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Autor: Goverde, Marcel / Granados, Julian / Erhardt, Andreas

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Host-plant selection in three different moth larvae

MARCEL GOVERDE[1,3], JULIAN GRANADOS[2] & ANDREAS ERHARDT[1]

Feeding preferences in three species of polyphagous noctuid larvae (*Spodoptera littoralis*, *S. eridania*, and *Heliothis virescens*) were studied in a greenhouse experiment. Five different tropical humid forest plant species were offered to second and third instar larvae of all three moth species. All larvae preferred mainly one plant species (*Gonolobus viridiflorus*, Asclepiadaceae) and hardly fed on *Thinouia tomocarpa* (Sapindaceae) and *Swietenia macrophylla* (Meliaceae). The latter may be protected from herbivory by their high leaf concentrations of polyphenols and condensed tannins. We correlated larval feeding probabilities with leaf tissue characteristics. Best fit was found for water concentration and specific leaf area while, surprisingly, leaf nitrogen and C/N-ratio did not seem to be the most relevant factor for larval choice behaviour. Furthermore, we could not find a general negative correlation between feeding probability and leaf concentrations of polyphenols and condensed tannins.

Key words: *Spodoptera littoralis*, *S. eridania*, *Heliothis virescens*, Noctuidae, plant-insect interaction, plant defence.

INTRODUCTION

Host-plant quality and abundance mediate growth and development of herbivorous insects (BERNAYS & CHAPMAN, 1994; PRICE, 1997). For these insects it is therefore important to find their most suitable host-plant. Normally, the first host-plant choice is made by ovipositing females. Visual and olfactory cues lead females to their preferred host-plants (BERNAYS & CHAPMAN, 1994; SCHOONHOVEN *et al.*, 1998). After landing, females examine the leave surface by drumming or scratching before laying their eggs (e.g. BAUR *et al.*, 1998; RENWICK & CHEW, 1994). After hatching, larvae normally start to feed on the plant on which the maternal female oviposited. However, at a certain age larvae might decide to leave their host-plant to seek a more appropriate one. Accordingly to this, we observed that freshly emerged larvae of *Coenonympha pamphilus* (Satyridae) show no preference among five different grass species offered. However, after 36 h of feeding larvae searched for their most preferred host-plant (M. GOVERDE, unpubl. data). Larval choice is determined by internal plant constituents such as sugar, protein, water, the presence and composition of allelochemicals and, furthermore, by leaf odour and surface structure (e.g. volatiles, waxes, trichomes) (MATTSON, 1980; ROSENTHAL & BERENBAUM, 1991; BERNAYS & CHAPMAN, 1994; CHAPMAN, 1998). A combination of these stimuli appears to be the major clue to host-plant acceptance (BERNAYS & CHAP-

[1] Department of Integrative Biology, Section of Conservation Biology, University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland.
[2] Department of Integrative Biology, Section of Botany, University of Basel, Schönbeinstrasse 6, CH-4056 Basel, Switzerland.
[3] Corresponding author; e-mail: goverde@mail.com

MAN, 1994). These leaf characteristics, however, differ among plant species and depend on biotic and abiotic factors (e.g. BARBOSA *et al.*, 1991; AYRES, 1993; CARTER *et al.*, 1997; BUSE *et al.*, 1998; GOVERDE *et al.*, 1999). There is clear evidence that host-plant quality mediates larval choice behaviour (BERNAYS & CHAPMAN, 1994; SCHOONHOVEN *et al.*, 1998).

In the present study we aimed to detect potential preferences and feeding limitations in three well known, polyphagous noctuid moth species frequently used in laboratory investigations, i.e. *Spodoptera littoralis* BOISDUVAL, *S. eridania* STOLL, and *Heliothis virescens* FABRICIUS. Five different tropical humid forest plant species were offered as host-plants. We correlated larval feeding probabilities with plant characteristics measured, i.e. concentrations of water, nitrogen, carbon, polyphenols, condensed tannins and specific leaf area (SLA).

