 1$, $F = 42.60$, $p < 0.001$, Figure 5A). The frequencies of the np, N2, and N3 waveforms of non-virulent SBPH on DCY-50 treated seedlings were considerably increased compared to control paddy seedlings ($df = 1$, $F = 19.10$, $p < 0.001$ for np; $df = 1$, $F = 18.10$, $p < 0.001$ for N2; $df = 1$, $F = 35.40$, $p < 0.001$ for N3, Figure 5B).

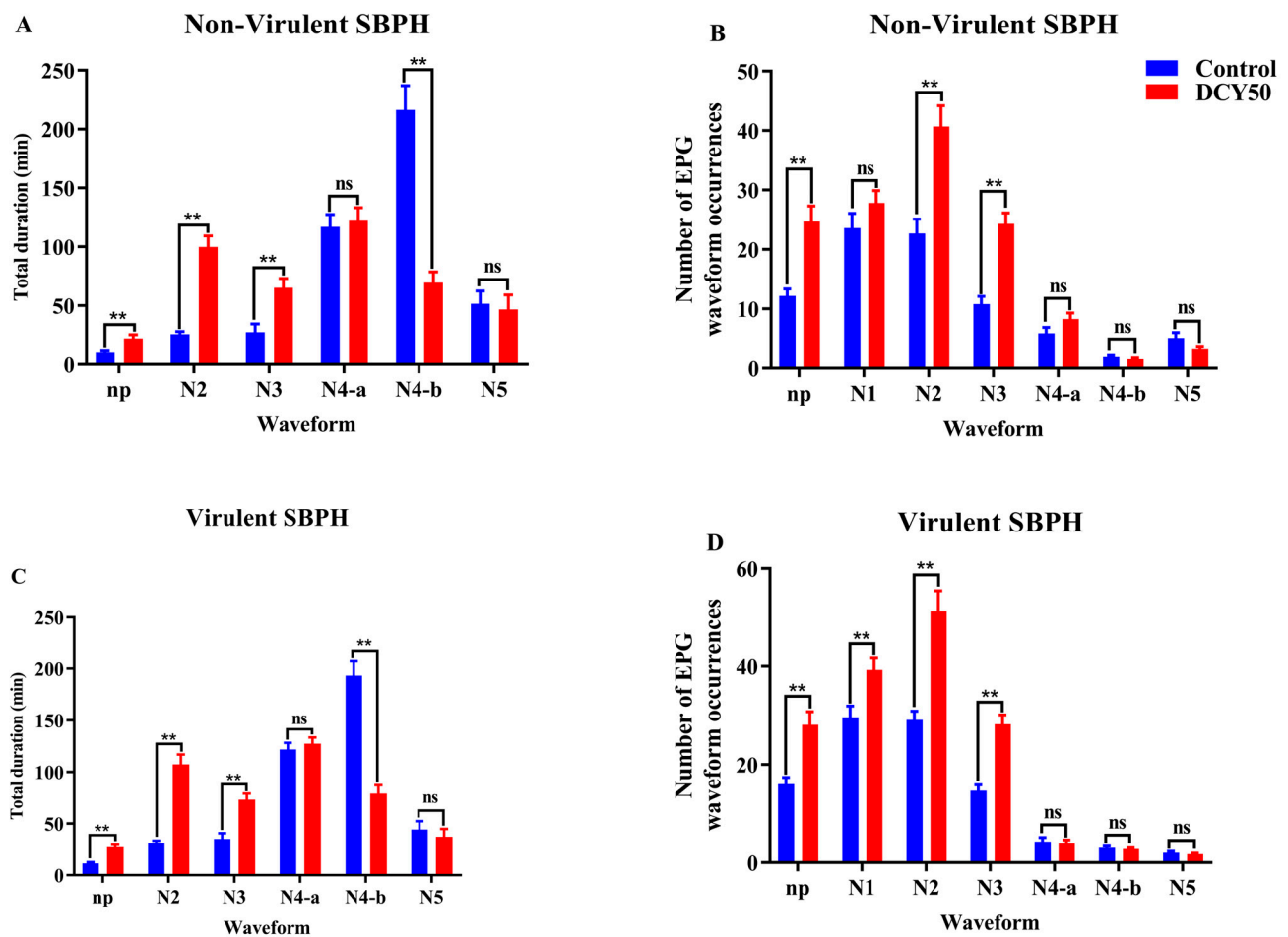


Figure 5. EPG waveform frequency and duration of SBPH feeding on rice. Different EPG waveform durations (A) and occurrences (B) recorded from non-virulent SBPH feeding on control and DCY50-treated rice plants. Different EPG waveform durations (C) and occurrences (D) recorded from virulent SBPH feeding on control and DCY50-treated rice plants. Asterisks (**) indicate significant ($p < 0.05$, Tukey's HSD test). The data were expressed as the mean \pm SE.

The same EPG recording of different waveforms was also detected for RSV-virulent SBPH on paddy seedlings. The periods of the np, N2, and N3 waveforms of RSV-virulent SBPH on rice seedlings raised from DCY 50 treated were considerably higher than control paddy seedlings ($df = 1$, $F = 33.50$, $p < 0.001$ for np; $df = 1$, $F = 61.50$, $p < 0.001$ for N2; $df = 1$, $F = 