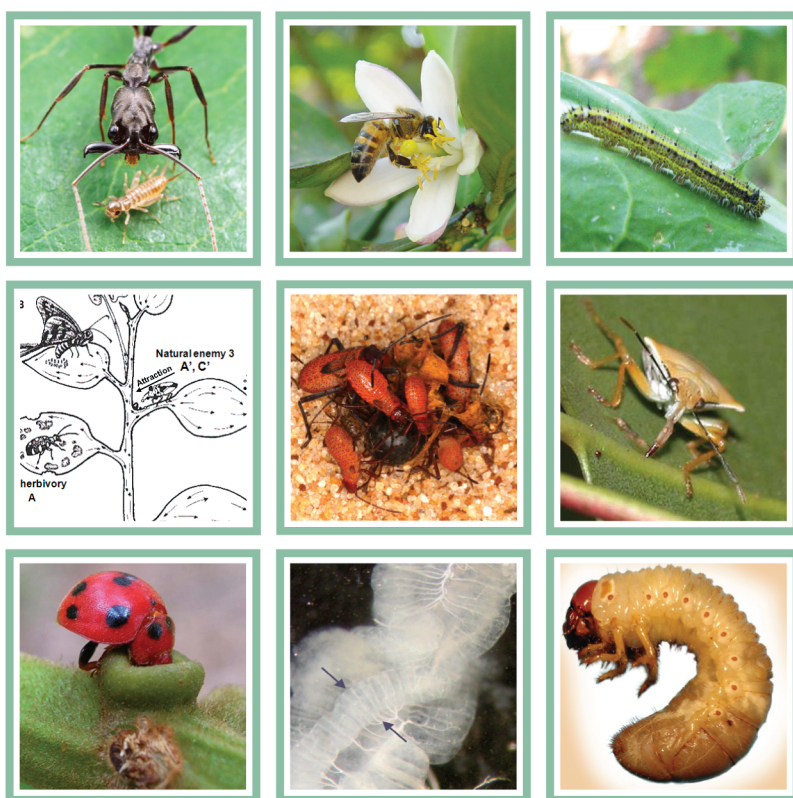


Insect Bioecology and Nutrition for Integrated Pest Management



Edited by
Antônio R. Panizzi
José R. P. Parra



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Foreword

After a deep freeze shriveled mulberry leaves near Avignon, France, silkworm growers needed alternative food plants to feed the newly hatched larvae. The growers sought out Jean Henri Fabre and begged for his help. The time was the late 1800s and Fabre was known in the region for his interest in plants and insects. “Taking botany as my guide,” wrote Fabre, “suggested to me, as substitutes for the mulberry, the members of closely-related families: the elm, the nettle-tree, the nettle, the pellitory (*Anacyclus pyrethrum*, a composite). Their nascent leaves, chopped small, were offered to the silkworms. Other and far less logical attempts were made, in accordance with the inspiration of the individuals. Nothing came of them. To the last specimen, the new-born silkworms died of hunger. My renown as a quack must have suffered somewhat from this check. Was it really my fault? No, it was the fault of the silkworm, which remained faithful to its mulberry leaf.” Fabre (1823–1915) pioneered the study of insect feeding behavior; he was puzzled by the host specificity of many insect species. This same puzzle continues to challenge scientists today.

It is estimated that of the more than one million species of insects that have been described thus far, about 45 percent feed on plants; the others are either saprophagous or predacious. Aside from the need to satisfy their pure scientific curiosity about the complexities of insects’ feeding behavior and nutritional physiology, entomologists realize that what insects eat is, in great part, what makes them economically important for humans. In agriculture, insects compete with humans for the same food resources. In cities and villages they contaminate human habitats and, if not controlled, often destroy those habitats. In cities, villages, and farms, insects vector disease organisms to humans and their domestic animals. Understanding insect feeding and host selection behavior, their feeding ecology, and physiology provides indispensable tools in the continuous fight against insect pests and in the protection of those insects that are beneficial.

Following in Fabre’s footsteps, generations of entomologists dedicated their careers to the study of insects and their relationship to food. An early extensive compilation on the subject was the 1946 book *Insect Dietary: An Account of the Food Habits of Insects* by Charles Thomas Brues. “A monophagous insect will deliberately starve to death in the absence of its proper food plant,” wrote Brues, “and most oligophagous species with highly restricted dietary will do the same. We cannot appreciate such instinctive intolerance.”

A potential key to solve the mystery of this complex behavior had already been found in studies by the Dutch botanist E. Vershaffelt, who in 1919 published a paper on interactions of the cabbage butterfly with its preferred crucifer host plants. For the first time, plant secondary compounds, in this case the glucosinolates, were implicated in the host selection process of an insect.

The role of secondary compounds was vigorously emphasized in the classic, albeit controversial 1958 paper by Godfried Fraenkel, published in *Science*. Fraenkel claimed that the *raison d’être* of plants’ secondary compounds was defense against phytophagous insects. In time a few insect species evolve the capacity to overcome those defenses and eventually “learn” to use the same defensive compounds as cues to identify what becomes a preferred host plant. This hypothesis was later expanded and further substantiated in a paper published in 1964 by Paul Ehrlich and Peter Raven in which they advanced the concept of coevolution of insects and plants.

The role of secondary plant compounds in insect–plant interactions continued to gain support from research on a variety of insect–plant systems. Research proliferated on the effect on insect host selection and feeding behavior related to Cruciferae glucosinolates, Solanaceae alkaloids, Fabaceae anti-proteinase and phenolic compounds, and Umbelliferae furanocoumarins, to mention only a few.

Concurrent with the publication of Fraenkel’s paper on plant defenses, however, another school of thought was rising among entomologists focused on aphid feeding behavior. In the early 1950s,

John S. Kennedy produced fundamental work in this area, claiming that nutrients were as important as secondary compounds in aphid host selection behavior. Kennedy proposed the “dual discrimination theory” later emphasized by A.J. Thorsteinson, in the 1960 *Annual Review of Entomology*. This theory postulated that secondary compounds, as token stimuli, as well as primary nutritional metabolites, were both implicated in the host selection process. Later it was demonstrated by detailed electrophysiological studies that insects possessed the sensorial capacity to detect both types of compounds. These findings gave rise to the “dual discrimination hypothesis.”

While major strides were being made in the study of insect host selection behavior, equally important advances were made in insect nutritional physiology. By the mid-1900s insect nutritional requirements were well defined. Fraenkel's emphasis on secondary compounds related to his assumption that basic nutritional requirements of phytophagous insects were essentially similar and available in most green plants. This assumption was not supported by research on the European corn borer, *Pirautia nubilalis*, conducted by Stanley Beck at the University of Wisconsin. Beck's research and evidence from research from other laboratories showed that there were qualitative and quantitative differences in nutritional requirements that influenced an insect's range of host plants.

Knowledge of insect nutrition improved with development of chemically defined artificial media that satisfied all requirements for larval growth and development, and production of viable adults. Nutritional physiological studies required development of adequate measurement of food intake and utilization by insects. Landmark work in this area was done by Gilbert Waldbauer, a former student of Fraenkel's at the University of Illinois. Waldbauer adapted the nutritional indices developed for the study of domestic farm animals for application to insect alimentary physiology. These indices remain the backbone of research on insect nutritional physiology and ecology; our understanding of insect nutritional ecology after the 1970s is a direct result of these advances.

The field of insect nutritional ecology blossomed in the late 1970s through the early 1980s, mainly with the research of entomologists such as Mark Scriber and Frank Slansky, then at the University of Wisconsin. In the 1981 *Annual Review of Entomology* they stated, “nutritional ecology is central to proper interpretation of life history phenomena (e.g., manner of feeding, habitat selection, defense, and reproduction) both in ecological and evolutionary times.” Thus nutritional ecology extends across many basic life sciences fields such as ecology, nutrition, behavior, morphology, physiology, life history, and evolutionary biology.

The editors of this volume developed professionally while the field of nutritional ecology was maturing into what it has become today, and were associated with institutions where most of the action was taking place. I had the pleasure of hosting José Roberto Postali Parra in my laboratory at the University of Illinois where he spent one sabbatical year as a visiting scholar. He conducted a series of elegant experiments comparing five basic methods used in the measurement of food intake and utilization by insects. That study consolidated the methodology and added powerful tools to the definition of the indices proposed by Waldbauer. Antônio Panizzi received his PhD at the University of Florida working with Frank Slansky. Panizzi had already established a reputation as a leading researcher on the nutritional ecology of Heteroptera: Pentatomidae associated with soybean. Upon returning to Brazil, both Parra, at the Escola Superior de Agricultura Luiz de Queiroz, in Piracicaba, São Paulo, and Panizzi, at the Centro Nacional de Pesquisa de Soja, in Londrina, Paraná, helped establish two centers of excellence in the research of insect nutrition and nutritional ecology of tropical insects.