MATERIAL & METHODS

In a greenhouse at the Botanical Institute of the University of Basel, five tropical humid forest plants (*Thinouia tomocarpa* STANDLEY, Sapindaceae; *Swietenia macrophylla* KING, Meliaceae; *Gonolobus viridiflorus* (WOODSON) STEVENS, Asclepiadaceae; *Cynanchum schlechtendalii* (DECNE.) STANDLEY & STEYERM., Asclepiadaceae; *Mansoa* sp., Bingoniniaceae) originating from Mexico were germinated. One single seedling was planted in a five litre pot containing a soil mixture of quartz sand and loess (1:1). In total eight pots per plant species were established. Plants were grown for one year under controlled environmental conditions simulating the Mexican tropical humid forest.

To characterize food plant quality, we used sub-samples of each plant (1–4 leaves per plant) and measured leaf water concentration (proportional difference between fresh and dry leaf mass), and the specific leaf area (SLA, cm^2/g dry mass) using a planimeter (LI-3100 Area Meter, LI-COR, inc., Lincoln, Nebraska USA). Nitrogen and carbon concentrations were determined from dried leaves (60° C) using a CHN analyser (LECO Instruments, Model 932, St. Joseph, Michigan USA), which uses a combustion procedure. For polyphenol and condensed tannin (CT) analysis, 70 mg dried leaf samples were extracted in 10 ml of 70% acetone over night (15 h) at 4° C in the dark. After filtration, CT concentration (estimated at 550 nm and expressed with coefficient extinction $E^{‰}{}_{550} = 150$ in units of milligrams per gram; condensed tannins anthocyanidin equivalent) was assessed using the acid butanol assay (PORTER *et al.*, 1986). For polyphenols, the Prussian blue assay (PRICE & BUTLER, 1977) was used with a standard curve of absorption at 725 nm established with commercial tannic acid (Catechin, Fluka Chemie AG, Switzerland).

Larval host-plant preference of three different noctuid generalists (*Spodoptera littoralis*, *S. eridania* and *Heliothis virescens*) was determined in a petri dish experiment. Caterpillars were reared on a synthetic medium by Novartis (P. Schneiter, Novartis, 4332 Stein AG, Switzerland). Five seven days old (second instar, I_2) respectively three 10 day old (third instar, I_3) caterpillars were placed in the middle of a petri dish (Ø 9 cm). Petri dishes contained equal-sized parts of the five tropical plants placed on water soaked Kleenex to maintain air humidity and covered with nylon mesh and the petri dish lid. Petri dishes were kept in the lab at room temperature. Host-plant preference was determined by estimating the eaten area after 24 h and 72 h, and additionally for the I_2 caterpillars after 120 h. Surviving caterpillars were counted.

