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Effect of Host Age on the Oviposition and Performance of *Ascia monuste* Godart (Lepidoptera: Pieridae)

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Efeitos da Idade do Hospedeiro na Oviposição e Performance de *Ascia monuste* Godart (Lepidoptera: Pieridae)

RESUMO - *Ascia monuste* Godart, conhecida como a lagarta-da-couve, é especialista em Brassicaceae e representa um dos principais herbívoros dessa família na região neotropical. O objetivo do presente estudo foi determinar a performance e a preferência de oviposição de *A. monuste* por folhas de couve *Brassica oleracea* (Brassicaceae, var. *acephala*) de diferentes idades. Os parâmetros utilizados para medir a performance foram tempo para pupação e para emergência, porcentagem de emergência, índices digestórios, taxas de consumo e crescimento relativos, número de ovos por fêmea, porcentagem de eclosão e peso dos imagos. Análises químicas e físicas de folhas jovens e velhas de couve foram feitas. Em geral, imaturos que se alimentam de folhas jovens exibem melhor performance que aqueles que se alimentaram de folhas velhas. Entretanto, não houve diferença no número de ovos por fêmea, indicando mecanismos de compensação, uma vez que folhas velhas possuem menor quantidade de nitrogênio e maior dureza. Fêmeas de *A. monuste* preferem ovipositar em folhas jovens.

PALAVRAS-CHAVE: Insecta, preferência de oviposição, idade da folha, comportamento alimentar

ABSTRACT - *Ascia monuste* Godart, known as the kale caterpillar, has a specialized diet on Brassicaceae and represents one of the main herbivores of this family in the Neotropical region. The objective of the present study was to determine the performance and oviposition preference of *A. monuste* for common kale *Brassica oleracea* (Brassicaceae, var. *acephala*) of different ages. The parameters used to assess performance were time to pupation and emergence, emergence rate, digestive indices, relative consumption and growth rates, number of eggs per female, hatching rate, and weight of the imagoes. Chemical and physical properties of young and old kale leaves were determined. In general, caterpillars feeding on new leaves showed better performance than those feeding on old leaves. However, no significant difference in the number of eggs per female was observed, indicating a strategy of compensation, as old leaves contain a lower amount of nitrogen and are harder than young leaves. *A. monuste* females prefer to lay eggs on young leaves.

KEY WORDS: Insecta, oviposition preference, leaf age, feeding behaviour

Numerous studies have been carried out in an attempt to better understand the interaction between insects and plants. One of the main areas of investigation is the relationship between oviposition preference of females for a specific host and the performance of immature insects on these plants (Thompson 1988, Scheirs 2002). Most herbivores show highly specialized behavior of host plant selection (Zucoloto 1987), which relies on olfactory and taste sensors that respond to taxon-specific plant substances (van Loon & Dicke 2001).

For holometabolous insects, whose larvae are relatively immobile, female choice of oviposition site is of essentially

important since, depending on its choice, the performance of the immature insects and the number of descendants can be seriously affected in a positive or a negative manner (Rausher 1979).

The feeding behavior of the animals reflects their physiological needs, with their metabolic ability frequently being able to compensate for the lack of adequate environmental resources (Warburg & Yuval 1996). According to Simpson & Simpson (1990), there are basically three strategies to compensate for a diet of low nutritional value or for less abundant food: 1) the insect can alter its diet intake rate until a sufficient amount of the limited

nutrient has been consumed, 2) the insect can select another diet or another part of the same plant, and 3) the insect can alter its metabolic and digestive efficacy by using more efficiently the nutrients ingested.

Plant characteristics that affect the performance of the insect include nutritional composition, the presence of allelochemicals, physical characteristics such as toughness, size, shape and texture, temporal and spatial distribution, and abundance (Tabashnik & Slansky 1987). In addition, these factors can be determinant for host recognition (Slansky & Scriber 1985, Thompson & Pellmyr 1991, Dodds *et al.* 1996).

