INSECT AND MITE NUTRITION

SIGNIFICANCE AND IMPLICATIONS IN ECOLOGY AND PEST MANAGEMENT

edited by J. G. RODRIGUEZ

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THIS BOOK RESULTED FROM TOPICS OR PAPERS DISCUSSED AT THE INTERNATIONAL CONFERENCE ON THE **SIGNIFICANCE OF INSECT AND MITE NUTRITION**
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PREFACE

This volume comes as a result of the Conference on Significance of Insect and Mite Nutrition held at the University of Kentucky Carnahan House Conference Center in April 1972. This conference developed after colleagues had been queried and had responded relative to its justification and relevance. Response was enthusiastic and convincing that insect nutritionists would support a conference and many problem areas were suggested for discussion. Our beliefs were confirmed, for example, that advances in the field have been rapid, even dramatic in recent years, that many scientists are working in specialties that impinge on the general area of nutritional physiology via a wide array of pathways and that many specialists are searching for a greater integration of the results of their investigations into other areas or disciplines.

An Organizing Committee was then named and this group developed the structure of the conference. International in scope and the first of its kind, the meeting sought to bring about much needed discourse on problems confronting scientists working in arthropod nutrition. The stated aim was to evaluate the role of insect and mite nutrition in the solution of biological problems and its unique, significant contribution to other biological disciplines and to environmental questions. The areas germane to the conference objective were identified and developed with the overall view to not only delineate and evaluate what has been accomplished but also to suggest where future research should lead. Each member of the Organizing Committee was given the responsibility of developing a particular area and section; this colleague subsequently served as moderator of the section and as section editor.

The papers that comprise this volume were presented at the conference in an informal manner by the discussants. Later the discussants, having had the benefit of reappraising their work, submitted a manuscript for publication to their section editor. As general editor it was my duty to arrange and focus material more effectively. Any editorial errors that may appear in this volume occurred through oversight in my part.

Grateful acknowledgement is made of the cheerful assistance and splendid cooperation rendered by numerous colleagues at the University of Kentucky. To my fellow members of the Organizing Committee, named separately in these pages, who were most cooperative and unstinting of their energies and enthusiastic over bringing the whole endeavor into fruition, I cannot express enough gratitude. Other colleagues gave valuable support and assistance to this undertaking but especially I would like to mention H. L. House and Calvin A. Lang. I would also be remiss if I did not acknowledge the spirited response of all conference participants and especially I would like to thank the discussants who submitted papers. My task in editing was lightened with the generous assistance of my daughters, Carmen and Teresa, and my wife, Lorraine, who gave of their time to provide a photo-ready manuscript. Many thanks are due Mrs. Alice Kidd who typed long hours and accomplished a professional job. Lastly, I would like to acknowledge the sponsoring agencies whose support made the international conference possible. These were:

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October, 1972

J. G. Rodriguez
Lexington

ORGANIZING COMMITTEE

Stanley D. Beck
Marion A. Brooks
R. H. Dadd
Ernest Hodgson
G. P. Waldbauer
B. S. Wostmann
J. G. Rodriguez, Chairman

DEDICATION

The following resolution was approved by the Conference:

"This conference, on the Significance of Insect and Mite Nutrition meeting at the Carnahan House, Lexington, Kentucky, April 25-28, 1972 dedicates the book resulting from the Conference to our colleague, Gottfried Fraenkel, as a token of appreciation of his pioneering contributions to the field."

CONTENTS

NUTRITION, ADAPTATION AND ENVIRONMENT

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The planning and organization of a conference entitled "Significance of Insect and Mite Nutrition" necessarily involves adoption of the premise that the subject does indeed have significance. Thus, we are not gathered here to test the validity of that premise, or to convince each other of its validity. Rather, we have come together in order to exchange information and to assess the current status of our varied research interests in diverse aspects of arthropod nutrition. Out of these three and a half days, we may individually gain some concept of the most significant problems and the most productive avenues that call for greater research emphasis, even though we may not reach some collective consensus. Such a collective consensus is not particularly important in any case. What is important is that there be a spirit of informal communication; that there be open and frank mutual exchange of insights and experimental information. This is the real significance of our conference, and the degree to which this is accomplished will be the measure of our success.

The conference program shows a wide variety of subjects, from metabolic specificities to aspects of pest management, all of which have been forced under one umbrella--the general rubric of nutrition. Obviously, the conference organizers have taken a very broad view of how the term 'nutrition' may be defined. This was done deliberately, of course, in order to bring into focus not only the central subject of specific biochemical nutritional requirements, but also all of the biological implications and peripheral aspects that contribute so much to the real significance of the broad subject of food habits, behavior, and nutritional adaptions that contribute to the impressive biological success of the insects and related arthropods.