22.80$, $p < 0.001$ for N3, Figure 5C). Although the time period of the N4-b waveform of RSV-virulent SBPH on DCY-50 treated seedlings was 74.71% lower than control seedlings ($df = 1$, $F = 50.50$, $p < 0.001$, Figure 5C). The frequencies of np, N1, N2, and N3 of RSV-virulent SBPH on DCY-50 treated seedlings were considerably increased compared to control paddy seedlings ($df = 1$, $F = 16.20$, $p < 0.001$ for np; $df = 1$, $F = 8.51$, $p = 0.009$ for N1; $df = 1$, $F = 23.90$, $p < 0.001$ for N2; $df = 1$, $F = 35.70$, $p < 0.001$ for N3, Figure 5D).

3.6. Honeydew Weight of Different Populations of SBPH on DCY-Treated Rice

The amount of honeydew extraction from both SBPH female populations (RSV-virulent and non-virulent) was studied in response to DCY treatments (Figure 6 and Table S1). ANOVA showed that SBPH and DCY treatments significantly influenced SBPH honeydew extraction (Table S1). The amount of honey extracted from RSV-virulent and non-virulent SBPH females was significantly changed with DCY application ($F = 20.981$, $df = 1$, $p < 0.001$). Among DCY treatments, significant variations in SBPH female honeydew extraction were also observed ($F = 48.619$, $df = 3$, $p < 0.001$) (Table S1).

