

Oviposition Preference and Nutritional Indices of *Papilio polytes* L. (Papilionidae) Larvae on Four Rutaceous (Sapindales: Rutaceae) Host Plants

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OVIPOSITION PREFERENCE AND NUTRITIONAL INDICES OF *PAPILIO POLYTES* L.
(PAPILIONIDAE) LARVAE ON FOUR RUTACEOUS (SAPINDALES: RUTACEAE) HOST PLANTS

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ABSTRACT. Oviposition preference and larval developmental performance of the butterfly, *Papilio polytes* L. on four rutaceous host plants, *Citrus aurantifolia* (Chrism.) Swing, *Citrus reticulata* Blanco, *Citrus hystrix* DC, and *Murraya koenigii* (L.) Sprengle, were investigated in outdoor cages. Maxima of eggs were laid on *C. reticulata*, followed by *C. aurantifolia*, but the numbers laid on the two host plants were not significantly different from each other; however, these numbers differed significantly ($F = 155.70$; $P < 0.01$) from those laid on *C. hystrix* and *M. koenigii*; the last host plant was the least preferred for egg laying. Leaves were significantly the preferred site (and in turn the underside of leaves) over stems for deposition of eggs in all host plants; negligible number of eggs was also laid on plant pots. The duration of 5th instar larval development was the shortest on *C. reticulata* and significantly different ($P < 0.01$) from that on *M. koenigii*, but did not differ significantly between the three *Citrus* species. The nitrogen content in leaves of all four host plants differed significantly ($P < 0.01$), with *C. reticulata* containing 4.52%, followed by *C. aurantifolia* (4.37%), *C. hystrix* (4.29%), and *M. koenigii* (3.73%), while the water content of leaves was significantly the lowest in *M. koenigii* (71.72%), compared to the three *Citrus* species (76.38–79.12%) among which the water content did not significantly differ. Relative consumption rate (RCR) and fecal dry weight of 5th instar larvae feeding on *M. koenigii* were the highest and significantly different ($P < 0.01$) from the other three host plants. Pupal dry weight, relative growth rate (RGR), efficiency conversion of digested food (ECD), efficiency conversion of ingested food (ECI) of *M. koenigii* were significantly lowest compared to the three *Citrus* species. The values of RGR, ECD, and ECI of the 5th instar larvae were similar for the three *Citrus* species; the approximate digestibility (AD) values were similar for all four host plants. This study shows that *C. reticulata* was the best host plant among the three *Citrus* spp. and *M. koenigii* was the least preferred.

Additional key words: Oviposition, larval performance, nutrition indices, host plant

The common mormon butterfly, *Papilio polytes* L. (Lepidoptera: Papilionidae) is a tropical or subtropical papilionid butterfly distributed from Southeast Asia to the Southwestern Islands of Japan (Corbet & Pendlebury 1992; Nakayama *et al.* 2003; Nakayama & Honda 2004). *Papilio polytes* is known to feed on various genera of Rutaceae, such as *Murraya*, *Triphasia*, *Glycosmis*, *Aegle*, *Zanthoxylum*, *Toddalia*, *Euodia*, *Atalantia* and *Poncirus* in the forests (Corbet & Pendlebury 1992). In recent years, this butterfly has adapted to the urban/suburban environments and is found to feed on citrus plants (Corbet & Pendlebury 1992); this feeding adaptation has made *P. polytes* a potentially serious pest in citrus orchards.

In Lepidoptera, host plant selection for larval development and propagation is commonly assumed to be the prerogative of the ovipositing female (Singer 1984; Udayagiri & Mason 1995). Based on this assumption, many studies have been conducted on the relationship between adult host preference and larval performance (Singer 1984; Nylin & Janz 1993; Berdegue *et al.* 1998; Jallow *et al.* 2001; Forister 2004).

In phytophagous insects, larval growth and longevity as well as fecundity of the adult are influenced by the nutritional value of the host plants (Bernays & Chapman 1994). Larval development and survival depend on the food quality determined by nutrient content and the presence of secondary compounds. The

food quality affects larval developmental time as well as larval mass. A quantitative analysis of the consumption and utilization of host plants by herbivorous insects is a commonly used tool in studies of plant-insect interactions (Scriber & Slansky 1981). For these herbivores, time to achieve pupation and pupal mass are good measures of the suitability of a particular host plant (Penz & Araujo 1990).