The task of compiling the wealth of information that has accumulated since the publication of Brues's book would be overwhelming for a single author. For production of this volume, Parra and Panizzi assembled a cadre of Brazilian authors who represent the best in the field, along with several chapters in collaboration with international authorities who have spent time in Brazil. This volume offers the most authoritative compilation of up-to-date research on the ecology of insects with emphasis on nutrition and nutritional ecology, as well as the implications for the development of integrated pest management programs applied to the neotropics, arguably the most complex and diverse of the world's biogeographic zones. This volume is a landmark in a relatively young, multidimensional science, and will greatly contribute toward much-needed further research.

Were it possible for Fabre to witness the research developments of the past 120 years, he most certainly could now address the plight of the distressed silkworm growers. The industry today no longer depends on the health of the mulberry trees. Even though natural food still is the most efficient way to produce healthy silkworms, artificial diets have been developed that are suitable for maintenance of colonies should a crop of leaves fail. Had Fabre had this information, his reputation as a bona fide quack would have remained unblemished.

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Preface

We initially conceived of a book on insect bioecology and nutrition as related to integrated pest management (IPM) back in 1985, at the Brazilian Congress of Entomology, held in Rio de Janeiro. The book (in Portuguese) was finally published in 1991, and was very well received by South American entomologists because it offered a much needed resource on the subject in a language accessible to both Portuguese and Spanish readers.

Eighteen years later the field has grown so much that we thought it was time to produce a second edition. Consequently, the book grew substantially in content. From the original nine it expanded to twenty-six chapters, including those on insect feeding guilds not covered in the first edition, plus chapters on insect feeding and nutrition covering subjects that have blossomed in those two decades. Examples are the role of symbionts on insect nutrition, chemical ecology versus food, and insect cannibalism. As result of this expansion of the subject matter, the book no longer could be considered a second edition of the 1991 title, but instead it was offered as an entirely new book. Therefore, in 2009 the book *Bioecologia e Nutrição de Insetos: Base para o Manejo Integrado de Pragas* (A.R. Panizzi and J.R.P. Parra, editors), Embrapa Informação Tecnológica, Brasília, 1,164 p., was published in Brazil.

Interest in the Portuguese version of the book prompted us to edit a further expanded version of the 2009 book, now to be published in English. The present publication by CRC Press basically is a translation of the 2009 book with updates and adaptations in most chapters and the inclusion of an entirely new one.

The book is organized in three parts. The first part (General Aspects) includes nine chapters, with an introductory chapter on insect bioecology and nutrition as basis for integrated pest management. The next two chapters cover nutritional indexes to measure food consumption and utilization, and the development of artificial diets and their interactions with science and technology. Chapters 4 through 9 cover molecular and evolutionary physiology of insect digestion, insect–plant interactions, symbionts and nutrition, multitrophic interactions mediated by chemical signals, insect cannibalism, and impact of entomopathogenic agents on insect behavior and nutrition.

The second part of the book is dedicated to specific feeding guilds, including ants, social bees, defoliators (Lepidoptera), seed-sucking bugs (Heteroptera), seed-chewing beetles, root-feeding beetles, gall makers, detritivores, pests of stored grains, fruit flies, sieve feeding aphids, parasitoids (Hymenoptera), predatory bugs (Heteroptera), predatory beetles (Coccinellidae), predatory lacewings, and hematophagous insects. Although not all feeding guilds were covered, we believe that the ones that were included should provide readers with a comprehensive view of the incredible diversity of the ways insects exploit feeding resources in nature, and how those resources affect insects' biology.

The final part of the book includes two chapters. The first is dedicated to the field of applied entomology known as host plant resistance. This chapter explores ways in which plant resistance influences insect bioecology and nutrition. The final chapter of the book presents a case study of heteropterans on soybean to illustrate how research on bioecology and nutrition may serve as a basis to design and deploy sophisticated and efficient integrated pest management systems.

We are aware that the field of insect nutritional ecology as defined by Frank Slansky, Jr., John Mark Scriber, and others in the 1980s (see references below) focuses on how insects deal with nutritional and non-nutritional compounds (allelochemicals), and how these compounds influence their biology and shape different lifestyles in evolutionary time. No attempt, in that original nutritional–ecological literature was made to fit the information within a framework applicable to the management of insect pests in agriculture. Therefore, we opted to avoid use of the expression “nutritional ecology,” and adopted instead the more conservative terminology of insect bioecology and nutrition, with inclusion of chapters on applied aspects related to the main topic. Much of the research on which chapters were written was

done in Brazil and based on its neotropical fauna. It is our hope that the complexity and diversity of the neotropics should afford readers from all zoogeographical regions to readily translate to their specific conditions the information provided herein.

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Editors

Antônio Ricardo Panizzi is a senior research entomologist at the Wheat Research Center at Embrapa (Brazilian Enterprise of Agricultural Research), in Passo Fundo, Rio Grande do Sul, Brazil. He earned his BS in agronomy in 1972 from the University of Passo Fundo, his MS in entomology in 1975 from the Federal University of Paraná, both in Brazil, and his PhD in entomology in 1985 from the University of Florida. He is the recipient of the Alexandre Rodrigues Ferreira Prize given by the Brazilian Society of Zoology and editor-in-chief of the *Annals of the Entomological Society of Brazil* (1993–1998). Currently, Dr. Panizzi is associate editor and president of the Entomological Society of Brazil. He served as a member of the advisor committee for agronomy (entomology) at the National Council for Scientific and Technological Development (CNPq) of Brazil from 1997 to 1999 and from 2009 to 2011. He has been an invited speaker at several congresses and symposia in different parts of the world and an invited scientist at the National Institute of Agro-Environmental Sciences, Tsukuba, Japan (1991). He coedited *Insect Nutritional Ecology and Its Implications on Pest Management* (Manole/CNPq, São Paulo, 1991) and *Heteroptera of Economic Importance* (CRC Press, Boca Raton, FL, 2000). Dr. Panizzi has published extensively on Hemiptera (Heteroptera), over 150 peer-reviewed publications, including an *Annual Review of Entomology* article on wild host plants of Pentatomidae. He teaches a course on insect nutritional ecology at the Federal University of Paraná, where he serves as advisor for MSc and PhD students. His current research focuses on the interactions of heteropterans (mostly Pentatomidae) with their wild and cultivated host plants, and the management of pest species on field crops.

José Roberto Postali Parra is a full professor of the Department of Entomology and Acarology at the College of Agriculture (ESALQ) of the University of São Paulo (USP). He is a member of the Brazilian Academy of Sciences and of the Academy of Sciences for the Developing World (TWAS). He was trained in insect rearing techniques and nutrition for biological control purposes at the University of São Paulo and the University of Illinois, Urbana–Champaign. Since the end of the 1960s, he has conducted research in biological control and is currently doing research on classical and applied biological control, with emphasis on *Trichogramma* and on the biological control of sugarcane and citrus pests. He has published more than 200 peer-reviewed papers and edited books, and he has supervised 55 MS and 40 PhD students. He was the president of the Entomological Society of Brazil and dean of ESALQ (USP), and he received awards from Embrapa, the Entomological Society of Brazil and the Zoological Society of Brazil. He also received honors from the state of São Paulo government and from the Brazilian government for his contributions in the biological control area. He is vice-president of the International Organization for Biological Control.



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Introduction to Insect Bioecology and Nutrition for Integrated Pest Management (IPM)

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1.1 Introduction

All living organisms are, in general, a result of the food they consume. In the case of insects, many aspects of their biology, including behavior, physiology, and ecology are, in one way or another, inserted within the context of food. The quantity, quality, and proportion of nutrients present in the food, and of secondary or nonnutritional compounds (allelochemicals), cause a variable impact on the insect biology, shaping its potential reproductive contribution to the next generation (fitness).