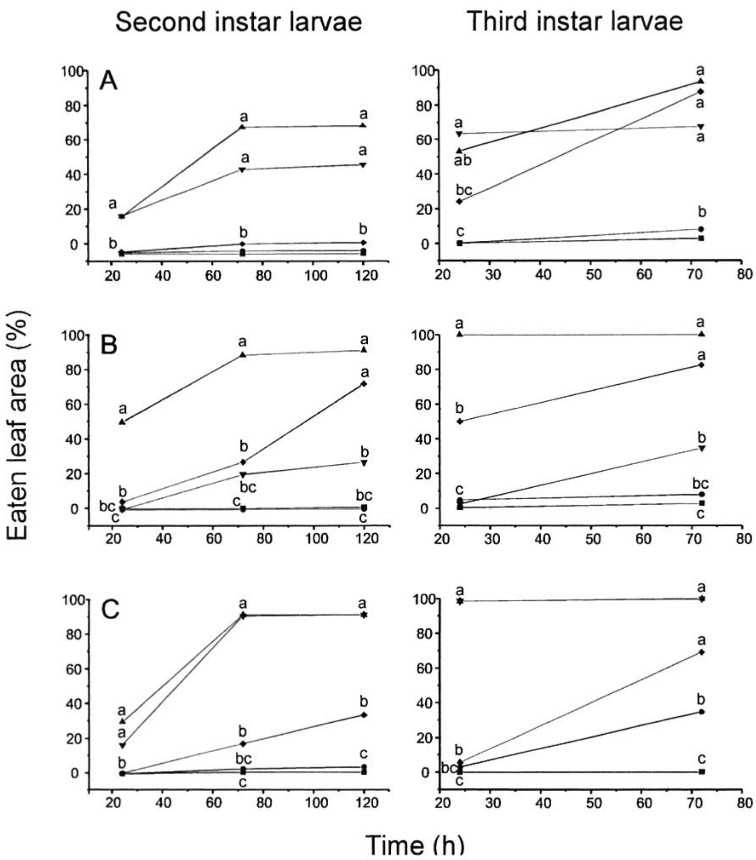

Fig. 1: Proportion of eaten leaf area by second and third instar larvae of *H. virescens* (A), *S. eridania* (B) and *S. littoralis* (C) on five different tropical humid forest plant species . (■) *Thinouia tomocarpa*, (●) *Swietenia macrophylla*, (▲) *Gonolobus viridiflorus*, (▼) *Cynanchum schlechtendalii*, (◆) *Mansoa* sp. Different letters indicate significant differences (all data are square-root transformed, Tukey-Kramer HSD corrected by Bonferroni $p = 0.017$ for second instar larvae and $p = 0.025$ for third instar larvae).

RESULTS AND DISCUSSION

Food-plant preference and mortality

Larvae of all three moth species showed clear preferences among the five plant species offered. Larvae fed on *G. viridiflorus*, *C. schlechtendalii* and *Mansoa* sp., except for young (I_2) *H. virescens*, which hardly fed on *Mansoa* sp., and older *S. littoralis*, which were additionally feeding on *S. macrophylla* (Fig. 1, Tab. 1A). A preference among the three noctuids for different host-plants also appeared in some cases. *S. eridania*, for example, seemed to prefer *G. viridiflorus* over *Mansoa* sp. over *C. schlechtendalii* while *S. littoralis* clearly preferred the two Asclepiadaceae over the other three plant species (Fig. 1). Thus polyphagous species, like the moth species used in this study, may feed on a great diversity of plant species but show clear preferences between different plant species and certainly do not indiscriminately accept all green plants. Even classic polyphagous insects like the desert locust (*Schistocerca gregaria*), which feeds on a wide range of plants, exhibits pronounced preferences for particular plants (CHAPMAN, 1990).

Larval mortality after the first feeding period (72 h for I_2 and 24 h for I_3 larvae) was low except for I_2 *H. virescens* (Tab. 2). The high mortality at the end of the experiment (Tab. 2) may be due to moving around and feeding on different plant

Tab. 1A: Feeding preference of three moth species on five tropical humid forest plant species. --, -, +, ++, +++: intensity of feeding from very low (--) to high (+++).

Plant species	**Total feeding probability**	Feeding preference of moth species *H. virescens*	*S. eridania*	*S. littoralis*
Thinouia tomocarpa	**<1%**	--	--	--
Swietenia macrophylla	**3%**	--	--	-
Mansoa sp.	**20%**	+	++	++
Cynanchum schlechtendalii	**30%**	++	+	+++
Gonolobus viridiflorus	**46%**	+++	+++	+++

