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Effects of Solanum viarum Cuticular Leaf Extracts and Its Fractions on the Oviposition of Helicoverpa armigera (Hübner) (Lepidoptera: Noctuidae)【Research report】

Solanum viarum 葉面表皮萃取物及其分餾物對番茄夜蛾 Helicoverpa armigera (Hübner) 產卵之影響【研究報告】

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Abstract

We investigated the effects of the leaf cuticular extracts of the tropical soda apple, Solanum viarum, on the oviposition of the tomato fruitworm, Helicoverpa armigera, a worldwide phytophagous pest. In a dual-choice laboratory assay, the cuticular extracts of the leaves of S. viarum showing significant attraction ($p < 0.05$) to H. armigera females for oviposition was fractioned by the use of normal-phase silica Sep-Pak cartridges. Five fractions eluted with diethyl ether in hexane (F1, F2, F3, F4, and F5) were compared for efficiency, as assessed by the mean number of eggs laid, in stimulating oviposition by the female. Only fractions F2 (40% ether) and F3 (60% ether) showed significant effects of stimulating oviposition. Scanning electron microscopy revealed the presence of sensilla trichodea and sensilla coeloconica on the antennal hairs which might bear receptor neurons for the detection of plant semiochemicals.

摘要

本實驗探討熱帶刺茄Solanum viarum (Dunal)，葉面表皮萃取物對於分布全世界的重要植物害蟲番茄夜蛾Helicoverpa armigera (Hübner)產卵的影響。在雙重選擇實驗分析下，利用常相silica Sep-Pak cartridges分析顯示，S. viarum葉片表皮的萃取物對雌番茄夜蛾產卵具顯著誘引效果($p < 0.05$)。5個分級(F1, F2, F3, F4及F5)乃以正己烷洗提稀釋不同濃度乙醚，並用以刺激雌蟲產卵，來比較產卵平均數的效果。只有F4 (40% ether)及F3 (60% ether)對刺激產卵有相當大的影響。掃描式電子顯微鏡指出在番茄夜蛾觸角上的觸毛有感覺毛(sensilla trichodea)及腔內感覺器(sensilla coeloconica)的存在，其可能具有接收神經可偵測植物訊息化學物(plant semiochemicals)。

Key words: Helicoverpa armigera, Solanum viarum, oviposition, sensilla, plant semiochemicals
關鍵詞: Helicoverpa armigera、Solanum viarum、產卵、感覺毛、植物訊息化學物

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Effects of *Solanum viarum* Cuticular Leaf Extracts and Its Fractions on the Oviposition of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae)

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ABSTRACT

We investigated the effects of the leaf cuticular extracts of the tropical soda apple, *Solanum viarum,* on the oviposition of the tomato fruitworm, *Helicoverpa armigera*, a worldwide phytophagous pest. In a dual-choice laboratory assay, the cuticular extracts of the leaves of *S. viarum* showing significant attraction ($p < 0.05$) to *H. armigera* females for oviposition was fractioned by the use of normal-phase silica Sep-Pak cartridges. Five fractions eluted with diethyl ether in hexane (F_1, F_2, F_3, F_4, and F_5) were compared for efficiency, as assessed by the mean number of eggs laid, in stimulating oviposition by the female. Only fractions F_2 (40% ether) and F_3 (60% ether) showed significant effects of stimulating oviposition. Scanning electron microscopy revealed the presence of sensilla trichodea and sensilla coeloconica on the antennal hairs which might bear receptor neurons for the detection of plant semiochemicals.