Studies on bioecology and insect nutrition greatly evolved during the last 50 years, from the definition of the basic nutritional requirements for survivorship and reproduction (see Chapter 2) to the evaluation of their influence in insect behavior and physiology, with ecological and evolutionary consequences (see Chapter 5 on insect/plant interactions). This is called insect nutritional ecology and its concept and development occurred during the last 20-plus years (e.g., Scriber and Slansky 1981; Slansky 1982a, b; Slansky and Scriber 1985; Slansky and Rodriguez 1987). In this introductory chapter, we will touch in summary on the natural food and artificial diets, food consumption, digestion and utilization, multitrophic interactions including symbionts, and the interface between food and chemical ecology. Variable feeding guilds and the implications of bioecology and insect nutrition of pest species within the context of integrated pest management (IPM) will be covered as well.

1.2 Food

1.2.1 Natural Food

Natural food (i.e., food obtained in nature) has variable nutritional quality. From the time insects appeared on Earth (see Chapter 5), an evolutionary adaptation process started with the appearance of different lifestyles. This allowed insects to explore an array of foods in all of their diverse forms. If on one hand, insects adapted to explore nutritional sources (e.g., vegetable and animal organisms), these, on the other hand, evolved to be less susceptible to being consumed, in an endless coevolutionary process. The fact that insects have a legendary ability to explore the more diverse habitats in search of food, with unique adaptive success, make them the only living creatures to challenge human beings in their total hegemony on Earth.

In addition to the variable quality of foods, their seasonality make exploration an even greater challenge. The abiotic environment, including temperature, humidity, and photoperiod makes natural food not constantly available, which “forces” the insects to adapt during less favorable periods. These adaptations include drastic changes in the physiology (e.g., diapause) and less pronounced changes (e.g., oligopause/quiescence). In both cases, energy storage such as lipids supports survivorship. Another strategy to face less favorable conditions is to search for suitable habitats through migration that demands stored energy to sustain steady flight.

Natural foods vary in their quality, and often toxic secondary compounds or allelochemicals are present (see Chapters 5 and 26). Beyond chemical compounds, physical defenses (i.e., pilosity, thorns, and tough and thick tissues) make natural foods often out of reach and/or undigestible. Therefore, natural foods present a constant challenge to insects even to those specialized on certain foods (monophagous). Artificial diets may solve this problem for biological studies in the laboratory, but do not always yield favorable results (i.e., the case of artificial diets for pentatomids is still a challenge to be overcome).

1.2.2 Artificial Diets

The development of artificial diets for insects, mostly from the 1960s on, provided conditions for refinements on studies on their nutritional requirements. Today there are over 1,300 species of insects raised on these diets (see Chapter 3 and references therein). These advances in insect rearing using artificial diets allowed us to learn that some particular group of insects need nucleic acids and liposoluble vitamins in their diets. Sophisticated techniques were developed with artificial diets that allow raising parasitoids *in vitro* (i.e., excluding the natural host). Although artificial diets for parasitoids and predators have been developed (Cohen 2004), phytophagous insects of the orders Lepidoptera, Coleoptera, and Diptera concentrate 85% of the artificial diets. These diets allowed great advances in basic and applied studies in entomology, including insights in public education and in human and animal nourishment (see Chapter 3).

1.2.3 Food Consumption, Digestion, and Utilization

Insect nutrition can be focused on two aspects: qualitatively (i.e., the chemical nature of the nutrients) and quantitatively (i.e., the proportion of nutrients that encompass the food that is ingested, digested, assimilated, and converted into tissue for growth). The measurements of food consumption and utilization, including physiology and behavior in selecting host plants, leads to several applications not only on basic nutrition, but in the ecology of insect communities through host plant resistance and biological control (see Chapter 2 and Cohen 2004).

The basic concepts of food consumption and utilization were developed by nutritionists relating food quality and its effects on growth and development of animals. The interactions of nutrients and allelochemicals have been determined by nutritional indexes. These indexes allow understanding the impact of variable factors to the insect life, including temperature, humidity, photoperiod, parasitism, allelochemicals, cannibalism, and so forth (see Chapter 2 and references therein).

Coudron et al. (2006) proposed the term *nutrigenomics* or *nutritional genomics* that provide information on the impact of nutrition based on biochemical parameters through the investigation of how nutrition alters genetic expression. These studies with molecular markers of insects could be used to indicate initial responses to nutritional sources, providing cues to the biochemical, physiological, and genetic regulation of insect populations, with multiple implications.

1.2.4 Multitrophic Interactions

1.2.4.1 Symbionts

The success of insects as organisms able to colonize every habitat is due to their enormous ability to feed on an array of food sources. In addition, the exploitation of less suitable food resources is done through the association with microorganisms in a symbiotic process. This allows utilization of novel metabolic pathways with mutual benefits in the course of evolutionary time (see Chapter 6 and references therein).

A wide variety of microorganisms is involved in the feeding process of insects. These microorganisms include external symbionts that cultivate fungi, such as the Ambrosia beetles of the subfamilies Scolytinae and Platypodinae, ants of the subfamily Myrmicinae, tribe Attini, and termites of the subfamily Macrotermitinae, and internal symbionts such as protozoans and bacteria that can play a secondary role (bacteria in Heteroptera) or a primary role or be obligated (e.g., *Buchnera*, *Wigglesworthia*, and *Blochmannia*—see Chapter 6).

The study of insect symbionts has gained momentum due to the development of molecular techniques that allowed a better understanding of insect–symbiont interactions previously unknown. The development of complete genomes of endosymbionts with a wide ecological and phylogenetic diversity will open opportunities for better comparisons to test actual evolutionary models. The possibility to manipulate bacteria symbionts of insects' vectors of human diseases such as malaria, dengue, and Chagas open up potential strategies to reduce a bug's longevity or to mitigate the parasites that cause such diseases. With regard to crop pests, revealing the interactions of insects and their symbionts may yield sophisticated and efficient control measures. Once revealed, the role of symbionts, their manipulation through genomics, biochemical, or conventional means (e.g., elimination of symbionts using antibiotics) will create a real possibility to mitigate the impact of pests on crops (see Chapter 6, and Bourtzis and Miller 2003, 2006, 2009).

1.2.4.2 Food and Chemical Ecology

Trophic interactions of insects and their hosts include many chemical signs, the so-called *infochemicals*. These signs have great influence in finding hosts. There are constitutive volatiles: those normally produced and induced volatiles and those produced due to plant–herbivorous–natural enemy interactions, such as volatiles of plants eliciting pheromone production by insects (see Chapter 7 and references therein).

Chemical signs utilized by insects include *allelochemicals* that mediate interspecific interactions and in general aid in finding food, both for phytophagous and zoophagous, which act like *allomones*, *kairomones*, *synomones*, or *apneumones*, and *pheromones*, which act as intraspecific signaling. These latter include trail, aggregation, and sexual pheromones, which act in setting directions and sexual attraction, but also play a role in finding food. Some pheromones act in association with allelochemicals, increasing the success of finding the conspecifics (e.g., synergic action of aggregation pheromones and plant components—Reddy and Guerrero 2004).

Several pheromones are commercialized for management of pest species. Recently, these include the effects of plant volatiles on pests, predators, and parasites (see Chapter 7 and references therein). The discovery that plants attacked by herbivores react by activating indirect defenses by alerting predators and parasites of the presence of their specific hosts (De Moraes et al. 1998) had a great impact. This led to investigations of biochemical mechanisms and ecological consequences of such interactions, and potential use of these compounds in agriculture (Turlings and Ton 2006). The myriad of trophic interactions among plants, herbivores, and their natural enemies (insect bioecology and nutrition and chemical ecology) open up a research area that is sophisticated and has great potential to be exploited in its most variable basic and applied aspects (see Chapter 7).

1.3 Feeding Habits

1.3.1 Feeding Habits of Social Insects

Feeding habits of social insects are among the most sophisticated of the Class Insecta. Ants (Hymenoptera) and social bees (Bombini, Apini, Meliponini (Hymenoptera)) included in this volume (Chapters 10 and 11, respectively) touch on this subject.

Ants function as important predators in trophic chains (Floren et al. 2002) and as main herbivores in tropical forests exploiting exsudates of phytophagous sucking insects (e.g., Homoptera) and flower nectaries (Davidson et al. 2003) beyond cultivated fungi for their nourishment. As predators and herbivores more important due to their abundance and wide distribution, in over 100 million years of evolution ants have had a major impact on other organisms and ecosystems (Holldöbler and Wilson 1990, see Chapter 10). Foraging strategies in ants are legendary and demonstrate a unique level of organization among living organisms (Fowler et al. 1991).