Understanding the host plant selection behavior and the effects of various host plant species on growth and larval performance of *P. polytes* is an important prerequisite for developing pest management strategies for this insect (Nylin & Janz 1996; Janz & Nylin 1997; Barros & Zucoloto 1999; Catta-Preta & Zucoloto 2003). In the present study, the oviposition preference of *P. polytes* on three species of commercially grown citrus [*Citrus aurantifolia* (Christm.) Swing., *Citrus hystrix* DC. and *Citrus reticulata* Blanco] and a commonly domesticated spicy leaf rutaceous species, *Murraya koenigii* (L.) Sprengel was evaluated and the life cycle of this butterfly on four rutaceous host plants was studied. The performance of *P. polytes* larvae on the host plants in terms of nutritional indices was also assessed.

MATERIALS AND METHODS

Host plants. Selection of the rutaceous host plants for this study was based on their potential value as commercial plants. Three commercially grown citrus species, *C. aurantifolia*, *C. hystrix* and *C. reticulata*, and a partially domesticated spicy leaf species, *M. koenigii*, popularly used as an ingredient (curry leaf) in local food in Malaysia were selected. The citrus seedlings were supplied by a local nursery in Penang, Malaysia, while *M. koenigii* seeds were collected from wild plants in Penang, and planted in the nursery at the School of Biological Sciences, Universiti Sains Malaysia (USM), Penang, Malaysia. The young seedlings of citrus and *M. koenigii* were planted in plastic bags (25 cm diameter and 35 cm high) containing a 3:1:1 mixture of podsolic, compost, and manure, respectively. Each plant was fertilized on fortnightly basis with a half-teaspoonful of artificial fertilizer and 100 g manure.

The insect. Larvae of *P. polytes* were collected in July 2005 from citrus trees at the USM main campus in Penang. The collected larvae were reared in the laboratory on *Citrus microcarpa* to avoid potentially confounding effect of dietary history on host plant preference. The larvae were placed in a screen cage measuring 50 × 50 × 50 cm and were maintained at 24–26 °C, 60–85% relative humidity, and a photoperiod of L12:D12, until emergence. The emerged *P. polytes* adults were transferred to a field cage (2 × 2 × 2 m) to facilitate mating and oviposition. Flowers of *Ixora* sp.

collected from the plants at USM campus were supplied as food for the caged adult *P. polytes*. The flowers contained in a glass jar filled with water were sprayed with 10% sucrose solution twice daily to ensure sufficient provision of nectar and placed in the cage; they were replaced with fresh flowers every three days.

Oviposition preference. Four plastic bags with each containing one seedling (50–60 cm high) of the four host plant species were placed opposite to each other in an experimental cage measuring 2 × 2 × 2 m. The plants were positioned one meter apart and any one plant was at least 50 cm away from the wall of the cage. Two pairs (2 males and 2 females) of newly emerged *P. polytes* were introduced into the cage. The number of eggs laid by the females on each host plant was recorded daily, until the females died. The host plants were replaced daily with fresh new plants. In this experiment, one cage represented one replication; the experiment was repeated 10 times (Greenberg *et al.* 2002; Nansen & Phillips 2003; Smyth *et al.* 2003).

Duration of immature stages. The eggs laid on each of the four host plants were recovered and were placed in four respective petri dishes (10 cm diameter), each dish layered with a wet tissue paper. Each petri dish contained 50 eggs. A plastic screen cover with a ventilation window made of fine wire (2 × 2 cm) was placed over each petri dish. The duration of the egg stage on each host plant was noted from the time of egg laying to hatching of first instar larva. Thirty newly hatched active larvae from each petri dish were selected and were reared individually on each of the four respective host plants serving as treatment. For this, a total of 120 cages (each 50 × 50 × 50 cm) were used, with 30 separate cages employed for each host plant. For example, for *C. reticulata*, 30 cages were used with each cage containing a newly hatched *P. polytes* larva placed on a young *C. reticulata* twig (two leaves) cut from a mother plant and placed in a bottle (one cm diameter, 10 cm high) filled with water. In this manner, newly hatched *P. polytes* larvae were individually reared on each of the other three host plants as well. As for *M. koenigii*, the larvae were provided with a young twig with four to five leaves. The leaves in each bottle were daily replaced with fresh leaves. Observations were made daily for the duration of larval stages and the data recorded until the larvae metamorphosed to the pupal stage. The duration of pupal stage was also recorded. These observations were replicated thirty times for each host plant.

