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Prediction of Whitefly Population and Infestation Based on Multitrophic Analysis between Competitor Pest, Plant Traits and Natural Enemy

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Abstract: Interaction among arthropods (insect-acarine) was investigated at all trophic levels in agro-ecosystem and affects the population dynamic and diversification of arthropod pests and intensity of natural enemy (parasitism) as well as stimulates the plant chemical defence. In the present study of two cropping periods, nutrient concentration and early infestation of plant-sucking pests are known to trigger different degrees of interactions (plant's parameters) which potentially alert abundance and diversity of the insect pests. Clearer interaction and magnitude of impact could be assessed (multivariate analysis of variance (MANOVA) and redundancy analysis (RDA)) and observed between arthropods (insect-acarine) community and plants' parameters from the strongest to the lowest effects. The two factors could have affected the community of insect-pests with various degrees of pressure effect and interaction that occurred naturally, thus leading to the predictable abundance of insect-acarine populations under eggplant leaves in response to plant physical characteristics (e.g., size of leaves, number of leaves and plant height) and biochemical constituents (flavonoid, phenolic, peroxidase and β-1,3-glucanase). Based on multivariate analyses of multitrophic interaction, MANOVA and RDA have the potential to elucidate the complex interaction among plant performance, abundance of pests and activity chemical defence compounds. Both analyses interpreted similar interactions of measured parameters in different ways. Whitefly population in this study was predictable by aphids, thrips and total phenolic contents in eggplant. Eggplant has capable defence systems against insect-acarine pests after stimulation (pre-infestation). In relation to IPM strategy, early stages of plant growth are known as susceptible periods for pests attack but the plant becomes more tolerant during the fruiting stage.

Key words: Multitrophic, insect interaction, whitefly, aphids, thrips and eggplant.

1. Introduction

Arthropods (insect and acarine) distribution and their relationship to biological parameters of plants are important for developing an effective control strategy [1, 2]. At all trophic levels, interaction, population dynamic and diversification of arthropod pests and intensity of natural enemy (parasitism) stimulate the plant chemical defence [3-6]. Indeed, this interaction-response complex helps to better understand the ecological aspects of pests which may lead to fast development of agricultural ecology [7]. In multitrophic systems, feeding behavior depends on various factors including the aggressiveness of pests as well as its intensity [8, 9]. In tropical agricultural ecosystems, the biology and ecology of multitrophic system components are not fully understood resulting in plenty of unproven assumptions and unanswered questions [7]. Dyer and Coley [10] found that variation in the degree of food consumption (nutrient content) eventually affected diversity of the pest communities. In the tropical agro-ecosystems, this

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pattern of diversity and alteration (variation) in the food consumption is unique as predation, chemical defence and multitrophic mutualisms are more complicated because insect pests are more diverse compared to other area [11].

Generally, plant responds to the pests attack through various ways called plant defence mechanisms. Against herbivores, for example, plant leaves were found to be tougher with high concentrations of toxic compounds [12]. Consequently, herbivore populations are strongly influenced by the bottom-up effect of greater plant defences and the top-down force of superior enemy densities [13]. In addition to that, the co-evolution among the hosts, herbivorous insects and parasites is an important process controlling the community structure in the agro-ecosystem [14]. The theory of co-evolutionary is often considered as an important selective mechanism that shapes the structure of predators and parasitoids communities [15].

On the other hand, nutrient concentration and early infestation of plant-sucking pests are known to trigger different degrees of interactions which potentially alert abundance and diversity of the insect pests [16]. That in turn will result in creating different patterns of plants defence mechanisms especially chemical response [17, 18]. With regard to the interaction between high and low trophic components, Polis and Strong [19] observed obvious increase in the diversity at a particular trophic level associated with significant weakness in the effect of consumption at the lower trophic levels which may be related to competition (e.g., intraguild predation), diet shifts, omnivory as well as other buffering mechanisms. Meanwhile, high diversity can also affect the resource availability for upper trophic levels due to increase in the competition, decrease in the host availability for specialists and changes in the plant chemical defence mechanisms [10]. Due to various limitations (related to high diversity of species), the comprehensive understanding of different interactions in the agro-ecosystem, analyzed the entire ecosystems are still rather difficult [9, 20].

Early infestation by whitefly (pre-infestation treatment) on the eggplants played an important role in reducing whitefly population in the field in a bitrophic system. Chemical defense is evidently induced by plant-sucking pests (e.g., whitefly and aphid) as stated by Mayer *et al.* [21] and Hopkins and Hüner [22]. Hence plant chemical defence may affect the pest itself, competitor pests or higher trophic organism (e.g., parasitoid).

In this study, three major ecological aspects in the multitrophic system were considered: first, biochemical and physiological aspects of the host plant (e.g., chemical defense), second, agronomic aspect of nutrient application such as nutrient concentration was highlighted due to the fact that nutrient concentration is arbitrarily used by the farmers to improve the crop production, and third, this study also sheds the light on various ecological aspects and relationships of insect-acarine communities.

Additionally, this study emphasized and selected most of key insect-pests present simultaneously on the eggplant leaves [23]. There is a substantial lack in the comprehensive understanding of insect-acarine-plant interaction with reference to different trophic levels, plants (e.g., eggplants) and region (e.g., tropics). This study provides baseline data to predict what and which parameters play important role in influencing insect-acarine on eggplants at multitrophic interaction levels with consideration to the effect of plant response (e.g., pests infestation), competitor pests (e.g., aphids, thrips, mite and spider mite) parasitoid activity (*Encarsia hitam*) and agronomic practices (nutrient concentration levels) on whitefly population. The study also provides necessary information for integrated whitefly management as the relationships among trophic levels and plants defence mechanisms were examined. Furthermore, mutual effects of lower and higher trophic levels and the interaction between trophic levels in a single system have been rarely studied [24].