Social bees, similar to ants, are also highly specialized in their ability to explore nutritional resources and they also demonstrate sophisticated foraging behavior. Seeking pollen and nectar in flowers and honey production are two of the most complex biological systems among living organisms (see Chapter 11 and references therein).

1.3.2 Feeding Habits of Phytophagous Insects

The feeding habits of phytophagous insects are extremely variable, and include leaf chewers (Chapter 12), seed suckers (Chapter 13), seed chewers and borers (Chapters 14 and 18), root feeders (Chapter 15), gall makers (Chapter 16), frugivores (Chapter 19), and leaf, bud, and fruit suckers (Chapter 20) that are detailed in this volume.

Leaf chewers are species of the orders Coleoptera, Hymenoptera, and Lepidoptera, which in general are specialized in one or few plant families. Therefore, their evolutionary relations are narrow and the chemical defenses of plants to the leaf chewers are abundant (e.g., Bernays 1998). In general, caterpillars consume a relatively large amount of food, have big guts, and rapidly digest food. However, by being less selective, they often ingest plant parts that are not highly nutritional such as leaf veins or other metabolic poor tissues (see Chapter 12).

Seed suckers (true bugs) include heteropterans of several families that prefer to feed on immature seeds, although some feed on mature seeds. They insert their stylets (mandibles + maxillae) in the seed and inject salivary enzymes that make up slurry, which is sucked in, carrying the nutrients. Because of the feeding activity, total or partial damage occurs, creating seedlings with low viability. The impact of seed suckers on seed and fruit production is discussed at length in the literature of economic entomology due to its worldwide effect (see Chapter 13, and Schaefer and Panizzi 2000).

Seed chewers (borers) include species of Coleoptera and Lepidoptera, but only coleopterans have chewing mouthparts during the larval and adult stages. Among the coleopterans, seed weevils are a classical example (see Chapter 14). Their larvae develop exclusively from nutrients of seed contents, while adults feed on pollen and nectar. Although polyphagous, they prefer legumes of several species, most considered of economic importance (Vendramin et al. 1992).

Root feeding insects are represented mostly by coleopterans that feed on live root tissues. However, their feeding habits include boring roots, stems, and tubers, making galleries or cutting root tissues from outside (see Chapter 15 and references therein). Many larvae are able to feed on roots externally and adults feed on the foliage, not necessarily of the same species fed by larvae. Beyond feeding on roots, larvae may explore organic matter, decaying wood (xylophagy), feces (coprophagy), and dead animals (necrophagy) (Oliveira et al. 2003).

Gall makers are found on all orders of phytophagous insects (Hemiptera, Thysanoptera, Coleoptera, Hymenoptera, Lepidoptera, and Diptera) except for Orthoptera. Galls are characterized by being reactions of plants due to the damage caused by insects. They are classified as the organoid type, which show similar growth pattern as to the plant tissue and the plant structure colonized keeps its identity (e.g.,

intumescences and callosities), and the histioid type, which show a wide variety of abnormal growing tissues (see Chapter 16).

Frugivorous insects belong to several orders. In this book, fruit flies (Tephritidae) are covered in detail (Chapter 19). Tephritids are a fruit-feeding guild related to the feeding habits of immatures. Adults feed on fruits exsudates, bird feces, decaying organic matter, nectar, pollen, and so forth. Although larvae stay inside the fruits, they may feed on their own exoskeleton, on larvae of other insects and of their own, and on worms (Zucoloto 1993). Fruit fly females lay their eggs on the fruit skins, and larvae penetrate fruits as they hatch. Life cycle is completed on the ground where they pupate, originating a new adult (Christenson and Foote 1960).

Among insects that suck leaves, buds, and fruits (e.g., psilids, whiteflies, and other Stenorrhyncha specialized in phloem feeding) aphids are an interesting guild that will be covered in Chapter 20. Aphids (Hemiptera: Aphidoidea) penetrate the vegetable tissue to suck the sieve, affecting plant growth and causing localized or systemic lesions, aphids commonly transmit virus and this is a highly specialized insect/plant interaction. Several authors treat feeding and nutrition of aphids, with relevant aspects of the role of saliva, and adaptative mechanisms (see references in Chapter 20).

1.3.3 Feeding Habits of Carnivorous Insects

Some of the feeding habits of carnivorous insects include parasitoids (Hymenoptera) (Chapter 21), predatory hemipterans (Chapter 22), predatory beetles (Coccinellidae) (Chapter 23), and predatory lacewings (Neuroptera) (Chapter 24), which are presented in this volume.

Parasitoids (Hymenoptera) are insects that adapt to the parasitic way of life either utilizing the limited nutritional resources of the immatures or acquiring nutrients from adults. Larvae are adapted to maximize the utilization of nutritional sources in different ways (see Chapter 21). Their development is closely dependent of their hosts. Parasitoids can explore eggs, eggs and larvae, larvae, larvae and pupae, pupae or adults; they can be endo or ectoparasitoids, solitary or gregarious (Askew 1973).

Predatory hemipterans (Heteroptera) include several species of the genera *Orius* (Anthocoridae), *Geocoris* (Lygaeidae), *Nabis* (Nabidae), *Podisus*, *Brontocoris*, and *Supputius* (Pentatomidae), *Macrolophus* (Miridae), and *Zelus* and *Sinea* (Reduviidae). Many predators show phytophagy (see Chapter 22 and references therein). To reach the “perfect” nutrition, the ecological tritrophic interaction is involved; that is, the third level (the entomophagous), the second level (the host), and the first level (the plant that feed the host). Therefore, the coexistence of entomophagy and phytophagy is highly important for predatory heteropterans.

Predatory beetles (Coccinellidae) are among Coleoptera the most important predators. Feeding habits of larvae and adults are similar, and their mandibulae are similar. Many species feed on aphids, coccids, and mites; some species show phytophagy and their mandibulae are adapted to cut and chew plant tissue, mostly of plants that belong to the families Cucurbitaceae and Solanaceae (see Chapter 23). Coccinellids are efficient predators in finding and eating their prey in all environments, mostly preying on aphids (Hodek 1973).

Lacewings (Chrysopidae) are predators as larvae and as adults feed on nectar, pollen, and/or honeydew (Canard 2001). Prey are small arthropods, less mobile, and with soft tegument that allow being perforated by the mouth parts, such as mites, whiteflies, aphids, scales, eggs and small larvae of Lepidoptera, psocopters, trips, and eggs and small larvae of Coleoptera and Diptera (see Chapter 24 and Albuquerque et al. 2001).

1.3.4 Feeding Habits of Hematophagous Insects

Insects that feed on blood (hematophagous) are important in transmitting pathogenic agents. Species of Diptera, Hemiptera, Phthiraptera, and Siphonaptera, for example, are vectors of such agents, causing devastating diseases such as dengue, malaria, leishmaniasis, Chagas disease, and bubonic plague. Hematophagy is a feeding habit of immatures and adults of both genders, or exclusively by females that seek hosts for their oogenesis (Forattini 2002). Some species, although not hematophagous, cause

allergic reactions due to the action of the saliva or by ingesting toxic compounds. Others develop inside their vertebrate hosts, feeding on tissues and blood, causing lesions and development of secondary infections associated with bacteria and fungi (see Chapter 25).

1.3.5 Other Feeding Habits

Other feeding habits less known include insects that feed on detritus. Detritus may contain relatively few nutrients as in the case of dead logs, feathers, and so forth, or a great amount of nutrients such as in carcasses and feces. Detritivory is a rather sophisticated feeding habit shown by insects belonging to several orders. However, this subject is little known (see Chapter 17).

1.4 The Coverage and Implications of Studying Bioecology and Nutrition of Insects

Studies in the area of bioecology and insect nutrition passed through a series of transformations. Initially, research efforts concentrated on determining feeding habits and qualitative nutritional needs (i.e., which basic nutrients such as aminoacids, vitamins, mineral salts, carbohydrates, steroids, lipids, nucleic acids, and water were needed for normal development and reproduction of insects). In this context, several classic studies were published a long time ago, such as the revision of insect nutrition and metabolism by Uvarov (1928), the feeding regime of insects by Brues (1946), and the dietary requirements of insects by Fraenkel (1959). These studies lead to the development of artificial diets later on (Singh 1977 and Singh and Moore 1985), which created conditions for mass rearing of insects in the laboratory with multiple purposes in integrated pest management programs. The quantitative approach, including concentrations and proportions of nutrients, followed. Several techniques to measure food consumption and utilization were developed and updated (Waldbauer 1968; Kogan 1986). Literature reviews on quantitative aspects of insect nutrition were published (Scriber and Slansky 1981; Slansky and Scriber 1982).