Key words: *Helicoverpa armigera*, *Solanum viarum*, oviposition, sensilla, plant semiochemicals

Introduction

The tropical soda apple, *Solanum viarum* Dunal (Solanaceae), is an herbaceous annual weed (Aranha *et al.,* 1982) native to South America (Nee, 1991). *S. viarum* is considered to be a serious weed threat and has been included in the list of noxious weeds by the Florida Department of Agriculture and Consumer Services (1994). This weed has spread into other geographical regions including Central America, the Caribbean, India, China, Africa (Chandra

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and Srivastava, 1978; Coile, 1993), and South Florida (Mullahey *et al*., 1993). Because of its alkaloid contents, the solution of the boiled-leaf of this weed is used as a drug in Senegal by young teenagers. In another part in West Africa, Chad, a solution of *S. viarum* roots is locally used as a tooth medicine. In India it is also regarded as a medicinal crop (, N. S. Talekar, pers. comm.). The spread of this weed in pastures was very fast in South Florida. Its rapid spread in South Florida can be partially attributed to the plant's ability to grow in sandy loamy soils (Chandra and Srivastava, 1978), its great reproductive potential (Mullahey *et al.,* 1993), and the effective seed dispersal by cattle and wildlife (Mullahey and Colving, 1993).

In spring 1988, while screening eggplant and related wild *Solanum* species for resistance to cotton leafhopper, a heavy infestation of *S. viarum* foliage by larvae of the tomato fruitworm, *Helicoverpa armigera* (Hübner), was noted by the Asian Vegetable Research and Development Center, Taiwan (Anonymous, 2000). Various instar larvae were found to be voraciously feeding only on *S. viarum,* and several subsequent laboratory studies confirmed that females of *H. armigera* preferred to oviposit on this wild crop over its natural host, the tomato plant. Laboratory and cage bioassays performed at the National Pingtung University of Science and Technology (NPUST), Taiwan also confirmed such a stimulatory power of the plant on the insect females. This suggested that *S. viarum* is highly preferred by females of *H. armigera*, which opened the possibility of using this wild plant as a trap crop. However since trap crops may occupy a lot of field area, the identification and synthesis of those leaf-chemicals involved in the oviposition attractiveness and stimulation of the female *H. armigera* could lead to their formulation of an ovitrap and its use in the continuous trapping of *H. armigera* females. Such potential applicability of these semiochemicals may help farmers through an integrated pest management (IPM) approach to control *H. armigera*. This paper confirms, from our laboratory investigation, the oviposition stimulatory effects of *S. viarum* leaf extract on the oviposition of *H. armigera*.

Materials and Methods

Helicoverpa armigera rearing

Adults of *H. armigera* were initially obtained from the Taiwan Agricultural Chemicals and Toxic Substances Research Institute (TACTRI), Taichung, Taiwan. The colony was maintained at the Department of Tropical Agriculture and International Cooperation (DTAIC) laboratory, at National Pingtung University of Science and Technology, in continuous culture at 27 ± 2°C and 68% ± 2% relative humidity (RH). Moths were grouped into 15 pairs each and placed in 33-cm-high × 15-cm-diameter acrylic cylinders, the inner surface of which was lined with rough tissue paper to facili- tate oviposition. A cotton plug, soaked in a solution containing 400 ml honey, 60 ml Taiwan beer, 20 g ascorbic acid, 12 g methyl para-benzoic acid, and 1000 ml distilled water, was hung from the top of the cylinder to serve as food and a mating stimulant. The cylinders were placed in a laboratory under ambient light. Eggs laid on the tissue paper were collected daily and disinfected with 7% formaldehyde for 25 min and rinsed in clean water for 2 h. After disinfection, eggs were maintained at one of the two temperatures, 27 or 30°C, and 68% ± 2% RH. Newly hatched larvae were reared on a wheat germ-based artificial diet (Kao, 1995). From the 3rd instar onwards, larvae were individually reared in separate containers. The containers and diets were changed every 2 days. Pupae were sorted by sex, and male and female pupae were placed in separate containers.

Adults were allowed to emerge, and the emergence date was recorded. Two newly emerged females were paired with 2 newly emerged males for mating in a cylinder as described above, and gravid females along with males were used for the experiments.

