How feeding on young and old leaves affects the performance of *Ascia monuste orseis* (Godart) (Lepidoptera, Pieridae)

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ABSTRACT. How feeding on young and old leaves affects the performance of *Ascia monuste orseis* (Godart) (Lepidoptera, Pieridae). In the field, immature individuals of *Ascia monuste orseis* (Godart), the kale caterpillars, migrate in great proportion to other regions of the host in order to complete their development; there, they find leaves of different ages and are exposed to the nutritional variation of these leaves. The objective of this study was to find out how the change to leaves of different ages affects the *A. monuste orseis* performance. The experiments were carried out providing one kind of leaf during the three first instars, and afterwards providing leaves of different ages during the fourth and fifth instars, since it is in these two instars that the changing movement prevails in that species. The parameters to measure performance were time of development (both to complete the three first instars and the fourth and fifth instars), ingestion of food, incorporated biomass, digestive indices that evaluated efficiency in food utilization, relative growth and intake rates, percentage of emergence, weight and size of the adults. In general, the caterpillars which were first fed on new leaves presented a better performance, but this study concluded that the *A. monuste orseis* caterpillars have shown skills to compensate food with lower nutritional value or less abundant in nature.

KEYWORDS. Feeding behavior; food mixture; insects; migration.

RESUMO. Como a alimentação com folhas novas e velhas afetam a performance de *Ascia monuste orseis* (Godart) (Lepidoptera, Pieridae). No campo, uma grande proporção dos imaturos de *Ascia monuste orseis* Godart, a lagarta da couve, migra para outras regiões do hospedeiro para completar seu desenvolvimento se deparando com folhas de idades diferentes e ficando sujeita à variação nutricional dessas folhas. O objetivo deste trabalho foi averiguar como a mudança para folhas de idades diferentes afeta a performance de *A. monuste orseis*. Os experimentos foram realizados fornecendo um tipo de folha nos três primeiros ínstares e depois mudando para outra folha de idade diferente nos quarto e quinto ínstares – já que são nesses dois últimos que o movimento de mudança prevalece nessa espécie. Os parâmetros para medir a performance foram: tempo para o desenvolvimento (tanto para completar os três primeiros ínstares como também o tempo do quarto e quinto ínstares), ingestão de alimento, biomassa incorporada, índices digestórios que avaliaram a eficiência na utilização do alimento, taxas de crescimento e consumo relativos, porcentagem de emergência, peso e tamanho dos adultos. De um modo geral, as lagartas que se alimentam primeiro de folhas novas apresentaram melhor performance, mas esse estudo concluiu que as lagartas de *A. monuste orseis* mostram habilidades para compensar alimentos com menor valor nutritivo, ou menos abundantes na natureza.

PALAVRAS-CHAVE. Comportamento alimentar; inseto; migração; mistura de alimento.

The *Ascia monuste orseis* (Godart 1819) larvae, known as kale caterpillars, feed themselves in the oviposition site until about the third instar, when they migrate in great proportion to other regions of the host or to other plants to complete their development. This movement becomes frequent in the fourth instar and prevails during the fifth larval instar (Barros-Bellanda & Zucoloto 2003). After oviposition, the *A. monuste orseis* caterpillars feed themselves basically on kale leaves or other brassicaceas of several ages (Barros-Bellanda & Zucoloto 2003, Bittencourt-Rodrigues & Zucoloto 2005), being exposed to the nutritional variation inherent to the leaf age variation (Scriber & Slansky 1981).

The plant characteristics which affect the insect performance include chemical composition, as nitrogen content, carbohydrates, water content and substances of the secondary metabolism; physical characteristics as hardness, size, form and texture (Renwich 1983, Tabashinik & Slansky 1987), temporal and spatial distribution and abundance (Tabashnik & Slansky 1987), among others. Besides that, these factors can be determinant to recognize the host (Slansky & Scriber 1985, Thompson & Pellmyr 1991, Dodds *et al*. 1996).

