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The Hidden Influence: Host Plant Suitability as a Key Factor in Acaricide Susceptibility of *Raoiella Indica*

Daniel L. Silva[1] | Maria Isabel de Oliveira Lopes Gomes[1] | Antônio A. Paz Neto[1] | José W. S. Melo[1] | José E. M. Oliveira[2] | Manoel G. C. G. Júnior[3] | Debora B. Lima[1]

[1]Department of Zoology, Centro de Biociências, Universidade Federal de Pernambuco, Programa de Pós-graduação em Biologia Animal, Recife, PE, Brazil | [2]Embrapa Semiárido, Petrolina, PE, Brazil | [3]Departamento de Fitotecnia, Universidade Federal Rural de Pernambuco, Rua Dom Manuel de Medeiros, s/n - Dois Irmãos, Recife, Prince Edward Island, Brazil

Correspondence: Debora B. Lima (debora.limamelo@ufpe.br)

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ABSTRACT

The susceptibility of herbivorous mites to acaricides can be influenced by the host plants they inhabit, which may impact the effectiveness of pest management strategies. Red palm mite (*Raoiella indica*) is a polyphagous mite that infests a variety of plant species, but its interactions with different hosts and susceptibility to acaricides are not fully understood. This study assessed whether differences in suitability of red palm mite to host plants could affect their susceptibility to different acaricides (abamectin, azadirachtin, fenpyroximate, and pyridaben). The following host plants were evaluated: coconut palm (*Cocos nucifera*), christmas palm (*Adonidia merrillii*), and foxtail palm (*Wodyetia bifurcata*). Host suitability was investigated through the instantaneous rate of population growth (*ri*), while susceptibility to acaricides was investigated using dose–response curves. The susceptibility to acaricides was inversely related to the suitability of the host plant. Thus, coconut palm plants provided the highest *ri* for red palm mite, and these populations were also the least susceptible to acaricides (abamectin, fenpyroximate, and pyridaben). Azadirachtin failed to reach 100% mortality even at the highest concentrations. Our results suggest that coconut palm is a more suitable host for red palm mite, possibly contributing to the mites' enhanced fitness and tolerance to acaricides. This study highlights the importance of considering host plant effects in pest management strategies and suggests that host adaptation may play a role in acaricide tolerance in red palm mite populations.

1 | Introduction

Herbivorous arthropods have been associated with host plants since the early Devonian period (Labandeira 2013). In response to the damage caused by herbivores, plants have evolved both direct defences (e.g., chemical and physical barriers) and indirect defences (e.g., volatile organic compounds, VOCs) that attract or enhance the effectiveness of natural enemies of the herbivores (Dicke and Sabelis 1988; Turlings et al. 1995; Kessler and Baldwin 2002; Heil 2008; Poelman et al. 2008; Mithöfer and Boland 2012). Plants defend themselves with a wide array of chemical defences, which can be produced constitutively or induced by herbivory (Stam et al. 2014; Haeger et al. 2020). Constitutive and inducible phytochemicals affect the physiology and behaviour of herbivores, playing a central role in the defence strategy against arthropods (Richards et al. 2015). Consequently, herbivores are under strong pressure to adapt to the chemical defences of their host plants, constantly developing countermeasures (an "evolutionary arms race," see Fraenkel 1959, and Ehrlich and Raven 1964).

In the struggle against the influences and toxicity of plant chemicals, herbivores develop adaptability through various strategies, including feeding avoidance, plant secondary metabolite detoxification and metabolisation, and even their eventual sequestration for their own use (Ratzka et al. 2002; Després et al. 2007; Heckel 2014; Schuman and Baldwin 2016). The activities of metabolic enzymes (e.g., P450s and glutathione-S-transferases (GSTs)) are involved in the detoxification of secondary plant metabolites and play key roles in the adaptability of herbivores to host plants, including the expression of these detoxification enzyme genes (Nagare et al. 2021; Kshatriya and Gershenzon 2024). At the same time, many of these enzymes also play a role in detoxifying pesticide molecules (Cheng et al. 2017; Ye et al. 2022). Thus, exposure to plant secondary metabolites not only results in the adaptation of insects to plant defences but also affects their ability to detoxify pesticides, influencing both tolerance and resistance to pesticides in arthropod herbivores (Després et al. 2007; Alyokhin and Chen 2017; Zhang et al. 2022).