Besides the nutritional differences observed in plants, there are reports indicating the existence of nutritional differences between parts of the same host (Fernandes-da-Silva & Zucoloto 1993, 1997, Catta-Preta & Zucoloto 2003), or, in the case of leaf-eaters, nutritional differences according to leaf age (Schweitzer 1979, Alonso & Herrera 2000). The ability of insects to respond to differences in the nutrient concentration represents a mechanism that helps in the location of the most adequate part (Edwards & Wratten 1981). The nutritional quality of the host is an important selection criterion, with females tending to select diets with a high nitrogen and water content (Honda 1995).

Leaf age has been reported as one of the main determinants in the selection of food resources in leaf-eating insects, with some insects being restricted to a certain leaf age (Larsson & Ohmart 1988, Steinbauer *et al.* 1998). Water content, toughness and the amount of nitrogen, among others, are parameters that change with age (Raupp & Denno 1983).

Studies have been carried out on *Ascia monuste* Godart (Lepidoptera: Pieridae) in the laboratory and in the field in order to determine factors that influence copulation, oviposition, development, and the physical characteristics of the individuals (Lordello & Rodrigues 1952, Shima & Gobbi 1981a, 1981b). Felipe & Zucoloto (1993) described the feeding behavior of immature insects from this species and stated that the nutritional value of the diet is decisive for their evolutive process.

The *A. monuste* caterpillars are considered some one of the most important herbivores of Brassicaceae plants in the Neotropical region (Chew 1988), resulting in considerable damage to their hosts and strongly competing with man, since Brassicaceae are widely used in the human diet.

Brassicaceae are characterized by the presence of glucosinolates, whose concentration varies according to the age of the plant and growth conditions (Tabashnik & Slansky 1987). Glucosinolates are believed to be responsible for host recognition by the butterfly (Chew 1988), although these substances are repellent or toxic to non-adapted species (Blaw *et al.* 1978, Futuyma & Mark 1992).

The objectives of the present study were to determine: 1) possible differences in the amount of nitrogen and water and in the toughness between young and old kale leaves; 2) how these differences influence the host selection and performance of *A. monuste*, and 3) if there is a positive correlation between the performance of immature insects and host selection by adult females.

Material and Methods

Performance. Eggs were collected from kale leaves in a vegetable garden where no insecticides are used, located 1.5 km from the Department of Biology, FFCLRP-USP, Ribeirão Preto, SP, Brazil (47°81'02"W - 21°17'75"S), and transported to the Laboratory of Insect Nutrition and Feeding Behavior, where the present study was carried out. At the time of hatching, caterpillars were divided into two groups according to the type (age) of leaf they would be exposed to. Each group consisted of 10 acrylic boxes measuring 10 x 10 x 4 cm (1 box = 1 replicate), each containing seven newly hatched caterpillars. Preliminary observations in the field showed that larvae are gregarious until the third instar, when they disperse. The boxes, covered with moist paper towels (Felipe & Zucoloto 1993), were maintained in an incubator at $29 \pm 2^\circ\text{C}$ and a relative humidity of approximately 80%, with luminosity being controlled by a fluorescent lamp (400 lux) (Barros & Zucoloto 1999). Food was changed daily when the boxes were also cleaned.

The following aspects were considered to differentiate leaf age: 1) the arrangement of the leaves on the plant, with the more apical being the younger leaves; 2) leaf color, with older leaves becoming darker as they mature and yellow stains being observed at the border; 3) leaf size, with older leaves being larger, and 4) thickness, which is greater for older leaves.

The parameters used to measure insect performance were the time to pupation and adult emergence (days), percent emergence, number of eggs per female, percent hatching, weight of the imago (mg), and various measures of host consumption: approximate digestibility (AD, %), efficiency in the conversion of the ingested food (ECI, %), efficiency in the conversion of the digested food (ECD, %), food intake and feces excretion (mg), and the relative growth rate (RGR) and relative consumption rate (RCR).