The young leaves of *Brassica oleracea* (Brassicaceae = Cruciferae, var. *acephala*) Latreille 1819, the typical host of *A. monuste orseis*, present higher water and nitrogen content and are less hard than the older leaves (Bittencourt-Rodrigues & Zucoloto, 2005), changes which are common during the leaf development (Mattson 1980, Scriber & Slansky 1981, Slansky & Wheeler 1992). Due to these factors, some herbivorous insects grow more, survive in higher numbers, and increase their weight when they eat the younger leaves (Schewitzer 1979, Dodds *et al*. 1996). In the species under study, the immature insects, when fed exclusively on young leaves, develop in a shorter period, however they obtain the same gain in mass and the same fecundity as the individuals which feed on old leaves, showing skills in food compensation (Bittencourt-Rodrigues & Zucoloto, 2005). One ought to know whether this movement to different parts of the host also causes a different performance.

The change to other hosts or to other parts of the same host occurs when: 1) the larvae feed on specific tissues of the host (Zalucki *et al*. 1986); 2) the insects lay many eggs in the same site (Floater 1996) as is the case of the species under study; or 3) when the individuals eat small plants (Walhberg 2000). Thus, the change can be provoked by exhaustion of resources, due to the marked increase in ingestion that occurs with the caterpillars growth (Chew 1975), by the consequent reduction in the plant capability to bear larger caterpillars (Gaston *et al*. 1991), or else by the variation in the nutritional needs of the immature individuals (Despland & Simpson 2000).

A number of studies have found deleterious effects on the immature individuals performance caused by the change to other hosts (Scriber 1981, Cunningham & West 2001). These effects can vary from temporary reduction of food intake to supression of growth rate, reduction in food utilization, lower pupal weight and increased mortality levels. However, other studies have found that depending on the sequence of hosts, the catterpillar can even be benefited (Stoyenoff *et al*. 1994a, Moreau *et al*. 2003). Thus, a host can be more appropriate in the first instars, while it is not in the final instars (Stoyenoff *et al*. 1994b). Therefore, the aim of this study was to evaluate how the change to leaves of different ages, in the same ontogenetic phase, can affect the *A. monuste orseis* performance in the laboratory.

MATERIAL AND METHODS

Biologic material and rearing of the immature individuals. The *A. monuste orseis* eggs were obtained from a vegetable garden where no agrotoxic substances were used, 1.5 km far from the FFCL-RP-USP/SP Biology Department. The eggs were taken to the Insects Nutrition and Feeding Behavior Laboratory where this study was carried out.

Larvae of *A. monuste orseis* were fed on young and old leaves of *B. oleracea*. To distinguish the two foliar age classes the following characteristics were considered: size (the old leaves are larger), color (the old leaves are dark green and the young leaves are light green), disposition in the stalk (the old leaves are basal and the young leaves are apical) and thickness (the old leaves are thicker). From the apical region down, the six first leaves were considered new and from the tenth on they were considered old. The *ad libitum* offered food was daily renewed during all the larval development.

The caterpillars were maintained in boxes or in glasses lined with moistened absorbent paper in a muffle at 28 ± 2^{o}C with relative umidity about 80%. Luminosity was controlled using fluorescent light (400 lx) during 12 hours a day (Felipe & Zucoloto, 1993).

Performance of the immature insects. The parameters used to measure performance of the immature insects were: time to complete the development from first to third instar, and from fourth instar to pupae, time for adult emergence, percentage of emergence and digestive indices. The values were registered once a day between 8 and 9 a.m. Percentage of emergence corresponds to the total number of imagoes emerged in relation to the initial number of caterpillars.

Time and emergence. Newly ecloded caterpillars were placed in standardized acrylic boxes (10 x 10 x 4 cm), 10 boxes (1 box = 1 repetition) with 7 caterpillars each (Barros-Bellanda & Zucoloto 2003). The caterpillars were allocated into four groups treatments: 1) fed on young leaves during all the larval phase (Y-Y); 2) fed on young leaves until the third instar and afterwards with old leaves (Y-O); 3) fed on old leaves during all the larval phase (O-O); and 4) fed on old leaves until the third instar and afterwards on young leaves (O-Y). The fourth instar was chosen for transference to different leaves because former studies (Barros-Bellanda & Zucoloto 2003) found that the caterpillars migrate more often from that instar on.

Digestive indices. Digestive indices, relative growth and intake rates of each group treatment were calculated during the third and fifth instars. To calculate the digestive indices in the third instar, 20 caterpillars were reared on young leaves and 20 caterpillars were rerared on old leaves. When they entered the third instar, they were individualized in standard glasses (50 ml) with food sufficient for 24 hours. The calculation in the third instar was made maintaining the type of leaf provided in the former instars since in nature feeding does not change in this instar.