Plant cultivation

Potted *S. viarum* plants were raised in a greenhouse at the DTAIC. Plants were fertilized once a week with N: P: K: Mg (20: 19: 15: 0.5), at 3 g/ 1000 ml. Mancozeb and cyromazine were applied to control *Alternalia solani* and *Bemisia* spp., respectively, when necessary. No chemicals were applied 2 weeks prior to the plants being used in the experiments. New plants were sown weekly to ensure a sufficient supply of test plants at different phenological stages for use in the experiments.

Solvents

Hexane (*n*-hexane) (85%, HPLC/spectro HS-2722) used in the extraction was purchased from Tedia Company Inc. (Fairfield, OH, USA. Diethyl ether (Baker DRY™) was purchased from Baker Analyzed ®, J.T. Baker, Inc. (Philipsburg, NJ, USA).

Extraction of cuticular leafs

S. viarum plants, 55 days after being transplanted, were cut at 0.1-0.15 m above the ground. The leaves were separately dipped four times in a two 2-l beakers containing 600 ml of hexane. The duration of dipping was 5 s each. The solution was filtered through folded filter paper containing sodium sulfate (Na_2SO_4) and then concentrated by rotary evaporation to 5 ml.

Sep-Pak extraction

Sep-Pak silica cartridges were provided by the Institute of Zoology, Academia Sinica, Taipei, Taiwan; extracts were eluted with diethyl ether in hexane in five different proportions as reported in Table 1. The extraction procedure is described in Fig. 1.

I-tube bioassay set-up

The behavioral response of *H. armigera* adults toward *S. viarum* leaf extract was observed in an I-tube olfactometer. The I-tube is a clear acrylic cylinder with dimensions of the three portions of 1.0 × 0.5 × 1.0 m with a diameter of 0.3 m each. The solvent-concentrated extracts and the solvent both containing a volume of 0.5 ml respectively, were coated onto 90-mm filter paper (Toyo Roshi Kaisha N°73171175, Tokyo, Japan). After 5 min to evaporate the solvent, the filter paper containing the solvent extract was hung on a nylon net to cover one side of the I-tube while the filter paper containing the solvent control covered the opposite side. Both nylon nets were attached with a rubber band. In our setup, airflow (0.5 m/s), regulated by a controller, was pumped up into the two ends of the tube. Each replicate was bioassayed separately, employing a clean I-tube. The bioassays were conducted at a room temperature of 26 ± 2°C with a RH of 70 ± 2%. During the bioassay 2-day-old mated adults were individually released into the middle portion of the I-tube. The tube was covered with black cloth to avoid light interference. We recorded the number of eggs laid on the net and on the cylinder at a distance of 0.2 m from the bottom of the I-tube after 2 days. After each test, the apparatus was cleaned with detergent, acetone, and distilled water. Each bioassay was replicated four times.

Scanning electron microscopy (SEM)

H. armigera antennae were fixed for 2h at room temperature in 2.5% glutaraldehyde. After fixation they were rinsed in 0.1 M cacodylate buffer for 10 min. They were post-fixed in 1% osmium tetroxide (OsO_4) and left overnight. They