Dealing with the toxicity of secondary metabolites can be costly, requiring energy and resource allocation for the adaptation and survival of herbivores (Kliot and Ghanim 2012). Therefore, it is plausible to assume that feeding on a suboptimal host imposes general stress on the herbivore, which may negatively affect its susceptibility to pesticides. The red palm mite (*Raoiella indica* Hirst (Acari: Tenuipalpidae)) is an excellent model to test this hypothesis. This species was first described from specimens collected on coconut (*Cocos nucifera* L.) in southern India (Hirst 1924). Its distribution remained restricted to the Old World until it was detected damaging coconut palms on the Caribbean Island of Martinique in 2004 (Flechtmann and Etienne 2004; Dowling et al. 2008). Since its introduction to the New World, this mite has not only reached large populations and spread rapidly, but it has also greatly expanded its host range (Vásquez et al. 2008; Carrillo et al. 2012; Navia et al. 2015; Melo et al. 2018). Currently, about 100 plant species are known to be attacked by red palm mite; these belong to the families Arecaceae, Cannaceae, Cycadaceae, Heliconiaceae, Musaceae, Pandanaceae, Strelitziaceae, and Zingiberaceae (Cocco and Hoy 2009; Carrillo et al. 2012; Vásquez and de Moraes 2013; Gómez-Moya et al. 2017). The main hosts of this species are palm trees (Arecaceae), with coconut palm considered its primary host (Carrillo et al. 2015). The aim of the present study was to evaluate whether the suitability of the host plant for red palm mite is related to its susceptibility to acaricides. For this purpose, the interaction of three plant species is considered hosts of red palm mite (coconut palm, christmas palm (*Adonidia merrillii* [Becc.] Becc.), and foxtail palm (*Wodyetia bifurcata* Irvine)), and four acaricides (abamectin, azadirachtin, fenpyroximate, and pyridaben) recommended and/or used against this species.

2 | Material and Methods

2.1 | Local and Experimental Conditions

Toxicity experiments were conducted at the Universidade Federal de Pernambuco (UFPE). The experiments about biological parameters were carried out at Universidade Federal Rural de Pernambuco (UFRPE).

2.2 | Mite Sources

Red palm mite individuals were collected from coconut palm leaflets at Universidade Federal de Pernambuco (UFPE) campus, and christmas palm and foxtail palm leaflets at Universidade Federal Rural de Pernambuco campus (UFRPE).

2.3 | Acaricides

The acaricides used were: abamectin (Abadin 72 EC CropChem Ltda.), azadirachtin (Azamax 12 EC E.I.D. Parry Limited), fenpyroximate (Ortus 50 SC Nichino do Brasil Agroquímicas Ltda.) and pyridaben (Sanmite 200 EC EW Iharabras S.A. Indústrias Químicas).

2.4 | Experimental Procedure for Determination of the Instantaneous Growth Rate

Seedlings of each host plant were obtained from commercial nurseries. The seedlings were properly identified and maintained throughout the experiment in the UFRPE greenhouse, at an average of 28.5°C and 70% ± 10% relative humidity and 12 h of photophase. The seedlings were 2–3 years old and measured between 1.2 and 1.7 m in height. The leaflets of each seedling were cleaned with cotton moistened with distilled water and each plant was placed individually inside cages made of voile to prevent the colonisation by other mites or organisms.

Adult males of red palm mite have guarding behaviour, remaining attached to teliocrisalid females until the latter reach the adult stage, for copulation. Thus, pairs of red palm mite were initially identified, consisting of an adult male mated to a female in the deuterochrysalis phase on the leaflets of each host plant (coconut palm, christmas palm and foxtail palm). After identifying couples at specific stages of development, they were transferred to experimental units carefully using fine hair brush. Each Petri dish (9 cm in diameter) contained a polyethylene sponge of the same diameter and 1 cm thickness, moistened with distilled water and covered with 9 cm diameter filter paper, in which one fragments (3.5 × 2.5 cm) of leaflets from each host palm were placed (experimental unit). The edge of the fragments was covered with hydrophilic cotton moistened with distilled water to maintain humidity and prevent mites from escaping.

