HERBIVOROUS INSECTS

Host-Seeking Behavior and Mechanisms

Edited by

SAMI AHMAD

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Preface

With herbivorous insects the sequence of selecting a host is catenary, beginning with recognition of the host plants from a distance, followed by arrival of the insect at the host and subsequent feed and/or oviposition. During this process, several environmental cues interact at the different behavioral levels that eventually result in host acceptance. The material presented in this book addresses itself to the initial aspects of this chain of events, specifically to mechanisms of searching behavior leading ultimately to host location. Our intention is to synthesize current data and ideas on host location research for behaviorists, ecologists, entomologists, evolutionary biologists, and physiologists.

The topics in this volume are divided into four sections: neurophysiology; the diversity of behavioral induction cues; searching mechanisms as affected by insects' breadth of diet; and, finally, an evolutionary analysis of the behavioral and physiological adaptations in insect/host plant relations. Clearly, this volume is not an end point in the development of scientific thought on host location by herbivorous insects, but we hope that it will provide direction toward developing a unifying theme and improving our ability to unravel the complexities of insect/plant interactions.

I am particularly grateful to the staff of Academic Press for their invaluable help with this publication, to Dr. V. G. Dethier (Zoology Department, University of Massachusetts, Amherst) for writing the Introduction, and to the authors for the thoroughness of their contributions. In many cases the reviews are combined with the results of many years of research which are presented for the first time. The authors also made many useful suggestions during the early stages of organizing this volume. They were very cooperative and understanding, and their help made editing this book a pleasant task.

I would also like to thank Mrs. Evelyn Weinmann and Miss C. von Gruchalla for skillfully typing a number of sections of this volume. Thanks also are due to my colleagues Dr. J. H. Lashomb and Dr. M. L. May for many valuable discussions and to Dr. H. T. Streu for his enthusiastic support of my efforts. The editorial work was supported in part by a grant (URF-G-82-370-NB-11) from the Research Council of Rutgers University. This publication (No. C-08130-01-82) was also partially supported by state funds and Hatch Act funds (NJAES-08130) through the New Jersey Agricultural Experiment Station. The authors also were supported by several grants that are acknowledged in their chapters.

Sami Ahmad

Introduction

Every herbivorous insect is associated with a specific range of host plants. Regardless of the breadth of this range, whether it consists of a single species of plant or encompasses many, the maintenance of stable host/insect relations and the evolution of new ones depends first on the ability of insects to find the plants with which their species is historically associated. These plants must be discovered and identified against a background of many irrelevant species within diverse and often varying quantitative and spatial vegetational contexts.

Having located the host plant in space, the herbivorous insect verifies its identity before ovipositing or feeding. Host selection thus becomes a matter of search and assessment. Each of these processes is effected by an orderly sequence of behavior patterns steered by successive stimuli relevant to the situation. This global view of host-plant selection has required no fundamental revision since it was expounded thirty years ago.

During the intervening period, the subject of insect/plant relations has stimulated the organization of numerous meetings to discuss fundamental issues. The impetus to encourage discussion began with a symposium on insect/plant relations organized by Jan de Wilde in conjunction with the IXth International Congress of Entomology convened in Amsterdam in 1951. This symposium proved to be the genesis of a continuing series of quadrennial Insect Plant Symposia held in Wageningen, The Netherlands in 1957, 1969, and 1982, in Budapest in 1974, and in Slough, England, in 1978. In 1980 a Gordon Conference on Chemical Aspects of Plant–Herbivore Interactions was held in Santa Barbara, California. In addition to the published proceedings of the quadrennial international symposia the following works have appeared: Insect/Plant Relationships, a Symposium of the Royal Entomological Society of London, 1973; Comportement des Insectes et Milieu Trophique, Tours, France, 1976; Biochemical Aspects of Plant and Animal Coevolution (J. B. Harborne, ed.), 1978; and Herbivores (J. A. Rosenthal and D. H. Janzen, eds.), 1979.

