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Oxidative enzymes in coconut cultivars in response to *Raoiella indica* feeding

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The increase in oxidative enzyme activities is related to diminished mite infestation. Some biological aspects of *Raoiella indica* Hirst reared on the coconut cultivars ('Jamaican Tall' (JT), 'Malayan Yellow Dwarf' (MYD), Niu Leka (NL) and a hybrid JT x MYD) were studied under laboratory conditions. Aditionally, changes in oxidative enzyme activities (peroxidase and polyphenol oxidase) as response to *R. indica* feeding were studied in the cultivars where red palm mites showed highest and lowest biological parameters values. Longer time spans and lower oviposition rates observed on the JT suggest this cultivar to be more resistant to *R. indica* feeding. Cultivar JT showed the highest value in PPO/POX ratio, being about twice the value shown by MYD in the infested plants. The observed enzyme activity ratios in both genotypes showed a slight increase 24 h after mite infestation, suggesting these enzymes could be related to plant resistance to *R. indica*. However, this relationship is still unclear. The biological parameters of *R. indica* together with higher enzyme activity, particularly on JT suggest this cultivar could be considered as a more resistant cultivar as compared to MYD. More detailed studies are required to determine the effect of these enzymes on coconut resistance to red palm mites.

Key words: Coconut, peroxidase, polyphenol oxidase, red palm mite.

INTRODUCTION

Plant defense mechanisms can be expressed permanently, without the presence of any stress factor (constitutive resistance), or can be induced in response to biotic or abiotic environmental stresses (induced

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resistance) (Agrawal and Karban, 2000; Kessler and Baldwin, 2002; Agrawal, 2005; Sunoj et al., 2014). Both permanent and induced responses are crucial for arthropod resistance management (Kant, 2006). Plant induced resistance involves defense mechanisms including structural barriers, increase of toxic substance level (Grubb and Abel, 2006), and protease inhibitors (Chen et al., 2005). However, some of these compounds obtained as a function of induced resistance can be auto-toxic (Gog et al., 2005) or activated relatively late in the interacting plant-herbivore (Morris et al., 2006), thus involving a high metabolic cost for the plant (Walters and Boyle, 2005). Oxidative stress is a complex chemical and physiological phenomenon that accompanies virtually all biotic and abiotic stresses in higher plants and develops as a result of overproduction and accumulation of reactive oxygen species (ROS) (Demidchik, 2015). Different ROS types are able to evoke oxidative damage to proteins, DNA and lipids (Apel and Hirt, 2004). The cellular damage by ROS appears to be due to their conversion into more reactive species such as the formation of •OH, which is dependent on both H_2O_2 and $O_2^{\bullet-}$ and, thus, its formation is subject to inhibition by both superoxide dismutase (SOD) and catalase (CAT) (Sharma et al., 2012). Besides SOD and CAT, there is a complex of enzymatic components of the antioxidative defense system that comprise several antioxidant enzymes such as guaiacol peroxidase (GPX), enzymes of ascorbateglutathione (AsA-GSH) cycle ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and glutathione reductase (GR) (Noctor and Foyer, 1998). Peroxidases (POX) are involved in many physiological processes in plants, involving responses to biotic and abiotic stresses, the biosynthesis of lignin in the polymerization of the precursors of lignin, and in the scavenging of reactive oxygen species (ROS). The ROS are partially reduced forms of atmospheric oxygen, highly reactive and capable of causing oxidative damage to the cell, and can either scavenge or be a source of hydrogen peroxide (H_2O_2) (Vicuña, 2005). Also, peroxidases may be involved in defense against pathogens (López-Curto et al., 2006) or insects (Dowd and Lagrimini, 1998). The expression of different peroxidase isoenzymes depends upon the plant developmental stage and on environmental stimuli (Valério et al., 2004). The increase in POX activity during pathogen/herbivore attack has been associated with phenolic compounds binding to the cell wall in soybeans and beans (Lamb and Dixon, 1997). POX activity has been shown to increase in tomato or hop after *Tetranychus urticae* Koch or *Tetranychus cinnabarinus* Boisduval feeding (Stout et al., 1994; Kielkiewicz, 2002; Trevisan et al., 2003). Similarly, higher oxidative enzyme activity has been associated with lower *Steneotarsonemus spinki* Smiley density on tolerant rice varieties (Fernández et al., 2005). Polyphenol oxidase (PPO) is considered an important oxidative enzyme involved in several physiological functions; however, greater activity has been reported in damaged tissue, therefore PPO's are also considered plant defense proteins (Pinto et al., 2008). Sunoj et al. (2014) demonstrated that reduced activity of PPO and an increased membrane stability index in some coconut seedlings indicate that even under abiotic stress, oxidative stress was reduced by the enzymatic protection mechanisms in operation, suggesting that coconut seedlings were able to maintain membrane stability. Previous studies showed a negative relationship between PPO activity and developmental rate of *Heliothis zea* (Boddie) in tomato leaves, probably due to chelating of amino acids and leaf proteins, with subsequent nutritional quality reduced in the infested foliage (Felton et al., 1989). More recently, caterpillars of several noctuid species (*Spodoptera exigua* (Hübner), *Spodoptera litura* (F.) and *Helicoverpa armigera* Hübner) showed decreased weight gains and consumption rates when feeding on transgenic tomato lines showing PPO expression (Mahanil et al., 2008; Bhonwong et al., 2009).