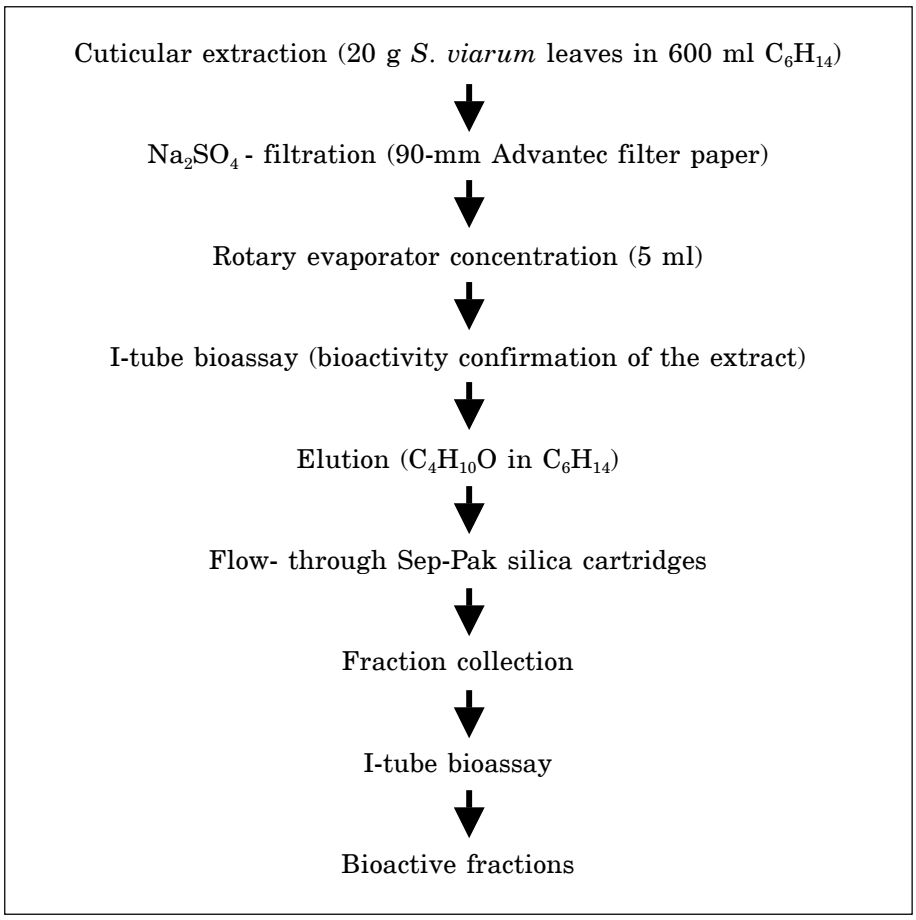

Fig. 1. Flow diagram of the Sep-Pak extraction.

were then rinsed in 0.1 M cacodylate buffer for 10 min. Specimens were dehydrated in 50, 70, 80, 90, 95 and 100% ethanol for 20 min and left overnight. The next day, the specimens were dehydrated again in two series of 100% ethanol for 20 min each, and finally dehydrated in 1:1 (ethanol: iso amyl acetate) and 100% iso amyl acetate for 2 h each. The specimens were dried at the critical point of CO_2 (in a critical-point dryer: Hitachi HCP-Z), mounted on aluminum stubs with double sticky tape, and coated with gold-palladium for 3 min (Hitachi E-1010 ion sputter). Specimens were viewed using a Hitachi S-3000N scanning electron microscope (Hitachi High Technologies, Ontario, Canada) at 25 kV.

Statistical analysis

Data on the ovipositional preferences of the female *H. armigera* were subjected to unpaired *t*-test analysis using Graphpad analytical software. Data were square root (SQRT)-transformed when necessary before analysis.

Results

Results on the bioassay of the crude cuticular leaf extract, from the ovipositional responses (described as the mean number of eggs laid), showed that *H.*

Table 1. Sep-Pak fractions and dilution compositions

Fractions	Percent ether in hexane	Dilution compositions
F_1	20	0.6 ml ether + 2.4 ml hexane + 1 ml CE [1)]
F_2	40	1.2 ml ether + 1.8 ml hexane + 1 ml CE
F_3	60	1.8 ml ether + 1.2 ml hexane + 1 ml CE
F_4	80	2.4 ml ether + 0.6 ml hexane + 1 ml CE
F_5	100 (ether only)	3 ml ether + 1 ml CE

[1)] CE, concentrated cuticular leaf extract.