The present study aimed to investigate the influence of all variable sets together; biological traits of eggplant (leaf size, leaf number and plant height) and chemical defence (total flavonoid content (TFC), total phenolic content (TPC), peroxidase (POD), β-1,3-glucanase (GCS)) on abundance of insect-pests (whitefly, aphid, thrips spider mites and mites) and natural enemy (parasitoid).

2. Materials and Methods

2.1 Location of Study

This study was carried out for two cropping periods in a rain shelter at Agriculture Centre, Relau and at the Food Technology Analysis Laboratory University Sains Malaysia, Pulau Pinang, meanwhile for laboratory studies, sorting, counting and identification of several arthropod species were carried out in Entomology Laboratory, School of Biology Sciences, Universiti Sains Malaysia.

2.2 Experimental Design

Selected F1-hybrid eggplant Polybags were arranged in four blocks at 1 m apart between plants and 1 m between blocks. This experiment was carried out for two cropping periods: August to October 2010 and between February and May 2011 for the first and second crops, respectively.

There were 36 samples collected in four replicates and all the variables were measured at three layers of the trophic system including host plant, insect and its natural enemies for both cropping periods. The pest species residing on the underside of eggplant leaves were sampled and counted using a stereomicroscope (20×).

2.3 Sampling and Sample Analysis

Chemical defence analysis of productions of two secondary metabolites was estimated. Thus, plant response to the pest attack was measured based on the amount of non-protenaceous secondary metabolites (the TFC and TPC) produced in the leaves in the first cropping period.

Three leaf samples were cut from three plants receiving each treatment and placed inside the labelled zip-lock plastic bag. The leaves were dried in an oven at temperature of 48 °C for 3 d. Then, the leaves were finely ground in a blender. Leaf extracts were prepared by soaking the ground leaves in 50 mL ethanol in a conical flask at a ratio of 100 g dried leaves to 1 L of ethanol. The flasks (leaves) were covered by aluminium foil to prevent vaporization of methanol and incubated at room temperature for 48 h. The extracts were filtered through filter paper (125 mm) and cotton wool. The extract was kept at room temperature for further analysis.

In this study, the TPC of eggplant leaves was analyzed in the laboratory determined according to Taga *et al.* [25] using Folin-Ciocalteu's method while TFC was analysed following the procedures of Barros *et al.* [26] with slight modification.

The protenaceous secondary metabolites in the form of enzyme activity (POD and GCS) were measured in the second cropping period. Two types of enzymes in the leaves, POD and GCS were analysed.

Fresh leaves excised from the plants were washed gently in cold water and kept in labeled zip-lock plastic bags. The samples were brought back to the laboratory and stored in a freezer at -20 °C to prevent enzyme degradation and activity prior to biochemical analysis. Ten grams (10 g) leaf sample for each treatment was weighed using a digital scale and mixed with 6.25 g polyvinylpolypyrrolidone (PVPP-Sigma-Aldrich). The mixture was ground in a pre-chilled blender for about 1 min with 50 mL of cold distilled water (2-4 °C) then filtered using a sieve cloth (Miracloth) and subsequently centrifuged at 10,000 *g* for 15 min. The supernatant (extracted leaves sample) was divided equally into two vials for enzymes POD and GCS analyses, respectively. The supernatant of each vial (treatment) was divided equally into four test tubes for each enzyme analysis: three replicates and a blank. In the field experiment, combination of three nutrient levels and three levels of pre-infestation in four replicates (blocks) led to 36 samples all together to be analysed for this experiment.

Three solutions: Dinitrosalicyclic acid (DNS), reagent A (300 g sodium phosphate (Na_3PO_4) dissolved in 500 mL distilled water) and B solution (10 g DNS reagent and 16 g sodium hydroxide (NaOH) dissolving in 200 mL distilled water) were prepared. Both were mixed and filled up with water (1 L solution). While for Lamina solution (2% *w*/*v*) was prepared by dissolving 0.2 g laminarin powder (Sigma) in 10 mL of 0.2 M sodium acetate buffer (pH 5.0) (equivalent to 20 tested tubes). Then, the mixed solution was immersed in a water bath at 100 °C for 1 min and ready for use. Whereas, to determine GCS activity in eggplant leaves was followed the procedures by Abeles and Forrence [27] with slight modification.

2.4 Data Analysis

The main concern in this study is to investigate the combined influence of all variables sets: biological traits of eggplant (leaf size, leaf number and plant height) and secondary metabolites (TFC, TPC, POD, GCS) on abundance of insect-pests (whitefly, aphid and thrips) and natural enemies (mite, spider mites and parasitoids).

For this purpose, multiple regression, multivariate analysis of variance (MANOVA) of Statistical Package for Social Science (SPSS version 15, 2006) and redundancy analysis (RDA) of CANOCO software package (version 4.5) [28] was used to examine the influence of all variables on abundance of whitefly, insect-acarine and natural enemies. The significance value of the produced model of RDA was obtained using Monte Carlo test at $p < 0.05$ with 499 permutations. RDA was selected because the data were obtained within the range value which was assumed as linear relationship.

3. Results

3.1 Effect of Multitrophics Interaction (Plant Parameters, Competitor Pests and Parasitoid) on Whitefly Population

In the first cropping period, seven independent variables (population of aphid, thrips, mite, spider mites, parasitoid, TFC and TPC) explained 39.6% of the total variance in whitefly population (Table 1). As illustrated in Table 1, there was no relationship between the residuals and predicted values, which was consistent with the assumption of linear interaction among variables (linearity). Therefore, population of aphids and TPC were good predictors of the changes in the whitefly population during the first cropping period ($F_{(7,64)} = 5.999$, $p < 0.01$).