To calculate during the fifth instar, 30 caterpillars were bred with young leaves, and when they entered that instar they were allocated into two groups: they were individualized, 15 of them received young leaves and 15 received old leaves. The same procedure was made for the caterpillars bred with old leaves. Altogether, 60 caterpillars were used. The digestive indices and the relative intake and growth rates were calculated according to Slansky & Scriber (1985), whose formulae are: Approximate Digestibility (DA) = (Ingestion – Feces) x 100; Efficiency in Converting the Ingested Food (ECI) = (Incorporated Biomass/Ingestion) x 100; Efficiency in Converting the Digested Food (ECD) = Incorporated Biomass/ Ingestion – Feces) x 100; Relative Intake Rate (RCR) = Ingestion/Time x Average Biomass incorporated by the group, and Relative Growth Rate (RGR) = Biomass/Time x Average Biomass incorporated by the group.

To calculate the indices, the young and old kale leaves were longitudinally cut, one half was offered to the individualized caterpillars and the other half was dried and weighted, giving an estimate of the initial dry weight of the food (Felipe & Zucoloto 1993). After 24 hours, the food was renewed, and the remaining leaves were dried and weighted giving the final dry weight of the food and consequently the daily intake value of dry matter. This procedure was repeated until the end of the experiment.

To calculate biomass for the total period, the initial weight of the caterpillars was obtained using the average weight of five individuals, randomly chosen from the group before the experiment. The final weight calculated for the third instar was the dry weight of the caterpillars at the very moment they change the exoskeleton for the fourth instar, and the final weight of the fifth instar was the dry weight of the pupae; the feces were weighted when dry, each 24 hour period. All material used to determine the dry weight was maintained in a muffle at 80ºC for 24 hours or until constant weight (Felipe & Zucoloto 1993).

The third instar performance data were analyzed by the t-test when distribution was normal or by the Mann-Whitney test when a normal distribution was not observed, $P<0.05$. The performance data calculated during the fourth and/or fifth instars were analyzed by the One Way Analysis of Variance, $p < 0.05$.

Weight and size of the adults. To evaluate the accumulation of biomass and how the utilization of each kind of leaf reflects in the adults, weight and size of the imagoes were determined, weight referring to dry weight and size referring to the sizes of the $M_3 – Cu_{1a}$ rear right wing veins of 20 males and 20 females of each group. The measurements were carried out with a stereomicroscope coupled to a computer, the images were captured and the veins measured with the SigmaScan Pro (5.0), Jandel Inc., 1995.

The data were analyzed by the One Way Variance Analysis.

RESULTS

Table 1 shows that, depending on the larval phase, the age of the leaf influences the *A. monuste orseis* performance. The caterpillars fed on young leaves in the three first instars took less time to develop than the caterpillars fed on old leaves in the same period.

The percentage of emergence did not present a significant difference between the treatments. However the standard deviation of the results shown by the caterpillars that were fed on old leaves during all larval stage was the highest among the groups, indicating more marked individual differences. Also, the parameters used to measure the imagoes performance did not present significant statistic difference (Table I). The parameters intake, feces and incorporated biomass of *A. monuste orseis* caterpillars fed on young leaves in the third instar were lower than those of the caterpillars fed on old leaves, however the digestive indices did not present differences between the groups (Table II).

Just as intake varied among the groups of the third instar, a significant variation was also observed in the fifth instar caterpillars (Table II). Apparently, when young leaves are ingested, ingestion is similar in spite of the previous food. However, when old leaves are ingested, intake varies according to the previous food: if young leaves, ingestion decreases. As concerns feces, the values depend exclusively of the kind of leaf: the amount of feces is smaller when the insects feed on young leaves (Table II).

Approximate digestibility (DA) and ECI depend on the kind of leaf the caterpillars are receiving and not on the previous food: caterpillars which receive young leaves present better DA and ECI. However, differences were not observed for ECD among the groups, showing signs of metabolic compensation.

The results of the relative growth and intake rates calculated in the third instar show a significant difference among the groups: the caterpillars fed on young leaves during that period had higher growth and intake rates, that is, they eat and grow more quickly. The results of these rates, calculated during the four experimental groups fifth instars, did not present significant differences as concerns the growth rates; however, the intake rates were the same for the groups fed on young leaves, independently of the previous food, and higher than the rates of the caterpillars fed on old leaves. Among these, influence of the previous food was observed, and that was to be expected since the same was observed concerning the intake rate.