Early 20th century workers, in viewing the enormous range of insect food habits, tended to postulate that both sensory and nutritional factors were operative in delimiting feeding specificity. The very great range of food habits was thought to reflect, in part, differences in the food value of the various substrates and corresponding differences in the specific chemical nutrients required by the insects subsisting successfully on those substrates. This hypothesis was reflected, at least to a degree, in Uvarov's 1928 review of insect nutrition and metabolism. Some of the early biologists took a surprisingly modern view of the problem of insect food habit specificity, including especially Brues (1920) and Folsom & Wardle (1934). In the 1920's and 1930's, however, nutrition as a field of biochemical endeavor was

Insect and mite nutrition – North-Holland – Amsterdam, (1972)

in its infancy, and very little work on insect nutritional requirements had been carried out. That insects might differ in some very significant ways from higher animals in respect to their nutritional requirements was shown by Hobson's 1935 demonstration that blowfly larvae required a dietary source of cholesterol.

Concurrently with the isolation and identification of the water-soluble vitamins, our knowledge of insect nutrition was magnificently advanced by the work of Gottfried Fraenkel, beginning in the early 1940's. In a classical series of papers published between 1941 and 1947, Fraenkel and his associates elucidated the principal specific biochemical requirements of several stored products insects (for a summary, see Fraenkel, 1959a). This research, more than any other, really established the significance of the field of insect nutrition. And to a large extent it also set the pattern of experimental design and fixed the criteria of evaluation according to which most subsequent nutritional research has been pursued.

It is not my intention to review step-by-step the history of research on insect nutrition during the thirty years that have elapsed since the early 1940's. But a few important points merit emphasis, as they have direct bearing on the concepts that guide us in this conference in 1972. The work of those past years has firmly established the concept that insects do not differ markedly in their fundamental qualitative requirements for biochemical nutrients that must be obtained by ingestion and assimilation. Nor do they show fundamental differences from other animal forms. To be sure, some differences and specializations occur, as for example, in respect to sterol identity, ascorbic acid requirement, and requirements for choline, carnitine, and some of the lesser B-vitamins. But these specialized differences do not seem to be of a magnitude any greater than the differences found among species of mammals or species of birds. It would seem, then, that the great range of insect food habits cannot be dealt with meaningfully by any experimental program that investigates only the insect's nutritional requirements in the strict sense. The general similarities in insect nutritional requirements were so impressive that Fraenkel (1959b) was led to postulate that the basic nutritional requirements of all plant-feeding insects are identical, and that any phytophagous insect could thrive on the tissues of any green plant, if the insect could be induced to eat enough of it. Food habits and host plant specificity were postulated to be determined by the effects of secondary plant chemicals that attracted or repelled the insects and influenced the insect's locomotor, ovipositional, and feeding behavior patterns.

Although simplistic in its original form, Fraenkel's theory served well to encourage a shift of emphasis from the purely biochemical determination of minimum requirements for various amino acids, vitamins, etc., to a broader consideration of what we might call "insect dietetics." As reflected by the program of this conference, we are dealing here with insect dietetics rather than with the more narrowly defined nutrition in the strict sense. The simplistic nature of Fraenkel's original theory was apparent when it was shown that even if insects were induced to feed on a variety of nonhost plant tissues, they grew and survived much better on some plant species than on others (Waldbauer, 1962, 1964; House, 1961, 1969; Bongers, 1970). Such results showed that insect dietetics involve more than a more-or-less standard array of nutrient factors plus appropriate behavioral releasers. This had also been demonstrated earlier when we (Beck, 1957; Beck and Stauffer, 1957; Beck and Smissman, 1960) had shown that growth inhibiting and toxic substances were present in corn foliage and a number of other plants, and that these substances exerted adverse effects on the survival and growth of European corn borer, *Ostrinia nubilalis.* Much of the advances in our understanding of insect dietetics over a ten year span was reflected in Fraenkel's 1969 much-needed re-evaluation of the role of secondary plant substances in insect-host plant relationships.

We have now reached a point where we are beginning to appreciate realistically that the effects of an insect's dietary substrate are not simply nutritional in the strict sense. We must also deal with the influence of factors affecting digestion, utilization, and conversion as well as factors affecting metabolism, form determination, reproduction, longevity, and general behavior.

The feeding insect must not only ingest a dietary substrate, but the material ingested must also be suitable for conversion into the energy and structural substances required for development and other biological functions. Digestibility of the diet is an important factor determining utilizability, and has been shown to be of particular significance in insect-host plant relationships. Protease inhibitors occur in some plant tissues as part of the plant's defense against herbivores. Such inhibitors have long been known to occur in legumes and grains, and have been recently reported in solanaceous plants. Green and Ryan (1972) found that feeding activity of larvae and adults of the Colorado potato beetle, *Leptinotarsa decemlineata,* on potato and tomato plants induced the formation of a protease inhibitor that was a powerful antagonist of the major intestinal proteases of insects and mammals. Applebaum (1964) studied the effects of plant-borne and antiproteases on the host specificity of Bruchid beetles, and has postulated that some of the specificity of these insects may be dependent on their having overcome the barrier of such a plant defense mechanism.