species some of which may have been toxic. The two most preferred plants, *G. viridiflorus* and *C. schlechtendalii*, belong to the family of Asclepiadaceae, which are known to contain high quantities of alkaloids (HEGNAUER, 1964). These allelochemicals are known to be deterrent to herbivores (ROSENTHAL & BERENBAUM, 1991) and, therefore, might have been lethal to the caterpillars. This is confirmed by a feeding experiment performed in the greenhouse where 360 *S. littoralis* larvae were allowed to feed freely on the same plants described above. After two weeks of growth we found some faeces and traces of feeding but not a single caterpillar had survived (M. GOVERDE, unpubl. data). This suggests that freely moving caterpillars fed on most plants and that at least one of these plants was deadly. In contrast, we were able to grow *S. littoralis* larvae on *G. viridiflorus* leaves in the lab (mortality <30%) reaching pupal stage without any problems. Thus feeding on this particular plant was not fatal while moving between different food-plants was. Similarly to this, BERNAYS (1999) observed that host-plant choice can be a problem for the generalist whitefly *Bemisia tabaci*, which showed reduced performance when a mixture of food-plants was presented. Thus the behaviour of our generalists shows that a more diverse resource availability can have a negative effect on the performance of polyphagous species.

Tab. 1B: Foliar chemistry of five tropical humid forest plant species and coefficient of determination (r^2) between larval feeding probability and leaf characteristic. Different letters indicate significant differences among species ($p = 0.05$, Tukey-Kramer HSD). Correlation between feeding probability and leaf characteristics are shown in Fig. 2.

Plant species		Water conc. (%)	SLA (cm^2/g)	N conc. (%)	C conc. (%)	Polyphenolic (mg/g)	Cond. Tannin (mg/g)
Thinouia tomocarpa		65.8 ± 2.9^{a}	284.7 ± 10.6^{a}	3.48 ± 0.13^{a}	43.85 ± 0.28^{a}	18.86 ± 2.63^{a}	1.76 ± 0.21^{a}
Swietenia macrophylla		69.3 ± 1.2^{a}	339.5 ± 13.9^{a}	1.90 ± 0.11^{c}	46.12 ± 0.30^{b}	39.93 ± 3.28^{b}	14.50 ± 1.25^{b}
Mansoa sp.		76.2 ± 1.2^{b}	386.8 ± 29.3^{ab}	2.32 ± 0.29^{bc}	46.04 ± 0.22^{b}	7.60 ± 0.40^{c}	0.92 ± 0.12^{ac}
Cynanchum schlechtendalii		85.1 ± 0.7^{c}	517.54 ± 40.2^{c}	2.49 ± 0.14^{b}	43.07 ± 0.37^{a}	11.32 ± 0.62^{cd}	0.62 ± 0.04^{c}
Gonolobus viridiflorus		86.0 ± 0.8^{c}	473.32 ± 39.2^{bc}	3.27 ± 0.15^{a}	43.08 ± 0.46^{a}	12.36 ± 0.47^{d}	1.12 ± 0.14^{ac}
Correlation between feeding probability and leaf characteristics	r^2	0.920	0.766	0.052	0.327	0.382	0.291
	p	**0.01**	**0.05**	**0.75**	**0.31**	**0.27**	**0.35**

Tab. 2: Mortality of second and third instar larvae of three moth species after 24 h, 72 h and 120 h, respectively. Larvae were allowed to feed on five different tropical humid forest plant species (*Thinouia tomocarpa*, Sapindaceae; *Swietenia macrophylla*, Meliaceae; *Gonolobus viridiflorus*, Asclepiadaceae; *Cynanchum schlechtendalii*, Asclepiadaceae; *Mansoa* sp., Bingoniniaceae).

	Second instar		Third instar	
	72 h	120 h	24 h	72 h
Heliothis virescens	40.0 %	73.3 %	10.0 %	43.3 %
Spodoptera eridania	10.0 %	53.3 %	13.3 %	40.0 %
Spodoptera littoralis	0.0 %	73.3 %	0.0 %	50.0 %

Correlation of feeding probability and leaf characteristics

Attraction to a host-plant often involves both olfactory and visual cues to herbivores. Since caterpillars have very limited visual acuity, odour as well as the first bite might be more important for their selection of host-plants (BERNAYS & CHAPMAN, 1994). In the present study the water concentration and the specific leaf area (SLA) correlated best with the larval feeding probability (Tab. 1B, Fig. 2). Leaves with low water concentration and low SLA were most unattractive for caterpillars. A low SLA indicates thick and/or tough leaves which are difficult to feed on especially for young caterpillars (SLANSKY, 1993; SCHOONHOVEN *et al.*, 1998).