The Petri dishes were kept in an incubator at 27°C, 70% ± 10% relative humidity and 12 h of photophase. These previously identified and separated couples were monitored daily until the females reached the adult phase and mated. Before transferring the adult females of red palm mite, a new experimental unit was made on each leaflet of the host on its abaxial region. Leaflets were selected from fully developed leaves of similar ages to minimise the impact of leaf age on the instantaneous growth rate. Three plants of each species was used and the leaflets of the plant were properly labelled and their area was delimited with entomological glue (coconut palm 15 cm × 3 cm, christmas palm 15 cm × 7 cm, foxtail palm 10 cm × 4 cm), in order to isolate the females and prevent possible escapes. The females adults were separated and transferred to leaflets of the seedling of the respective host species from which they were collected. On each

host plant, two females were transferred to each leaflet. From 5 to 8 replicates per host plant (20 to 23 replicates in total by treatment) were performed, each one corresponds to one repetition. Eggs and immature stages were counted daily for 7 days. Using this data, the instantaneous growth rate was calculated using the equation: $ri = \ln (N_f/N_0)/\Delta t$, where: N_f is the total number of mites, N_0 is the initial number of mites, Δt is the time interval between the beginning and the end of the bioassay (Stark et al. 1997; Walthall & Stark 1997). Positive values of *ri* mean that the population is growing, $ri = 0$ indicates that the population is stable, while negative values of *ri* indicate that the population is declining and heading towards extinction.

2.5 | Statistic Analysis

The instantaneous growth rate data were compared using the non-parametric Kruskal-Wallis test; using the SAS statistical program (SAS 2008).

2.6 | Toxicity Experiments

The susceptibility method no. 004 established by the Insecticide Resistance Action Committee (IRAC) was used for the toxicological experiments (IRAC 2009). To find a range of doses for toxicological tests, we carried out preliminary tests with mite populations from different hosts, using three concentrations of acaricides diluted by a factor of 10 (from 0.1 mg of active ingredient/L). After finding the dose range that caused mortality between 0 and 100% of the mite population, six or seven concentrations were established, in addition to the control (only distilled water).

The experimental units used were similar to the setup described in the previous section to maintain the couples of red palm mite for mating, except that the fragments used for their construction contained residues of either acaricides or distilled water (as the control treatment). Rectangular fragments (3.5 × 2.5 cm) of leaflets from each host palm were fully submerged for 5 s in 40 mL of either an acaricide solution or distilled water; then left to dry for 30 min. Only after the fragments had dried were they used to construct the experimental units.

Five adult females of red palm mite from each host palm were transferred with a brush to the respective leaflet fragments of the experimental units. Each unit was made with only one fragment. Four experimental units were used for each concentration, totalling 20 mites per concentration and 140–160 mites per acaricide. Experiments were carried out twice (in different days) from mite populations of distinct host palm. The experimental units were kept in the laboratory at 27°C, 70% ± 10% relative humidity and 12 h of photophase. The evaluation was performed after 24 h, quantifying the live and dead mites, considering dead those that were unable to move after a light touch of the brush.

2.7 | Statistic Analysis

Data from tests performed on different days were evaluated for equality and parallelism of the curves. The replicates that did not show differences between the intercepts and slope of the line were grouped to obtain the concentration–response curves using the DRM function of the *drc* package, using the R software (Posit Team 2024).

3 | Results

3.1 | Host Plant Interference on the Instantaneous Growth Rate of the Red Palm Mite

Red palm mite exhibited the highest rate of population growth (*ri*) on coconut palm and christmas palm, with no difference between them. No difference was found between christmas palm and foxtail palm, but *ri* differed significantly between coconut palm and foxtail palm (Figure 1).

3.2 | Toxicity Experiments

It was not possible to obtain concentration-response curves for the acaricide azadirachtin on coconut palm and foxtail palm due to the low mortality levels observed, even at the highest tested concentrations. The highest mortality on coconut palm was only 53.13% at 12.000 mg/L, while on foxtail palm it was 61.4% at 10.000 mg/L. In coconut palm experiments, 15.63% of the mites left the leaflet onto the cotton layer in the highest concentration, indicating a possible repellent effect of azadirachtin on red palm mite. For christmas palm, the LC_{50} of azadirachtin was determined as 0.398 mg/L (0.293–0.607).

The concentration-response curves fit the probit model, showing low χ^2 and high p values > 0.10. The population from coconut trees was consistently less susceptible (higher LC_{50}) to all acaricides (Table 1 and Figures 2, 3 and 4). Abamectin was the most toxic acaricide to all red palm mite populations evaluated, with the lowest LC50 values (Table 1 and Figures 2, 3 and 4). It was most toxic to the christmas palm population, followed by foxtail palm and coconut palm (Table 1 and Figure 2). The response to pyridaben was similar to that of abamectin, with the highest toxicity to the christmas palm population (Table 1 and Figure 3). For fenpyroximate, there was no difference in susceptibility between red palm mite populations from christmas palm