In the second crops, however, combination of seven independent variables explained approximately 19.0% of the total variance in whitefly population (Table 2). Meanwhile, populations of thrips showed to be a potential predictor ($F_{(7,64)} = 2.151$, $p < 0.05$) for changes in the whitefly population (Table 2).

3.2 Multitrophic Interactions between Abundance of Insect-Acarine, Biological Traits of Eggplant, Competitor Pests and Parasitoid

As shown in the MANOVA results (Table 3), all physical characteristics (number of leaves, plant height and size of leaves) did not influence the abundance of all infesting arthropods. As TFC obviously affected only spider mites ($p < 0.05$), TPC also influenced significantly ($p < 0.05$) the populations of whitefly, thrips and mites.

Table 4 shows the effect of plant parameters on abundance of insect-acarine species in the second cropping period. No significant effect was found between plant parameters on all insect-acarine species. Meanwhile, POD and GCS influenced significantly ($p < 0.05$) abundance of the aphid but not the other pests.

Table 1 Multiple regression results of whitefly population versus biological parameters of the plant and abundance of insect-acarine in the first cropping period.

	Coefficient	SE	*t*	*p*	R^2
Whitefly (a)					
Constant (b)	-9.790	9.313	-1.051	0.297	0.396
Aphid	1.949	0.911	2.139	0.036*	
Thrips	-1.551	1.742	-0.890	0.377	
Mite	0.056	0.989	0.057	0.955	
Spider mite	-0.296	0.174	-1.701	0.094	
Parasitoid	0.778	2.966	0.262	0.794	
TFC	1.991	1.900	1.048	0.299	
TPC	3.603	0.884	4.078	0.000*	

(a) Dependent variable: population of whitefly; (b) Predictors: (constant), total phenolic content (TPC), total flavonoid content (TFC), parasitoid (*Encarsia hitam*), population of mite, population of aphid, population of spider mites, population of thrips; *significant at $p = 0.05$; SE: standard error.

Table 2 Multiple regression results of whitefly population versus biological parameters of the plant and abundance of insect-acarine in the second cropping period.

	Coefficient	SE	*t*	*p*	R^2
Whitefly (a)					
Constant (b)	-6.221	19.591	-0.318	0.752	0.190
Aphid	-0.029	0.028	-1.015	0.314	
Thrips	0.770	0.333	2.309	0.024*	
Mite	-0.886	0.834	-1.062	0.292	
Spidermite	-0.076	0.110	-0.692	0.491	
Parasitoid	-0.892	2.441	-0.365	0.716	
POD	403.52	426.20	0.947	0.347	
GCS	0.136	0.182	0.751	0.456	

(a) Dependent variable: population of whitefly; (b) Predictors: (constant), peroxidase (POD), β-1,3-glucanase (GCS), parasitoid (*E. hitam*), population of mite, population of aphid, population of spider mites, population of thrips; *significant at $p = 0.05$; SE: standard error.

Table 3 The relationship results between physical parameters of eggplants and insect-acarine abundance for all treatments using MANOVA in the first cropping period (WAT 2 and WAT 8).

Species parameters	Whitefly	Aphid	Thrips	Spider mites	Mites	Parasitoid
	(a)	(b)	(e)	(d)	(c)	(f)
Cor. model	$F_{(4,67)} = 13.38$; df = $p < 0.01$	$F_{(4,67)} = 4.53$; $p < 0.01$	$F_{(4,67)} = 3.54$; $p < 0.01$	$F_{(4,67)} = 1.78$; $p < 0.01$	$F_{(4,67)} = 2.00$; $p < 0.01$	$F_{(4,67)} = 1.18$; $p < 0.05$
No. of leaves	$F_{(1,67)} = 0.01$; $p > 0.05$	$F_{(1,67)} = 0.22$; $p > 0.05$	$F_{(1,67)} = 0.16$; $p > 0.05$	$F_{(1,67)} = 0.46$; $p > 0.05$	$F_{(1,67)} = 0.11$; $p > 0.05$	$F_{(1,67)} = 3.68$; $p > 0.05$
Size of leaves	$F_{(1,67)} = 3.76$; $p > 0.05$	$F_{(1,67)} = 0.02$; $p > 0.05$	$F_{(1,67)} = 0.04$; $p > 0.05$	$F_{(1,67)} = 0.22$; $p > 0.05$	$F_{(1,67)} = 0.23$; $p > 0.05$	$F_{(1,67)} = 0.091$; $p > 0.05$
Plant height	$F_{(1,67)} = 1.55$; $p > 0.05$	$F_{(1,67)} = 1.29$; $p > 0.05$	$F_{(1,67)} = 0.23$; $p > 0.05$	$F_{(1,67)} = 0.53$; $p > 0.05$	$F_{(1,67)} = 0.01$; $p > 0.05$	$F_{(1,67)} = 2.28$; $p > 0.05$
TFC	$F_{(1,67)} = 0.47$; $p > 0.05$	$F_{(1,67)} = 1.36$; $p > 0.05$	$F_{(1,67)} = 0.69$; $p > 0.05$	$F_{(1,67)} = 0.42$; $p < 0.05$	$F_{(1,67)} = 7.77$; $p > 0.05$	$F_{(1,67)} = 0.062$; $p > 0.05$
TPC	$F_{(1,67)} = 7.81$; $p < 0.05$	$F_{(1,67)} = 1.23$; $p > 0.05$	$F_{(1,67)} = 10.7$; $p < 0.05$	$F_{(1,67)} = 4.31$; $p < 0.05$	$F_{(1,67)} = 2.01$; $p > 0.05$	$F_{(1,67)} = 0.053$; $p > 0.05$

Computed using alpha = 0.05; (a) $R^2 = 0.432$ (adjusted $R^2 = 0.389$); (b) $R^2 = 0.255$ (adjusted $R^2 = 0.199$); (c) $R^2 = 0.158$ (adjusted $R^2 = 0.094$); (d) $R^2 = 0.247$ (adjusted $R^2 = 0.190$); (e) $R^2 = 0.349$ (adjusted $R^2 = 0.300$); (f) $R^2 = 0.127$ (adjusted $R^2 = 0.061$).