The most important factor for insect growth is commonly assumed to be the nitrogen concentration of food (MATTSON, 1980; SCRIBER & SLANSKY Jr., 1981). In our study, however, the nitrogen concentration seemed not to have been the most important factor for larval choice behaviour. The plant species with the highest nitrogen concentration, *T. tomocarpa*, was not attractive for any moth species investigated (Tab. 1A). However, we find a correlation between feeding probability and nitrogen concentration when we omit *T. tomocarpa* ($r^2 = 0.975$, $p = 0.03$). The leaf carbon concentration differed among species but did not correlate with larval feeding probability (Tab. 1B, Fig. 2).

Plants produce secondary compounds to protect themselves against herbivores (FRITZ & SIMMS, 1992). Low concentrations of deterrents can be ineffective to polyphagous insects but in higher concentrations the same compound can be deterrent (BERNAYS & CHAPMAN, 1994). In our study we found no general negative correlation between larval feeding probability and polyphenolic or condensed tannin concentration. We still suggest that these compounds might have protected *S. macrophylla* and *T. tomocarpa* from herbivory, since both plant species had the highest levels of these allelochemicals compared to the other plant species (Tab. 1B).

Finally, physical properties such as leaf thickness, trichomes or waxes on the leaf surface influence the attractiveness of larval host-plants. As mentioned above, in our study, we were able to correlate SLA with larval feeding probability, indicating that tough leaves are less attractive for caterpillars. Trichomes as physical barriers seemed irrelevant in our experiment since caterpillars fed on *C. schlechtendalii*, which has many trichomes but avoided *T. tomocarpa* and *S. macrophylla*, which have no trichomes. However, we would like to point out that many other leave tissue factors not measured in the present study, are also involved in host-plant selection, and that the combination of these stimuli seems to be the major clue to host-plant acceptance.