The time for development was counted from the first day of hatching. Percent emergence is defined as the number of emerged adults divided by the number of initial caterpillars multiplied by 100; the digestion indices $AD = [(ingestion - feces) / ingestion]$, $ECI = [incorporated\ biomass / ingestion]$, and $ECD = [incorporated\ biomass / (ingestion - feces)]$, as well as the $RGR = [incorporated\ biomass / (time \times mean\ biomass\ incorporated\ per\ group)]$ and $RCR = [ingestion / (time \times mean\ biomass\ incorporated\ per\ group)]$, were calculated according to Slansky & Scriber (1985) for the last larval stage which lasted between three and four days. Previous studies (Felipe & Zucoloto 1993, Barros & Zucoloto 1999) have suggested that this phase is representative of the complete larval phase (but see Zalucki 2002).

In order to perform the digestive indices one larvae was kept per standard glass flask (150 cm³) (10 replicate per group) containing food sufficient for 24h. The kale leaves were cut longitudinally, with half the leaf being given to the caterpillar and the other half being dried and weighed to determine the initial food weight. The remaining food and feces were weighed and the total intake was calculated. To calculate the incorporated biomass, the initial weight was

obtained from the mean weight of three caterpillars at the beginning of the 4th instar for each group. To obtain the weight last the caterpillars were again weighed as soon as they pupated. All material used to determine dry weight was dried in an incubator at 80°C for 24h.

To obtain adults, experimental groups identical to the experimental groups were used. The weight of the imagoes was obtained by drying and weighing 20 pairs of each group at the time of emergence. The adult insects were killed by freezing and dried in an incubator at 80°C for 24 h.

The experiments using adult insects to determine the number of eggs per female were carried out in 1 x 1 x 1.5 m cages (8 replicates per group), with a couple of butterflies being placed in each cage. The eggs were counted daily and the pots were replaced as soon as oviposition was observed. Percent hatching was determined for 10 clusters with more than 25 eggs each.

Oviposition Preference. These experiments were carried out in two steps: in the laboratory and in the field. In the laboratory, each pair was placed in a cage (20 replicates) as described previously, with the kale pots containing the two types of leaves in an equal proportion. Eggs were counted and removed daily from the cages until the death of the female. Plants were replaced each three days. In the field, eggs were counted on 80 *Brassica oleracea* individual plants in a vegetable garden containing four beds. The plants were chosen randomly as long as they possessed young and old leaves on which eggs were identified.

Host Analysis

Water Content. New and old kale leaves (n = 15) were collected from different individuals in the vegetable garden. The leaves were weighed (fresh weight), dried in an incubator at 80°C for 48 h and then weighed again (dry weight). Water content is reported as percentage: 100 x (fresh weight - dry weight/fresh weight).

Nitrogen Content. New and old kale leaves were collected as described for the water content measurement. The leaves were weight, dried in an incubator at 40°C until reaching a constant weight (dry weight). Nitrogen was determined in young and old leaves of different plants (n = 5) by the method of Kjeldahl (Allen *et al.* 1974).

Leaf Toughness. The toughness of young and old leaves was determined as described by King (1988) using a penetrometer, which indicates the pressure necessary to perforate a given area of the leaf. Measurements were obtained in three different regions of the leaf and the mean per leaf was calculated (10 replicates).

Results

Young leaves generally led to a better performance of caterpillars, such as shorter duration of development (Mann-Whitney, $P < 0.05$) and a higher survival rate (Mann-Whitney, $P < 0.05$). However, the number of eggs per female was the same as that observed for females reared on old leaves (Mann-Whitney, $P > 0.05$) (Table 1).

No difference was observed in ingestion (Test-t, $P > 0.05$), feces excretion (Test-t, $P > 0.05$) or AD (Test-t, $P > 0.05$) between groups when calculated for the first 24h of the last larval stage (Table 2). In contrast, the ECI and ECD values were higher (Test-t, $P < 0.05$) for caterpillars, which fed solely on new leaves throughout the larval stage.

When calculated for the complete 5th instar, the indices indicated that caterpillars feeding on old leaves consumed larger amounts of diet (Test-t, $P < 0.05$) but took less advantage of the food ingested as shown by the decrease in the ECI (Test-t, $P < 0.05$). However, a relative increase in the ECD was observed for caterpillars that consumed old leaves, with this increase similar to that observed for caterpillars feeding on young leaves.