TFC = total flavonoid content; TPC = total phenolic content; WAT 2 = vegetative stage; WAT 8 = fruiting stage.

Table 4 The relationship results between physical parameters of eggplants and insect-acarine abundance for all treatments using MANOVA in the second cropping period (WAT 2 and WAT 8).

Species Parameters	Whitefly	Aphid	Thrips	Spider mites	Mites	Parasitoid
Cor. model	(b) $F_{(4,67)} = 2.62$; $p < 0.05$	(b) $F_{(4,67)} = 2.95$; $p < 0.01$	(e) $F_{(4,67)} = 4.69$; $p < 0.01$	(d) $F_{(4,67)} = 1.14$; $p > 0.05$	(c) $F_{(4,67)} = 1.28$; $p > 0.05$	(f) $F_{(4,67)} = 1.28$; $p < 0.05$
No. of leaves	$F_{(1,67)} = 0.09$; $p > 0.05$	$F_{(1,67)} = 0.53$; $p > 0.05$	$F_{(1,67)} = 0.03$; $p > 0.05$	$F_{(1,67)} = 0.34$; $p > 0.05$	$F_{(1,67)} = 0.60$; $p > 0.05$	$F_{(1,67)} = 3.49$; $p > 0.05$
Size of leaves	$F_{(1,67)} = 3.19$; $p > 0.05$	$F_{(1,67)} = 0.02$; $p > 0.05$	$F_{(1,67)} = 1.65$; $p > 0.05$	$F_{(1,67)} = 2.41$; $p > 0.05$	$F_{(1,67)} = 1.25$; $p > 0.05$	$F_{(1,67)} = 0.02$; $p > 0.05$
Plant height	$F_{(1,67)} = 0.37$; $p > 0.05$	$F_{(1,67)} = 0.59$; $p > 0.05$	$F_{(1,67)} = 0.27$; $p > 0.05$	$F_{(1,67)} = 0.04$; $p > 0.05$	$F_{(1,67)} = 0.02$; $p > 0.05$	$F_{(1,67)} = 0.58$; $p > 0.05$
GCS	$F_{(1,67)} = 1.95$; $p > 0.05$	$F_{(1,67)} = 7.02$; $p < 0.05$	$F_{(1,67)} = 0.27$; $p > 0.05$	$F_{(1,67)} = 1.58$; $p > 0.05$	$F_{(1,67)} = 0.08$; $p > 0.05$	$F_{(1,67)} = 0.54$; $p > 0.05$
POD	$F_{(1,67)} = 2.20$; $p > 0.05$	$F_{(1,67)} = 7.21$; $p < 0.05$	$F_{(1,67)} = 0.95$; $p > 0.05$	$F_{(1,67)} = 1.09$; $p > 0.05$	$F_{(1,67)} = 0.10$; $p > 0.05$	$F_{(1,67)} = 0.01$; $p > 0.05$

Computed using alpha = 0.05; (a) $R^2 = 0.199$ (adjusted $R^2 = 0.138$); (b) $R^2 = 0.224$ (adjusted $R^2 = 0.165$); (c) $R^2 = 0.100$ (adjusted $R^2 = 0.031$); (d) $R^2 = 0.093$ (adjusted $R^2 = 0.024$); (e) $R^2 = 0.282$ (adjusted $R^2 = 0.228$); (f) $R^2 = 0.222$ (adjusted $R^2 = 0.163$).

POD: peroxidase; GCS: β-1,3-glucanase; WAT 2 = vegetative stage; WAT 8 = fruiting stage.

Table 5 Means ± SE of eggplant characteristics and arthropods measured during the two distinctive stages of the growth in the first cropping period.

	Parameters	WAT 2	WAT 8
1	Host plants (eggplant)		
	TFC (mg/mL)	3.18 ± 0.39	3.55 ± 2.90
	TPC (mg/mL)	13.56 ± 0.78	2.91 ± 0.57
	Plant height (cm)	23.24 ± 0.87	72.97 ± 1.27
	Leaf number (per plant)	8.65 ± 0.29	70.15 ± 2.94
	Leaf size (cm^2)	152.08 ± 8.30	164.65 ± 5.56
2	Pest and competitor pest		
	Whitefly (per leaf)	47.81 ± 7.20	1.03 ± 0.34
	Aphids (per leaf)	4.69 ± 0.94	0.22 ± 0.14
	Thrips (per leaf)	3.31 ± 0.54	0.53 ± 0.10
	Mites (per leaf)	3.22 ± 0.89	0.083 ± 0.061
	Spider mites (per leaf)	13.69 ± 5.75	0.056 ± 0.038
3	Parasitoid (*E. hitam*) (per leaf)	0	0.53 ± 0.28

TFC = total flavonoid content; TPC = total phenolic content; WAT 2 = vegetative stage; WAT 8 = fruiting stage; SE: standard error.

3.3 Multitrophic Interaction between Insect-Acarine and Biological Traits of Eggplant, Competitor Pests and Parasitoid

Data from various trophics levels obtained during the first and the second cropping periods at initial vegetative and fruiting stage of eggplant are summarized in Tables 5 and 6.

