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## The dynamic interplay of host plant resistance and HIPVs in rice defense against the leaf folder, *Cnaphalocrocis medinalis*

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### Abstract

Olfactometer bioassays were carried out to know the effect of HIPVs emitted by rice plants upon leaf folder herbivory, on the parasitism by *T. chilonis*, with a focus on the role of host plant resistance. The results of the study indicated that *T. chilonis* significantly preferred infested plants over healthy ones, when given a choice between the two of same variety. The infested plants of W1263 attracted the highest per cent of 91.20 parasitoids over healthy plants. The results of dual choice preferences for different infested cultivars showed that *T. chilonis* had different attraction rates for volatiles from different rice varieties. The volatiles from W1263 were efficient in attracting the highest per cent parasitoids followed by the varieties TN 1 and TKM 6. The study confirms that a variation in volatile emission exists with the genotype of a plant species which in turn affects the behavior of natural enemies.

**Keywords:** Olfactometer, tri-trophic interaction, volatiles, rice cultivars

### Introduction

(*Oryza sativa* L.) is a vital crop that feeds more than 65 per cent of the world's population. It is cultivated in 112 countries all over the globe (Raju, 2003) [29]. However, its productivity is threatened by various biotic stresses, including insect pests such as stem borers, plant hoppers, leaf folder, gall midge etc., (Savary *et al.*, 2019) [33]. Among the insect pests, leaf folder, *C. medinalis* (Guenee) is one of the wide spread and destructive pests (Ramasamy and Jaliecksono, 1996) [31]. The larva causes damage by folding the leaves longitudinally into tubular structures and feed on the leaf by scrapping the green matter resulting in white, transparent streaks leading to reduced photosynthesis (Fletcher, 1914; Herdt, 1991) [8, 15].

Plants defense begins with the perception of the herbivore's activities like feeding, oviposition or walking on the plant surface (Shi *et al.*, 2019). Upon perception, plants display indirect and induced defense mechanism by emitting volatiles (Turlings and Wackers, 2004) [47]. The volatiles released upon herbivory are called herbivore-induced plant volatiles (HIPVs). HIPVs are volatile organic compounds that are released by plants in response to herbivore attack and can attract natural enemies of herbivores (Dicke and Baldwin, 2010; Vet *et al.*, 2018) [51]. The natural enemies of the insect pests depend on these volatiles to locate their insect hosts (Turlings *et al.*, 1991; Steinberg *et al.*, 1993) [46, 38].

Host plant resistance is a promising strategy for managing the pests, but its effectiveness can be influenced by a range of factors, including the emission of herbivore-induced plant volatiles (HIPVs). Several studies have demonstrated the potential of HIPVs to enhance the efficacy of host plant resistance against herbivores. Plant variety is one of the crucial factors in determining the volatiles emitted upon herbivory (Dicke *et al.*, 1990; Turlings *et al.*, 1993; Takabayashi *et al.*, 1994; Takabayashi and Dicke, 1996 and Geervliet *et al.*, 1997) [45, 40, 6]. Different plant varieties can vary in the amount and composition of the volatile organic compounds they produce in response to herbivory or other environmental stimuli. This variation can be influenced by genetic factors, as well as environmental factors such as temperature, light, and nutrient availability and can result in varied attraction to natural enemies (Li *et al.*, 2019) [20].

In this study, we investigated the effect of HIPVs emitted by rice plants upon leaf folder herbivory on the parasitism by *T. chilonis*, with a focus on the role of host plant resistance. Many studies were carried out on the influence of oviposition induced plant volatiles on the egg parasitoid behavior. But in the natural context, oviposition and herbivory often coincide with each other. So in this study, the egg parasitoid, *T. chilonis* was used to know its behaviour towards HIPVs of different rice cultivars.

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## Materials and Methods

The study was conducted at the ICAR- Indian Institute of Rice Research during the years 2021- 2022. The rice varieties used in the study were TKM 6, TN 1, and W1263. The bioassay of the parasitoids was studied with a Y tube

olfactometer. Plants of each variety that were used in the experiment were thirty days old after transplanting. The experiment had three treatment combinations and five replications.