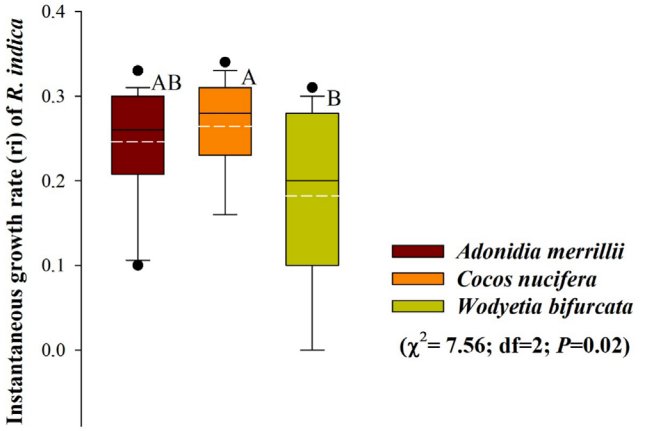

FIGURE 1 | Instantaneous growth rate (*ri*) of red palm mite on different hosts. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 | Relative toxicity to red palm mite from different hosts.

Acaricides/ Model/Hosts	$LC_{50} \pm SE$[a]	χ^2[b]	DF[c]	*p*
Abamectin				
Global model (LL.2)	—————	29.86	36	0.75
Wodyetia bifurcate (LL.2)	0.04 (0.02–0.05)[b]	8.04	12	0.78
Adonidia merrillii (LL.2)	0.01 (0.01–0.05)[c]	12.41	14	0.57
Cocos nucifera (LL.2)	0.16 (0.12–0.20)[a]	9.41	10	0.49
Pyridaben				
Global model (LL.2)	—————	12.22	34	1.00
Wodyetia bifurcate (LL.2)	6.68 (4.14–9.22)[b]	1.81	12	1.00
Adonidia merrillii (LL.2)	3.64 (1.87–5.41)[c]	2.23	12	1.00
Cocos nucifera (LL.2)	29.19 (16.54–41.84)[a]	8.18	10	0.61
Fenpyroximate				
Global model (LL.2)	—————	27.80	36	0.83
Wodyetia bifurcate (LL.2)	1.03 (0.44–1.63)[b]	11.25	12	0.51
Adonidia merrillii (LL.2)	0.97 (0.45–1.49)[b]	8.21	12	0.77
Cocos nucifera (LL.2)	58.72 (39.55–77.90)[a]	8.34	12	0.76

Note: Means followed by the same letter in columns do not differ significantly from each other by overlap of the confidential interval.
[a]Lethal concentration to 50% of the population (LC50) together with their 95% confidence intervals (95% CI).
[b]Qui-square.
[c]Degree of freedom.

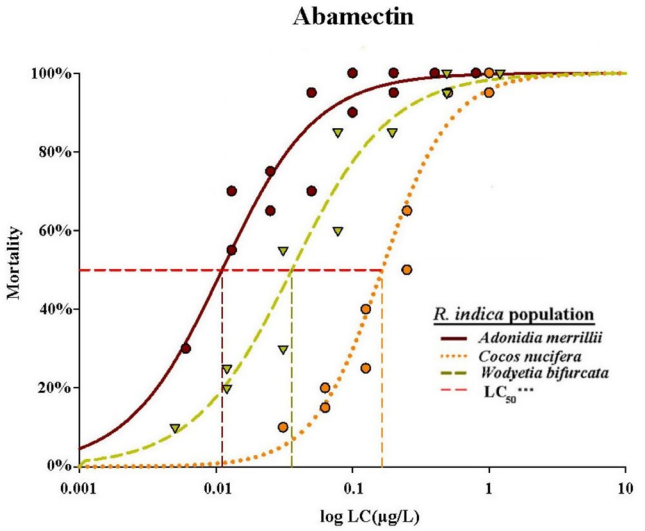

FIGURE 2 | Dose–response curve of red palm mite from different hosts exposed to abamectin. [Colour figure can be viewed at wileyonlinelibrary.com]