Generally, all insect-pests infesting eggplant leaves declined drastically during the fruiting stage (week after transplanting (WAT) 8) compared to the vegetative stage (WAT 2) in the first cropping period. Similar trend was observed in the second cropping period for all insect-acarine except mite (*Phytoseiulus* sp.). Parasitism rate increased at the harvesting stage as plants reached maturity in both cropping periods but higher parasitism was recorded in the second cropping period. Plant height and number of leaves were found to increase as plant grew, but leaf size decreased as the phenology of plant changed from the vegetative to the fruiting stage. Meanwhile, the amounts of phenolic (secondary metabolites) as well as the activity of GCS and POD decreased in the fruiting stage. However, the amount of flavonoid increased during the fruiting stage.

The RDA biplot (Fig. 1) shows that the TFC and leaf size in the first axis explained 35.8% of the total variance in the population of insect-pests in the first

Table 6 Means ± SE of eggplant characteristics and arthropods measured during the two distinctive stages of the growth in the second cropping period.

	Parameters	WAT 2	WAT 8
1	Host plants (eggplant)		
	GCS (nmol)	63.38 ± 2.56	55.13 ± 1.56
	POD (nmol)	0.041 ± 0.00075	0.0314 ± 0.00076
	Plant height (cm)	14.09 ± 0.68	65.87 ± 1.87
	Leaf number (per plant)	16.60 ± 0.61	70.56 ± 2.55
	Leaf size (cm^2)	245.67 ± 8.74	152.33 ± 6.83
2	Pest and competitor pest		
	Whitefly (per leaf)	25.25 ± 4.37	8.86 ± 1.27
	Aphids (per leaf)	51.19 ± 19.49	0.42 ± 0.21
	Thrips (per leaf)	9.33 ± 1.63	1.19 ± 0.27
	Mites (per leaf)	1.44 ± 0.54	3.14 ± 0.41
	Spider mites (per leaf)	8.42 ± 5.08	0.81 ± 0.25
3	Parasitism activity of		
	E. hitam (per leaf)	0	0.833 ± 0.21

GCS: β-1,3-glucanase; POD: peroxidase; WAT 2 = vegetative stage; WAT 8 = fruiting stage; SE: standard error.

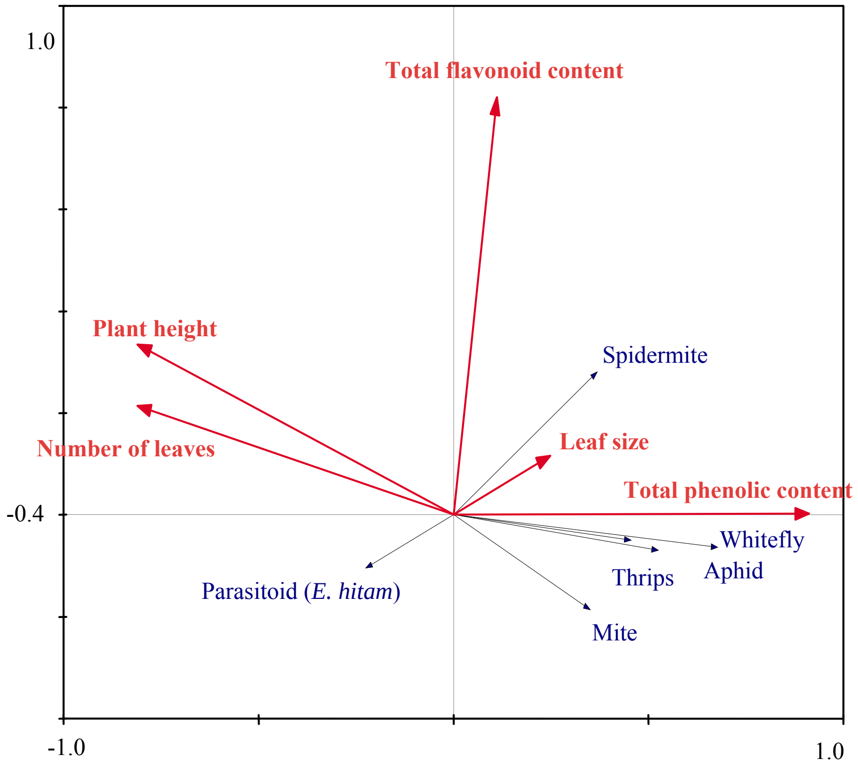

Fig. 1 Two-dimensional ordination of the first two axes from RDA analysis showing the relationship between species from various multitrophic levels including competitor pests, natural enemies and selected parameters such as secondary metabolites and biological characteristics in the first cropping period.

The eigenvalue of the first axes in the RDA model is 0.358 (F-ratio = 36.864, $p = 0.002$).

The eigenvalue of all canonical axes is 0.386 (F-ratio = 8.283, $p = 0.002$).