**Table 1:** Genetic background of rice varieties:

| S. No. | Variety                 | Parentage                           | Pest response       | Pest/disease   | Reference                                       |
|--------|-------------------------|-------------------------------------|---------------------|--|---|
| 1      | TKM 6                   | GEB 24 X Co 18.                     | Multiple Resistance | Stem borer, Green Leaf Hopper, Brown Plant Hopper, Leaf folder, Thrips, Bacterial Leaf Blight, Rice Tungro Virus and Grassy Stunt. | Jayaraj and Uthamasamy, 1990 <sup>[53]</sup> .  |
| 2      | Taichung Native 1 (TN1) | Dwarf Chow-wu-gen x Tsai-Yuan-Chunj | Susceptible         | Green leafhopper, leaf folder, White backed plant hopper, brown plant hopper, gall midge, rice stem borer, Bacterial Blight.       | Li <i>et al.</i> , 2019 <sup>[20]</sup>         |
| 3      | W1263                   | Donor accession                     | Resistant           | Stem borer, Leaf folder.   | Padmavathi <i>et al.</i> , 2019 <sup>[25]</sup> |

## Insect Culture

To establish the *C. medinalis* colony, naturally occurring adults were collected from rice fields and placed in cages on rice plants of the variety TN1 to mate and lay eggs. A cotton swab soaked in sucrose solution was provided as a food source. The eggs were left on the same plant to hatch, and once the larvae began feeding on the plants, they were moved to new potted plants for further development. Experiments were conducted using late third instar larvae.

Nuclear culture of the egg parasitoid, *T. chilonis* was sourced from National Institute of Plant Health Management (NIPHM), Hyderabad as tricho-cards. The culture was maintained on the eggs of *Corcyra cephalonica* in the laboratory. Each day the newly emerged wasps were collected into clean glass tubes with access to both water and honey solution.

## Olfactometer setup

The Y-tube olfactometer consisted of a Y-shaped glass tube (3.5 cm diameter, stem length 20 cm, arm length 10 cm) fabricated locally. Each arm is connected to an aerator that facilitates the flow of air into a flask filled with charcoal for purification. The purified air then proceeds through another tube into a flask filled with distilled water where it is humidified. The humidified air then flows into closed jars containing plants that serve as the source of odor. Before placing the plants in the jars, they were removed from the pot and the root of the plants was wrapped in moist cotton and then in aluminum foil to prevent the interference of below ground volatiles with HIPVs. The infested plant was kept intact with the leaf folder larvae in its fold. As the humidified air enters the jars, it carries with it the volatile compounds released by the plants and pushes them along with the airflow into the arms of the Y-tube olfactometer. The parasitoids were released at the base of the Y-tube stem and given two minutes to make a choice. The parasitoids moved towards the odor source and entered one of the arms of the Y-tube. The response or choice of the parasitoid was then recorded.

## Dual choice preference test: Infested vs healthy plants

In the dual choice preference test, each plant was infested with two third instar larvae of the leaf folder, 24 hours before the olfactometer studies. The healthy plants of each variety were kept free of infestation throughout the experiment. The infested plant of one variety was kept in a closed glass jar connected to one arm of the olfactometer. The other arm was

connected to another jar where the healthy plant of the respective variety was placed. The egg parasitoid, *T. chilonis*, was released at the end of the olfactometer stem to receive the volatiles emitting from the infested and healthy plants of the same variety through the arms of the olfactometer. The parasitoids were given two minutes to move to any one of the arms of the olfactometer. When the parasitoid moved to any one of the arms within two minutes, its choice was recorded. The experiment was conducted with three treatment combinations, and for each replication, 40 parasitoids were tested for their preference.

The treatment combinations were:

- Infested TN 1 x Uninfested TN 1
- Infested TKM 6 x Uninfested TKM 6
- Infested W1263 x Uninfested W1263

## Dual choice tests – Varietal differences (infested vs infested)

In the dual choice tests for varietal differences, each plant was infested with two third instar larvae of leaf folder 24 hours before the olfactometer studies. The infested plants of three varieties were compared against each other to identify the relative preference of genotypes to the parasitoid. The infested plant of one variety was kept in a closed glass jar connected to one arm of the olfactometer, while the infested plant of another variety was placed in the other arm. The parasitoid was released at the end of the olfactometer stem to receive the volatiles emitting from the infested plants of different varieties through the arms of the olfactometer. The experiment was conducted with three treatments, and for each replication, 40 parasitoids were tested for their preference.