A perusal of these volumes will reveal that although the matter of locating host plants in the environment was never neglected, it was subordinated, in terms of research effort expended, to other aspects of host-plant selection. That this relative neglect occurred is hardly surprising considering the enormous difficulties attendant upon observing the behavior of individual flying insects in their natural environment, a difficulty that is amply illustrated in this volume and one that still challenges progress. It is salutary, therefore, that an attempt has been made to focus on the search phase of host selection. This volume is a sampling of current research in that area. While the number of contributions is necessarily restricted, their combined bibliographies provide a comprehensive view of current knowledge.

Of the eight contributions, six deal directly with host-seeking behavior and allied patterns of behavior. The first paper serves as an introduction to the chemical sensory system as it relates to host selection in general. The concluding paper examines evolutionary aspects of the process.

The ability of an insect to find and assess a plant obviously depends on an appropriate sensory system conveying the requisite quantity of information about the environment. The sensory systems most intimately involved are the visual and the chemical. Volumes have been written about these two sensory modalities, but knowledge of how they operate in the field with respect to plants and what the natural adequate stimuli are is still rudimentary.

A paucity of information that becomes particularly restrictive is that relating to differences in visual capacities among different species of insects and, more particularly, how different species perceive their botanical environment. Data describing spectral sensitivity, form perception, and edge and contrast perception, to mention but a few characteristics of visual systems, are scanty. Even less complete are data describing hue, saturation, reflectance, transparency, and other optical properties of leaves.

As Feeny, Rosenberry, and Carter note in their discussion of oviposition by swallowtail butterflies, the weight to be assigned to vision in orientation and recognition varies even among closely related insects. Furthermore, different phases of the coordinated search procedure may depend primarily on vision or primarily on olfaction. Several of the contributors to this volume refer to the lacunae in this area of research; it is regrettable that this subject has not been explored more fully at this time.

The difficulty of relating intrinsic sensory capacities to behavior in the field also appertains to olfaction. Insofar as this sense relates to oviposition, evidence from Feeny's studies of swallowtail butterflies indicates that specific chemicals acting as "token stimuli" play a dominant role. On the other hand, as May and Ahmad point out, studies of orienting behavior of Colorado potato beetles indicate that a ratio of nonspecific compounds representing a profile of a plant's essence constitute the perceived stimulus.

Interpretation of behavior toward odors is further complicated by uncertainty regarding the characteristics of odor plumes. Recent studies of the internal structure of odor plumes indicate that a flying insect experiences a far more complex stimulus situation than formerly assumed.

Another aspect of response to odors of botanical origin, which is discussed by Lanier, is the contribution made by members of the species that have already found the host. With bark beetles, in particular, pheromones are active constituents of the total stimulus complex. The searching beetle presumably is required to integrate information from pheromone receptors, receptors responsive to volatile constituents of plants, and visual receptors.

Some perceptions of the intrinsic capacities of the chemical senses of herbivorous insects, the nature of the stimuli, and the potential information carrying capacities of the system are described by Hanson. As Lance has pointed out, however, we still are ignorant of the volume and kind of information about a total plant that are actually gleaned by the chemical senses. For example, not all toxic substances are detected by gustation or olfaction; nor are stimuli mediating deterrence necessarily indicative of a nutritionally unsuitable plant. Furthermore, chemical senses are not able invariably to provide complete assessments of nutritional suitability. Postingestive physiological mechanisms that influence locomotion, and hence dispersal, may operate effectively in plant selection where sensory systems fail.

While the intrinsic capacities of visual and chemosensory systems set the upper limits of perception, the context in which stimuli are presented in nature sets the actual limits. Regardless of whether host location is achieved by visual or chemical cues or by some combination of both, environmental features are limiting factors. As Stanton describes, the discovery of host plants depends very much on circumstances of host distribution in space, the size of stands, the diversity of species within a stand, the identity of nonhost species in mixed stands, and the edge characteristics of a patch. It depends also, as Stanton, Lanier, May, Ahmad, and Lance have pointed out, on whether the searching insect is a specialist or a generalist, adult or immature. It further depends on a nexus of transient variables in any given individual insect, as Papaj and Rausher have outlined.