The red palm mite, *Raoiella indica* Hirst, has been considered a serious pest for coconut (*Cocos nucifera* L.) and Areca palms (*Areca catechu* L.) in India (Daniel, 1981; NageshaChandra and Channabasavanna, 1984), and date palms (*Phoenix dactylifera* L.) in Egypt (Zaher et al., 1969). After being reported in the Caribbean in 2004, *R. indica* quickly spread through that region, reaching Florida (USA) and the northern area of South America (Gondim Jr. et al., 2012; Vásquez and Moraes, 2013). *R. indica* inflicted serious damage to Arecaceae, primarily to the coconut trees, but also to Musaceae and other botanical families (Carrillo et al., 2012; Rodrigues and Irish, 2012). It has been observed that coconut seedlings may die from pest attack, while older plants show discoloration and consequent yield reduction. This information has not been systematically quantified (Welbourn, 2005; Peña et al., 2006). Considering the economic impact of *R. indica* in the Caribbean area, resistance in coconut cultivars should be addressed in order to improve knowledge on how sustainable strategies could contribute in red palm mite population management. For this reason, peroxidase and polyphenol oxidase activities in response to *R. indica* feeding were evaluated in different coconut palm cultivars used commercially in Venezuela.

MATERIALS AND METHODS

Plant material

A study was conducted at the Universidad Centroccidental Lisandro Alvarado, in the state of Lara, Venezuela (10°01'04" N; 69°17'03"W) during 2012. Forty 1-2 years-old plants from each of the coconut cultivars were planted in plastic containers (60×40 cm) containing a substrate of ground soil + rice hulls + sand (1:1:1). One month before the test was initiated, the plants were fertilized with NPK (15-20-20) and treated with Mancozeb (3 g) in 300 ml

Table 1. Mean (±SD) developmental time (days) and oviposition rate of *Raoiella indica* on different coconut cultivars (29 ± 1.0°C, 60±10% RH and 12 h light photoperiod).

	Developmental time					Oviposition
	Egg	Larva	Protonymph	Deutonymph	Egg-adult	Mean egg number/female/day
Jamaican Tall	6.7±1.8^{b}	5.8±0.7^{a}	4.7±0.5^{a}	4.8±0.7^{a}	21.9±2.7^{a}	1.7 ± 1.3^{b}
MYD x JT	7.6±0.5^{a}	4.4±0.5^{b}	3.8±0.8^{b}	4.0±0.8^{b}	19.8±1.0^{b}	2.4 ± 1.5^{a}
Niu Leka	7.7±0.5^{a}	3.7±0.7^{c}	3.8±0.9^{b}	3.9±0.9^{b}	19.0±1.3^{b}	2.2 ± 2.1^{ab}
Malayan Yellow Dwarf	6.0±0.5^{b}	4.3±0.5^{b}	2.6±0.8^{c}	4.0±0.6^{b}	16.9±0.9^{c}	2.4 ± 1.9^{a}