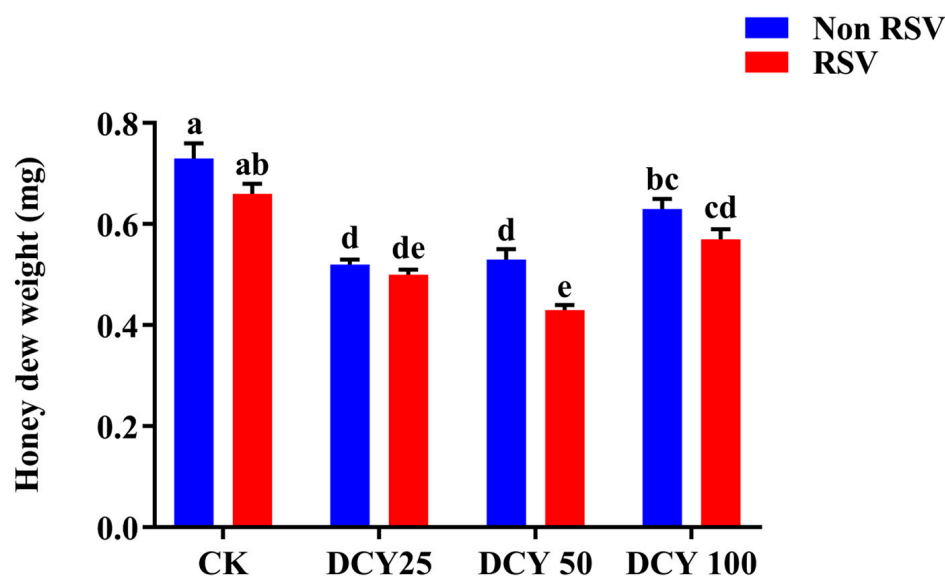


Figure 6. Honeydew weight of different populations of female SBPH on DCY-treated rice. Significant differences between treatments are indicated by different letters ($p < 0.05$, Tukey's HSD test).

In general, DCY decreased the amount of honeydew extraction from both virulent and non-virulent SBPH female populations fed on rice seedlings. In comparison, among both populations, the amount of honeydew extraction from non-virulent SBPH was significantly lower than that from virulent SBPH. Furthermore, in the DCY treatments, the amount of honeydew extraction from both SBPH female populations (virulent and non-virulent) was lowered as compared with the control. Among DCY treatments and SBPH populations (interaction), the non-virulent SBPH females fed on DCY 50 extract (0.53 mg) as compared with virulent SBPH females fed on DCY 50 treated rice extract (0.43 mg), which is 23.25% significantly lower than virulent SBPH (Figure 6).

3.7. Effects of DCY on RSV Transmission

The RSV inoculation rates by SBPH were not significantly affected by DCY treatments ($df = 3$, $\chi^2 = 4.40$, $p = 0.22$) (Table 1). The ratio of RSV-positive plants in different DCY-treated rice seedlings fed by virulent SBPH nymphs was not significantly different from control.

The RSV acquisition rates by SBPH were not significantly affected by DCY treatments ($df = 3$, $\chi^2 = 3.88$, $p = 0.27$) (Table 2). The ratio of RSV-positive SBPHs in the offspring of virulent SBPH females fed on different DCY-treated rice seedlings was not significantly different from the control.

Table 2. RSV acquisition rate of SBPH fed on DCY-treated rice.

| DCY | Concentration (mg L ⁻¹) | No. of Valid Insects | No. of Nymphs Acquiring RSV | Virus Transmission Rate (%) | Chi-Square (χ^2) Test |
|-----|-------------------------------------|----------------------|-----------------------------|-----------------------------|------------------------------|
| | 0 | 50 | 2 | 4.00 | $\chi^2 = 3.88$ |
| | 25 | 50 | 1 | 2.00 | $df = 3$ |
| | 50 | 30 | 3 | 10.00 | $p = 0.27$ |
| | 100 | 51 | 5 | 9.81 | |

The RSV vertical transmission rates by SBPH were not significantly affected by DCY treatments ($df = 3$, $\chi^2 = 2.70$, $p = 0.44$) (Table 3). The ratio of RSV-positive SBPHs in the offspring of virulent SBPH females fed on different DCY-treated rice seedlings was not significantly different from the control.

Table 3. RSV vertical transmission rate of SBPH fed on DCY-treated rice.

| DCY | Concentration (mg L ⁻¹) | No. of Valid Insects | No. of Nymphs Acquiring RSV | Virus Transmission Rate (%) | Chi-Square (χ^2) Test |
|-----|-------------------------------------|----------------------|-----------------------------|-----------------------------|------------------------------|
| | 0 | 96 | 73 | 76.04 | $\chi^2 = 2.70$ |
| | 25 | 95 | 65 | 68.42 | $df = 3$ |
| | 50 | 95 | 70 | 73.68 | $p = 0.44$ |
| | 100 | 96 | 64 | 66.67 | |