The three treatment combinations were:

- Infested TN 1 x Infested TKM 6
- Infested TN 1 x Infested W1263
- Infested TKM 6 x Infested W1263

## Statistical analysis

Chi squared goodness of fit was used to determine whether the overall distribution of the parasitoids over the two odour sources tested. The level of significance was set at  $p < 0.05$ .

## Results

For each of the dual-choice odor preference experiments, a total of 600 egg parasitoids, *T. chilonis* were subjected to olfactometer testing. Parasitoids that did not exhibit a preference for either odor were eliminated from the analysis.

### Dual choice preferences for infested and healthy plants

The results of the study indicated that the egg parasitoid, *T. chilonis* exhibited a significant preference for infested plants over healthy ones when given a choice between the two (Figure I). Specifically, when offered a choice between infested and healthy plants of the rice variety W1263, 91.20 per cent of the parasitoids significantly preferred infested plants, while only 8.80 per cent chose healthy plants. Similarly, for the rice variety TN 1, 70.40 per cent of the parasitoids moved towards infested plants, while 29.60 per cent chose healthy ones. For the rice variety TKM 6, 79.60 per cent of the parasitoids moved towards infested plants, while 20.40 per cent chose healthy ones.

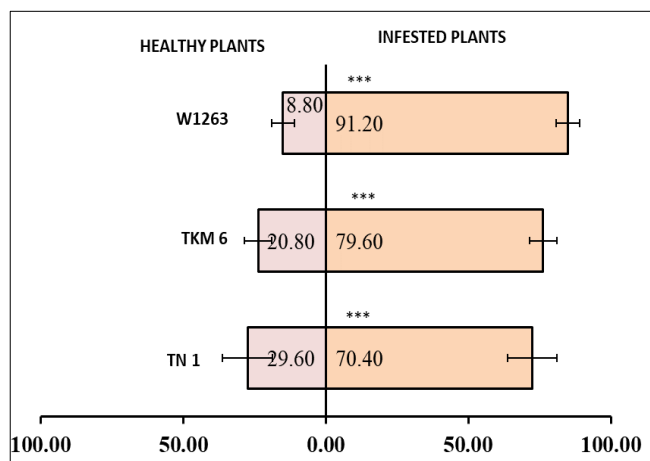


Fig 1: Y-tube olfactometer response of the parasitic wasp,

*Trichogramma chilonis* (N = 40) to volatile profiles of rice cultivars with leaf folder infestation against healthy plants (Chi squared goodness of fit was used to determine whether the overall distribution of the parasitoids over the two odour sources deviated from 50:50 (H<sub>0</sub>:  $\mu = 0.5$ ))

The preference of parasitoids for infested plants varied among the rice varieties tested, with the order being W1263 > TKM 6 > TN 1. When considering both infested and healthy plants across all varieties, the order of parasitoid preference was infested W1263 (91.20 per cent), infested TKM 6 (79.60 per cent), infested TN 1 (70.40 per cent), healthy TN 1 (29.60 per cent), healthy TKM 6 (20.40 per cent), and healthy W1263 (8.80 per cent).

### Dual choice preferences for different infested cultivars

The results on dual choice preferences for various infested cultivars showed a significant variation in the rate of attraction of parasitoids across different rice varieties (Figure II). The percentage of parasitoids that chose different infested cultivars ranged from 27.10 per cent to 72.90 per cent. The egg parasitoid, *T. chilonis*, was given three combinations of three different rice varieties to choose between (Figure II). In the first combination, TN 1 and W1263, 29.00 per cent of the parasitoids moved towards the rice plants of variety TN 1, while the remaining 71.00 per cent moved towards the variety W1263. In the second combination, TN 1 and TKM 6, 27.10 per cent of the parasitoids moved towards the rice plants of variety TKM 6, and 72.90 per cent moved towards the variety TN 1. In the third combination, TKM 6 and W1263, 69.00 per cent of the parasitoids chose the rice plants of variety TKM 6, and 31.00 per cent chose the variety W1263.