The so-called “insect dietetics” (Beck 1972; Beck and Reese 1976) or “quantitative nutrition” (Scriber and Slansky 1981) expanded to include insect physiology and behavior that vary according to the presence of different nutrients and secondary or nonnutritional compounds (allelochemicals). Beyond biotic, abiotic factors shape the behavioral and physiological patterns of insects, such as migration or diapause, with the decrease of temperature and photoperiod or increase in production of metabolic water when facing low humidity. These patterns cause, in the long run, ecological and evolutionary consequences with the appearance of new lifestyles (Slansky 1982). The development and evolution of this research is called nutritional ecology and its model was formed as follows: for a particular species and population, there is a set of states that result in the achievement of maximum fitness (i.e., the maximum reproductive contribution to the next generation). With the variability in the environment, biotic and abiotic, insects change their behavior and physiology in an attempt to compensate for less favorable conditions to achieve their maximum potential. Their responses implicate in ecological consequences for fitness (for details see Slansky 1982a, b; Slansky and Scriber 1985).

1.5 Insect Bioecology, Nutrition, and Integrated Pest Management

By definition, integrated pest management (IPM) includes the utilization of multiple control methods. For its implementation it is necessary to understand and plan the agroecosystem, to analyze the cost/benefit net result of its adoption, to understand the tolerance of the crops to insect damage, to know the right time for insect utilization, and finally, to educate people to understand and accept the IPM principles (Luckmann and Metcalf 1982; Kogan and Jepson 2007).

The concept of integration of several tactics for management of insect pests includes those related to the bioecology and feeding/nutrition of insects (see Chapters 26 and 27). Plants resistant to insects, with physical or/and chemical attributes that make them less suitable for the insect biology (antibiosis) or less

preferred for feeding and/or oviposition (antixenosis) are good examples. In addition, ecological resistance by host escape such as noncoincidence of plant and insect phenology, and induced resistance by modification of the environment to negatively affect the insect biology are included here (e.g., Maxwell and Jennings 1980; Kogan 1982; Kogan and Jepson 2007).

The use of attractive plants (preferred food sources) to concentrate insects in order to manage them to mitigate their impact to crops is another tactic that is included in the context of insect feeding behavior. There are many examples of attractive plants that are used as trap crops; sometimes parts of these attractive plants are mixed with insecticides and used as bait, causing bugs to die (see Chapter 27). Furthermore, the cultivation of plants in a consortium creating agricultural landscape mosaics and/or growing crop plants in between uncultivated landscapes (e.g., Ferro and McNeil 1998; Elkbom et al. 2000) makes them less conspicuous and therefore less suitable for pests. Supplement of nutrients to attract natural enemies or to concentrate insect pests in a particular site to facilitate control and use of attractants, repellents, and agents that disrupt the feeding process are management tactics with a strong ecological–nutritional appeal. Most of those are yet to be fully exploited in IPM programs because they are poorly understood, seldom evaluated, and, therefore, little known.

1.6 Final Considerations

The study of insects under the scope of bioecology and nutrition (nutritional ecology) include the integration of several areas of research such as biochemistry, physiology, and behavior within the context of ecology and evolution (Slansky and Rodriguez 1987). A great amount of information is generated about the biology of insects that is accumulated over time; however, this data has not been analyzed in conjunction with the areas of knowledge mentioned above. The analysis of such data considering the holistic view of the bioecology and nutrition (nutritional ecology) certainly will generate questions whose answers are currently unknown. For instance, in considering an agroecosystem where we know the species of insects that inhabit it, questions can be raised such as the following: What are the effects of inter- and intraspecific competition of species to their biology and to the crop? How do insect pests and their associated natural enemies react to the fluctuation of temperature and change in photoperiod? How are the feeding behavior and physiology affected by a change in quality of food over time? How does a parasitized insect behave regarding feeding, reproduction, and dispersion? Which factors make secondary pests become primary pests? These and many other questions that are generated should be analyzed and answered considering the paradigm of bioecology and nutrition (nutritional ecology).

It is clear that many of the ecological, physiological, and behavioral processes are linked to the feeding and nutrition context. Therefore, it is important to develop acknowledgment on feeding preference, feeding habits, nutritional requirements, and their consequences to growth, survivorship, longevity, reproduction, dispersal, gregarism, and so forth. This will allow the design of control strategies that will include a myriad of tactics. For example, once aware of the feeding preference of an insect for a particular plant species, such a plant can be used as a trap to facilitate pest control; knowing the insect and plant phenologies, one can manipulate planting time to avoid insect damage to target plants. Furthermore, physical (e.g., pilosity, tissue hardness, thorns) and chemical (lack of nutrients, presence of toxic allelochemicals) create opportunities for their manipulation in order to mitigate the pests' impact. Studies on basic and applied aspects considering the bioecology and nutrition (nutritional ecology) will not only help to understand the different insect lifestyles but will also yield data to generate holistic integrated pest management programs.

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Nutritional Indices for Measuring Insect Food Intake and Utilization

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2.1 Introduction

Nutrition may be studied both qualitatively and quantitatively. Qualitative nutrition deals exclusively with nutrients needed from the chemical aspect. In this case, it is well known that, independently of the systematic position and the feeding habits of insects, qualitative nutritional needs are similar and that these needs, except for a general need for sterols, are close (with rare exceptions) to those of the higher animals. The basic nutritional needs of insects include amino acids, vitamins and mineral salts (essential nutrients) and carbohydrates, lipids, and sterols (nonessential nutrients), which should be adequately balanced, especially in the ratio of proteins (amino acids): carbohydrates (see Chapter 3).

There have been many papers on nutrition since the beginning of the last century (Uvarov 1928), and after the revisions by Brues (1946) and Fraenkel (1953), especially since the 1970s, there have been a large number of publications on the subject (Rodriguez 1972; Dadd 1973, 1977, 1985; House 1972, 1977; Reinecke 1985; Parra 1991; Anderson and Leppla 1992; Thompson and Hagen 1999; Bellows and Fisher 1999; Cohen 2004). The development of artificial diets for insects, mainly since the 1960s, has refined research on nutritional needs (Singh 1977), and in 1985 there were artificial diets for more than 1,300 insect species (Singh 1985). This advance in rearing techniques resulted in the discovery that some restricted insect groups need nucleic acids and even liposoluble vitamins, such as A, E, and K₁. Sophisticated production techniques for parasitoids *in vitro* (excluding the host) have even been developed (Cônoli and Parra 2002), with these authors referring to 73 parasitoid species reared *in vitro*, 16 Diptera and 57 Hymenoptera. The artificial diets used for phytophages today have the same composition as those developed in the 1960s and 1970s (see Chapter 3). A recent revision was published by Cônoli and Grenier (2010).

It was some time before significant attention was paid to quantitative nutrition due to the technical difficulties in measuring food utilization. However, today, it is known that food intake and utilization is a basic condition for growth, development, and reproduction. Food quantity and quality consumed in the larval stage affects growth rate, development time, body weight, and survival, as well as influencing fecundity, longevity, movement, and the capacity of adults to compete. Larvae that are inadequately fed result in pupae and adults of “bad quality.” For example, an artificial diet for *Pseudoplusia includens* (Walker) that does not contain wheat germ oil (a source of linoleic and linolenic acids) leads to deformed wings in all the adults (J. R. P. Parra, personal observation). Similar results were recorded by Bracken (1982) and Meneguim et al. (1997) for other lepidopterous species.

Quantitative (Scriber and Slansky 1981) or dietetic nutrition (Beck 1972) considers that not only are the basic nutritional requirements important for the insect but also the proportion (quantity) of food ingested, assimilated, and converted into growth tissue. This quantity varies not only in function of the nutrients but also the nonnutrient contents (such as the allelochemicals) in the food. Some researchers (e.g., Slansky and Rodriguez 1987a) considered quantitative nutrition more important. Thus, when the behavioral and physiological changes are examined in an ecological context (in constant change), by identifying the ecological consequences and the evolutionary aspects of such behavior, insect nutrition reaches a wider meaning, transforming it into the nutritional ecology. According to these authors, most, if not all these ecological, physiological, and behavioral processes in insects happen within a nutritional context, which includes feeding, growth, metabolism, enzyme synthesis, lipid accumulation, diapause, flight, and reproduction.