In perusing these eight presentations one notes the recurrence of familiar fundamental questions, themes, dilemmas, and frustrating lacunae, some of which emerged repeatedly in earlier literature and remain to obstruct our understanding. Designation of the breadth of host acceptability and suitability is one problem. It is clear, as several contributors have emphasized, that patterns of search behavior differ for specialists and generalists. What constitutes a specialist or a generalist is itself unclear because, as pointed out long ago, the terms monophagy, oligophagy, and polyphagy are arbitrarily selected points along a continuous spectrum. In any case, the specialist's task of locating a single species of plant in a mixed floral community requires different tactics than those that are effective for a generalist capable of accepting more than one alternative species. It is in this context that generalizations may fail and that models designed to delineate efficiencies of particular search tactics must take into account breadth of diet.

Another recurring theme relates to variations introduced into behavioral responses by the environment, by the host plant, and by changes within the insect itself. The host plant can, for example, influence such components of orientation as rate of turning, or the insect can modify its behavior as a consequence of experience. Papaj and Rausher discuss these and other modifying conditions. Among internal factors are age, ovarian cycle, hormonal cycles, level of satiation, and competing events such as tendency to migrate or mate.

The emphasis in this volume is on host-finding behavior and mechanisms. If one did not already realize it before reading these articles, it becomes clear that host-finding behavior must be studied in relation to the total behavior pattern of which it is a part. Then the forbidding complexity and diversity of the host/herbivore relationship reveals itself. Can one hope to extract from the mass of data any valid generalizations or unifying theme? Futuyma in the concluding article is not very optimistic. Considering two alternative possibilities, a mechanistic theme or an evolutionary theme, he believes that there is more hope of discovering the latter. He examines cost–benefit models and optimization models.

Whenever one may seek a unifying theme in herbivore/plant relations, whether it be evolutionary or otherwise, more information about mechanisms is sorely needed. Only then will it be possible to assemble knowledge gained from studying separate aspects of total coordinated behavior patterns. The great service that this volume provides is that of focusing for the first time on the initial phases of host/plant relations, that is, on search and location. It thus provides a stimulus for further work in this challenging area. Furthermore, by examining this aspect of behavior in the context of the total insect/plant relationship, it takes its place among those volumes that are indispensable reference works for graduate students and established scholars and for specialists and generalists alike.

V. G. Dethier

Contents

PART I

Neurophysiological Aspects

1

The Behavioral and Neurophysiological Basis of Food Plant Selection by Lepidopterous Larvae*

FRANK E. HANSON

I. INTRODUCTION

Host-plant selection by insects in their feeding stages is composed of three distinct behavioral phases: (1) attraction to a potential food plant, (2) arrest or cessation of locomotion, and (3) stimulation (or deterrence) of feeding on that plant. Although visual and mechanical stimuli are utilized to some extent in various phases of the overall feeding behavior, the primary agents controlling

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these interactions are the phytochemicals. Thus the critical interface between plant and insect is between the plant chemicals and insect chemoreceptors, the understanding of which will be necessary for an explanation of the basic mechanisms of herbivory.

Accordingly, the ensuing discussion of current knowledge and new directions in the study of behavioral and physiological mechanisms of host selection will follow three approaches: (1) description of the herbivore's feeding behavior, (2) identification of the chemicals in the host plant that elicit feeding behavior, and (3) determination of the physiological responses of insect chemoreceptors to these chemicals.