Means followed by different letters within each column are significantly different according to the Tukey test (P< 0.05).

water per palm. Then, plants of each cultivar were divided into two groups; the first group being females infested with 25 *R. indica* on each one of the three leaflets of well-developed middle leaves, while the second group was kept mite free and used as a control. A leaf section (about 4 cm^2) was taken from each of five infested plants per cultivar, and from the control group at 0, 24, 72, 120 and 264 h after mite infestation. Samples were wrapped in a piece of foil and brought in an icebox to the laboratory. Leaf samples were weighed and stored at -20°C until being processed.

Biological aspects of *R. indica* on several coconut genotypes

The biological cycle of *R. indica* was studied using rearing units on four distinct coconut cultivars. The cultivars studied were: the Jamaican Tall (JT), Malayan Yellow Dwarf (MYD), the Niu Leka (NL), and a hybrid cultivar (JT x MYD) provided by the Instituto Nacional de Investigaciones Agrícolas (INIA), Irapa, Sucre state, Venezuela. Each rearing unit consisted of a coconut leaf disc (3 cm diameter) placed with the lower surface on a polyurethane layer, continuously maintained wet by the daily addition of distilled water (Vásquez et al., 2015). One 3-5 day old female was put on each of the thirty rearing units of each cultivar to obtain one egg per rearing unit. After 24 h, the females were removed and just eggs were kept in rearing units. The units continued to be examined in 12-h intervals to determine the duration of each developmental stage. Leaf disks were replaced by new disks every 3-4 days to ensure a physiologically adequate rearing substrate throughout the work. Oviposition was studied in 30 mated-females for each cultivar. The study was carried out under room conditions (29 ± 1.0°C, 60 ± 10 % RH and 12 h photoperiod).

Biochemical changes in coconut cultivars induced by *R. indica* feeding

Total proteins (TP)

Content of total protein was determined using the Bradford (1976) method. Absorbance of each dilution was measured using a spectrophotometer (GENESYS 10S UV-Vis) at 595 nm. Induced biochemical response to *R. indica* feeding were determined on coconut cultivars in which *R. indica* showed the lowest and highest biotic potential in the experiment above, those being JT and MYD. Biochemical responses in leaf tissue included total protein (TP) content, polyphenol oxidase (PPO), peroxidase (POX) and lipid peroxidation.

Enzyme extract

Enzyme extract was done following Martínez et al. (2013), with some modifications. 300 mg of leaf sample from each cultivar (infested and uninfested plants) was ground in liquid nitrogen and homogenized with 50 mM Tris-HCl buffer (pH 5.7), containing 1% polyvinylpyrrolidone (PVP) and 1 mM EDTA. Plant extract was centrifuged at 12,000 rpm, 4°C for 20 min, and the supernatant was used to determine total proteins and enzyme activity.

Quantification of peroxidase (POX) activity

POX activity was measured by spectrophotometry. The guaiacol oxidation rate by POX mediated by H_2O_2 was measured on 470 nm absorbance of the light spectrum absorbed by oxidized guaiacol. Changes in optical density were determined every 15 s for 1 min. Enzymatic activity was expressed in mM of tetraguaiacol min^{-1} μg^{-1} of protein.

Quantification of polyphenol oxidase activity (PPO)

PPO activity was quantified by the oxidation rate of pyrogallol (Alexander et al., 1964). Pyrogallol was prepared in a buffer solution of sodium acetate (50 mM, pH 5.5). Enzyme activity was measured at 15 s intervals for 3 min in a spectrophotometer at 420 nm and expressed in mM of quinone min^{-1} μg^{-1} protein.