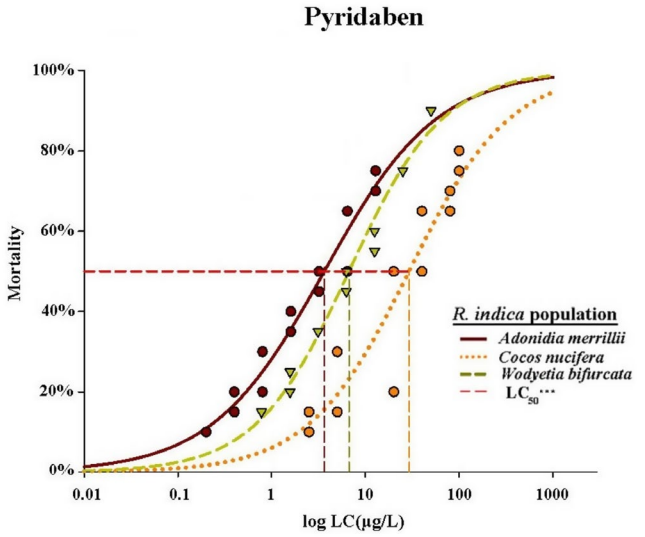

FIGURE 3 | Dose–response curve of red palm mite from different hosts exposed to pyridaben. [Colour figure can be viewed at wileyonlinelibrary.com]

and foxtail palm, but they differed from the coconut palm population, which exhibited a higher LC_{50} (Table 1 and Figure 4).

Red palm mite from coconut palm exhibited the highest LC_{50} for fenpyroximate, indicating that this acaricide is less effective in controlling red palm mite on this host. Conversely, pyridaben was the least toxic to the red palm mite populations on christmas palm and foxtail palm (Table 1 and Figures 2, 3 and 4).

4 | Discussion

Our study is one of the few to demonstrate how susceptibility to acaricides varies in polyphagous mites with the plant species on which they happen to feed when treated. More specifically, we demonstrated that coconut palm plants provided the highest instantaneous growth rates for red palm mite, and these populations were also the least susceptible to the acaricides (abamectin, fenpyroximate, and pyridaben). In other words, susceptibility to acaricides was inversely related to the suitability of the host plant.

A substantial body of evidence indicates that the host plant can influence a mite's fitness and performance. Our study demonstrates that the host plant affected the instantaneous growth rate of red palm mite. This variation in growth response is most likely linked to the nutritional quality of the host plant. Poor-quality hosts can impair the fitness and performance of herbivores by reducing the production and activity of enzymes responsible for detoxifying secondary metabolites (Awmack and Leather 2002; Wilson et al. 2019). Detoxifying enzymes play a crucial role in the evolution of herbivore-plant interactions by allowing

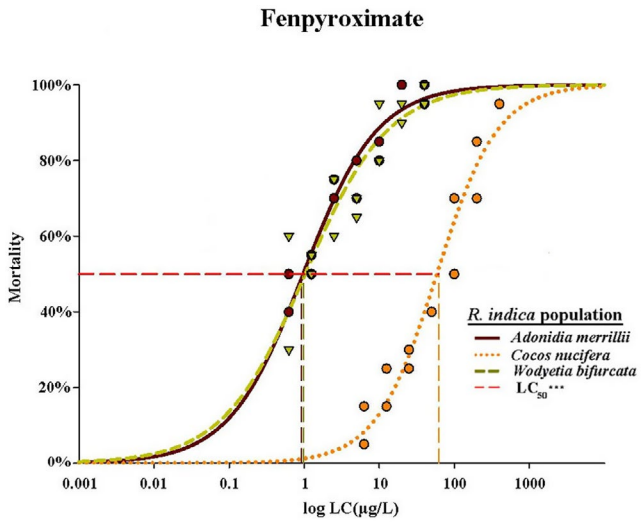

FIGURE 4 | Dose–response curve of red palm mite from different hosts exposed to fenpyroximate. [Colour figure can be viewed at wileyonlinelibrary.com]

herbivores to neutralise host chemical defences (Kshatriya and Gershenzon 2024). Moreover, many enzymes involved in the detoxification of plant secondary metabolites are also responsible for deactivating pesticide molecules (Gordon 1961; Mullin and Croft 1983; Islam 2019), which influences the toxicity of these synthetic compounds to pests.