II. BEHAVIORAL RESPONSES TO POTENTIAL FOOD PLANTS

A. Preference Levels for Host and Nonhost Plants

All plants contacted elicit behavior from phytophagous insects: some are rejected, some accepted. Although host plants are in the latter category, they are not all equally preferred; furthermore, some nonhosts are acceptable as well. This raises the question as to where the boundary should be drawn between host and nonhost. Probably the best answer is the ecological one: host plants are those on which the animal completes normal development in nature. The insect's "physiological host range," however, includes some nonhost plants, because many of these elicit feeding and are nutritionally adequate. It follows that screening by the sensory and central nervous systems must be sufficiently broadly tuned to accept a wider group of plants than just those on which the animal is found in nature. Perhaps a continuum of preferences exists, with rejected nonhosts located beyond some hypothetical threshold of acceptability. This threshold is poorly defined and fluctuates with environmental conditions and prior feeding experience.

The factual basis for the previous discussion has been somewhat sketchy; adding flesh to this skeleton requires behavioral assays that permit quantitative comparisons of the feeding preferences for all plants tested. Early efforts in quantitative measurements of feeding tended to be subjective, with feeding estimates scaled from 0 to 5 or with pluses and minuses. An improvement was introduced by the disk test (Fig. 1), which allows quantitative comparisons of preference for different plant species (using leaf disks) or chemicals (using filter-paper disks) (Stadler and Hanson, 1978). By keeping one plant or a control chemical common, the preferences of many plant species or chemicals can be compared quantitatively.

Evidence that all host plants are not equally preferred has been obtained using

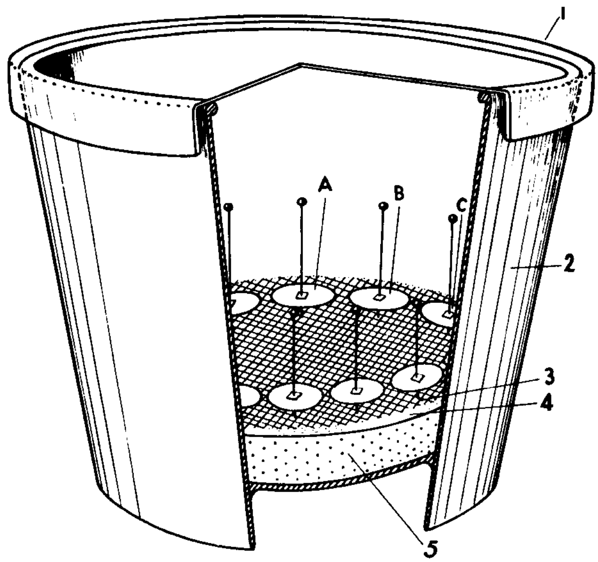

Fig. 1. The disk test. Disks cut with a cork borer from leaves of species A, B, and C are mounted on pins and held by small acetate squares 1 cm above the wax substrate. 1, Cover; 2, plastic or paper cup; 3, wire screen; 4, moist filter paper; 5, paraffin wax layer. The caterpillar is placed in the center; feeding is scored as area of disk eaten. (From Jermy *et al.*, 1968; used with permission.)

this method. For example, larvae of the tobacco hornworm (*Manduca sexta*), reared on tomato leaves, were given a choice between leaf disks of tomato and another plant species. The results were normalized to the consumption of tomato. The relative feeding preferences for nine different host solanaceous plants are shown in Fig. 2. All of these host plants are acceptable, although considerable differences are evident between the most and the least preferred of the solanaceous plants.

The discrimination between host and nonhost can also be seen in Fig. 2. The cruciferous plants rape and radish and the legume cowpea have feeding scores that are comparable or lower than the least preferred of the tested solanaceous plants. Nevertheless, larvae can be reared successfully on these nonhosts in the laboratory, showing that they can support larval development. Less acceptable nonhosts also can be tested and compared quantitatively (Fig. 3).

Preference hierarchies for the tobacco hornworm were previously reported for a wide variety of solanaceous plants by Yamamoto and Fraenkel (1960c). Although the methods used were different, similar conclusions were drawn.

In summary, there is evidence that the tobacco hornworm discriminates among host plants as well as between host and nonhost. As suggested by the theoretical