The PPO/POX ratio was used as an indirect measurement to visualize the behavior of the genotypes after herbivore feeding. This decision was made due to the lack of information on which specific PPOs or POXs are induced.

Statistical analysis

The results were subjected to variance analysis and mean values were compared by Tukey test at p< 0.05. POX and PPO activities were correlated with the number of mites per leaflet, using Statistix software version 8.0.

RESULTS AND DISCUSSION

Biological aspects of *R. indica* reared on different coconut cultivars

Life cycle of *R. indica* was influenced by the coconut cultivar tested (Table 1). Higher developmental time was observed on JT cultivar (21.9 days), while it was about 23% lower on MYD cultivar. Developmental time was intermediate on JT×MYD hybrid and NL, being reduced by 9.6 and 13.4%, respectively in relation to JT. Furthermore, effect of coconut cultivar on *R. indica*

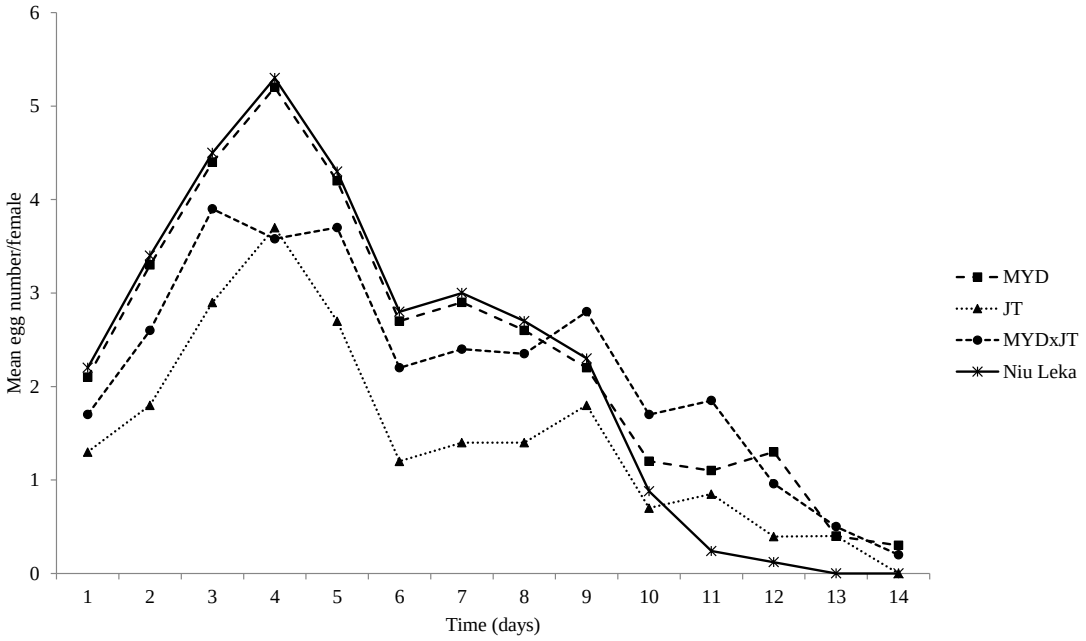

Figure 1. Daily oviposition of *R. indica* reared on different coconut genotypes leaf disk (29 ± 1.0°C, 60 ± 10% RH and 12 h light photoperiod).

oviposition was also observed (Table 1 and Figure 1). The highest oviposition rate was observed in *R. indica* females reared on MYD and on hybrid MYD×JT leaf disks (2.4 eggs female^{-1}day^{-1}), while the oviposition rate on the JT cultivar was about 30% lower than on MYD. Daily oviposition was intermediate on NL.

