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FLIGHT BEHAVIOR OF *MANDUCA* MOTHS AS A FACTOR IN HOSTPLANT SITE SELECTION

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ABSTRACT

Field surveys in late September showed that larvae of *Manduca sexta* (L.) *(Lepidoptera: Sphingidae)* were found on the upper leaves and floral parts of mature tobacco plants whereas larvae of *M. quinquemaculata* were consistently found on young shoots of tobacco plants cut at ground level. Behavioral analyses of both species of moths showed that they preferred young, growing leaves of tobacco over maturer leaves for oviposition. However, the host-seeking flight pattern of *M. sexta* was high and *M. quinquemaculata* was low in relation to the floor of an experimental cage. The flight patterns may account for the difference in site distribution of larvae.

INTRODUCTION

A common feature among phytophagous insects is their restricted feeding habits. They do not share all plants but rather apportion themselves on different species or groups of plants. Some insects are rigidly confined to certain plants and do not or cannot feed on others. These are the hostplant-specific or oligophagous insects. Fraenkel (1953, 1956) has persuasively argued that the oligophagous insects are restricted feeders because they respond to specific plant chemicals, the so-called secondary plant substances. These are limited in distribution and act as token or feeding stimulants. Chemical, behavioral, morphological, and electrophysiological evidence to date have clearly substantiated this viewpoint (Schoonhoven 1967, 1969, Schoonhoven and Dethier 1966, Dethier 1970). Within the range of plants possessing a particular or related token stimulant for an insect, other chemicals in some of the plants act as deterrents, repellents, or toxins and thus further narrow the number of plants suitable as food (Fraenkel 1969). Examination of the foodplants of the Colorado potato beetle, *Leptinotarsa decemlineata* Say (Hsiao and Fraenkel 1968a, 1968b) and the tobacco hornworm, *Manduca sexta* (L.) (Yamamoto and Fraenkel 1960a) shows the variety of interactions which may occur. Some plants are readily consumed, some are slightly consumed, some are suitable for growth, while some are toxic or inhibit development. Although investigations into the requirements for feeding show that simple compounds such as sugars, salts, and certain amino acids act as feeding stimulants, they are not as decisive as the token stimulants or deterrents in determining choice of plants for feeding or for oviposition. Evolution of phylogenetic groups of insects, especially the butterflies, has been linked with the evolution and distribution of the complex chemicals which regulate their behavior (Ehrlich and Raven, 1965), and thus, when viewed in the perspective of today, the hypothesis that complex plant chemicals regulate the selection of plants by insects has stimulated research at various levels of biological organization.

In a geographical area, the suitable hostplants of an insect usually outnumber the plants actually chosen. Preferences for particular species of plants are manifested. The factors which govern preferences are not identical to the token stimulants which identify hostplants from non-hostplants for insects. For example, the tobacco hornworm moth, *M. sexta*, preferentially oviposits on tobacco (*Nicotiana tabacum* L.) and tomato (*Lycopersicum esculentum* Mill.) although many other solanaceous plants growing in the same area and containing the requisite stimuli for feeding by the larvae and oviposition by the adults are ignored (Yamamoto and Fraenkel 1960a, 1960b). Since plant selection is a function of the moths in *M. sexta*, preference factors may likely be odorous components (attractants) although supplementary contact stimuli cannot be discounted entirely. On the supposition that attractants are involved, the question then arises whether responses of the moths to the attractants are fixed by virtue of their possession of antennal chemoreceptors particularly attuned to them or whether the moths learn to respond to the attractants because of prior association with them. An analysis of the host-seeking behavior of the moths was initiated in order to critically examine the role of attractants in fixed and learned responses (Yamamoto et al, 1969).

There are several components in the flight behavior of gravid *M. sexta* moths. These can be listed as dispersal, host-seeking, approach, landing, and oviposition. The host-seeking flight in a large cage is non-random and somewhat undulating, the moths following a circular path varying between 60 to 90 cm above the floor of the cage. Some moths descend and fly close to the floor in a circular path. From this flight path, they approach objects and plants placed at various heights in the cage. Visual stimulation rather than odors initiate approach to objects. When large, potted tobacco plants are placed in the cage, oviposition occurs mainly on the uppermost leaves or even on flower buds if they are present. The upper leaves might have been selected for oviposition either because they were closest to the flight path of the moths or because they contained higher concentrations of attractants. A combination of both factors might also have influenced the moths. Field observations also indicate that most of the eggs and larvae are found on the upper 1/3 of mature, flowering, tobacco plants. There is thus evidence for the propensity of *M. sexta* moths to select young leaves on the upper part of tobacco plants.

When research on the hostplant specificity of *M. sexta* was initiated in Illinois some 15 years ago, larvae were found naturally only on tomato and two species of *Nicotiana* (Yomamoto and Fraenkel 1960a). However, the larvae of another species, the tomato hornworm, *Manduca quinquemaculata* (Haw.), were found not only on tomato but also on a groundcherry, *Physalis* sp., on purple nightshade *Solanum dulcamara* L. on a matrimony vine, *Lycium halimifolium* Mill. The tomato hornworm is a more robust insect than *M. sexta*, the larva possessing characteristic V-shaped, lateral stripes on the body and the moth possessing 5 orange spots on the abdomen. In recent years, *M. quinquemaculata* has increased in numbers near Oxford, North Carolina, and some research was initiated on this species, particularly in respect to its culture in the laboratory (Soto and Yamamoto, 1972). Preliminary behavioral analysis of the moths in cages showed that they also preferentially oviposited on young, growing leaves of tobacco. But in contrast to *M. sexta*, the host-seeking flight path of *M. quinquemaculata* was consistently low and close to the floor of the cage.

In late September at Oxford, North Carolina, a tobacco field in which some of the plants were cut to ground level was surveyed for hornworm infestations. Young

shoots abounded on the stems of the cut tobacco, some growing laterally and some growing upward. Large numbers of *M. quinquemaculata* larvae were found on these young shoots. When terminal young leaves and flower buds of mature, uncut tobacco were examined, only small numbers of *M. sexta* larvae were found on them. Although direct observations of the moths in the field were not made, the distribution of the larvae would indicate that *M. quinquemaculata* moths selectively oviposited on young leaves at or near ground level.

Comparative analyses of the chemical factors influencing selective oviposition in both species of *Manduca* moths are required if firm conclusions are to be drawn concerning their preferences for tobacco. It would seem, on the other hand, that the differences in the elevation of their host-seeking flight paths can account for the differences in selection of oviposition sites on the same plant such as tobacco and also may account for the finding of larvae of *M. quinquemaculata* on low-lying solanaceous plants such as *Physalis* and *S. dulcamara*

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