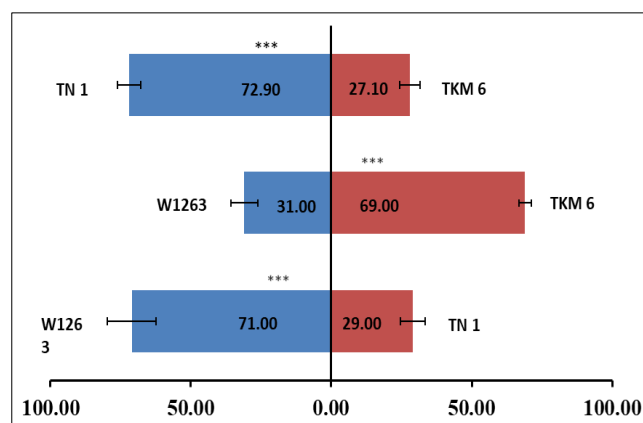


Fig 2: Y-tube olfactometer response of the parasitic wasp,

*T. chilonis* volatile profiles of rice cultivars with leaf folder infestation (Chi squared goodness of fit was used to determine whether the overall distribution of the parasitoids over the two odour sources deviated from 50:50 (H<sub>0</sub>:  $\mu = 0.5$ ))

### Discussion

Plants have developed complex mechanisms to defend herbivore attack in the natural environment. These mechanisms of defense include constitutive and induced defenses. Induced defenses constitute direct and indirect defenses. Plants can be induced to produce toxins or digestion inhibitors against herbivores. Indirect induced defenses are used to attract natural enemies of herbivores through odour cues. The volatiles thus produced by a plant upon herbivore attack to attract its natural enemies are called herbivore induced plant volatiles (HIPVs) (Price *et al.*, 1980; Stenberg *et al.*, 2015) [28, 39]. Therefore, direct defense mechanisms can affect herbivore preference for host plants, while indirect induced defense mechanisms involve the attraction of natural enemies of the herbivores (Arimura *et al.*, 2009; Dudareva *et al.*, 2006) [1, 7]. Plants have developed the ability to recognize the chemical compounds in oral secretions and oviposition fluids of insects, and to emit a blend of odours that can attract natural enemies when foraging for a host or prey (Giunti *et al.*, 2016) [11]. The attraction of natural enemies to a specific host is due to the qualitative and quantitative differences in volatile emissions between healthy and herbivore-infested plants (Shiojiri *et al.*, 2010) [35]. The HIPVs emitted upon herbivore feeding, serve as odour cues to attract the foraging natural enemies to the host plant (Ayelo *et al.*, 2021a; Conchou *et al.*, 2019; Thomas-Danguin *et al.*, 2014) [2, 4, 43]. The results of dual choice preferences for infested and healthy plants indicate that volatiles were emitted from the leaf folder infested plants from different rice varieties which had an effect on the attraction of the egg parasitoid, *T. chilonis*. The volatiles from infested rice plants were more attractive to individuals of the parasitoid than to those from healthy ones. A difference was observed among the varieties of infested plants in attracting the individuals of the parasitoids in dual choice preferences for infested and healthy plants study. The infested rice variety W1263 (91.20 per cent) registered highest parasitoid attraction followed by TKM 6 (79.60 per cent) and TN 1 (70.40 per cent). This indicates that the volatiles of infested W1263 were more effective in attracting the parasitoids compared to the other two varieties. Egg parasitoids have been observed to prefer infested plants over healthy ones when given a choice between plants of the same

variety (Ayelo *et al.*, 2021b; Giunti *et al.*, 2016; Lou *et al.*, 2006; McCormick *et al.*, 2012; Shiojiri *et al.*, 2010)<sup>[35, 11, 3, 22, 23]</sup>. This preference is thought to be due to the emission of herbivore-induced plant volatiles (HIPVs) by infested plants, which attract natural enemies of the herbivores (Arimura *et al.*, 2009; Dudareva *et al.*, 2006; Halitschke *et al.*, 2001; Hare, 2011; Hilker and Meiners, 2010; Indhumathi *et al.*, 2018; Penafior *et al.*, 2011; Price *et al.*, 1980; Spiteller and Boland, 2003; Stenberg *et al.*, 2015; Takabayashi and Shiojiri, 2019; Turlings and Erb, 2018; Verhage *et al.*, 2010a)<sup>[1, 7, 28, 44, 39, 36, 13, 37, 49]</sup>. When considering both infested and healthy plants across all varieties, parasitoid preference was in the order, infested W1263 (91.20 per cent) > infested TKM 6 (79.60 per cent) > infested TN 1 (70.40 per cent) > healthy TN 1 (29.60 per cent) > healthy TKM 6 (20.40 per cent) > healthy W1263 (8.80 per cent). A minor attraction of the individuals of the parasitoid to the healthy plants was observed. This was because, healthy plants also emit traces of volatiles constitutively, but the plants emit higher amounts of HIPVs upon herbivore infestation (Takabayashi and Shiojiri, 2019)<sup>[36]</sup>. HIPVs are synthesized *de novo* only after herbivore damage to the plant to which the natural enemies rely on for foraging (Pare and Tumlinson, 1999)<sup>[46]</sup>.