Since the measures of food consumption and use are the limit between feeding physiology and the selection behavior of the host plant, their study has a series of applications, not only in the basic area of nutrition, community ecology, and behavior, but also in applied areas of control through plant resistance and biological control (Kogan and Parra 1981; Cohen 2004; Jervis 2005).

The basic concepts of food consumption and use have been developed by nutritionists who related the quality of the food consumed with its effect on animal growth and development (Klein and Kogan 1974). The ecologists used this type of analysis as a basis for studies on community energy flows (Mukerji and Guppy 1970; Latheef and Harcourt 1972). Researchers in pest management can use consumption and growth rate measures to develop simulation models for determining pest economic injury levels (Stimac 1982) or even to evaluate which plant part is preferred by the insect (Gamundi and Parra, unpublished).

TABLE 2.1

Relative Consumption Rate, Relative Growth Rate, Relative Metabolic Rate, Approximate Digestibility, Efficiency of Conversion of Ingested Food, Efficiency of Conversion of Digested Food, Metabolic Cost, and Mortality for *Spodoptera frugiperda*, *Heliothis virescens*, and *Diatraea saccharalis* Larvae Reared on Artificial Diet at 25°C and 30°C, RH of 60 ± 10%, and a 14 h Photophase

Nutritional Indices*	<i>S. frugiperda</i>		<i>H. virescens</i>		<i>D. saccharalis</i>	
	25°C	30°C	25°C	30°C	25°C	30°C
RCR (g/g/day)	0.5653 ± 0.1364a	0.5620 ± 0.0231a	0.8139 ± 0.0333b	1.2289 ± 0.0472b	0.8848 ± 0.0497b	1.0899 ± 0.0667a
RGR (g/g/day)	0.0835 ± 0.0060b	0.1407 ± 0.0040a	0.1500 ± 0.0036b	0.2315 ± 0.0041b	0.0771 ± 0.0016b	0.1142 ± 0.0026a
RMR (g/g/day)	0.2057 ± 0.1260a	0.0748 ± 0.0084a	0.3026 ± 0.0315b	0.5264 ± 0.0474b	0.1879 ± 0.0132b	0.4619 ± 0.0619a
AD (%)	42.04 ± 3.39a	38.90 ± 1.00a	54.55 ± 2.22b	60.64 ± 1.68a	31.43 ± 1.37b	50.91 ± 2.16a
ECI (%)	19.67 ± 1.44b	26.26 ± 1.40a	19.77 ± 0.95a	19.53 ± 0.56a	9.52 ± 0.39b	11.64 ± 0.60a
ECD (%)	53.30 ± 5.06b	67.06 ± 3.04a	40.07 ± 2.99a	33.73 ± 1.66a	31.87 ± 1.51a	24.23 ± 1.45b
MC (%)	46.70 ± 5.06a	32.94 ± 3.04b	59.93 ± 2.99a	66.27 ± 1.66a	68.13 ± 1.51b	75.77 ± 1.45a
Mortality (%)	58.0 ± 14.00b	52.0 ± 25.80a	18.0 ± 6.60a	20.0 ± 12.60a	12.0 ± 9.80a	20.0 ± 17.90a

Source: Souza, A. M. L., C. J. Ávila, and J. R. P. Parra. *Neotrop. Entomol.*, 30:11–17, 2001.

Note: RCR = relative consumption rate, RGR = relative growth rate, RMR = relative metabolic rate, AD = approximate digestibility, ECI = efficiency of conversion of ingested food, ECD = efficiency of conversion of digested food, MC = metabolic cost.

* Means followed by the same letter on the row do not differ significantly, based on the Tukey test ($P \geq 0.05$), for each species in two temperatures.

The process that determines host plant selection by an insect, that is, the insect/plant relationship (see Chapter 5 for more details), is an application of the measures of insect intake and utilization. The interaction of allelochemicals and nutrients has been determined from nutritional indices that have helped in understanding the mechanisms of plant resistance to insects (Reese 1977). The study of nutritional indices may be done with natural or artificial diets and explains the phenomena that occur under variable conditions of temperature (Souza et al. 2001), relative humidity, photoperiod, parasitism, and even soil nutrients (Oliveira et al. 1990), allelochemicals, transgenic plants, enzymatic studies, or cannibalism (Nalim 1991). For artificial diets, a diet's nutritional suitability or even deciding which is the most suitable container can be done through measuring food intake and utilization. Thus, Souza et al. (2001), using food consumption and indices concluded that for *Spodoptera frugiperda* (J. E. Smith) the best rearing temperature is 30°C while for *Heliothis virescens* (F.) and *Diatraea saccharalis* (F.), there is no difference between 25°C or 30°C (Table 2.1).

Coudron et al. (2006) proposed the term “nutrigenomics” or “nutritional genomics,” which has the aim of supplying information on the impact of nutrition on biochemical parameters by investigating how it alters the standards of global gene expression. Insect molecular markers would be identified that could be used as initial indicators of the response to different nutritional sources. Such molecular markers could be chosen based on the degree of expression and evaluated for their suitability as nutritional markers by examining development and expression by generation. Ideal markers would be those that are strongly expressed, that would appear in a development stage in the first generation, and that would be consistent over many generations. The authors demonstrated the first example with *Perillus bioculatus* (F.) (Heteroptera: Pentatomidae), by rearing it on optimum and suboptimum diets and analyzing the presence of expressed genes differentially in the two treatments. According to the authors, future research in this area can supply a better definition of biochemical, physiological, and genetic regulation of suitability, quality, and high performance in insect populations. It could be useful in evaluating the degree of risk of introduced natural enemies, since it is a faster method for identifying and evaluating potential alternative hosts; in a wider context, it could be important for the effective use of biological control and other control methods, as well as improving agricultural sustainability.

2.2 Nutritional Indices for Measuring Food Intake and Utilization

The first studies on insect food intake and utilization were made with natural foods, with no standardization and using methods with variable degree of precision, which resulted in much confusion. Waldbauer (1968) made a revision and standardized the indices for measuring consumption and use by herbivorous insects. Even today, this work is the basis for those researchers who study quantitative or diet nutrition, although Kogan and Cope (1974) and Scriber and Slansky (1981) have suggested some alterations that have been accepted by the scientific community. These indices are as follows:

- a. Relative Consumption Rate (RCR)

$$RCR = \frac{I}{B \times T}$$

- b. Relative Metabolic Rate (RMR)

$$RMR = \frac{M}{B \times T}$$

- c. Relative Growth Rate (RGR)

$$RGR = \frac{B}{B \times T}$$

d. Efficiency of Conversion of Ingested Food (ECI)

$$ECI = \frac{B}{I} \times 100$$

e. Efficiency of Conversion of Digested Food (ECD)

$$ECD = \frac{B}{I - F} \times 100$$

f. Approximate Digestibility (AD)

$$AD = \frac{I - F}{I} \times 100$$

The meaning of the variables of the different formulae is as follows:

T = Time of duration of feeding period

I = Food consumed during T

B = Food used during T_i

$$B = (I - F) - M$$

F = Undigested food + excretory products

M = (I - F) - B = food metabolized during T (part of assimilated food that was used in the form of energy for metabolism)

$\bar{I} - F$ = Food assimilated during T (represents the part of I which was used by the insect for conversion into biomass and for metabolism)

\bar{B} = Mean weight of insects during T (some ways to determine this are described in Kogan 1986)

2.2.1 Experimental Techniques

The data needed to determine the indices include the quantity of food consumed in time T, the insect weight gain in the period T, and the total excretion (including exuviae, secretions, cocoons, and feces). Besides this data, the volume of CO₂ produced during respiration can be necessary in certain types of study. It is important that in the determination of nutritional indices a standard be adopted using the weights of fresh or dry materials for the parameters. It is preferable to use dry weights especially when the indices are determined in artificial diets since water loss from the medium is significant, making it difficult to make corrections for working with fresh weights. The indices calculated on the basis of fresh weight cannot be compared due to the difference in the percentage of water in the food, feces, and tissues of the insect. However, knowing the amount of water is fundamental for understanding adaptations to different lifestyles in which its use has important ecological consequences (Slansky and Scriber 1985). The selection of the period (e.g., the whole cycle, a stage, or one or two instars) to measure consumption and utilization is important. Periods defined physiologically offer the advantage of being able to be reproduced and be compatible with results from other experiments.

