

## Feeding Performance of Daphnis nerii on Three Apocynaceae Plant Species 【Research report】

### 夾竹桃天蛾(Daphnis nerii)(鱗翅目:天蛾科)在三種夾竹桃科植物上的取食表現【研究報告】

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#### Abstract

This research was conducted to assess the feeding performance of Daphnis nerii (L.) (Lepidoptera: Sphingidae) on three Apocynaceae plant species (Allamanda cathartica L., Catharanthus roseus L., and Thevetia peruviana Merr.). Both long- and short-term feeding trials were conducted to evaluate variations in insect performance among different plant species. To evaluate the effects of foliage quality on insect feeding performance, leaf tissues from all plant species were collected and assayed for water and nitrogen contents. Results showed substantial among-species variation in insect feeding performance. Larvae survived and grew very well on foliage of Catharanthus roseus L.; but all larvae died when fed foliage of Allamanda cathartica L.; Chemical analysis also revealed that foliar nitrogen content differed significantly among plant species. This study shows that D. nerii larvae perform differently on three Apocynaceae plant species, and the difference may due to variations in foliar nutritional and allelochemical factors.

#### 摘要

本研究在探討夾竹桃天蛾在三種夾竹桃科植物(軟枝黃蟬、日日春、及黃花夾竹桃)上的取食表現。為了評估此蟲在三種植物上的生長情形,使用兩種餵食分析方法。同時為了了解樹葉品質對昆蟲取食表現的影響,這三種植物的葉子在昆蟲餵食分析的同時也被收集,用來分析樹葉含水及含氮量。結果顯示夾竹桃天蛾在這三種夾竹桃科植物上的取食表現顯著的不一樣,食用軟枝黃蟬樹葉的幼蟲全部死亡;而食用日日春樹葉的幼蟲,其存活率及生長速率都非常高。化學分析也發現植物化學物質的含量在這三種植物之間相差很顯著,尤其是含氮量,在三種樹葉上的含量都不一樣。本研究顯示夾竹桃天蛾在不同的夾竹桃科植物上的表現不同,而根據化學分析的結果發現,此種的不同表現可能受到植物的營養及防禦物質所影響。

**Key words:** Daphnis nerii, Allamanda cathartica, Catharanthus roseus, Thevetia peruviana, feeding performance. **關鍵詞:** 夾竹桃天蛾、軟枝黃蟬、日日春、黃花夾竹桃、取食表現

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# Feeding Performance of *Daphnis nerii* on Three Apocynaceae Plant Species

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### ABSTRACT

This research was conducted to assess the feeding performance of *Daphnis nerii* (L.) (Lepidoptera: Sphingidae) on three Apocynaceae plant species (*Allamanda cathartica* L., *Catharanthus roseus* L., and *Thevetia peruviana* Merr.). Both long- and short-term feeding trials were conducted to evaluate variations in insect performance among different plant species. To evaluate the effects of foliage quality on insect feeding performance, leaf tissues from all plant species were collected and assayed for water and nitrogen contents. Results showed substantial among-species variation in insect feeding performance. Larvae survived and grew very well on foliage of *Catharanthus roseus* L.; but all larvae died when fed foliage of *Allamanda cathartica* L.; Chemical analysis also revealed that foliar nitrogen content differently among plant species. This study shows that *D. nerii* larvae perform differently on three Apocynaceae plant species, and the difference may due to variations in foliar nutritional and allelochemical factors.

Key words: Daphnis nerii, Allamanda cathartica, Catharanthus roseus, Thevetia peruviana, feeding performance.

## Introduction

The relationship between preference of ovipositing females for certain plant species and performance of offspring on those plants (survival and reproduction) has been a main issue in the theory of insect/plant interactions (Thompson, 1988; Barros and Zucoloto, 1999). Consequently, this relationship between adults and immature characteristics influences how insect species come to be distributed among plant species (i.e., host-plant selection) over evolutionary time (Thompson, 1988). A frequent assumption of models of host-plant selection is that adult females can rank hosts according to the fitness they impart to offspring (Mayhew, 1997). In turn, the performance of immature stages, such as insect pupal weight, can affect fitness of adult stages.