Assimilation and conversion into insect tissue must follow digestion, and plant tissues differ greatly in the degree to which they meet this requirement. Waldbauer (1964, 1968) studied assimilation and conversion in the tobacco hornworm, *Manduca sexta,* on a wide variety of solanaceous and nonsolanaceous plants, and demonstrated that these factors are of real importance in the dietetics of the hornworm. Even relatively polyphagous species such as grasshoppers and armyworms do not utilize all hosts equally efficiently. Among the plants fed on by larvae of the southern armyworm, *Prodenia eridania*, digestibility ranged from a highly satisfactory 76% down to only 36% in the poorest host plant; conversion into insect tissue showed a range of efficiency of from 56 to 16% (Soo Hoo and Fraenkel, 1966).

Although insect feeding habits are not determined primarily by the insect's specific biochemical nutritional requirements, it must certainly be recognized that not all dietary substrates are equally nutritious. Plant parts and plant products vary in their content of nutrients required by insects, with such variation being dependent on developmental stage, physiological condition, and plant genotype. These variations have been shown to influence both the behavior and developmental success of plant-feeding insects. In studies of the pea aphid, *Acyrthosiphon pisum,* Auclair *et al.* (1957) found that the amino acid content of an aphid-resistant variety of peas was quantitatively different from that of an aphid-susceptible variety; they postulated that resistance was caused by a relatively low content of free amino acids. Similarly, Colorado potato beetle larvae were shown to grow faster with highest survival rates on young potato foliage than on older foliage, presumably because of a more favorable amino acid content in the younger tissue (Cibula *et al.*, 1967). Grison (1958) observed that adult Colorado potato beetles showed egg production rates that were positively correlated with the phospholipid content of the host plant foliage; senescent foliage was deficient in the phospholipids required for egg production. A number of other investigators have also reported differences in nutrient content of plant structures of different ages, and their apparent effects on growth, survival, and reproduction of insects. Whether in a host plant, synthetic diet, or other nutritional substrate, the importance of the dietary proportions of required nutrients may be of greater importance than their absolute quantities (House, 1969, 1971). Such nutrient ratios may also influence feeding behavior, and they are almost certain to be important factors in the efficiency of the conversion of ingested food into energy and insect tissues.

This very short survey of the different facets of insect nutrition has dealt with but a few of the ways in which the subject has significance. Because of the reviewer's particular bias, emphasis has been on insect-plant interactions, and equally important aspects--such as parasitic, medically important, storage product, and household insects--have been largely ignored. The practical importance of scientific knowledge concerning insect nutrition is apparent in all of these areas of concern. The economic importance of insect nutrition studies has come most sharply into focus in the development and use of mass-rearing programs that underlie the conception and execution of pest management systems involving sterile-male releases, pheromonal manipulation, and lethal gene introductions (Smith, 1966).

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ASPECTS OF INSECT AND ANIMAL NUTRITION

INTRODUCTION
by

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Besides providing data on nutrient requirements pertaining to a specific insect species, the study of insect nutrition appears to offer two distinct potentialities. On the one hand, because of the often quoted similarity in nutritional requirements among the various insects, and even between insects and mammals, nutritional data obtained with insects may have a much wider applicability. On the other hand, differences in requirements have become apparent, especially when mutant strains are considered, which may present a specific insect as an almost tailor-made model for the study of a certain nutritional problem.

Considering nutrition in general, even while assuming much more similarity than dissimilarity in metabolic systems throughout the more complex representatives of the animal kingdom, our final emphasis will often be on mammalian nutrition. However, in our studies, any small size animal with a relatively short life cycle may prove to be a tool of importance, provided that a reasonable generalization of experimental data appears warranted. Years ago, protozoans of the genus Tetrahymena were used extensively to assess the nutritional quality of proteins. Davis' paper, "Application of Insect Nutrition in Solving General Nutrition Problems," follows similar principles, describing the use of growth data from *Tenebrio molitor* larvae as a criterion for nutritional adequacy of various vegetable proteins.

But nutrition, nowadays, cannot be studied only in terms of what, or how much. Nutrition studies must eventually lead to an acceptable answer of the question why. As such, nutrition is only part of a larger picture, that of the totality of a coordinated metabolism. Here, insects, with their vast potential to produce specific, recognizable mutants appear to offer a welcome alternative to *in vitro* studies with mammalian tissues or tissue homogenates, or even cell constituents on the one hand, and the use of unicellular organisms on the other hand. As pointed out by Sang in his study, "The Use of Mutants in Nutritional Research," judicious use of mutants may often be advantageous, especially since, with the use of an integrated multicellular organism, the influence of metabolic control