A higher RGR (Mann-Whitney, $P < 0.05$) was observed

Table 1. Performance of *A. monuste*, whose immature insects fed on only one type of leaf (in laboratory conditions) and nutritional analysis of the different types of *B. oleracea* leaves.

| Measures | New leaves | Old leaves |
|--|-----------------|-----------------|
| Time to pupation (days) | 9.0 ± 0.3 a | 0.6 ± 0.6b |
| Time to emergence (days) | 15.0 ± 0.6 a | 1.4 ± 0.8 b |
| Percent emergence (arc-sin) | 90.0 ± 0.0 a | 67.3 ± 13.5 b |
| Female weight (mg) | 68.8 ± 9.0 a | 62.7 ± 6.4 a |
| Male weight (mg) | 62.0 ± 7.6 a | 61.3 ± 4.1 a |
| Number of eggs per female | 240.5 ± 129.7 a | 217.9 ± 142.0 a |
| Percent hatching (arc-sin) | 85.0 ± 10.6 a | 84.3 ± 9.4 a |
| Nutritional analysis | | |
| Leaf toughness (mmHg/mm ²) | 6.2 ± 0.7 a | 13.2 ± 1.3 b |
| Water content (arc-sin) | 70.1 ± 0.6 a | 69.6 ± 0.5 b |
| Nitrogen content (arc-sin) | 3.7 ± 0.1 a | 3.1 ± 0.1 b |

Data are reported as mean ± SD for each group. Different letters in the same line indicate a significant difference ($P < 0.05$).

Table 2. Digestive indices calculated for the first 24h of the last larval stage, for the last complete instar and relative growth (RGR) and consumption (RCR) rates of *A. monuste*, whose immature insects fed on only one type of kale leaf.

| Measure | | New leaves | Old leaves |
|---|---------------------------------|----------------|----------------|
| Ingestion (mg) | 24h 5 th instar | 211.0 ± 23.3 a | 205.0 ± 3.6 a |
| | complete 5 th instar | 420.9 ± 67.8 a | 589.0 ± 92.3 b |
| Feces (mg) | 24h 5 th instar | 116.0 ± 19.2 a | 107.0 ± 19.5 a |
| | complete 5 th instar | 226.8 ± 31.8 a | 406.3 ± 64.5 b |
| AD (arc-sin) | 24h 5 th instar | 42.5 ± 2.9 a | 43.5 ± 2.9 a |
| | complete 5 th instar | 42.7 ± 1.7 a | 33.4 ± 5.3 b |
| ECI (arc-sin) | 24h 5 th instar | 31.4 ± 3.6 a | 27.4 ± 1.4 b |
| | complete 5 th instar | 27.3 ± 1.2 a | 21.4 ± 2.5 b |
| ECD (arc-sin) | 24h 5 th instar | 51.0 ± 5.3 a | 42.3 ± 4.5 b |
| | complete 5 th instar | 42.8 ± 3.8 a | 45.0 ± 13.1 a |
| RGR (mg.day ⁻¹ .mg ⁻¹) | complete 5 th instar | 0.33 ± 0.04 a | 0.25 ± 0.03 b |
| RCR (mg.day ⁻¹ .mg ⁻¹) | complete 5 th instar | 1.60 ± 0.24 a | 1.90 ± 0.3 a |

Data are reported as mean ± SD for each group. Different letters in the same line indicate a significant difference ($P < 0.05$).

for caterpillars consuming a diet of young leaves, while the consumption rate was the same (Mann-Whitney, $P > 0.05$) (Table 2).

Host analysis showed that, besides higher water content (Test-t, $P < 0.05$), young leaves contained a larger amount of nitrogen (Mann-Whitney, $P < 0.05$) and were less tough (Test-t, $P < 0.05$) (Table 1).