Most insect herbivores are relatively specific, feeding on only one or a few genera or on a single plant family or

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subfamily (Bernays and Graham, 1988). Previous researches have revealed that host intrinsic quality, such as nutritive value and attraction, may govern host preference of particular plant species for insect herbivores (Ahman, 1985: Murugan and George, 1992; Babu et al., 1996; Barros and Zucoloto, 1999). In general, the host range of monophagous or oligophagous insect species is most likely to occur among chemically similar plants (Jaenike, 1990). However, limited researches were focused on the differential response of insect herbivores to chemically related plant species, especially for insect herbivores which feed on plant species which are generally considered toxic to most herbivores.

The oleander hawk moth, Daphnis nerii L., is a member of the family Sphingidae which is widely distributed in tropical and subtropical areas ranging from Africa to Southeast Asia (Ohba et al., 1999). The adult moth is a strong flier that can migrate great distances, for example from Africa to Europe (Ohba et al., 1999). Because it is a large, fast-growing, and oligophagous insect, D. nerii is a good model for studying larval feeding physiology and preference. The larva of this moth feeds on the oleander and other Apocynaceae plants (Abe et al., 1996; Lin, 1997; Ohba et al., 1999) although such plants are deleterious or toxic to most of other insect herbivores (Abe et al., 1996; Babu et al., 1996). Accordingly, the influence of oleander's nutritional and non-nutritional factors on food preference and utilization by D. nerii was previously established (Murugan and George, 1992; Babu et al., 1996). Relatively little is known about the larval performance of *D. nerii* on various Apocynaceae plant species.

In this study, we determined the feeding performance of *D. nerii* on three Apocynaceae plant species including *Allamanda cathartica* L., *Catharanthus roseus* L., and *Thevetia peruviana* Merr..

We predicted that the performance of *D. nerii* would vary among these Apocynaceae plant species.

# Materials and Methods

## Insects

For mass culturing of insects in the laboratory, *D. nerii* larvae were initially collected from leaves of the host plant *C. roseus* in a garden located near the building of the Institute of Botany, Academia Sinica, Taipei, Taiwan. These larvae were reared in cages  $(30 \times 30 \times 30 \text{ cm})$  and fed foliage of *C. roseus* collected from the garden. About 200 eggs were laid on leaves of *C. roseus* from three female moths. Newly hatched, first instar larvae were used for the insect bioassays.

## Plants

Three common Apocynaceae plant species were used in this study, including *A. cathartica, C. roseus, and T. peruviana*, which are abundant and easily found on the campus of Academia Sinica. *C. roseus* has previously been reported as a host plant of *D. nerii* (Lin, 1997); whether *A. cathartica* and *T. peruviana* are hosts of *D. nerii* is unknown.

### Feeding Trials

To evaluate the feeding performance of D. nerii on foliage of different plant species, we conducted two types of insect bioassays: long-term feeding trails and short-term feeding trials. Newly hatched larvae were reared in petri dishes (14 cm in diameter) at room temperature. They were fed foliage from local C. roseus plants (where we collected *D. nerii*) until being assayed. For experimental bioassays, insects were reared in the laboratory at a constant 22°C. Foliage of similar phenological age (new and fully expanded leaves) was randomly collected from throughout the campus of

Academia Sinica to be used in the bioassays.

Long-term feeding trails were conducted to assess the effects of foliage quality on insect development and growth over the entire larval feeding stage. trails commenced Feeding on 23 December 1999, when the eggs hatched. After larvae had hatched from eggs, they were fed C. roseus for 1~2 days and then used for the bioassay. Two larvae were weighed and put into a petri dish (14 cm in diameter) with a leaf from one of the three test plant species. Ten replicates were conducted for each plant species (20 larvae for each plant species). Larvae were fed in the petri dish until pupation. Leaf materials were changed every 2 days or as necessary. In order to understand the growth rate of insects over the entire larval stage, larval weights were recorded every 4-6 days. Upon pupation, pupal weights were recorded, and development times were calculated as the time elapsed from egg hatching to pupation. Mean and standard errors were calculated for larval weights, pupal weights, and development times for insects fed on foliage from different plant species. Moreover, to measure leaf water and nitrogen content, additional leaf materials from the test plants were collected at the beginning and end of the bioassay (25 December 1999; 5 January 2000) for later analysis. On both collection dates, new and fully expanded leaves were collected from all three plant species.