Larval nutritional indices. This experiment was conducted using fifth instar *P. polytes* larvae. Newly moulted 5th instars were reared individually on a twig of respective host plant in a screen cage (50 × 50 × 50 cm).

Weight of each larva and the host plant twig were recorded prior to releasing the larva on the twig. The host plant twig in the cage was placed in a bottle filled with water to maintain its vigour. The host plant twigs were replaced daily with fresh twigs from respective hosts. Unconsumed twig and the larval faeces were collected daily and dried in an oven at 60°C for seven days (Suwarno 1999). The experiment was continued until pupation of the larva. The prepupa was subsequently collected and dried in the oven at 60°C for seven days. All dry weights of the above components recorded for each host plant were used to calculate the nutritional indices for each host plant according to Slansky & Scriber (1985) as follows:

- i) Relative Consumption Rate (RCR) = F/HT (gram/day)
 - ii) Relative Growth Rate (RGR) = G/HT (gram/day)
 - iii) Efficiency of Conversion of Digested food (ECD) = G/F-E × 100%
 - iv) Efficiency of Conversion of Ingested food (ECI) = G/F × 100%
 - v) Approximated Digestibility (AD) = F-E/F × 100%.
- where G = additional larval weight; F = weight of consumed food; E = faeces weight; H = mean of larval weight [(the initial weight + the final weight)/2]; and T = duration of fifth instar larva.

Nitrogen content of host plant leaves. One hundred grams young leaves of each of the four experimental host plants were analyzed in the laboratory for nitrogen content using the standard micro Kjeldahl method (Hwang & Feng 2004; Eaton *et al.* 2005).

Water content of host plant leaves. Twenty young leaves from each *Citrus* species and *M. koenigii* host plants were collected. All leaves of each species were separately weighed for wet weight (WW) and dried in an incubator at 80°C for 24 h and then weighed again for dry weight (DW). The water content of leaves of each species was calculated as percentage (WW - DW/WW) × 100% (Barros & Zucoloto 1999).

Data analysis. Oviposition preference of *P. polytes* for the host plants, its development (life stage) on the

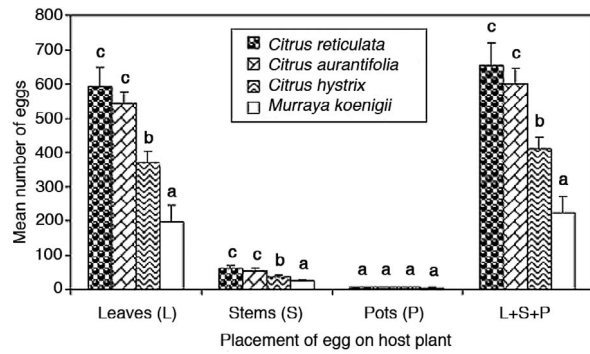


FIG. 1. Mean number of *Papilio polytes* eggs laid on leaves (L), stems (S), and pots (P) and on total plant, including pots (L+S+P) of host plants. Means accompanied by a different letters are significantly different ($P < 0.01$; Tukey's test).

hosts and the larval nutritional indices related to the host plants were evaluated using the one-way analysis of variance (ANOVA). When significant F value was indicated, means associated with each variable of the host plant were further separated using the Tukey's test (Rao 1998). All data were analyzed using the SPSS software version 12 (Dytham 2003; Pallant 2005).

RESULTS

Nitrogen and water content of host plants. The nitrogen as well as water content in the leaves of *M. koenigii* were the lowest and significantly different ($F_{3,8} = 7.198, P < 0.01$) from all three *Citrus* spp. analyzed. Nitrogen content in the leaves of *C. reticulata* was the highest and significantly different from the other two citrus species; however, the water content in the leaves of all three citrus species was somewhat similar (Table 1).

Oviposition preference. The number of eggs laid on *C. reticulata* was found to be the highest and significantly different ($P < 0.01$) from the numbers laid on *C. hystrix* and *M. koenigii*, but not significantly different from the numbers laid on *C. aurantifolia*. Between *C. hystrix* and *M. koenigii*, the former host plant was preferred by *P. polytes* as significantly more ($F_{3,36} = 155.70, P < 0.01$) eggs were laid on *C. hystrix*. Leaves were a preferred site for egg deposition as more eggs were observed on leaves of all host plants, whereas relatively small numbers were laid on the stems, and those deposited on the pots were negligible (Fig. 1).