Our study also demonstrated that the origin of red palm mite populations influenced the toxicity of the acaricides abamectin, fenpyroximate, and pyridaben, with populations from coconut palm being more resistant to all three products. Red palm mite was originally described from individuals found on coconut trees (Hirst 1924). Studies show that among several hosts evaluated, red palm mite favoured the coconut tree as its preferred host (Gondim et al. 2012; Kane et al. 2012; Vásquez et al. 2015; Otero-Colina et al. 2016; Gómez-Moya et al. 2017). A shorter development time, greater longevity, and higher intrinsic growth rate of red palm mite were observed on coconut palm compared to other palms, including christmas palm (Vásquez et al. 2014). This response may be due to a longer co-evolutionary period between red palm mite and this host. Therefore, the higher growth rate and lower pesticide toxicity may suggest that the coconut population of red palm mite possesses more efficient enzymes for deactivating the toxins of the coconut palm, and these enzymes may also be involved in deactivating synthetic chemical compounds. Herbivores with high enzymatic activity typically exhibit better fitness on hosts rich in toxic compounds and show reduced susceptibility to synthetic chemicals—a result observed in both insects (Brattsten et al. 1977; Zhang et al. 2023) and mites (Ibrahim 2009; Grbić et al. 2011). However, other factors, such as feeding rate, differential bioavailability, and enhanced enzymatic activity (Gordon 1961; Yu 1986; Wright and Verkerk 1995), may also contribute to this low susceptibility to acaricides, and further studies investigating these factors should be conducted.

The results presented here are consistent with other studies showing that the differential susceptibility of herbivores to pesticides is influenced by the quality of the host plant. For example, the migratory grasshopper *Melanoplus sanguinipes* (Fabricius) (Orthoptera: Acrididae) is significantly more susceptible to deltamethrin when fed oats, requiring only one-third of the dose needed to achieve the same effect as when feeding on rye (Hinks & Spurr 1998). Similarly, the aphid *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) has shown a 200-fold difference in insecticide susceptibility depending on the host plant (Ambrose and Regupathy 1992). In *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae), pesticide susceptibility was altered by dietary manipulation, where the presence of plant defence metabolites interfered with this species' susceptibility to pesticides (Xue et al. 2010). Furthermore, the *Spodoptera frugiperda* (Smith) corn-fed strain exhibited higher insecticide tolerance and detoxification enzyme activities compared to the rice-fed strain, with multiple detoxification genes upregulated in the corn-fed strain. Additionally, variations in microbiome composition were observed between the two strains (Gou et al. 2022). Collectively, these findings suggest that population-specific plasticity is related to the diet provided by the host plant.

In mites, this topic has been less explored. A study on the mite *Tetranychus urticae* Koch (Acari: Tetranychidae) found that populations from different host plants—including rose, beans, tomato, and cucumber—were subjected to various acaricides and exhibited different toxicity ratios. Rose-associated mites exhibited greater resistance to abamectin, bean mites to acrinathrin, and tomato mites to fenazaquin (Vassiliou and Kitsis 2013). However, according to Vassiliou and Kitsis (2013), the mites collected from crops that were being sprayed with these products, so simply relating mite resistance to the host population is not logical, and in fact, was not the central objective of this study. Resistance selection is a complex process involving many factors, and the physiological mechanisms behind changes in herbivore susceptibility to insecticides remain largely unknown (Dermauw et al. 2013, 2018). A recent study showed that the genetics of *T. urticae* populations from different hosts influence resistance mechanisms, such as metabolic resistance to acaricides, which can vary depending on the host plant (Huo et al. 2021). Evidence suggests that a generalist lifestyle alone does not predict rapid resistance evolution to pesticides. Instead, the prevalence of pesticide resistance in generalist herbivores likely reflects their economic importance as pests and the strong selection pressure imposed by intensive pesticide use (Dermauw et al. 2018). In our study, we used mite populations that were not under selection pressure from acaricides, meaning the differences in resistance ratios found for the acaricides tested were not influenced by previous exposure to these products. Therefore, in this case, the link between host adaptation and acaricide resistance is plausible.

In summary, our findings underscore the critical influence of host plant on the fitness and acaricide susceptibility of red palm mite. The observed relationships between host plant quality and pesticide susceptibility highlight the necessity of integrating ecological considerations into pest management strategies. By understanding the adaptive mechanisms employed by herbivores like red palm mite in response to their host plants, we can better anticipate the challenges posed by pest populations and develop more effective, sustainable approaches to mitigate their impact in agricultural systems. Future research should focus on elucidating the specific physiological and genetic factors that govern

these interactions, paving the way for innovative solutions in pest management that align with environmental sustainability.

Author Contributions

D.L.S. and M.I.O.L.G. conducted experiments. D.L.S., A.A.P.N., J.W.S.M., J.E.M.O., M.G.C.G.J., and D.B.L. wrote the manuscript. A.A.P.N., J.W.S.M., and D.B.L. analysed data. J.E.M.O. contributed to the toxicity part of the study. D.B.L. the methodology to be used. All authors read and approved the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.13984641, reference number 13984641.

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