Short-term feeding trials were conducted to evaluate the effect of foliage quality on growth rates, food consumption rates, and food processing efficiencies of fourth instar *D. nerii* larvae. Seventy newly hatched larvae were grown on *C. roseus* foliage until molting to fourth instars. Each assay consisted of one newly molted and weighed larva placed into a petri dish (9 cm in diameter) containing a leaf from one of the test

plant species (n = 12 replicates per plant species). Leaves were changed every 1-2 days during the bioassay. Upon molting to fifth instars, larvae were frozen, dried (60°C, 1 week), and weighed. Frass and uneaten leaf material were also collected, dried (60°C, 1 week), and weighed. Nutritional indices were calculated from standard formulas (Waldbauer, 1968) for approximate digestibility (AD), efficiency of conversion of digested food (ECD), and efficiency of conversion of ingested food (ECI). We used initial rather than average weights of larvae to calculate relative growth rates (RGR) and relative consumption rates (RCR) (Farrar et al., 1989). Initial dry weights were estimated based on a wet-to-dry weight conversion factor determined from 10 newly-molted fourth instars. Similarly, initial dry weights of leaves fed to insects were estimated by dry weight conversion using foliage collected from each plant species at the time of the bioassay. Means and standard errors were calculated for duration, absolute growth rate (AGR), relative growth rate (RGR), absolute consumption rate (ACR), relative consumption rate (RCR), total consumption (TC), approximate digestibility (AD), efficiency of conversion of digested food (ECD), and efficiency of conversion of ingested food (ECI) for insects fed on foliage from different plant species. Statistical analysis was used to compare insect performance among the plant species. Like the long-term feeding study, additional leaf materials from test plants were also collected during the bioassay to measure leaf water and nitrogen contents.

## Foliar Chemistry of Plant Materials

During the insect performance trials, samples of 25 leaves (new and fullyexpanded) were collected from each plant species (three plants/species), flash frozen in liquid nitrogen, freeze-dried, ground, and stored in a freezer (-20°C). Water content and total nitrogen were quantified for each plant sample. Water contents were determined by differences between wet and dry weights of leaf samples. We conducted standard micro-Kjeldahl assays for leaf nitrogen. Leaf samples were digested in acid (Parkinson and Allen, 1975), and aliquots were subjected to a Kjeltec auto system (Model 2300; Foss Tecator, Sweden) for quantification of nitrogen. Mean and standard errors were calculated for foliar water and nitrogen concentrations for each plant species.

## Results

#### Long-term Feeding Trials

During the feeding trial, all 20 larvae fed on *A. cathartica* died within 5 days, therefore, this species was

eliminated from the statistical analysis. Mean larval weights, pupal weights, and development times were only calculated for insects fed on leaves of C. roseus and Student t-test (PROC Τ. peruviana. TTEST; SAS Institute, 1988) was used to compare pupal weights and development times between these two plant species. Larval weights varied markedly between insects reared on different plant species; the range of variation was more than 7-fold from 10 days of age onward (Fig. 1). Larvae grew particularly well on foliage of C. roseus. Almost all 20 larvae fed on C. roseus went pupation, but only two insects fed T. peruviana survived until pupation. Pupal weights varied by a factor of 1.8 between insects reared on C. roseus and T. peruviana, and variation in development times was about 1.6-fold (Table 1).