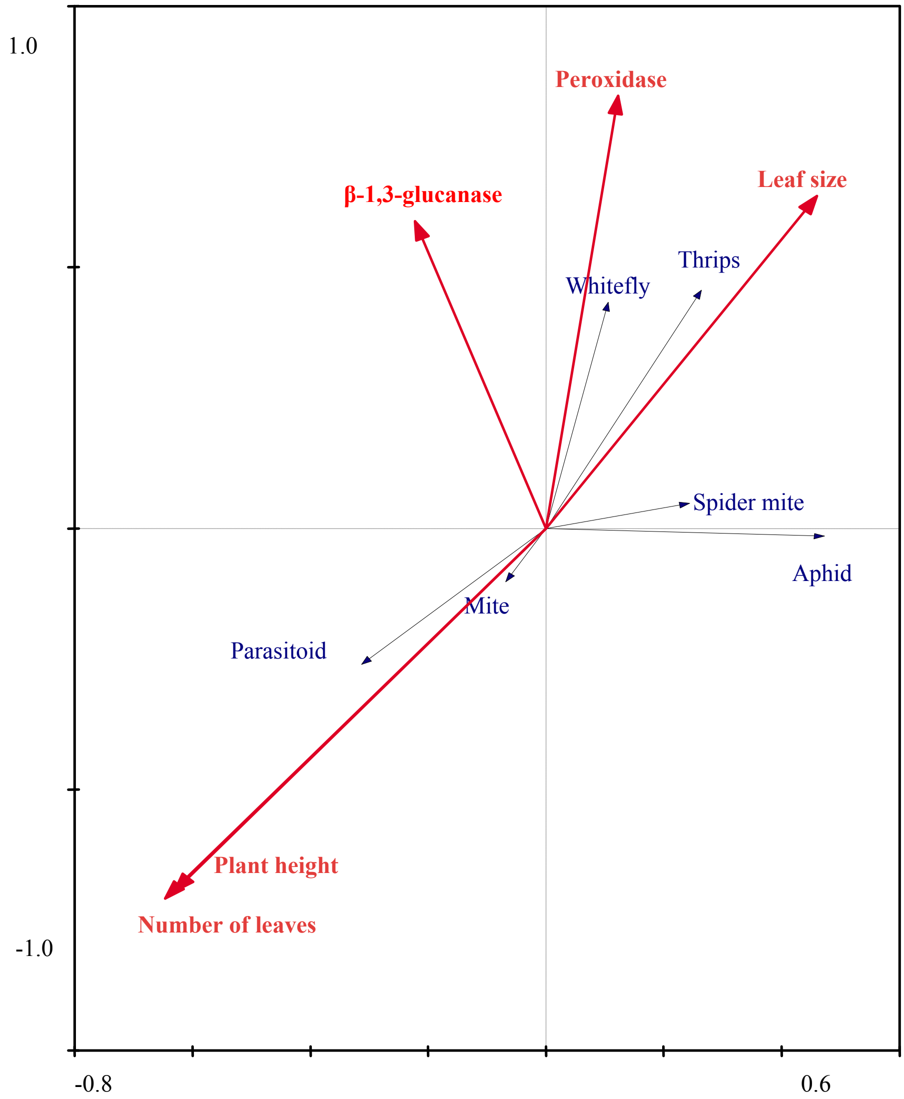

Fig. 2 Two-dimensional ordination of the first two axes from analysis showing the species relationship between species from various multitrophic levels including competitor pests, natural enemies and selected parameters and biological characteristics in the second cropping period.

The eigenvalue of the first axes in the RDA model is 0.192 (F-ratio = 15.641, $p = 0.002$).

The eigenvalue of all canonical axes is 0.213 (F-ratio = 3.574, $p = 0.002$).

cropping period. However, TPC, number of leaves and plant height were assigned in the second axis and explained only 2.6% of the total variance in the population of insect-pests. As shown in the RDA ordination plot, whitefly and aphid correlated positively with TPC. However, plant height as well as the number of leaves was negatively correlated to the abundance of insect-pests. Meanwhile, spider mites population had strong and positive relationship with TFC and leaf size.

Fig. 2 shows that the RDA selected POD, plant height, number of leaves and leaf size in the first axis and explained 19.2% of the total variance in the population of insect-pests in the second cropping period. However, the second RDA axis consisted of GCS with low amount of the variance explained (< 2%). In the second cropping, however, whitefly and thrips had strong and positive relationship with POD yet negative with plant height and number of leaves. Meanwhile, strong relationship was observed between plant characteristics (plant height and number of leaves) and abundance of parasitoid and mite.

However, GCS showed weak relationship with aphids in the second cropping period.

Meanwhile, physical characteristics of plants did not show consistent relationship probably due to variation in the composition and abundance of the pest population in the two cropping periods. The plants were severely attacked by major pests such as whitefly in the first cropping period and aphids in the second cropping period. Consequently, the variation in the plant performance in the two different cropping periods was remarkable leading to heterogeneity in the physical characteristics (Tables 5 and 6). Interestingly, all plant traits and chemical defence did not show significant correlation during the fruiting stage for both cropping periods. The main reason that may explain this scenario is occurrence of low population of all insect-pests during this stage compared to the fruiting stage (8 WAT).

4. Discussion

The present study revealed the variation among selected parameters of the eggplants (number of leaves, leaf size and plant height) which were probably due to variations in nutrient concentrations [29] applied to the plants and occurrence of early infestation (pre-infestation). The two factors could have affected the community of insect-pests [30] with various degrees of pressure effect and interaction that occurred naturally, thus leading to the predictable abundance of insect-acarine populations under eggplant leaves in response to plant physical characteristics (e.g., size of leaves, number of leaves and plant height) and biochemical constituents (flavonoid, phenolic, POD and GCS).

Some of these plant parameters studied remarkably contributed to insect's communities [31] that lead to the different degree of predictions as the main forces factor naturally occurring between trophic levels which is associated with direct and indirect effects [30], either positive or negative association. Based on the analyses of MANOVA and RDA, clearer interaction and magnitude of impact could be assessed and observed between insect-acarine community and plants' parameters. Additionally, the degree of plants parameters on the interaction among insect community was assessable from the strongest to the lowest effects including the insignificant effect.

4.1 Effect of Multitrophics Interaction on Whitefly Population on the Eggplant Leaves

Based on the regression models (Table 1), the present study revealed that the TPC and aphid population could be good predictors for variation in the whitefly population during the first cropping period.

The strong effect of TPC on the whitefly population may indicate intensive production of phenolic by the eggplant during the first crop. Lattanzio and Cardinali [32] found progressive production of the chemical compounds (including phenolic) as a defence mechanism after the insect feeding manifestation. Similar findings were also reported [3, 33] as the phenolic compounds including solasodine, phenols, phenolic oxidase enzymes which were produced in response to the insect feeding activities.