DISCUSSION

As the results of this study show, higher amounts of nitrogen and water and less hardness of the young leaves did not significantly affect survival of the immature insects or the accumulation of biomass in the adult, as they did not affect the number of eggs laid by each female according to previous studies (Bittencourt-Rodrigues & Zucoloto 2005). However,

Table I. Means (± SD) of the performance parameters of *A. monuste orseis* immature and adult individuals fed on young leaves during all larval stage (Y-Y); young leaves until third instar and afterwards old leaves (Y-O); old leaves during all development (O-O); and old leaves until third instar and afterwards young leaves (O-Y).

Parameters	Grupos			
Development	Y-Y	Y-O	O-O	O-Y
Time until the 3rd ínstar(days)	4.2 ± 0.3 a	4.3 ± 0.4 a	5.1 ± 0.4 b	5.3 ± 0.8 b
Time from the 4th instar until pupation (days)	4.9 ± 0.2 a	5.6 ± 0,8 a	5.7 ± 0.6 a	5.7 ± 1.1 a
Time for pupation (days)	9.1 ± 0.3 a	9.9 ± 0.9 b	10.6 ± 0.6 c	10.9 ± 1.3 c
Time for emergence (days)	15.0 ± 0.5 a	15.6 ± 0.8 ac	16.6 ± 0.6 b	16.3 ± 1.3 bc
% of emergence(arc sen)	83.2 ± 12.9 a	78.5 ± 15.3 a	71.9 ± 20.1 a	79.4 ± 15.4 a
Weight of the imagoes (mg)				
Male	55.4 ± 9.9 a	55.6±11.8 a	59.5±10.8 a	55.5±10.0 a
Female	58.0±10.0 a	60.5±9.6 a	59.1±11.4 a	61.2±7.7 a
Size of the imagoes wing (mm)				
Male	2.2±0.2 a	2.2±0.2 a	2.1±0.1 a	2.2±0.2 a
Fêmale	2.5 ± 0.3 a	2.3 ± 0.2 a	2.1 ± 0.2 a	2.2 ±0.21 a

The values indicate means ± standart deviation. Numbers followed by different letters in the same line indicate that there was a significant difference according to the One Way Analysis of Variance test ($p<0.05$)

Table II. Performance of *A. monuste orseis* whose larvae fed on young leaves during all the larval stage (Y-Y); young leaves until the third instar and afterwards old leaves (Y-O); old leaves during all the development (O-O); and old leaves until the third instar and afterwards young leaves (O-Y). The values were separately analyzed for each instar.

Parameters	3º ínstar		5º ínstar			
	New	Old	Y-Y	Y-O	O-O	O-Y
Ingestion (mg)	9.5±2.9 a	16.4±4.4 b	305.9±44.6a	464.8±81.9b	530.0±95.2c	314.2±61.5a
Feces (mg)	3.7±0.5 a	6.5±1.4 b	165.9±21.0 a	314.9±90.4 b	368.0±50.7 c	174.9±32.1a
Biomass (mg)	2.1±0.6 a	3.4±1.1 b	68.0± 9.5 a	61.7± 8.4 a	70.5± 8.8 a	65.4± 6.6 a
DA (%)	58.7±11.1a	58.6±11.7a	45.5±3.7 a	32.7±11.6 b	29.6±9.1 b	44.1±2.7 a
ECI (%)	23.3±6.5 a	21.4±8.0a	22.3±2.0 a	13.8±2.4 b	13.8±1.5 b	21.3±3.1 a
ECD (%)	41.7±17.3a	32.3 ± 12.3a	49.6±7.7 a	46.1±15.3 a	47.7±17.9 a	48.5±8.2 a
RGR (%)	0.9±0.21a	0.5±0.17b	0.3±0.05a	0.3±0.05a	0.3±0.02a	0.3±0.04a
RCR (%)	4.3±1.17a	2.5±0.71b	1.4±0.2a	2.4±0.4b	2.0±0.2c	1.5±0.2a

The values indicate the means ± standart deviation. Numbers followed by different letters in the same line indicate that there was a statistic difference. For the 3rd instar, the t-test was used (with exception of ECI and ECD- Mann-Whitney Rank Test) and for the 5th instar the One Way Analysis of Variance test, P< 0.05.

the time of development was affected mainly by the kind of ingested leaves in the three first instars, showing a positive correlation among the females oviposition behavior – 80% of the eggs are laid on young leaves where a faster development occurs (Bittencourt-Rodrigues & Zucoloto 2005).