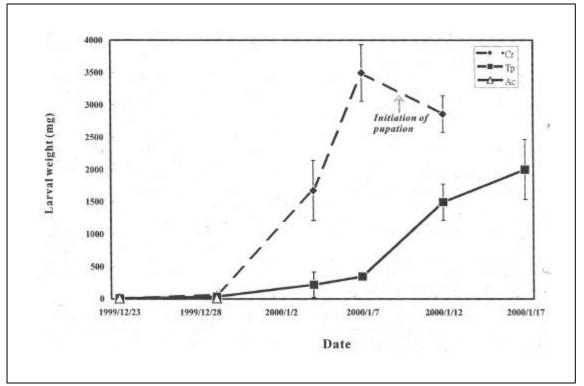


Fig. 1. Growth of *Daphnis nerii* larvae on three Apocynaceae plant species. Each point represents the mean value for weights of insects on foliage of *Catharant hus roseus* (ten replicates) and *Thevetia peruviana* (two replicates). Cr, *C. roseus*; Tp, *T. peruviana*.

#### Short-term Feeding Trials

In the short-term feeding trails, almost all larvae performed well on foliage of C. roseus and T. peruviana; but extremely poor on A. cathartica (Table 2). Similar to the long-term feeding trials, all larvae fed A. cathartica died within 3 days, therefore, no data are reported for larvae fed on this foliage. Mean performance parameters (growth rates, food processing efficiencies, etc.) were only calculated for insects fed on foliage of C. roseus and T. peruviana (Table 2). Student *t*-tests (PROC TTEST) were used to compare feeding performance parameters between these two plant species. The 1.5-fold between-species variation in relative growth rate (RGR) was due

primarily to a variation in digestibility (AD) and secondarily to a variation in conversion efficiency (ECD). The difference in relative consumption rate (RCR) also appeared to contribute to variation in growth, although this difference was not statistically significant. Generally, performance of insects in the short-term study paralleled that of insects in the long-term study, with the best performance on *C. roseus*, and the worst performance on *A. cathartica*.

#### Foliar Chemistry of Plant Materials

Concentrations of water and nitrogen assayed varied among plant species (Fig. 2). Levels of water varied by only 1.15-fold among plant species for both collecting times, whereas concentrations of nitrogen varied by 2.36 and 1.45-fold

Table 1. Pupal weights and developmental times for *D. nerii* fed foliage of two Apocynaceae plants (mean±SE, *n* = 10 and 2 insects for Cr and Tp, respectively)

Species	Pupal weight	Developmental time		
Species	(mg) *	(day)		
Cr	2,858 <del>±</del> 89	20.4±0.2		
Тр	1,615 <b>±</b> 315	32.5 <del>±</del> 2.5		
t	5.30	-4.82		
df	10	1.0		
Р	< 0.005	0.129		

Cr, Catharanthus roseus; Tp, Thevetia peruviana.

\*Significant difference (*t*-test, P < 0.005).

Table 2. Fourth instar oleander hawk moth feeding performance (mean $\pm$ SE, *n* = 12 insects)

Species	Survival	Duration	AGR	RGR	ACR	RCR	TC	AD	ECD	ECI
	(%)	(day)	(mg/day)	(mg/mg/day)	(mg/day)	(mg/mg/day)	(mg)	(%)	(%)	(%)
Cr	100	3.1±0.1	24.5±1.0	1.22±0.09	105.3±3.0	5.18±0.31	327.6±10.2	31.5±1.5	76.3 <del>±</del> 5.3	23.2 <del>1</del> 0.5
Тр	100	3.9±0.1	15.2 <u>±</u> 0.7	0.81±0.04	102.1±4.3	5.42±0.23	394.0±19.6	17.5±0.6	85.7 <u>±</u> 2.8	14.9 <u>±</u> 0.5
Ac	0	-	-	-	-	-	-	-	-	-
t	-	-5.24	7.50	4.07	0.62	-0.61	-3.01	8.78	-1.57	11.75
df		22.0	22.0	15.9	22.0	22.0	16.5	14.9	16.7	22.0
Ρ	-	< 0.001	< 0.001	< 0.001	0.542	0.548	0.008	< 0.001	0.135	< 0.001

AGR, absolute growth rate; RGR, relative growth rate; ACR, absolute consumption rate; RCR, relative consumption rate; TC, total consumption; AD, approximate digestibility; ECD, efficiency of conversion of digested food; ECI, efficiency of conversion of ingested food.