TABLE 1. Values of nitrogen and water content (mean ± SE) in leaves of four different rutaceous host plants of *Papilio polytes* butterfly. Means in the same column followed by a different letters are significantly different ($P < 0.01$; Tukey's test). All n = 3.

Host plant	Nitrogen content (%)	Water (%)
<i>Citrus aurantifolia</i>	4.37 ± 0.01c	78.47 ± 1.03b
<i>Citrus hystrix</i>	4.29 ± 0.01b	76.38 ± 0.79b
<i>Citrus reticulata</i>	4.52 ± 0.01d	79.12 ± 1.55b
<i>Murraya koenigii</i>	3.73 ± 0.01a	71.72 ± 1.46a

TABLE 2. Duration (mean no. of days \pm SE) for development of immature stages of *Papilio polytes* reared on four different rutaceous host plants. Means in the same column followed by different letters are significantly different ($P < 0.01$; Tukey's test). All $n = 30$.

Host plant	Mean \pm SE duration of stages (days)		
	Larva	Pupa	Total period [°]
<i>Citrus aurantifolia</i>	15.30 \pm 0.19 a	9.90 \pm 0.09 ab	29.20 \pm 0.24 ab
<i>Citrus hystrix</i>	14.73 \pm 0.13 a	10.13 \pm 0.09 b	28.87 \pm 0.17 ab
<i>Citrus reticulata</i>	14.63 \pm 0.22 a	9.77 \pm 0.09 a	28.40 \pm 0.25 a
<i>Murraya koenigii</i>	16.13 \pm 0.30 b	9.60 \pm 0.09 a	29.73 \pm 0.32 b

[°] Including eggs incubation period

Among the host plants, the number of eggs on the leaves and stems of *C. reticulata* were the highest and significantly different ($F_{\text{leaves}} = 160.04$, $df = 3,36$, $P < 0.01$; $F_{\text{stems}} = 40.04$, $df = 3,36$, $P < 0.01$) from those laid on *C. hystrix* and *M. koenigii*. There was no significance difference ($P > 0.05$) between the numbers of eggs on the pots on all host plants (Fig. 1).

Duration of larval and pupal stages. *Papilio polytes* required 28.40 to 29.73 days to complete their life cycle from egg to adult. All eggs hatched after three days. The larval development was completed in 14.63–16.13 days. There was a prepupal stage that lasted for only a day. The pupae took 9.6 to 10.13 days before adult emergence. Host plant had an effect on feeding period ($F_{\text{larva}} = 9.887$, $df = 3,116$, $P < 0.01$), pupal period ($F_{\text{pupa}} = 6.145$, $df = 3,116$, $P < 0.01$) and the duration of immature stages *P. polytes* ($F_{\text{total}} = 4.25$, $df = 3,116$, $P < 0.01$). The shortest immature period (egg until emergence, 28.40 \pm 0.25 days) was recorded on *C. reticulata*. The duration of immature on *C. reticulata* was significantly shorter ($P < 0.01$) than on *M. koenigii* (29.73 \pm 0.32 days), but not significantly different from those on other *Citrus* species. However, there was no significant difference in developmental time of immature stages among *P. polytes* reared on *C.*

aurantifolia, *C. hystrix* and *M. koenigii* (Table 2).

Papilio polytes spent the longest larval period on *M. koenigii*, which was significantly longer compared to all other host plants. Among the citrus species, the larval developmental period on *C. reticulata* was the shortest, but on *C. aurantifolia* and *C. hystrix* there was no significant time difference. The duration of pupal stage of *P. polytes* on *M. koenigii* was significantly shorter than that on *C. hystrix*, but no significant difference was detected in time duration of pupal stage on *C. aurantifolia* and *C. reticulata* (Table 2).

Larval nutritional indices. The fifth larval stadium of *P. polytes* was the longest in term of developmental time and its fecal dry weight was the highest when reared on *M. koenigii*. Similarly, the duration of pupal stage on *M. koenigii* was the longest and significantly different from all three *Citrus* species (Table 3). In contrast, the pupal dry weight of *P. polytes* developed on *M. koenigii* was the lowest and significantly different from the other three host plants (Table 3).