Host plant effect on phytophagous mite species reproduction was previously shown as growing, without effect, or decreasing (Ribeiro et al., 1988; Hilker and Meiners, 2002; Praslička and Huszár, 2004). Differences in *R. indica* developmental time was observed when reared on coconut cultivars, being 21.5 and 19.8 d on JT (in Trinidad) and on a hybrid MYDxJT (in Venezuela), respectively (Vásquez et al., 2015). Vásquez et al. (2008) hypothesized that reproductive parameters of *Oligonychus punicae* appeared to be negatively associated with flavonoid content in grape cultivars. These phenolic compounds can be synthesized in grapevine leaves and fruits in response to biotic or abiotic stress (Morrissey and Osbourn, 1999) and these compounds may act synergistically with tannins to provide plant resistance (Harborne, 1994; Bernards and Båstrup-Spohr, 2008).

Biochemical changes in coconut cultivars induced by *R. indica* feeding

Total proteins

TP content was significantly higher in JT cultivar as compared to MYD during the evaluation period (Figure 2). Although no significant variations were observed in TP content in JT after *R. indica* feeding, higher TP content was observed 72 h after infestation. In MYD, total protein content varied significantly ($p<0.01$, $F= 0.000$; $df=14$), being greater 120 h after infestation. Likewise, previous studies have shown TP increasing in response to different types of abiotic (García et al., 2003) or biotic stress (Kamal et al., 2010; Wang et al., 2011). This response has been considered as a protective strategy against stress factors, which may be associated with specific gene expression favoring induction of proteins only synthesized under non-optimal conditions (Pérez et al., 1997). Polyphenol oxidase (PPO) and peroxidase (POX) catalyze oxidation of phenols and consequently, quinones formed by oxidation of phenols, bind covalently to leaf proteins, and inhibit the protein digestion in herbivores (War et al., 2012). Consenquently, the conserved TP content in JT suggests this cultivar might be considered tolerant to the stress caused by mite feeding.

Enzyme activity

The PPO/POX ratio was similar in both non-infested genotypes in JT and MYD at 0 h. This ratio tended to decrease both in infested or non-infested JT plants, showing an increase after 72 h on infested plants. Ratio values were relatively similar along evaluation periods in MYD infested plants, ranging from 2.1 to 2.94 after 24 and 72 h, respectively (Figure 3). Mayer (2006) stated

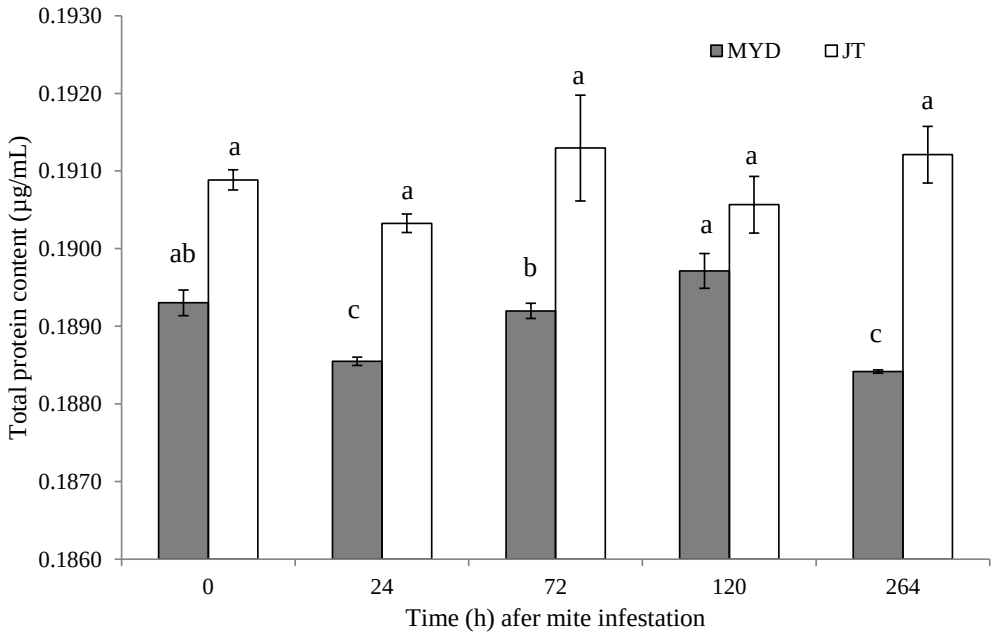

Figure 2. Variation in total protein content in MYD and JT coconut cultivars in response to *R. indica* feeding.