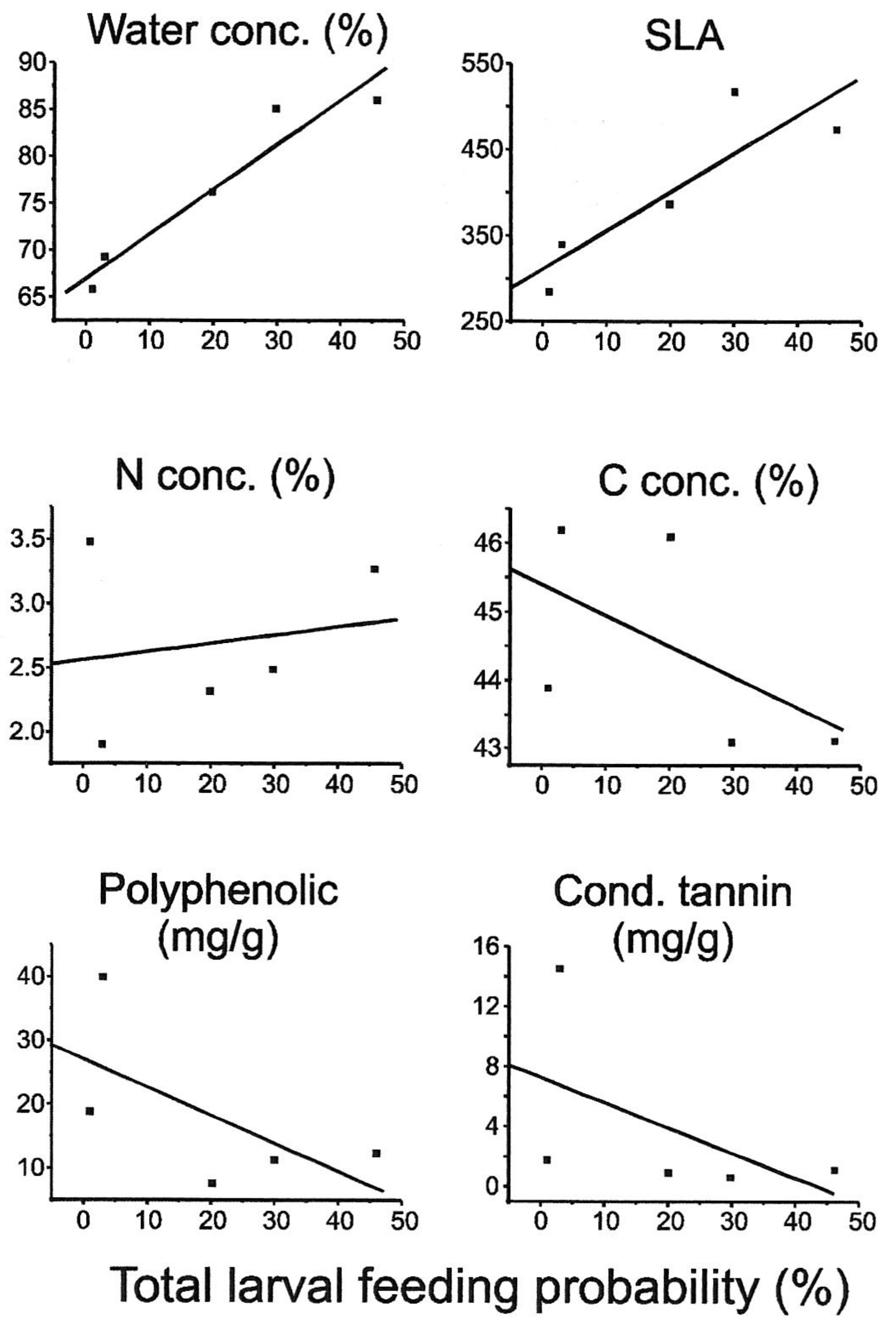

Fig. 2: Correlation between feeding probability and leaf characteristics. R- and p-values are given in Tab. 1.

CONCLUSION

Our results indicate that the investigated polyphagous noctuid larvae show clear host-plant preferences. This implies that also generalist insects chose between different host-plants, most likely based on some leaf quality factors. In our experiment, larval choice was correlated with water concentration and SLA but not with nitrogen and carbon concentrations of the presented host-plants. Although our data do not show a corresponding correlation, polyphenolics and condensed tannins in high concentrations are likely to protect a plant from herbivory. Finally, the high mortality of larvae indicates that probing several plant species including toxic species can be lethal for the larva.

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ZUSAMMENFASSUNG

In einem Gewächshausversuch untersuchten wir die Futterpräferenz von drei polyphagen Nachtfalterarten (*Spodoptera littoralis*, *S. eridania* und *Heliothis virescens*). Larven im zweiten und dritten Entwicklungsstadium erhielten die Möglichkeit aus fünf feucht-tropischen Pflanzenarten auszuwählen. Die Pflanzenart *Gonolobus viridiflorus* (Asclepiadaceae) wurde von allen Raupen deutlich bevorzugt. *Thinouia tomocarpa* (Sapindaceae) und *Swietenia macrophylla* (Meliaceae) wurden praktisch nicht gefressen. Dies ist vermutlich auf deren hohen Gehalt an Abwehrstoffen (Polyphenolen und kondensierten Tanninen) zurückzuführen. Die Fresswahrscheinlichkeit der Larven war nicht wie wir erwartet hätten durch den Proteingehalt oder das Verhältnis von Kohlenstoff zu Stickstoff (C/N-Ratio) bestimmt, sondern sie war vor allem mit dem Wassergehalt und der spezifischen Blattfläche korreliert. Auch konnten wir keine Korrelation zwischen der Fresswahrscheinlichkeit und den Abwehrstoffen nachweisen.

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