FEEDING ON NON-HOST PLANTS BY PARTIALLY
MAXILLECTOMIZED TOBACCO HORNWORMS
(MANDUCA SEXTA: Lepidoptera: Sphingidae)

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ABSTRACT

Tobacco hornworm larvae reared on diet or jimsonweed and with one or both pairs of maxillary sensillae styloconicae removed were given feeding tests with four non-host plants (collard, dandelion, cowpea and mullein). Increased feeding was observed for all larvae lacking medial, lateral, or both pairs of sensillae; these increases were greater for larvae that had been reared on jimsonweed. For larvae with both pairs of sensillae removed, all test plants were highly acceptable. For larvae with only the lateral sensillae removed, the test plants were only slightly more acceptable. Diet-reared larvae with the median sensillae removed found test plants slightly more acceptable than did control larvae. Jimsonweed larvae lacking only the median sensillae found dandelion, normally a rejected plant, almost completely acceptable. Possible physiological reasons for these behavior changes are discussed.

RESUMEN

Se hicieron pruebas alimenticias con cuatro plantas no hospederas a las larvas de Manduca sexta criadas con dieta artificial o con hierba hedionda Datura stramonium y con uno o dos pares de las sensillae styloconicas estirpadas de las maxilas. Las plantas experimentales fueron berza comun, Brassica oleracea, amargón, Taraxacum officinale, caupi, Vigna sinensis y gordolobo, Verbascum thapsus. Se observó alimentación mas extensiva para las larvas a las cuales les faltaron ambos o uno u otro par (medio o lateral) de sensillae. El aumento de alimentación fué mas grande en las larvas que habian comido hierba hedionda. Todas las plantas fueron aceptadas por las larvas sin ambos pares de sensillae. Las larvas sin las sensillae laterales, aceptaron un poco mas dichas plantas. Las plantas experimentales fueron un poco mas aceptables a las larvas crecidas con dieta y sin las sensillae medias, pero las larvas criadas en hierba hedionda y sin las sensillae comieron casi completamente el amargón (el cual normalmente es una planta no aceptable). Se discute la posibilidad de una base quimiosensorial que explique este comportamiento.
Studies on feeding behavior of Lepidoptera have emphasized electrophysiology and much progress has been made in determining the electrical responses of specific receptor cells to specific chemicals. Because of its large size, economic importance and ease of rearing, the tobacco hornworm, *Manduca sexta* (L.), has become a favorite experimental animal for feeding studies. Much of the research has centered on the median and lateral sensilla styloconica of the maxillae (Waldbauer & Fraenkel 1961, Waldbauer 1962, Schoonhoven & Dethier 1966, Schoonhoven 1969, Stadler & Hanson 1976) which function as both gustatory and olfactory receptors.

While electrophysiological studies tell us much about the responses of individual receptor cells, they still leave open the question of how these responses are integrated by the insects into behavior patterns. One possible approach is to surgically alter the receptors and observe how feeding behavior changes. Several experiments have been done in which the maxillae of *M. sexta* were removed or destroyed (Waldbauer & Fraenkel 1961, Waldbauer 1962). These showed that without their maxillae, *M. sexta*, normally oligophagous on the Solanaceae, became effectively polyphagous and fed on a wide range of plants that they would not accept under normal circumstances (however; de Boer et al. 1977 found that even *M. sexta* lacking both maxillae and antennae still showed some feeding selectivity because of receptors in the preoral cavity). In this paper we report the results of experiments in which *M. sexta* fed on two different diets had their sensillae styloconicae removed in various combinations and then were tested for feeding on four non-host plants.

**MATERIALS AND METHODS**

*M. sexta* larvae were obtained from a culture at North Carolina State University and two groups, one reared on artificial diet and the other reared on jimsonweed as described previously (Flowers & Yamamoto 1982), were used in these experiments. On entering the fourth instar, sensillae styloconica in three combinations were removed by confining the larvae to a block of paraffin in a dish which was then filled with water. This caused the larva to close its spiracles, thus building up CO₂ in the tracheal system which anesthetized the animal. (Using CO₂ gas directly proved unsatisfactory and caused a high mortality rate.) Sensillae were pinched off with sharpened jeweler's forceps under 200X magnification. Four treatments were used: all four sensilla styloconica removed, the lateral pair removed, the median pair removed, and a control group which were anesthetized but without an operation. All larvae were returned to their respective diets (artificial or jimsonweed) and allowed to feed until fifth instar.