Table 2. Ovipositional responses (on the net) (no. of eggs laid) of female *Helicoverpa armigera* to different fractions of cuticular leaf extract from *Solanum viarum*

Fractions		No. of eggs laid (Mean ± SD)	df	*p*-Values [1)]
F_1	extract	4.20 ± 5.35	3	0.8069 *ns*
	control	3.03 ± 2.05		
F_2	extract	63.00 ± 13.71	3	0.0066 **
	control	11.50 ± 3.42		
F_3	extract	72.50 ± 21.39	3	0.0056 **
	control	35.25 ± 26.79		
F_4	extract	110.25 ± 82.54	3	0.9429 *ns*
	control	101.00 ± 173.30		
F_5	extract	23.75 ± 23.07	3	0.2923 *ns*
	control	34.75 ± 37.57		

[1)] Graphpad analysis; ** $p < 0.01$; *ns*, $p > 0.05$.

armigera significantly preferred ($t = 3.65$, $p < 0.05$, $df = 3$) to lay eggs on the filter bearing the extract stimulus (698.36 ± 17.25 eggs) rather than on the solvent control (199.86 ± 14.33 eggs). That difference in oviposition indicated the presence of chemical cues which stimulated the female's oviposition. When we evaluated the bioassay responses of the 5 Sep-Pak fractioned crude cuticular leaf extract on the net-egg-laying preference (Table 2); we found that *H. armigera* females overwhelmingly preferred to lay eggs on fractions F_2 ($p = 0.0066$, $df = 3$) and F_3 ($p = 0.0056$, $df = 3$), which respectively contained elutions of 40 and 60% diethyl ether in hexane over the other fractions in which there dilution was < 40 or > 60%. The mean ovipositional responses of these fractions on the net were 63.00 ± 13.71 and 11.50 ± 3.42 eggs, respectively. This trend was found to be similar on the cylinder's ovipositional response (Table 3), where the female's egg-laying preference was also significantly observed on fractions F_2 (11.00 ± 3.16 eggs) ($p = 0.003$, $df = 3$) and F_3 (16.75 ± 4.35 eggs) ($p = 0.0249$, $df = 3$). The positive ovipositional attractiveness of the volatiles present from the *S. viarum* extract raises the possibility of finding insect olfactory sensilla linked to the detection of volatile cues.

The results of scanning electron microscopy of the antennae are presented in Fig. 2. The examination was focused on the external morphology and distribution of sensilla. The number of segments was slightly greater on the flagellum of the female (81 ± 0.32) than on the male (79.6 ± 0.65) ($n = 10$). The flagellar segments were reduced in length and diameter

Table 3. Ovipositional responses (on the cylinder) (no. of eggs laid) of female *Helicoverpa armigera* to different fractions of cuticular leaf extract from *Solanum viarum*

Fractions		No. of eggs laid (Mean ± SD)	df	*p*-Values [1]
F_1	extract	1.52 ± 1.95	3	0.6028 *ns*
	control	3.11 ± 3.68		
F_2	extract	11.00 ± 3.16	3	0.0043 **
	control	7.25 ± 2.75		
F_3	extract	16.75 ± 4.35	3	0.0249 *
	control	10.25 ± 2.63		
F_4	extract	42.75 ± 16.01	3	0.1429 *ns*
	control	45.50 ± 21.46		
F_5	extract	7.00 ± 7.02	3	0.8125 *ns*
	control	6.25 ± 5.38		

[1] Graphpad analysis; ** $p < 0.01$; * $p < 0.05$; *ns*, $p > 0.05$.

from the base to the apex of the antenna and had the same general organization and pattern of sensory structures. Different types of sensilla have been described as being olfactory receptor hair bearing plant volatiles and/or sex-pheromone responsiveness in adults *Helicoverpa* (Zhang *et al*., 2001). Chemoreceptive trichoid sensilla are the most-numerous types; sensilla coeloconica was also found in the antennae.