4. Discussions

The majority of insect pest management in rice involves the use of pesticides, but pesticides have led to a resurgence of insect pest populations due to increased fecundity in rice fields [24,56,57]. The widespread and inappropriate pesticide application also led to resistance development in insect pests and the eradication of bio-control agents, along with additional detrimental effects on humans and the environment [21]. Recently, microbial pesticide application has been considered the most appropriate approach to managing pest infestations in agriculture [25,26], as they are host-specific, effective even in small amounts, tend to degrade easily in the natural environment. [58]. The recent study was initiated with the same aim: to investigate the impact of a novel microbial biopesticide, DCY, against SBPH in rice. Prior studies reported that the DCY application decreased the fecundity of BPH and SBPH in rice [40,41]. Previously, Yang et al. (2017) reported that the non-virulent SBPH adult female has significantly lower fecundity than virulent SBPH fed on validamycin-treated rice [55]. In comparison, we also found that the fecundity of non-virulent SBPH was also significantly lower than that of RSV-virulent SBPH fed on DCY-treated rice (Figure 2). These results suggest the potential role of DCY in inducing SBPH fecundity.

According to Wang et al. (2022), the nymphal survival of SBPH was recorded as being lower on rice treated with Cyantraniliprole at lethal concentrations (LC 20 and LC 30) [59]. Furthermore, another study by Wen et al. (2021) also found a considerably lower SBPH nymphal survival on Triflumezopyrim (TZM) lethal dosage (LD 10, LD 20, and LD 30) treated rice [60]. On the contrary, our results showed that the nymphal survival of virulent SBPH was significantly higher than that of non-virulent SBPH fed on DCY-100 treated rice (Figure 3). Previously, Wang et al. (2021) reported that wheat seeds primed with calcium chloride provide protection against the wheat aphid, *Schizaphis graminum* [61]. Similarly, the exogenous application of the flavonols, kaempferol, and quercetin to TN1 rice seedlings increased their survival rates in response to white-backed planthopper *Sogatella furcifera* feeding [62]. Ma Chao et al. (2022) studied that rice seeds primed with DCY enhanced rice seedling survival against BPH infestation [41]. A recent study has also shown that the DCY application has enhanced the tolerance of rice against SBPH infestation. Previously, Wan et al. (2015) reported that the non-virulent SBPH female body's weight was considerably lower than that of the RSV-infected SBPH fed on rice, while the male body weight was not different for both non-virulent and RSV-infected SBPH [63]. In contrast, we recorded contradictory results, which revealed that the non-virulent SBPH female body's weight was significantly higher than that of virulent SBPH fed on DCY-treated rice (Figure 1A). In regards to the SBPH male body's weight, non-virulent SBPH was also considerably heavier than virulent SBPH fed on DCY-treated rice (Figure 1B). Formerly, Ma et al. (2022) observed that BPH feeding on DCY-treated rice significantly reduced the amount of honeydew excretion [41]. In comparison, our results also showed that the honeydew excretion of SBPH on DCY-treated rice was significantly reduced. Furthermore, the honeydew excretion of non-virulent SBPH was significantly higher than virulent SBPH on DCY-treated rice (Figure 6).

Prior, Attia et al. (2020) studied the effect of different plant growth-promoting rhizospheric bacteria (PGPR) such as *Bacillus subtilis*, *Achromobacter xylosoxidans*, and *Lysinibacillus*