After the moult to the fifth instar, acceptance of four non-host plants to the treated larvae was determined by placing individual larvae in a petri dish with an 8 mm diameter leaf disk of each of four test plants. Feeding after 24 hours by each larva was recorded to the nearest quarter of a disk for each test plant (further details in Flowers and Yamamoto 1982). Plants tested were collard (*Brassica oleracea* L., Cruciferae), dandelion (*Taraxacum officinale* L., Asteraceae), mullein (*Verbascum thapsus* L., Scrophulariaceae), and cowpea (*Vigna sinensis* L., Fabaceae). De Boer & Hanson (1984) have proposed a hierarchy of acceptability for plants: under their system, cowpea and collard would be considered “acceptable non-host plants” since *M. sexta* can be reared on them in the laboratory, while dandelion and mullein would fall into the category of unacceptable non-host plants. As in our previous paper, feeding indices (Flowers & Yamamoto 1982) were obtained from scoring fractions of the test plants consumed by larvae and multiplying by 100. Data were analyzed as a split-plot design with the larvae as a whole plot and the 4 test plants as sub-plots. Feeding indices and their 95% confidence limits are shown in Fig. 1-2.
Fig. 1. Responses of diet-reared larvae with the sensillae styloconica removed in different combinations: L-M-, both pairs of sensillae removed; L-, lateral pair removed; M-, medial pair removed. Test plants: P, cowpea; D, dandelion; C, collard; M, mullein. Vertical bars give 95% confidence limits.

RESULTS AND DISCUSSION

Feeding by intact control larvae on the four test plants roughly paralleled the results obtained earlier (Flowers & Yamamoto 1982): collard was highly acceptable, followed by mullein, with cowpea and dandelion showing low to very low acceptability. As in our previous study, cowpea and dandelion were slightly more acceptable to jimsonweed-reared larvae than to diet-reared larvae. Removal of both lateral and medial sensillae styloconica (L-M-; Fig. 1,2) resulted in dramatic increases in feeding on all test plants except collard (which was already almost completely acceptable), although cowpea remained slightly less acceptable than the other three in most cases. Removal of the lateral sensillae styloconica (L-; Fig. 1,2) increased feeding on cowpea, dandelion and mullein for both diet- and jimsonweed-reared larvae, with the jimsonweed-reared larvae showing slightly greater increases in consumption than the diet-reared larvae. Removal of the median sensillae (M-) resulted in small increases in feeding on cowpea and mullein, and a large increase in feeding on dandelion for diet-reared larvae (Fig. 1); while for jimsonweed-reared larvae (Fig. 2), there was a proportionally similar increase in feeding on dandelion, while increases in feeding on cowpea and mullein were somewhat greater than for diet-reared larvae.

These results suggest that both the median and lateral receptors respond to deterrent chemicals since removal of either one caused an increase in feeding. Schoonhoven and Dethier (1966) also postulate the presence of a stimulant receptor in the median sensilla; our experiments neither confirm nor disprove such a function for the median sensilla. The greater increase in acceptance of dandelion by L- and L-M- diet-reared larvae as compared to those reared on jimsonweed suggests that jimsonweed was desensitizing the deterrent receptors and that removal of these receptors caused a smaller change than did removal of the same receptors in diet-reared larvae.
Fig. 2. Responses of jimsonweed-reared larvae with the sensilla styloconica removed in different combinations: abbreviations as in Fig. 1.

Induction of feeding preference has been well studied in *M. sexta* and has been demonstrated in a broad range of other Lepidoptera and in other orders of insects as well (Szentesi & Jermy 1990). Our results with cowpea-reared larvae (Flowers & Yamamoto 1982, Yamamoto 1974) give some support to the hypothesis that oligophagy is the result of food imprinting. On the other hand, de Boer and Hanson (1984) found that *M. sexta* larvae reared on acceptable non-host plants still showed preference for normal hosts, although often at a reduced level. They concluded that oligophagy is inherited. Some of the apparent conflict is due to different tests: in this study and our 1982 study we did not directly compare hosts and non-hosts. De Boer & Hanson (1984) also explained differences between their data and Yamamoto's (1974) by differences in procedures and possible genetic differences in the *M. sexta* strains. To this could also be added possible differences in strains of plants used in the two experiments.

While electrophysiological studies are providing many new insights into receptor physiology, feeding studies are still needed to help understand how the insect processes the spike activities of the various receptors. In this study, selective ablation clarified how the hornworms responded to dandelion, the least acceptable plant used in our preference tests. Frazier & Hanson (1986) give three possible explanations for why a plant might be rejected by a phytophagous insect: stimulation of a “deterrent” cell; inhibition of an “acceptance” cell; or some “complex code” involving many cells. Additional feeding studies using pure chemicals (as was done using sucrose by De Boer et al. (1977) to test preoral cavity chemoreceptors) on larvae with single pairs of sensilla removed could provide additional information on how spike patterns observed in previous studies are interpreted in the central nervous system of the insect.

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NEW RECORDS AND SYNONYMY IN PATAGONIAN
ATRICHOPOGON (DIPTERA: CERATOPOGONIDAE)

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ABSTRACT

Atrichopogon obtubulus Ingram & Macfie from southern Argentina and Chile is
redescribed and figured. Two similar species from the same area described in the same
paper are junior synonyms of A. obtubulus: A. chilensis Ingram & Macfie and A.
assimilis Ingram & Macfie (NEW SYNONYMY). Atrichopogon obtubulus is the first
South American species to be assigned to the subgenus Meloeheleu Wirth, a group
known as ectoparasites of Meloidae and related beetles in the northern hemisphere. The
habits of A. obtubulus are unknown.