Table 4 shows the values of various parameters of *P. polytes* larval nutritional indices on the four host plants. The relative consumption rate (RCR) of *P. polytes* reared on *M. koenigii* was the highest but the values of relative growth rate (RGR), approximate digestibility

TABLE 3. Duration (mean \pm SE) for *Papilio polytes* 5th instar larval development, its fecal dry weight and pupal dry weight, when fed on four different rutaceous host plants. Means in the same column followed by a different letters are significantly different ($P < 0.01$; Tukey's test). All $n = 20$.

Host plant	5th instar duration (mean \pm SE, days)	Fecal dry weight (mean \pm SE, grams)	Pupal dry weight (mean \pm SE, grams)
<i>Citrus aurantifolia</i>	5.40 \pm 0.11 a	0.76 \pm 0.03 a	0.19 \pm 0.005 b
<i>Citrus hystrix</i>	5.35 \pm 0.17 a	0.76 \pm 0.03 a	0.19 \pm 0.003 b
<i>Citrus reticulata</i>	5.30 \pm 0.13 a	0.78 \pm 0.03 a	0.20 \pm 0.003 b
<i>Murraya koenigii</i>	6.05 \pm 0.15 b	0.91 \pm 0.04 b	0.15 \pm 0.003 a

TABLE 4. Values of mean \pm SE parameters of nutritional indices, relative consumption rate (RCR), relative growth rate (RGR), efficiency of conversion of digested food (ECD), efficiency of conversion of ingested food (ECI), and approximated digestibility (AD) of 5th instar *Papilio polytes* reared on different host-plants. Means in the same column followed by a different letters are significantly different ($P < 0.01$; Tukey's test). All $n = 20$.

Host plant	RCR (g.g ⁻¹ .d ⁻¹)	RGR (g.g ⁻¹ .d ⁻¹)	ECD (%)	ECI (%)	AD (%)
<i>C. aurantifolia</i>	1.84 \pm 0.06 a	0.23 \pm 0.01 b	38.54 \pm 2.19 b	12.87 \pm 0.30 b	34.88 \pm 1.45 a
<i>C. hystrix</i>	1.96 \pm 0.06 a	0.25 \pm 0.01 b	34.68 \pm 2.06 b	12.51 \pm 0.28 b	37.77 \pm 1.70 a
<i>C. reticulata</i>	1.88 \pm 0.04 a	0.25 \pm 0.01 b	40.63 \pm 1.76 b	13.14 \pm 0.28 b	33.53 \pm 1.64 a
<i>M. koenigii</i>	2.32 \pm 0.04 b	0.19 \pm 0.01 a	25.04 \pm 0.93 a	8.19 \pm 0.22 a	33.23 \pm 1.17 a

(AD), efficiency of conversion of digested food (ECD), and efficiency of conversion of ingested food (ECI) were the lowest and significantly different compared with those on all citrus species. However, the approximate digestibility (AD) was not significantly different among the four host plants. All studied parameters of nutritional indices of *P. polytes* larvae reared on three citrus species were not significantly different from each other (Table 4).

DISCUSSION

Oviposition and larval developmental performance of herbivorous insects are determined by the nutritional content of the host plants selected by the female. This study showed that *P. polytes* females preferred to oviposit the most on *C. reticulata* compared to other host plants; *M. koenigii* was the least preferred host. In several earlier studies, the host plants which had higher nitrogen content were shown to be the most preferred hosts (Udayagiri & Mason 1995; Hwang & Feng 2001; Kid & Orr 2001; Wheeler 2003; Chen *et al.* 2004; Moreau *et al.* 2006). In the present study, results of leaf analysis revealed higher nitrogen and water levels in *Citrus* spp. than in *M. koenigii*. These underlying properties presumably attracted the female to prefer *Citrus* spp. over *M. koenigii*. Among the three *Citrus* species, *C. reticulata* had the highest nitrogen and water contents; consequently, the larval developmental period of *P. polytes* reared on *C. reticulata* was shorter than on *C. aurantifolia* and *C. hystrix*. The butterfly spent the longest larval developmental period on *M. koenigii*.

The nitrogen content of leaves of *M. koenigii* was relatively lower (3.73%) than that of *C. reticulata* (4.52%), *C. aurantifolia* (4.37%) and *C. hystrix* (4.29%). Consequently, the developmental period of fifth instar larva of *P. polytes* reared on *M. koenigii* was relatively longer than those reared on *C. aurantifolia*, *C. hystrix*, and *C. reticulata*.