bacillus fusiformis and the combination of all these three strains against the tomato early blight disease *Alternaria solani* [64]. The results revealed that the combined mixtures of these bacterial strains enhanced plant growth and suppressed early blight disease in tomatoes. Another study was conducted by Ranganathan et al. (2006) to investigate the effect of pyridine N-oxide (PNO), 4-morpholinopyridine N-oxide (MNO), and Silicon dioxide as a Sodium metasilicate (SMS) in rice against yellow stem borer (*Scripophaga incertulus*) and rice blast disease (*Pyricularia grisea*). They showed that rice treated with MNO (100 mg kg⁻¹) and SiO₂ (150 mg kg⁻¹) reduced the blast disease incidence in rice-treated plants as compared to untreated [65]. Yang et al. (2017) studied that RSV inoculation rates were not significantly affected when virulent SBPH nymphs fed on prior Validamycin- and Triazophos-treated non-infected rice plants [55]. In comparison, our study showed similar results: the RSV inoculation rates were not significantly affected when virulent SBPH fed on pre-treated DCY healthy rice plants (Table 1). Formerly, Yang et al. (2017) studied that the application of Validamycin considerably increased the RSV acquisition rate of non-virulent SBPH fed on Validamycin RSV-infected rice, while Triazophos application did not significantly influence the RSV acquisition rate of non-virulent SBPH fed on Triazophos-treated RSV-infected rice [55]. We observed similar results with the Triazophos application; we detected that the RSV acquisition rate of non-virulent SBPH fed on prior DCY-treated RSV-infected rice was non-significant (Table 2). Yang et al. (2017) investigated that the number of RSV-positive progeny of virulent SBPH females was significantly enhanced when reared on Triazophos-treated rice as compared to control and validamycin-treated rice [55]. Our results revealed that the number of RSV-positive offspring of virulent SBPH was not considerably affected on DCY-treated rice as compared with the control treatment (Table 3).

Yang et al. (2018) investigated whether silica application in rice boosted the resistance against BPH by prolonging non-probing and stylet pathway activities through strengthening physiological barriers in order to reduce phloem sap-feeding [66]. Similarly, Wang et al. (2020c) found that the gravid WBPH females spent significantly more time in the np and pathway phases but considerably less time in the N4-b phase when rice was exposed to the chemical elicitor, 4-fluorophenoxyacetic acid [67]. Zhang et al. (2015) investigated whether tricin concentration in rice can prolong the np waveform duration of BPH [68]. Further, Ma et al. (2022) studied that rice plants treated with DCY significantly prolonged the time period and occurred more frequently in BPH feeding waveforms (i.e., np, N2, and N3); however, the waveform (N4-b) time period was considerably decreased [41]. Our results conform with the above-mentioned findings of previous studies. We observed that the DCY-primed rice seedlings significantly prolonged the time period and increased the frequencies of non-virulent SBPH feeding waveforms (i.e., np, N2, and N3), although the time period of the waveform (N4-b) was considerably reduced (Figure 5A,B). In contrast, in terms of RSV-virulent SBPH, the time periods of the np, N1, N2, and N3 waveforms were significantly prolonged, and the number of occurrences of the N4-b waveform was decreased on DCY-primed seedlings. These results revealed a slight reduction in RSV inoculation of SBPH on DCY-treated rice (Figure 5C,D).

The results regarding SBPH biological parameters, feeding behavior, and honeydew extraction with DCY priming enhanced the resistance of rice, but further study will be needed to explain the mechanism by which this resistance is augmented in rice against SBPH.

5. Conclusions

In conclusion, the findings of our study revealed that rice seeds primed with DCY adversely affected the life-table parameters of both RSV-virulent and non-virulent SBPH. In addition, SBPH's feeding behavior is also significantly altered by the DCY application. Honeydew extraction of viruliferous and non-viruliferous SBPHs was reduced by DCY application. Rice seedling mortality was reduced in DCY-treated rice fed by SBPH. Non-significant impacts of DCY application against nymphal survival and RSV transmission

rate were observed. Further study should carefully evaluate in the future how DCY affects the expression of rice genes involved in inducing resistance.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agronomy13030864/s1>, Figure S1: (A) Rice seedlings after non-RSV SBPH feeding; the label represents different concentrations of DCY. (B) Rice seedlings after RSV SBPH feeding; the label represents different concentrations of DCY; Table S1: Two-way analysis of variance for biological parameters of SBPH fed on DCY-treated rice under laboratory conditions.

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