that resistant genotypes had localized elevated levels of PPO formation which was rapidly induced following infection. Susceptible cultivars failed to accumulate PPO even after considerable time. These results suggest that increases in PPO/POX ratio in response to *R. indica* feeding could be considered as the first evidence of resistance expressed by coconut cultivars to mite feeding. It is still unclear whether PPO may be involved in resistance to the red palm mite in coconut palms; however, the observed enzyme activity ratios in both genotypes show a slight increase 24 h after mite infestation. Simultaneously, the biological parameters of *R. indica* together with the above, particularly on JT (Table 1 and Figure 1), suggest this cultivar could be considered as a more resistant cultivar as compared to MYD.

Changes in total protein content and levels of oxidative enzymes are considered the first plant response to feeding herbivores (Felton et al., 1994; Ni et al., 2001). These biochemical responses are in function to plant growth stages and stress intensity (Constabel and Barbehenn, 2008). Furthermore, POX activity is influenced by plant species and sampling time and it reaches higher levels during the first 3 days and tends to diminish as stress decreases (Ni et al., 2001). Peroxidases and polyphenol oxidases are involved in plant defense against phytophagous mites and insects, by the production and polymerization of phenolics and lignification and hypersensitive responses in injured tissues (Kielkiewicz, 2002).

The production of PPO as a defense response to herbivores involves a complex sequence of reactions starting with gene expression and then leading to the formation and activation of enzymes for substrate production (Mayer, 2006). However, the lower mRNA levels associated with this enzyme in some species suggests that its role in defense has evolved only in a few species (Constabel et al., 2000). Results associated with PPO activity and arthropod herbivore performance, using plant genotypes that vary in resistance to herbivory and ontogenetic variation in PPO activity within the plant and leaves treated with PPO, have been contradictory (Constabel and Barbehenn, 2008).

Previous studies dealing with the relationship between the plant resistance and the activity of POD and PPO are intriguing. Most of the results have shown that higher POX or PPO levels are associated with plant resistance to *Steneotarsonemus spinki* Smiley in rice cultivars (Fernández et al., 2005), *T. urticae* in strawberry (Steinite and Ievinsh, 2002) and hop (Trevisan et al. 2003), *T. cinnabarinus* (Kielkiewicz, 2002), common cutworm (*Spodoptera litura*) and the cotton bollworm (*Heliothis armigera*) in tomato (Thipyapong et al., 2006). More recently, Samsone et al. (2012) observed that high *Vasates quadripes* Shrimer infestation levels could evoke increases in POX activity in *Acer saccharinum* leaves. Conversely, higher levels of PPO in coffee leaves apparently was not associated with resistance to the coffee leaf miner (*Leucoptera coffeella*) (Melo et al., 2006; Ramiro et al., 2006). The induction of phenolic activity, and the enzymes peroxidase and polyphenol oxidase in response to insect attack might not be