2.2.2 Quantity of Food Consumed

This parameter results from the difference between the amounts of food offered to the insect at the beginning of the experiment and what is left over at the end of the study period. The starting weight has to be determined as fresh weight with the dry weight obtained from the fresh and the dry weight of an aliquot, which should be as similar as possible to the food offered. When leaves were used, Waldbauer (1964) and Soo Hoo and Fraenkel (1966) found that great precision is possible by cutting leaves into two symmetrical parts along the midrib and using one part as the food and the other as the aliquot. These

aliquots should be kept under the same conditions as the experimental batch. Food quality should be preserved, maintaining the humidity (especially with filter paper) in the recipient used and changing the food regularly (daily). In order that there is no alteration in the food to be offered the insect, ideally the determination should be done on the intact plant material without removing (e.g., leaf) the part to be consumed. Although this can be done by using cages that keep the insect together with the part to be consumed, this procedure is not always feasible. Thus, since the aliquot should be kept under the same conditions, the leaf could absorb water (if that is the case) and there might often be a “negative consumption” (the weight left over greater than the food offered). In order to avoid this problem, when the consumption of very small larvae is determined (first–second instars), then work should be done with groups of insects (Crócomo and Parra 1985). These errors are common, especially in early instars (Crócomo and Parra 1985, Figure 1; Schmidt and Reese 1986). In general, errors are reduced when studies are done measuring all the food consumed during the larval phase. Another aspect to be considered is that enough food should be supplied so that some is always left over. Therefore, previous knowledge of the insect’s feeding habits is necessary so that enough food can be supplied that is sufficient for the study period. Waldbauer (1968), Crócomo and Parra (1979), and Crócomo and Parra (1985) proposed a series of formulae to determine the weight of food ingested, based on area or weight, but there are large differences between the methods (Kogan 1986).

2.2.3 Weight Gains by the Insect

Since the insect’s dry weight cannot be measured at the start of the experiment, it is estimated from the percentage of dry weight of an aliquot of an identical larva, dried to constant weight (55°C–60°C). Very small larvae, such as some noctuids, should be weighed in batches of 100 because their very light weight does not register on normal balances (except for highly sensitive microbalances). Larvae should preferably be killed quickly thus avoiding the liberation of feces, or by freezing in a “freezer” or by immersing in liquid nitrogen, before drying the insect. The moment of weighing is fundamental to avoid errors. The food residue that remains in the gut can, at the beginning or at the end of the experiment, result in errors in determining weight gain. The gut may be empty before or soon after ecdysis, so that in general insects empty it before each molt. Keeping insects without feeding for a certain time does not always result in the elimination of all the feces (Waldbauer 1968), and some, when kept without food, retain more feces than the food they received due to the stress caused by interrupting feeding. Ecdysis can lead to errors of determination of weight gains. Thus, the insect reaches a maximum weight in each instar and loses

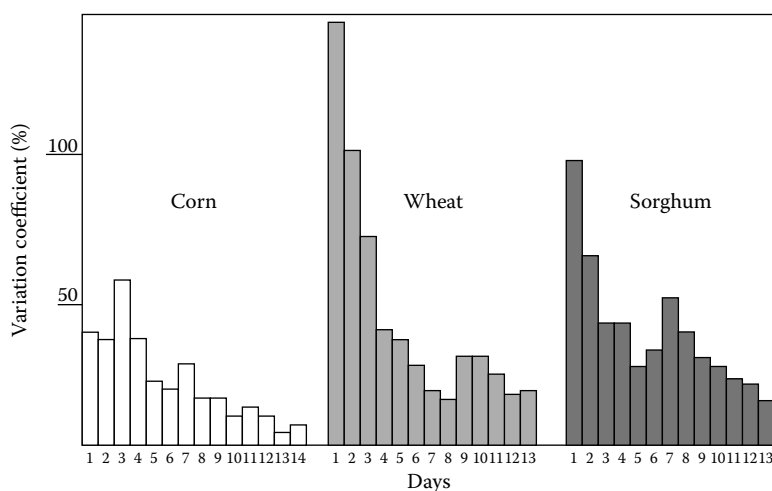


FIGURE 2.1 Coefficient of variation (CV) of the mean daily accumulated consumption of *Spodoptera frugiperda* larvae reared on corn, wheat, and sorghum. Temperature: 25°C ± 2°C, relative humidity: 60% ± 10%, and 14 h photophase. (From Crócomo, W. B., and J. R. P. Parra, *Rev. Bras. Entomol.*, 29, 225–60, 1985.)

weight during the molt because the molted cuticle and the energy used in ecdysis contributes to losses, which reach 45% (Waldbauer 1962). For studies with only one instar, the final instar should be preferred owing to the large amount of food consumed that will facilitate the weighings. The weight gain is calculated by subtracting the weight at the beginning of the experiment from that reached at the end.

2.2.4 Measuring Feces

Feces' dry weight can be measured directly, taking care to make frequent collections and dry the feces immediately to avoid decomposition and fungal growth. Feces fresh weight is difficult to measure due to water losses or gains. Feces of larval *Automeris* sp. (Lepidoptera) lose around 26% of their fresh weight in 24 hours (Waldbauer 1968). There are cases where it is difficult to separate out the feces, especially in artificial diets, because they are mixed in with the food. In these cases, the recommendation is to invert the rearing recipient so that the fecal pellets are collected in the lid. There are cases, such as in studies on stored grain pests, where it is impossible to separate the feces from the food. In these cases, indirect methods are used, such as the uric acid method (see uric acid method).

In the Department of Entomology and Acarology of ESALQ (Escola Superior de Agricultura Luiz de Queiroz), University of São Paulo (USP), in order to calculate these indices, special cards are used to collect the necessary data from the studies with artificial diets; today, information technology permits each person to elaborate a model for registering data.

2.3 The Meaning of the Different Nutritional Indices

2.3.1 Relative Consumption Rate

The relative consumption rate (RCR) represents the quantity of a food ingested per milligram of insect body weight per day, and is expressed as mg/mg/day. It can be altered in function of the amount of water in the food or the physical–chemical properties of the diet. Although insects consume a large percentage of food (more than 75%) in the last instar, in relation to the total amount of food consumed, the consumption is, proportionally to the size, greater in the first instars (Figure 2.2a and Table 2.2).

2.3.2 Relative Metabolic Rate

The relative metabolic rate (RMR) represents the quantity of food spent in metabolism per milligram of body weight (biomass of the insect per day) and is expressed in mg/mg/day (Figure 2.2b).

2.3.3 Relative Growth Rate

The relative growth rate (RGR) indicates the gain in biomass of the insect in relation to its weight and is expressed as mg/mg/day. It depends on host quality, the physiological state of the insect, and environmental factors (Figure 2.2c).

2.3.4 Efficiency of Conversion of Ingested Food

The efficiency of conversion of ingested food (ECI) represents the percentage of food ingested that is transformed into biomass. This index tends to increase up to the last instar. In the last instar, there are physiological changes and an extra energy expenditure in the stage before pupation, which provokes a proportionally lower weight gain in the insect in this instar (Figure 2.2d).