Aphids (Aphididae) and whiteflies (Aleyrodidae) have similar feeding mode which employed unique morphological adaptations, physiological food perception, digestion and excretion systems and feeding behaviours [34]. These traits allow them to use a regularly unique plant resource, nutritionally restrictive phloem sap [35]. Previous studies reported that both insects (whitefly and aphids) had slightly similar morphology and physiology of phloem feeding [36, 37] suggesting a crucial role for saliva in eliciting changes in plant gene expression [34]. Hence, aphid could be a good predictor to whitefly population especially when both populations were available in surrounding areas and the timing of infestation was almost similar. Additionally, according to Aquilino *et al.* [38], the population dynamic of different pests may show associated patterns. In this case, a strong association has been found between the population patterns of whitefly and aphids. Generally, several studies reported that populations of pests which coexist on the same host will be closely related (i.e., increase or decrease together) [39-41].

Different pattern of the relationship between the competitor pests and whitefly was observed in the second cropping period. The thrips population was the only determinant variable describing the changes in the whitefly population. There are probably two consecutive reasons, firstly other competitors, such as changing in population of aphids (outbreak), were represented by a great number of individuals and secondly remarkable presence of other pests in the surrounding area (i.e., thrips) [42, 43]. In addition, early infestation to the plants by whitefly and aphids may affect thrips, therefore close relationship to the whitefly population dynamic was observed [44]. As aphid changed their trend in second cropping, the determinant factor on whitefly population may change probably due to other factors such as abiotic factor (climatic). The climatic factor will also influence other trophic levels (natural enemy) which come from surrounding area [45]. Consequently, thrips have the ability to change their behaviour like aphids to compete whitefly infestation that makes them good predictor for changes in the whitefly population. On the underside of leaves, immature of thrips is highly mobile [46] while immature of whitefly is immobile [47]. These differences could make them live competitively with their unique biological traits [43, 48]. As aphids and thrips are presumably good predictors for the whitefly population, this study reveals that aphids and thrips are major competitors to whitefly.

It means although the first competitor pest attack the plant will take the full advantage for their survival reflecting to higher abundance, however, association other competitors or second competitor to the whitefly population could be changed or loss in the competition due to some reasons. Possibly analysis between predictor pest and the occurrence of major species abundance (whitefly) could be predicted using predictor pest abundance (data) of two or three weeks before.

4.2 Multitrophic Interaction between Insect-Acarine Abundance and Eggplants Parameters, Competitor Pests and Parasitoid

Multivariate results in the present study explained that plants responded to pest manifestation by producing chemical compounds such as the phenolic which mainly targeted whitefly, thrips and spider mites. In this study, the multivariate model (i.e., RDA) showed that abundance of whitefly and aphid was positively correlated with the TPC contents.

It is an acceptable fact that the behavior and tendency of whitefly population on eggplants depends mainly on the TPC activity which is produced by plants as a chemical defence [14, 49]. The TPC function is different from TFC compound when plants activated and responded to the pest infestation. Some chemical defence produced by plants [18] is species-specific which can function to suppress insect-pest population [17].

On the other hand, abundance of spider mites had a positive correlation with the TFC contents. It is also widely known that plants use constitutive and induced defence [14] which always has remarkable effect on structuring the community structure of herbivores including whitefly, thrips, mites and spider mites [23].

The present study, both multivariate analyses (MANOVA and RDA) produced somewhat identical outputs, thus they were interpreted similarly. Furthermore, both multivariate techniques (MANOVA and RDA) were used together to elucidate the complex interaction between plant parameters, pests abundance and chemical defence compounds.

As shown in the MANOVA outputs (Table 4), all insect-acarine populations showed no effect on the plant biological traits. On the other hand, aphid abundance was significantly affected by POD and

GCS activities in the eggplant leaves. The RDA model elaborated the explanation as it showed negative correlation between aphid abundance and activity of the GCS. Additionally, whitefly and thrips had strong and positive relationship with activity of the POD. At this end, the present findings indicated that abundance of aphids was negatively associated with GCS activities in the second cropping period.

Walling [14] reported that constitutive and induced defenses are only effective if the herbivore contacts the defense chemical. In this regard, allelochemicals (defence chemicals) are normally species-specific due to the selection by a pest (herbivore) on the plants, which is also affected by mode and site of herbivore feeding [50, 51]. Basically, some chemical defence produced by plants [18, 49, 52] can function to kill, inhibit the reproduction and development or mediating the insect-pest [17, 18]. Although no significant association was observed between parasitoid *E. hitam* and eggplant parameters in this study, it is noteworthy to mention that parasitisation rate by *Trichogramma turkestanica* is low when the host plant has higher number of leaves and thus dense canopy [31]. This is probably due to the reduction in prey searching ability and simple plant structure means parasitoids will search for their prey easily [42, 53].

In general, the present study revealed that whitefly, thrips and spider mites were more associated with TPC in the first cropping period, and only aphid was much related to POD activity in the second cropping period. In the meantime, it was hard to generalize the findings as the cropping periods showed obvious difference in the interaction patterns. However, biological traits of the eggplant did not show significant contribution in the interaction model of the multitrophic system. This scenario is probably due to the disparity in pest composition and rate of damage which consequently resulted in poor performance of plants.

Interestingly, after 8 WAT, all the pests' populations decreased abruptly on the eggplant. This may be due to low abundance of the insect-pests populations resulting from unfavourable conditions such as chemical defence [43, 54]. Additionally, the recent findings demonstrated that chemical defence could be one of major factors inhibiting feeding, oviposition, growth and development, settling, fecundity and longevity of insect-pests [14].