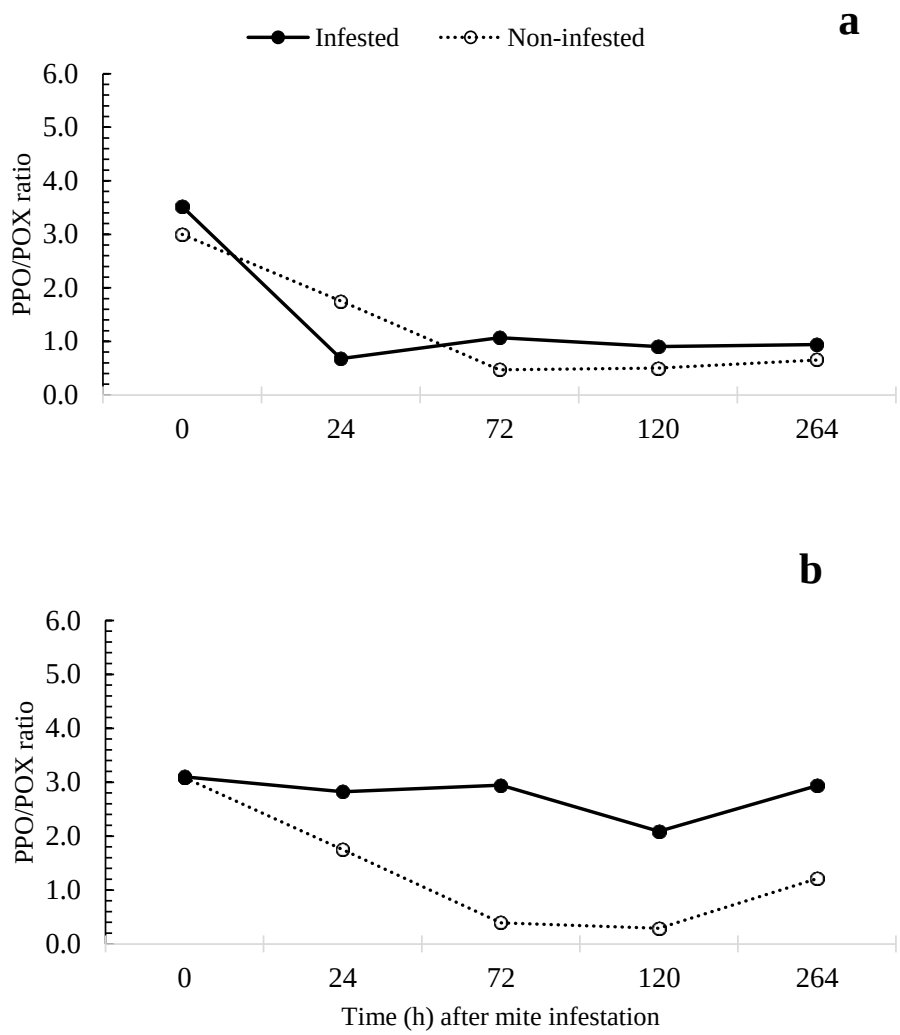

Figure 3. PPO/POX ratio in coconut cultivars Jamaican tall (a) and Malayan Yellow Dwarf (b) after *Raoiella indica* feeding.

concrete evidence that these substances participate directly in plant defense mechanisms (Ramiro et al., 2006). In addition, *Manduca quinquemaculata* caterpillars surprisingly showed greater performance on younger tobacco leaves, which contain higher PPO levels (Kessler and Baldwin, 2002). Given the tremendous variation in PPO expression patterns, activity levels, and potential substrates in different species, similar variation in the adaptive roles played by PPO in defense and other processes may be anticipated. Thus, correlations of PPO activity with defense may be confounded by the complexity of PPO gene families (Constabel and Barbehenn, 2008).

Similar to PPO production in response to plant-arthropod interaction, peroxidases catalyze synthesis of products with antimicrobial activity in plants, suggesting a role in plant defense by participating in phytoalexin synthesis (Almagro et al., 2009). Peroxidases are also involved in the binding of cell wall components. Extensin, phenolic compounds and polysaccharides act as a mechanical barrier for pathogen penetration (Brisson et al., 1994). In addition, these mechanical barriers, formed as result of strengthening cell walls, have been reported as a resistance mechanism in pericarp (García-Lara et al., 2004) and embryo in maize grain (García-Lara et al., 2007) to *Sitophilus zeamais*. Moreover, quinone oxidation in the developing grain pericarp regulated by peroxidases may contribute to plant resistance reducing digestibility for insect pests (García-Lara et al., 2007).

The observed enzyme activity increase soon after mite infestation, suggesting that the role of this enzyme should be further investigated. In this regard, more detailed studies are required to better understand mechanisms of plant response to arthropod herbivores and thus use this information for crop protection and sustainable crop production.

Conflict of Interests

The authors have not declared any conflict of interests.

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