Discussion

The preference of female *H. armigera* for *S. viarum* leaf extract indicates that there are certain oviposition-stimulating semiochemicals present in *S. viarum* leaves that attracted and triggered the ovipositional response of the female *H. armigera*. It is not clear whether or not a volatile compound from the leaf surface of *S. viarum* is acting as a contact stimulus for oviposition or as an olfactory orientation for host-plant selection prior to landing and surface evaluation by the tarsal and ovipositor of the female. The I-tube behavioral responses showed that the semiochemicals responsible for attracting and/or stimulating *H. armigera* females could be located on the leaf surface or the epidermis of a leaf of *S. viarum* as the fast cuticular method extraction might not have allowed the solvent to enter the leaf tissues. This is in agreement with a similar finding reported by Coates and Dennison (1998) where *H. zea* females were stimulated by phytochemicals extracted from the leaf of a wild tomato plant using hexane as a solvent. The egg-laying preference of *H. armigera* on the F_2 and F_3 fractions showed that those chemicals involved in *H. armigera* surface recognition and oviposition preference could be dissolved in a medium polarity of a mixture of solvents. This shows that the stimulatory effect may be influenced by the polarity of the solvent used; this was also confirmed by Degen *et al*. (1999) on carrot fly oviposition stimulant extracted from host plant leaves. Our results are also in agreement with those described by Jallow *et al*. (1999) suggesting that *H. armigera* is stimulated to oviposit by several different classes of compounds and/or solvents. This finding is an important factor to consider in the choice of a solvent aimed at extracting *S. viarum* semiochemicals to mediate the oviposition of *H. armigera*.

According to Yamamoto *et al*. (1969),

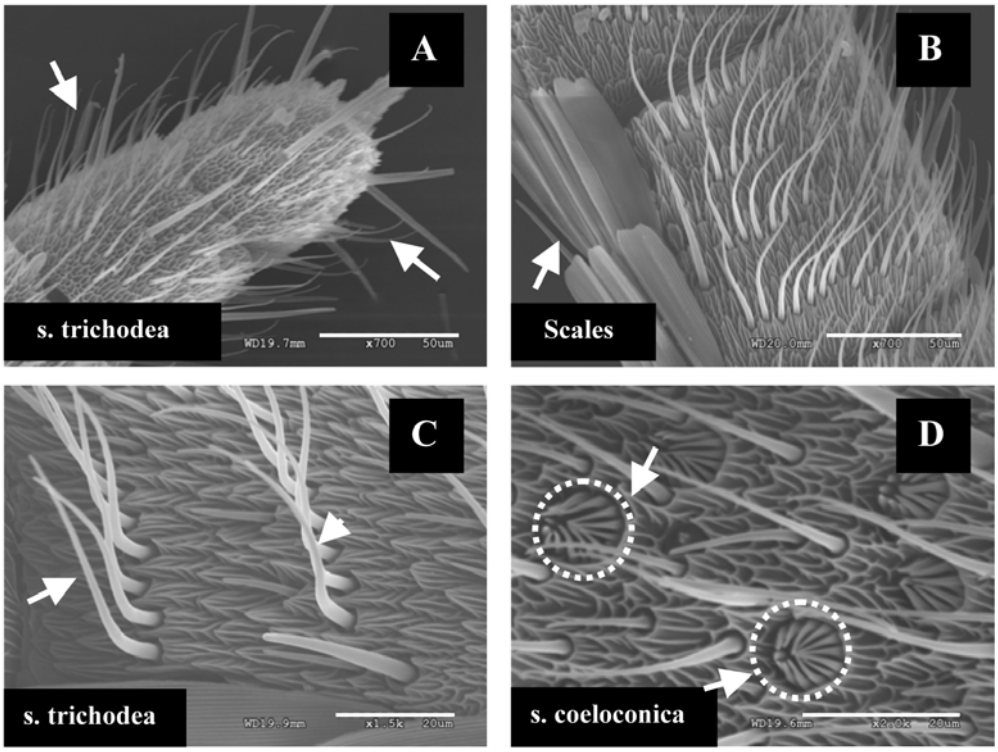

Fig. 2. Different types of sensilla on the female antennae of *H. armigera* moth identified by scanning electron microscope. A, view of sensilla trichodea (white arrows) in the two last segments of the distal part (scale bar = 50 μm); B, scales on a ventral part of a segment (scale bar = 50 μm); C, parallel rows of sensilla trichodea (white arrows) identified on the ventral side of the antenna (scale bar = 20 μm), D, sensilla coeloconica located on the ventral surface of the antenna (scale bar = 20 μm).