Many factors could have influenced the oviposition behavior of *P. polytes* on the host plants, such as the texture, nutrition and chemical compounds of the host

plant leaves. Morphologically, the upper surface of *Citrus* spp. leaves was smoother than *M. koenigii* leaf. However, nutritional and chemical contents of the host plants have been reported to be more important for purposes of oviposition and food preference by adult female butterfly and its larvae (Portillo *et al.* 1996; Barros & Zucoloto 1999; Ulmer *et al.* 1996; Smyth *et al.* 2003; Chen *et al.* 2004). In several laboratory experiments, the nitrogen and water contents of the leaf were found to be useful for prediction of upper limits of larval developmental performance (Scriber & Slansky 1981; Simpson & Simpson 1990; Ojeda-Avila *et al.* 2003). For instance, the nutrient content of the host plant—especially protein—has been reported to determine growth and larval performance of several insects, such as *Manduca sexta* (Lepidoptera: Sphingidae) (Ojeda-Avila *et al.* 2003), *Oxyops vitiosa* (Coleoptera: Curculionidae) (Wheeler 2003), *Pieris rapae crucivora* and *P. candida candida* (Lepidoptera: Pieridae) (Chen *et al.* 2004) and *Orius albidipennis* (Heteroptera: Anthocoridae) (Groenteman *et al.* 2006), on their respective host plants.

Besides nutrient contents, Nakayama & Honda (2004) found that contact chemical stimuli from the host plants play the decisive role at the final step of egg laying process. The compound *trans*-4-hydroxy-*N*-methyl-L-proline and 2-C-methylerythronic acid have been identified as oviposition stimulants for *P. polytes* from the host plant, *Toddalia asiatica*. Meanwhile, a compound identified as trigonelline (*N*-methylpyridine-3-carboxylic acid) from *Murraya paniculata*, exhibited moderate oviposition deterrence to female *P. polytes*.

In many *Papilio* butterflies, extreme synergism of multiple components has been reported to feature in their stimulatory system of oviposition (e.g., Nishida *et al.* 1990; Ohsugi *et al.* 1991; Nishida 1995; Ono *et al.* 2000a, b; Nakayama *et al.* 2002, 2003; Nakayama & Honda 2004). Nakayama *et al.* (2003) found that oviposition response of *P. polytes* to a 5% concentration of the chemical compound, *trans*-4-hydroxy-*N*-methyl-L-proline (HMP) from *Toddalia asiatica*, was 34.8%;

this response increased to 70.8% even at much lower concentration (0.25%) of HMP after the addition of an equivalent amount of acidic fraction from the same host, although 2-C-methyl-D-erythronic acid (MEA), isolated from acidic fraction of *T. asiatica* was almost inactive in itself (response below 10%). The combination of higher and lower amounts of HMP and MEA (0.4% and 0.1%, respectively) strongly stimulated oviposition by females of *P. polytes* to 95.3% response. The results suggested that *P. polytes* females make use of at least two simple compounds as the crucial chemical cues in recognizing *T. asiatica* as a host.

During this investigation, the lowest oviposition preference of female of *P. polytes* was on *M. koenigii*. This condition may be attributed to the presence of some chemical compound that could act as oviposition deterrents. In an earlier study, Nakayama & Honda (2004) found that trigonelline, a chemical compound isolated from *Murraya paniculata* foliage was responsible for the avoidance of *M. paniculata* by *P. polytes* females. Interestingly, although trigonelline deterred egg-laying process, the compound had no inhibitory effects on larval feeding. It is likely that *M. koenigii* contains this compound, which makes it less preferred by the ovipositing *P. polytes*.

The oviposition preference of *P. polytes* in the present study was indicated by placement of offspring by the female on the most suitable host plant. The larvae of *P. polytes* reared on all three *Citrus* spp. performed much better in term of development than those on *M. koenigii*. The dry weights of pupae developing on *Citrus* spp. were higher than the pupa developed on *M. koenigii* and this probably was a consequence of higher nitrogen content of the *Citrus* host plants compare to *M. koenigii*. It was observed earlier in Taiwan that the pupal weight of *Daphnis nerii* L. (Lepidoptera: Sphingidae) from the larvae fed on periwinkle Madagascar (*Chatharanthus roseus*) containing 3.86% nitrogen was significantly higher than those fed on yellow oleander (*Thevetia peruviana*) that contained 2.44% nitrogen (Hwang & Feng 2001). Wheeler (2003) found that the biomass of the prepupa, pupa, and adult of *Oxyops vitiosa* (Coleoptera: Curculionidae) was greater when fed on leaves that were fertilized with high N₂ fertilizers compared to the unfertilized leaves with N₂.