Nitrogen is an important nutrient for initial instars because it is a fundamental component for proteins composition and, consequently, for the larvae growth (Scriber 1982). Leaves with low content of nitrogen as occurs in *B. oleraceae* old leaves (Bittencourt-Rodrigues & Zucoloto 2005) would have to be ingested in larger amounts by the larvae to obtain an appropriate level of growth (Kerpler *et al*. 2006). That lenghtened time of development, however, indirectly affects survivorship since it increases vulnerability to predators, desiccation and the action of pathogens (Haggstrom & Larsson 1995). In addition, the hardness of the old leaves can also impair the young catterpillars mastication since their mandibular apparatus is very delicate (Gaston *et al*. 1991, Dodds *et al*. 1996, Bittencourt-Rodrigues & Zucoloto 2005).

Besides the increased intake of old leaves that is a typical mechanism of compensation using foods with lower nutritive value (Scriber 1982; Slansky & Wheeler 1989), there can be compensation through changes associated to the physiology of digestion, altering the animal efficiency in converting food in biomass (Rausher 1982, Simpson & Simpson 1990). That compensation is frequently observed when there is equivalence in the fecundity (same number of eggs by female) and mortality rates, which are similar in the species under study (Bittencourt-Rodrigues & Zucoloto 2005). In that case, such physiological compensation can be verified by the similarity of efficiency in the conversion of the digested food.

According to Barton-Browne & Raubenheimer (2003), eating more slowly can increase the efficiency of digestion, probably because the time of contact between enzyme and substrate is lenghtened, producing a better utilization of the food, though the time of exposition to parasites/predators can be greater. These compensatory responses apparently are common in herbivorous insects (Slansky & Wheeler 1989, Woods 1999).

As concerns the rates calculated during the fifth instar, there was a significant difference among the groups relative growth rates (RGR). This shows that in this instar the caterpillars manage to incorporate the same quantity of biomass, ingesting higher amounts of food in the same period of time. However, during the third instar, the amount of incorporated biomass was larger for the caterpillars fed on old leaves, possibly because of the longer period that the food remained in the digestive tract of the animal. Even though, this was not sufficient to achieve the growth rate of the caterpillars fed on old and new leaves in that stage.

The caterpillars fed on new leaves during the last phase of development have shown lower RCRs, both in the group fed on young leaves (Y-Y) and the group fed on old leaves (O-N) in the first stages of development, showing that the characteristics of the young leaves determine consumption. On the other hand, the caterpillars fed on old leaves at the end of the development presented different RCRs in the groups O-O and Y-O: the caterpillars fed previously on old leaves have a lower RCR than the other caterpillars previously provided with young leaves, showing that not only the characteristics of the old leaves (producing more ingestion) but also the previous food influenced RCR. Caterpillars that had previous contact with young leaves reached pupation ingesting a little less food during the fifth instar, and this can be the compensation to a kind of food with low nutritive value but with higher doses of allelochemicals (Slansky & Wheeler 1992).

The performance of the caterpillars fed only on new leaves or fed on new leaves until the third instar that have afterwards migrated to older leaves is practically the same. Why then the caterpillars migrate to those old leaves and do not remain in the young leaves, even when the young leaves still remain in the plant? Would there exist different microhabitats both in young and old leaves that could be identified by the caterpillar?

Some authors suggest that in certain cases the distance between the new and the old leaves is not sufficient to cause differences in the microhabitat (Moreau *et al*. 2003). However, other studies (e.g. Catta-Preta & Zucoloto 2003) indicate that the presence of predators can make the difference between continuing to eat a type of food or migrating to other sites. The migration of *A. monuste orseis* larvae when they reach a certain size to more basal regions of the kale plant, where the older leaves are, can be a protection against predators as well as a change to a more abundant part of the host in the absence of the other part (Kerpel & Moreira 2005), thus preserving the host. The observations made in nature indicate that the almost complete exhaustion of young leaves would be the main factor of change, since the old leaves intake in the final instars does not affect performance, because the requirement for nitrogen is lower or because tolerance towards hard food is greater (Gaston *et al*. 1991; Carroll 1999; Hochuli 2001: Schoonhoven *et al*. 1998). More studies should be carefully conducted in natural situations to compare the results with the ones obtained in laboratory experiments.

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