The results of dual choice preferences for different infested cultivars clearly showed that *T. chilonis* had different attraction rates for volatiles from different rice varieties. Host plant resistance is an important factor in which the volatile emissions differ from one variety to the other (Rathika and Nalini, 2011)<sup>[32]</sup>. The difference in the quantity and quality of volatiles emitted from each cultivar results in difference in attraction of the natural enemies (Rathika and Nalini, 2011)<sup>[32]</sup>. The volatiles from the resistant rice variety, W1263 were efficient in attracting the parasitoids compared to other two varieties. This outcome was due to the volatile profile difference between resistant and susceptible plants of the same species (Ghirardo *et al.*, 2012)<sup>[10]</sup>. The variation in the volatile composition of different plant cultivars influences the effectiveness of natural enemies (Takabayashi and Dicke, 1996; Geervliet *et al.*, 1997)<sup>[40, 9]</sup>. Similar to our results, the resistant PTB 33 was found to emit higher amounts of defensive volatiles upon herbivory by brown planthopper (Lou and Cheng, 1996)<sup>[21]</sup>. The attraction of the individuals of the parasitoid was higher towards the susceptible TN 1 infested plants compared to the variety TKM 6 that has multiple resistances. Upon infestation with rice leaf folder, the parasitoids, *Trichomma cnapalocrocis* Uchida and *Cotesia angustibasis* Gahan registered higher attraction towards the susceptible TN 1 compared to the resistant, PTB 33 and moderately resistant, IR 72 variety (Rathika and Nalini, 2011)<sup>[32]</sup>. The leaf folder infested resistant cultivars were found to emit lesser number of volatile compounds compared to that of susceptible TN 1 (Navyashree *et al.* 2019)<sup>[24]</sup>. The resistant PTB 33 was found to emit higher amounts of defensive volatiles upon herbivory by brown planthopper (Lou and Cheng, 1996)<sup>[21]</sup>. Induced defenses like HIPVs are synthesized by a network of plant hormones. Jasmonic Acid (JA) and Salicylic Acid (SA) are the important plant hormones that elicit induced defenses in plants. These hormones may work individually, synergistically or antagonistically depending on the stress factors faced by the plants (Verhage *et al.*, 2010b)<sup>[50]</sup>. JA induces plant defenses against chewing insects and necrotrophic pathogens (van Loon *et al.*, 2006)<sup>[48]</sup>. Jasmonic Acid (JA) signalling pathway

is widely for direct defenses in rice (Rakwal and Komatsu, 2000; Kim *et al.*, 2003)<sup>[30, 18]</sup>. Its accumulation occurs in affected plant tissues within minutes after herbivory (Koo and Howe, 2009)<sup>[19]</sup>. Leaf folder attack was found to activate Jasmonic acid (JA) biosynthesis which has a defensive role in plants. The JA signaling pathways promote the accumulation of defensive compounds like phenolamides and trypsin proteinase inhibitors (Zhuang *et al.*, 2021)<sup>[52]</sup>. Guo *et al.* (2019)<sup>[12]</sup> reported that the level of induced JA was much higher in resistant variety compared to the susceptible varieties upon infestation by leaf folder. Among six rice varieties that were mechanically injured and treated with JA, the total amount of volatiles emitted was significantly higher in the susceptible TN 1 (Lou *et al.*, 2006)<sup>[22]</sup>. Therefore, these results suggest that the HIPVs synthesized by various plant hormones play an important role in the mechanism of resistance of plants to herbivores. However, the HIPV emissions can be affected by various factors such as the plant cultivar, duration of infestation, stage of the herbivore, fertilization, host plant resistance etc.,

#### Declaration of interests

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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