The water and protein contents of the host plant are extremely important to herbivore insects. Low amount of water and protein will result in low values of RGR, ECD and ECI, reflecting poor growth, and reduced efficiencies of digestion and ingestion, respectively. As observed in *M. koenigii* in the present study, the values of RGR, ECD and ECI were the lowest and correlated

to its lower water and protein contents, compared to the three *Citrus* species. Scriber & Slansky (1981) reporting on the performance of *Papilio polyxenes* on several Umbeliferae hosts showed that it was closely paralleled to the nitrogen and water contents (2.0–4.5% and 66–89%, respectively) of the host leaves with an extremely strong correlation between ECI and leaf nitrogen. Furthermore, Barros & Zucoloto (1999) found that the pupal weight, ECD and ECI of *Ascia monuste* (Lepidoptera: Pieridae) larva living on *Brassica oleracea* (4.58 % nitrogen) were higher than those feeding on *Brassica juncea* (3.13 % nitrogen).

The value of ECI is strongly influenced by nitrogen content of the host plant because nitrogen is efficiently converted into body tissue of the larva. Low value of ECI is mainly due to decrease of ECD rather than AD because ECI and ECD are closely related to growth. Low nitrogen content in the food results in increase of RCR which consequently decreases the ECI. Furthermore, AD and ECD have also been found to vary inversely on the same food under different regimes of deprivation, but these results are confounded by differences in RCR (Simpson & Simpson 1990).

Papilio polytes larvae developing on *M. koenigii* took more food (higher RCR) than those reared on the three *Citrus* spp. host plants. The fifth larval stadium developmental time was longer; consequently the fecal dry weight was also heavier on *M. koenigii*. In contrast, the pupal dry weight was the lowest on *M. koenigii* compared with the other three *Citrus* spp. plant hosts. In a study with *Tyria jacobaeae* (Lepidoptera: Arctiidae), Tinney *et al.* (1998) found that the larval development time was negatively correlated to plant nitrogen content, whereas the larval weight, growth rate, and pupal weight were positively correlated to plant nitrogen content. Henriksson *et al.* (2003) also reported that low concentrations of water and nitrogen were the main factors reducing pupal mass of *Epirrita autumnata* (Lepidoptera: Geometridae).

More food intake (RCR) does not automatically increase the RGR because other factors, such as nutrient contents especially protein and water content contribute to the RGR. For example, the consumption rate of *O. vitiosa* larvae feeding on *Melaleuca quinquenervia* receiving low dose of fertilizer increased compared with the larvae feeding on *M. quinquenervia* receiving the higher dose of the fertilizer, but the biomass of pupae and adults on lower dose fertilizer was lower (Wheeler 2003). The digestion of food (AD, ECI, and ECD) also strongly affects the RGR. Ingested nutrients must meet an insect's requirement for growth and other metabolic processes. In this relationship, the amount of nutrients allocated to tissue growth and

storage represents the growth target, and the intake targets is the amount the insect must consume in order to meet its growth and metabolic needs (Simpson & Raubenheimer 1995 cit. Telang *et al.* 2001). Wheeler (2003) also found that larvae fed on leaves from highly fertilized plants converted absorbed food more efficiently to insect biomass than those fed on less fertilized plants.

The *P. polytes* larval AD values on all four host plants in the present study were not significantly different from each other. It was assumed that all these host plants were equally suitable for the larval development and none of them has chemical compound that could obstruct the digestive process. Scriber & Slansky (1981) reported that the value of AD was lower in the presence of higher content of fiber, lignin, tannin, waxes or silica. The decline of AD especially for leaf chewers is often associated with less selective feeding by later instars. Summarizing all nutrition indices Scriber & Slansky (1981) suggest that: $RGR = RCR \times ECI$ and $ECI = AD \times ECD$.

In summary, this study has shown a positive relationship between oviposition preference and larval developmental performance of *P. polytes*. The host plant oviposition preference hierarchy of *P. polytes* corresponds to nutritive value of the potential host plant selected for oviposition. Larval developmental performance was better when fed on plants (*Citrus* spp.) with higher nutritive values than those fed on lower nutritive value (*M. koenigii*); the hierarchy of oviposition preference of *P. polytes* on the studied host plants was *C. reticulata* \geq *C. aurantifolia* > *C. hystrix* > *M. koenigii*.

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