4.3 Multitrophic Interaction between Insect-Acarines and Biological Traits of Eggplant, Competitor Pests and Parasitoid

Production of chemical compounds by the plants is commonly known and widely reported which is induced by pest manifestation [49]. According to the literature, chemical defence compounds are not released by intact or mechanically damaged plants [55, 56]. Thus, it supports the principle that pest manifestation is the main factor enhancing the production of these chemical compounds. In the present study, importance of herbivore-induced chemical defence (TPC, TFC, POD and GCS) was highlighted as it significantly affected most of insect-acarine communities on the eggplant. As discussed earlier in this chapter, the pre-infestation can be considered as the main stimulus for producing and releasing these chemicals.

Furthermore, indirect defense also includes production of substances or structures in plants that may attract or enhance the negative effects of natural enemies on the second trophic level [57]. In this study, no significant relationship was found between parasitoids abundance and chemical defence compounds. It is also evident that pattern of this interaction highly depends firstly on the species involved [58], which pest attack earlier and availability of host plant to induce the secondary metabolites. Subsequently, the performance of plant growth also contributes to trigger secondary metabolite after pest attack which is also closely related to the concentration of the nutrients applied to the plants. It is also worth mentioning that age of the plant such as differences between vegetative and fruiting stage is the main determinant for its nutritional requirement and uptake rates which also may influence the relationship between plant performance and insect-pests population [59]. Furthermore, diverse insect-acarine species are responding to multiple trophic levels [49]. Thus, population size, early infestation and diversity of insect-acarine could lead to obvious differences in the plant response resulting in remarkable variation in the trends of plant-pests interaction. However, it was difficult to make an inference that the chemical induced caused by pest species solely because pathogen also influences the plants to induce chemical defence [14, 21, 60].

In agro-ecology, several studies found that classical interaction on how insect-acarine species responded and/or were influenced by lower trophic levels [38] will result in variation in plants parameters particularly physical (size of leaves, number of leaves and plant height) and chemical traits such as secondary metabolites. After 8 WAT, plant chemical defence (e.g., phenolic) was strongly associated with some herbivores (whitefly, thrips and spidermite). Frisvad and Filtenborg [61] reported that this secondary metabolite is used taxonomically to identify some species that infested the plant. It is known that phenolic is found to be one of the most abundant secondary metabolites and the most diverse compound in the plants [62].

Interestingly, the present study revealed that the chemical defence of the plants aggressively reduced insect-acarine populations via direct or indirect effect [56]. Direct effect of chemical defence especially phenolic commonly acts as a toxic substance to herbivores. In addition to toxicity, direct effect may include inhibition of feeding, growth, and reproduction [32, 63] reported that phenolic compound could affect the oviposition of insect, insect larval growth and thus survival of the offspring on the host plant. Indirect effect, however, may involve specific chemical compounds signaling natural enemies as communication system [64] to attack the plant pests [14, 49]. The latter indirect effect was not clearly observed in the present study presumably due to complexity of the studied multitrophic system which affected the effectiveness of indirect chemical defence in attracting natural enemies. It probably involved other factors (unexplained variables) which could strongly influence natural enemies against pest such as specific production of volatile allelochemicals [55] upon herbivory feeding activities.

In the present study, spider mites also exhibited strong and positive relationship with TFC. Flavonoid is known as a strong repellent that inhibits the reproduction and growth of insect-acarine population on eggplant [49]. Several feeding tests have shown sensitivity of insects to flavonoids [65-67]. Thus, flavonoids are known as strong anti-feedants with obvious deterrent effect on the herbivores insect [67].

POD and GCS were closely related to aphid population in the second cropping period. The POD plays a vital role in plant lignification and subsequently deters insect feeding [68]. Moreover, POD has the ability to produce oxidative radicals of phenolic compounds and toxins that can reduce the digestibility in insect.

There are several studies which reported occurrence of the induced plant volatile after manifestation of pests including herbivores such as moths, scarabeid and chrysomelid [69]. Additionally, repellence effect of some chemical has been identified and recorded on aphids [70]. Based on the above discussion, it is concluded that plant response to competitors, herbivores and pathogen indicating high ability of the plant to react with all trophic levels existed in its environment [49]. However, it is also suggested that further studies be needed for comprehensive understanding of the mechanism in how herbivores response to the volatiles released by the plants under various ecological and agronomical conditions.

In relation to this multitrophic system, the bottom-up and top-down effects occurred in very complex interaction between organisms and host plants, plants and natural enemies, and natural enemies and pests [14]. In general, when insect-pests are living and foraging simultaneously they cause serious damage to the plants [71]. However, the degree of damage probably depends on the strength of the interaction between specific pests and the plant performance which may always relate to effectiveness of plant defence system. Hence, this study revealed that pre-infestation has the potential to shape the insect-acarine community structure, composition and population size. Pre-infestation also influences the degree of infestation, plants tolerance (defense system) and natural enemy effectiveness on the plants [72].

5. Conclusions

To conclude, whitefly population in this study was predictable by aphids, thrips and TPCs in eggplant. It is also concluded that eggplant has a capable defence system against insect-acarine pests after stimulation (pre-infestation). Presence of phenolic and POD corresponded to obvious reduction in insect-pests communities after 8 WAT. In relation to IPM strategy, early stages of plant growth are known as susceptible periods for pests attack but the plant becomes more tolerant during the fruiting stage. Based on multivariate results of the multitrophic levels interaction, MANOVA and RDA have the potential to simplify the complex interaction between plant performance, abundance of pests and chemical defence. In this multitrophic study, several factors were controlled to overcome possible outbreak of major pests in the mass scale production. Thus, it is suggested that optimum nutrient levels should be applied according to the age progress through precision farming which may result in increase of the production as the pest attack will be minimized.

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