Cr., Catharanthus roseus; Tp, Thevetia peruviana; Ac, Allemanda cathartica.

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for the two collecting dates, respectively. *C. roseus* and *A. cathartica* had higher water content than *T. peruviana*, i.e., 85% versus 74%. Moreover, nitrogen content was much higher in *C. roseus*, with mean values of 3.86% dry weight, followed by 2.41% dry weight for *T. peruviana* and 2.16% dry weight for *A. cathartica*.

# Discussion

This study clearly demonstrates that the feeding performance of *D. nerii* varied significantly among the three Apocynaceae plant species, *A. cathartica, C. roseus*, and *T. peruviana.* Survival and growth of larvae at several stages, as well as food consumption and food processing efficiencies of fourth instars, differed substantially among plant species.

Several studies have documented the host range of D. nerii which include Alstonia scholaris L. R. Br., Vinca rosea L., Tabernaemontana coronaria L., Disverticillata Lour, Adenium solaena obesum Forsk, C. roseus L., Tabernaemontana divaricata L., Cerbera manghas L., and Nerium oleander (Murugan and George, 1992; Babu et al., 1996; Lin, 1997; Yeh et al., 1997). Many of these host plants are in the family Apocynaceae. Among these host plants, only a few studies have been conducted to assess the effect of leaf quality of N. oleander on the performance of D. nerii (Murugan and Babu et al., 1996). 1992; George, Extremely little is known, however, about the differential response of D. nerii to various Apocynaceae plant species.

In Taiwan, *D. nerii* was found to feed mainly on *Nerium indicum* Mill. and *C. roseus* (Lin, 1997). In this study, neonate larvae fed well on foliage of *C. roseus*; but extremely poorly on foliage of *A. cathartica* and *T. peruviana*. In accordance with the results of the long-term study, mature larvae also performed well on foliage of *C. roseus*; but very poorly on foliage of *A. cathartica*. In contrast to the result for neonate larvae, mature larvae grew well on foliage of *T. peruviana*.

Although results of the feeding performance suggest that *D. nerii* may have different host preferences and that preferences change during distinct larval stages, the reason for the variation is unknown. Our results of the comparative food utilization by fourth instar D. nerii indicate that the absolute growth rate, relative growth rate, approximate digestibility, and efficiency of conversion of ingested food were relatively higher for insects fed on C. roseus leaves than on T. peruviana leaves. In contrast, duration of the fourth instar, relative consumption rate, total consumption, and efficiency of conversion of digested food were relatively higher for insects fed on T. peruviana leaves than on C. roseus leaves. These results suggest that the greater growth rate and faster developmental time recorded for D. nerii larvae on C. roseus leaves rather than on other plant species might be due to the high assimilation capacity of larvae for C. roseus leaves.

Physicochemical factors are known to play important roles in affecting insect host preference; the physical nature of host plants as well as the chemical constituents, such as water, free amino acids, carbohydrates, proteins, nitrogen, and lipids, are potentially important parameters (Bernays and Chapman, 1975; Murugan and George, 1992). Therefore, the substantial variation in growth, food processing consumption and food efficiency of D. nerii larvae on foliage of different plant species may be due to the differential chemical compositions of the host plants (Murugan and George, 1992; Babu et al., 1996; Barros and Zucoloto, 1999). Studies have indicated that the growth rates of insects are usually more closely related with foliar