in the case of *Manduca sexta,* the arrival of this insect at a host plant requires two levels of attractants: those that stimulate the moth to fly to the host plant and those that stimulate the moth to oviposit. Similarly, Dethier *et al*. (1960) and Isoe *et al*. (1995) also reported that the oviposition attractant refers to the volatile compound acting on long-range behavior, while the oviposition stimulant mediates the actual act of oviposition. The long-range flying behavior of the moth for locating oviposition sites could be led by its olfactory senses present in the antennae which help in detecting a suitable substratum. This attraction effect could be guided by the insect sensilla. The ability of an insect to detect those compounds may depend on the fact that olfactory sensilla bear a number of different types of olfactory receptors present on the insect antennae that respond to those compounds. Raguso *et al*. (1996) reported that female antennae may bear larger populations of olfactory receptor cells (ORCs) that are responsive to plant volatiles. In the specific case of Lepidoptera, Zhang *et al*. (2001) described that olfactory sensilla either belong to the single-walled category (sensilla trichodea and sensilla basiconica) or to the double-walled sensilla coeloconica. In our study, the sensilla trichodea (Zhang *et al*., 2001) and sensilla coeloconica (Pophof,

1997) which might bear receptor neurons for detecting plant volatiles through the antennae of *H. armigera* were identified (Fig. 2). In addition to the olfactory attractiveness, the surface texture (trichome composition, density, and exudates) of the leaves appears to be an important factor affecting oviposition choice of an insect female. In the case of *S. viarum*, we did not investigate any morphological and anatomical characterristics of its trichomes; however, Georgievska (2001) who described different types of trichomes in *S. viarum* leaves (type-1 gland tipped finger trichomes, type-IV multicellular Trichomes, and type-VI stellate trichomes), reported that volatiles from host plant glandular trichomes served as an attractant for the nocturnal gravid female for oviposition. It was specifically reported by Yoshida *et al.* (1997) that malic acid in chickpea trichome exudate stimulates *H. armigera* oviposition during the vegetative and flowering stages, when its concentration was 0.1-0.7 μmol/cm^2.

This study demonstrated the presence of oviposition-stimulating chemicals in *S. viarum* leaf extracts. The separation of those chemicals and their elucidation by gas chromatography mass spectrometry alone or linked to an electroantennographic detector could lead to a better understanding of the female oviposition behavior towards *S. viarum* semiochemicals. Complete identification and characterization of those chemicals could lead to a formulation for use in ovitraps which can be incorporated into an integrated pest management system to manage *H. armigera* populations in the field.

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Solanum viarum 葉面表皮萃取物及其分餾物對番茄夜蛾 *Helicoverpa armigera* (Hübner) 產卵之影響

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摘　要

本實驗探討熱帶刺茄 *Solanum viarum* (Dunal)，葉面表皮萃取物對於分布全世界的重要植物害蟲番茄夜蛾 *Helicoverpa armigera* (Hübner)產卵的影響。在雙重選擇實驗分析下，利用常相 silica Sep-Pak cartridges 分析顯示，*S. viarum* 葉片表皮的萃取物對雌番茄夜蛾產卵具顯著誘引效果($p < 0.05$)。5 個分級(F1, F2, F3, F4 及 F5)乃以正己烷洗提稀釋不同濃度乙醚，並用以刺激雌蟲產卵，來比較產卵平均數的效果。只有 F4 (40% ether)及 F3 (60% ether)對刺激產卵有相當大的影響。掃描式電子顯微鏡指出在番茄夜蛾觸角上的觸毛有感覺毛(sensilla trichodea)及腔內感覺器(sensilla coeloconica)的存在，其可能具有接收神經可偵測植物訊息化學物(plant semiochemicals)。

關鍵詞：*Helicoverpa armigera*、*Solanum viarum*、產卵、感覺毛、植物訊息化學物