A. monuste females in the field (Wilcoxon, $P < 0.05$) (Fig. 1) and in the laboratory (Wilcoxon, $P < 0.05$) (Fig. 2) preferred young leaves for oviposition. Of all eggs found in the field (4 633), 94.7% were observed on young leaves and 5.3% on old leaves. The results obtained in the laboratory support the hypothesis that females prefer young leaves, with 95.9% of the 2, 868 eggs being found on new leaves.

Discussion

The nutritional quality of a leaf generally changes with age, with the decrease of water and nitrogen content and the increase of fiber content and toughness (Mattson 1980, Scriber & Slansky 1981, Slansky & Wheeler 1992). Herbivorous insects show a higher growth rate, higher survival rate and higher weight gain when feeding on young leaves (Schweitzer 1979, Dodds *et al.* 1996), a fact observed in the present study for *A. monuste* feeding on kale leaves.

Nitrogen content has been characterized as a critical factor for insects feeding on plants, since plants contain low concentrations of this nutrient compared to animal tissue (Slansky & Fenny 1977). In addition, nitrogen has been considered an important factor in host selection, especially for oviposition (Honda 1995). Since nitrogen is present at low concentrations in old leaves, a decrease in the

performance of caterpillars feeding only on this type of leaf and a lower preference of females are expected.

The duration of development of the group feeding on new leaves was shorter, with nitrogen content probably playing an important role in this process. Furthermore, excessively lignified fibers directly related to the tough consistency of leaves, as well as the low nitrogen level, might have resulted in metabolic impairment in caterpillars feeding on old leaves (Scriber 1982). The lower emergence rate may have been caused by the hard consistency of the leaves, since newly hatched caterpillars presented difficulties in feeding on leaves that were too old and died within 24h due to food deprivation. According to Quiring (1992), different herbivorous specialists are able to overcome the qualitative defenses of their hosts but are unable to overcome quantitative defenses and the low nutritional value of old leaves.

Feeding on old leaves prolonged the time of development of caterpillars, leading to higher energy expenditure and potentially a longer period of exposure to predators. This eventual energy expenditure can be compensated for by an increase in food intake or by changes in the digestive physiology, altering the efficiency at which food is converted into biomass (Rausher 1982, Simpson & Simpson 1990). The latter mechanism was observed in the present study by comparing the digestive indices. A higher ECD value was observed for caterpillars feeding on young leaves when measured during the first 24h of the 5th instar. However, when determined during the last complete larval stage, no significant differences were observed, in contrast to the findings of Stamp & Bowers (1990) who observed higher ECD values for *Hemileuca lucina* (Saturniidae) larvae that

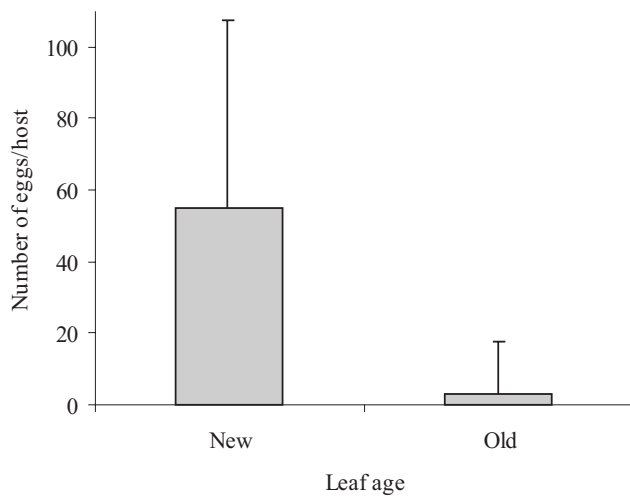


Figure 1. Mean number of eggs found on each type of leaf per kale plant (n = 80) in the field (Wilcoxon test, P < 0.05). There was a significant difference between groups.