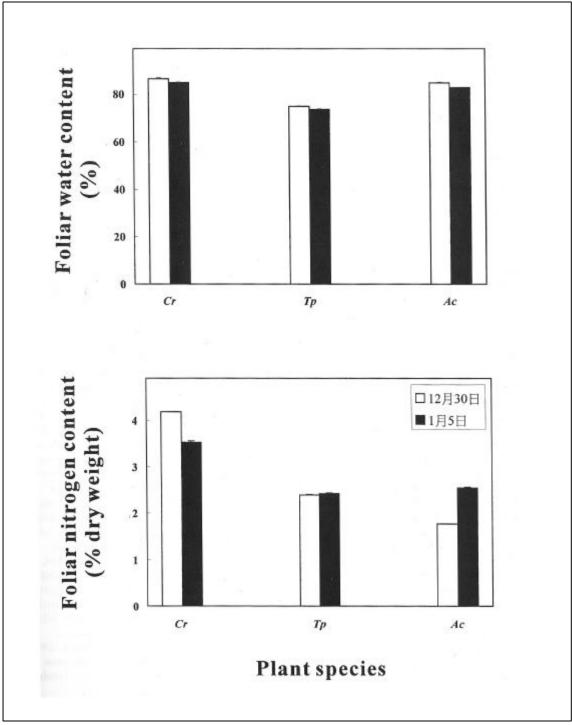


Fig. 2. Concentrations of water and nitrogen in different plant species. Vertical lines indicate±SE, (n = 3 plants for each plant species; , December 30; , January 5). Ac, Allamanda cathartica, Cr, Catharanthus roseus; Tp, Thevetia peruviana.

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water and nitrogen contents (Scriber and Feeny, 1979; Scriber, 1984). Murugan and George (1992) found that both consumption and growth rates were much higher when *D. nerii* fed on high-water-content leaves (78%) than on low-water-content leaves (65%), and significant reduction in food consumption and weight gain by larvae may be due to lower amounts of nitrogen in the foliage. Our results are consistent with their findings (Murugan and George, 1992) that D. nerii grew faster on foliage with high water and nitrogen contents than on foliage with lower water and nitrogen contents. However, this study also indicated that larvae cannot survive on foliage of A. cathartica which has a high water content, and the reason for this result may due to the effect of other aspects of the foliar chemistry.

Except for foliar nutritional contents, non-nutritional factors can also affect host plant suitability to phytophagous insects. Usually, host acceptibility is dependent in part on a wide variety of chemical cues (Dethier, 1980). It has been shown that allelochemicals can block the bioavailability of nutrients by reducing food processing efficiencies (Broadway and Duffey, 1986). Babu et al. (1996) found that the low growth rate of D. nerii fed on N. oleander foliage was probably due to the inhibiting effects of foliar phenolics and amino acids. For the plant species we used, numerous secondary chemicals, such as indole alkaloids, nrsolic acid, and thevetin, have been identified (Cheng and Chang, 1997). We found that D. nerii larvae died within 2-3 days after feeding on A. cathartica foliage. In the field, very little herbivory damage was found on A. cathartica foliage. Therefore, the foliar chemistry of A. cathartica may play an important role in its defense against insect herbivores. In summary, we found that foliar water and nitrogen contents may partially account for variations in feeding performance of *D. nerii* among the three plant species. However, there are no experimental data to confirm this effect yet. Additional and more comprehensive studies are needed to understand the actual role of phytochemistry on feeding performance and host preference of this insect species.

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# 夾竹桃天蛾(Daphnis nerii)(鱗翅目:天蛾科)在三種夾 竹桃科植物上的取食表現

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#### 摘 要

本研究在探討夾竹桃天蛾在三種夾竹桃科植物(軟枝黃蟬、日日春、及黃花夾竹 桃)上的取食表現。為了評估此蟲在三種植物上的生長情形,使用兩種餵食分析方法。 同時為了了解樹葉品質對昆蟲取食表現的影響,這三種植物的葉子在昆蟲餵食分析的 同時也被收集,用來分析樹葉含水及含氮量。結果顯示夾竹桃天蛾在這三種夾竹桃科 植物上的取食表現顯著的不一樣,食用軟枝黃蟬樹葉的幼蟲全部死亡;而食用日日春 樹葉的幼蟲,其存活率及生長速率都非常高。化學分析也發現植物化學物質的含量在 這三種植物之間相差很顯著,尤其是含氮量,在三種樹葉上的含量都不一樣。本研究 顯示夾竹桃天蛾在不同的夾竹桃科植物上的表現不同,而根據化學分析的結果發現, 此種的不同表現可能受到植物的營養及防禦物質所影響。

關鍵詞:夾竹桃天蛾、軟枝黃蟬、日日春、黃花夾竹桃、取食表現