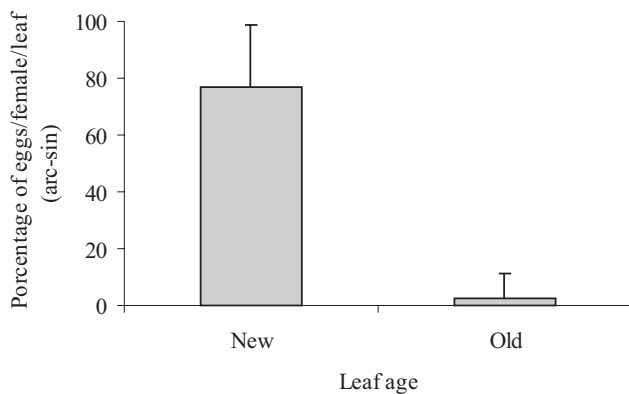


Figure 2. Percentage of eggs laid on each type of leaf per *A. monuste* female (n = 20) in the laboratory (Wilcoxon test, P < 0.05). There was a significant difference between groups.

fed on young leaves.

According to Scriber & Slansky (1981), this type of compensation, as well as an increase in food intake, is observed when resources are insufficient, while the final weight is usually lower. This was the case for *A. monuste* whose females showed a higher weight when feeding on young leaves in the larval stage. On the other hand, an increased consumption might be sufficient to compensate the deficit in certain nutrients such as nitrogen, thus not harming the individual.

The large amount of diet ingested and feces excreted by the group feeding on old leaves indicates that the insects took poor advantage of the ingested food, with a consequent lower ECI value. Another cost of feeding for prolonged periods of time and of consuming large amounts is the prolonged intake of secondary compounds, which can be toxic at high doses even to adapted animals and might exert a fatal effect (Slansky & Wheeler 1992).

Comparison of the relative growth and consumption rates revealed that caterpillars feeding on old leaves showed a lower growth rate even when maintaining the same consumption rate due to a prolonged feeding time.

In general, performance of the caterpillars feeding on old leaves was impaired in terms of the time to emergence and percentage of emerging adults, although the number of eggs per female were similar for the two groups. In lepidopterans plant quality during larval development is the determining factor for female fecundity and fertility (Stern & Smith 1960 *apud* Awmack & Leather 2002). In the present study, the amount of diet ingested was sufficient to compensate for the number of eggs, although the weight of females reared on old leaves was significantly lower.

The emergence rate in the laboratory for the group feeding exclusively on old leaves was approximately 82%, a value that, although lower than the emergence rate observed for the group feeding on new leaves, was still quite high. In the case of high competition for young leaves, like this case, oviposition on old leaves represents a strategic mechanism that guarantees a large number of descendants in the next generation.

However, considering the number of eggs per female and the emergence rate, which was lower in the group feeding on old leaves, the total number of descendants able to reproduce would decrease in each generation, leading to a long-term reduction in the population.

The individual compensations discussed previously may even generate ecological compensations for the species (Simpson & Simpson 1990), including changes associated with the feeding behavior of the immature insect or with the process of oviposition preference, leading to the selection of that part of the host that possesses a higher nutritional value.

Barros & Zucoloto (1999) demonstrated that adult *A. monuste* females choose between two species, i.e., kale and mustard, in terms of a better performance of the immature insects; in this case, kale is chosen because it contains a higher amount of nitrogen than mustard. In the present study, an oviposition preference of females for young leaves was observed both in the laboratory and in the field.

Previous studies have shown that *A. monuste* caterpillars start to feed at the site of oviposition, a fact that leads to an even greater dependence on the adequate selection of the oviposition site by the mother. In the present study, females preferred young leaves, although some eggs were laid on old leaves.

This variability in selection has been recognized as an important element in the evolution of insects and plants - when individuals encounter unfavorable conditions, this variability increases the chances of maintaining the population, even in the presence of environmental fluctuations (Schoonhoven *et al.* 1998). Therefore, survival on old leaves, which was approximately 82% in the present study, guarantees the continuation of the population under adverse environmental conditions. This fact indicates a highly refined behavior of *A. monuste*, whose females select the most adequate food source for their offspring, taking into account chemical and physical characteristics, the

presence of predators (Catta-Preta & Zucoloto 2003), and the availability of nutrients, which results in good performance at the lowest possible cost.

The results of the present study support the hypothesis that *A. monuste* females prefer hosts that offer the best performance for their offspring both in the laboratory and in the field.

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