2.3.5 Efficiency of Conversion of Digested Food

The efficiency of conversion of digested food (ECD) is an estimate of the conversion of assimilated material into biomass by the biological system (represents the percentage of ingested food that is converted

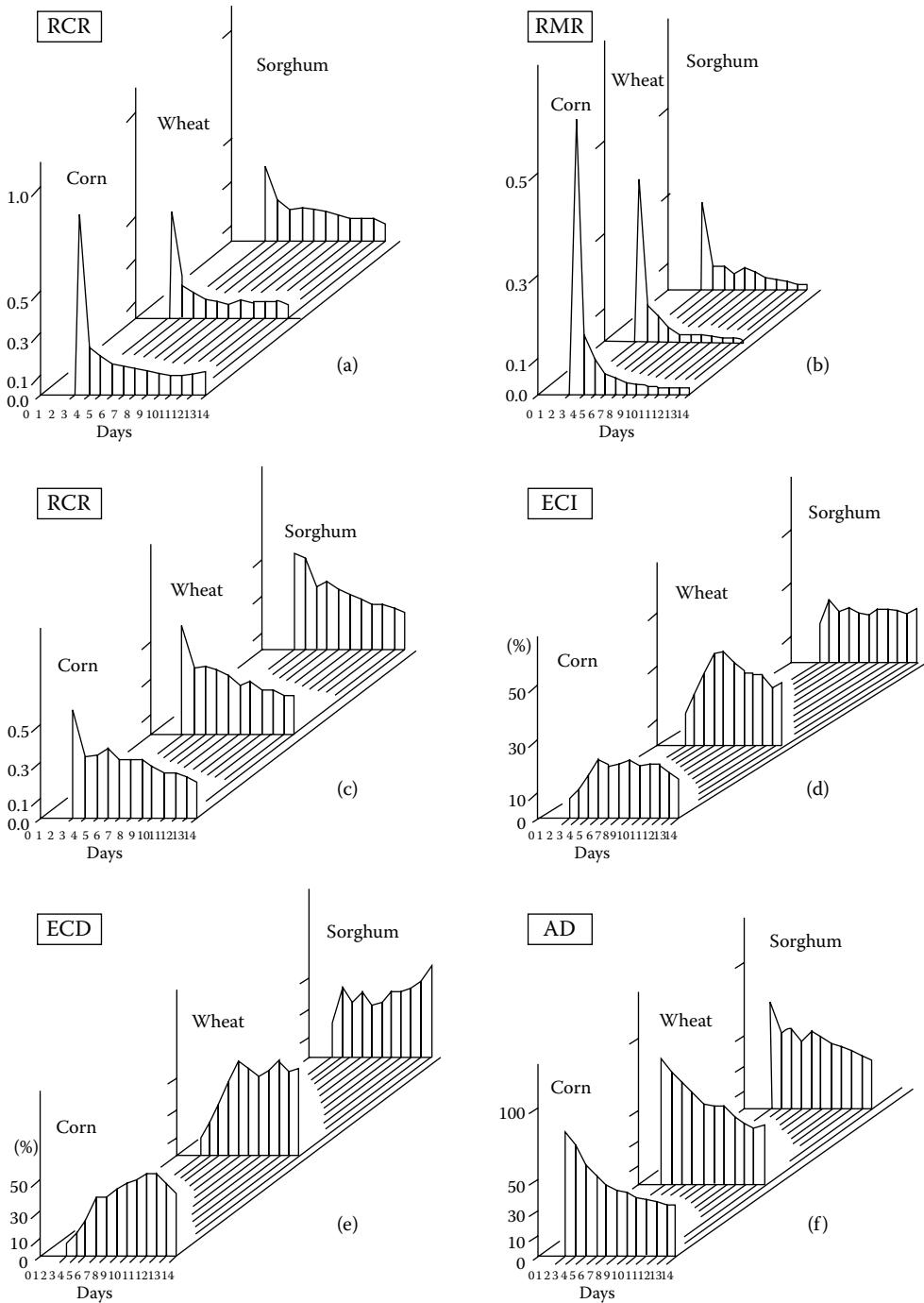


FIGURE 2.2 (a) Relative consumption rate (RCR), (b) relative metabolic rate (RMR), (c) relative growth rate (RGR), (d) efficiency of conversion of ingested food (ECI), (e) Efficiency of Conversion of Digested Food (ECD), and (f) approximate digestibility (AD) of *Spodoptera frugiperda* caterpillars feeding on leaves of corn, wheat, and sorghum. Temperature: $25^{\circ}\text{C} \pm 2^{\circ}\text{C}$, relative humidity: $60\% \pm 10\%$, and 14 h photophase. (From Crócomo, W. B., and J. R. P. Parra, *Rev. Bras. Entomol.*, 29, 225–60, 1985.)

TABLE 2.2

Food Consumed (%) per Instar of the Total Food Consumed during the Larval Stage

Insect and Food	% of Total Consumption per Instar						Reference
	I	II	III	IV	V	VI	
<i>Agrotis orthogonia</i> *							Waldbauer (1968)
<i>Triticum aestivum</i>	0.21	0.42	2.3	8.70	31.60	56.80	
<i>T. durum</i>	0.15	0.48	3.10	9.10	32.90	54.20	
<i>Protoparce sexta</i> †							
Tobacco leaves	0.08	0.53	1.90	10.50	86.40	–	Waldbauer (1968)
<i>Agrotis ipsilon</i> ‡							
Corn leaves	0.06	0.18	0.77	2.60	10.40	86.00	Waldbauer (1968)
<i>Pseudoplusia includens</i> §							
Soybean leaves	0.60	0.35	2.33	6.53	14.96	75.08	Kogan and Cope (1974)
<i>Eacles imperialis magnifica</i> ‡							Crócomo and Parra (1979)
Coffee leaves	0.37	1.43	3.78	15.13	84.87	–	
<i>Lononia circumstans</i> ‡							D'Antonio and Parra (1984)
Coffee leaves	0.18	0.46	1.30	4.14	13.90	80.02	
<i>Alabama argillacea</i> *							Carvalho and Parra (1983)
Cotton leaves	–	–	7.90§	11.26	81.00	–	
IAC-18							
<i>Erinnyis ello ello</i> *	0.37	0.93	3.49	15.38	79.83	–	Reis F° (1984)

* Measurement in dry weight.

† Measurement in fresh weight.

‡ Measurement in area.

§ Consumption from first to third instar.

into biomass). The ECD increases with insect development (Figure 2.2e). Variations can occur with age, as a variation of the RMR, lipid synthesis, and the rate of assimilation and activity by the organism (Slansky and Scriber 1985). The opposite of the EDC indicates the percentage of food metabolized into energy for maintaining life. Therefore, 100-ECD corresponds to the metabolic cost. Almeida and Parra (1988) demonstrated this cost to be greater at higher temperatures for *D. saccharalis* maintained on an artificial diet.

2.3.6 Approximate Digestibility (AD)

The approximate digestibility (AD) represents the percentage of food ingested that is effectively assimilated by the insect. This index is an approximation of the actual nutrient absorption through the intestinal walls, since the presence of urine in the feces makes accurate measurements of digestibility more difficult. In this case, fecal weight does not only represent the noningested food but added to this are the metabolic products discharged in the urine. The values obtained for approximate digestibility are, therefore, always less than the corresponding values of actual digestibility. This difference is minimal in phytophages. In general, digestibility diminishes from the first to the last instar (Figure 2.2f), with an inverse relationship between AD and ECD, since the smaller larvae digest the food better because they tend to select it, avoiding leaf veins that contain large quantities of fibers and feeding almost exclusively on parenchymatous tissue. Thus, most of the food consumed by the young larvae is spent in energy for maintenance and only a little is used for growth. In the older larvae, consumption is indiscriminate and includes leaf veins. In this way, less food is used for energy and a large amount is incorporated into body tissue, thus increasing the ECD. Digestibility is also affected by an unsuitable nutrient balance, water deficiency, or the presence of allelochemicals (Beck and Reese 1976). Nutritional indices have been discussed in great detail by Waldbauer (1968), Kogan and Cope (1974), Scriber and Slansky (1981), and Cohen (2004). According to Slansky and Scriber (1982) these nutritional indices vary considerably as follows: RGR = 0.03–0.39 mg/day.mg, RCR = 0.04–2.3 mg/day.mg, AD = 9%–88%, ECD = 18%–89%,

and $ECI = 0.6\%–68\%$. A summary of these values for *S. frugiperda* fed on sorghum, corn, and wheat is shown in Figure 2.3.

Rates and efficiencies for the consumption of specific compounds can also be calculated. Waldbauer (1968), and Slansky and Feeny (1977) proposed the following terms to describe the use of nitrogen (N): rate of N; that is, milligrams of biomass of N gain/day (NAR); consumption rate of N, that is, milligrams of N ingested/day (NCR); and use efficiency of N (NUE,) which is calculated as follows:

$$NUE = \frac{\text{milligrams of biomass of N gained}}{\text{milligrams of N ingested}} \times 100$$

The rate of biomass of N gained is obtained by multiplying the dry weight gained by the mean percentage of N in a control larva. The conversion efficiency of N assimilated in biomass of N of the larva assumes that it is 100%. Since part of the N assimilated is feces, such as uric acid, allantoinic acid, or other compounds, the NUE is underestimated from these calculations. Gamundi (1988) observed that the NUE is greater in soybean leaves (upper or lower) compared to Bragg soybean pods for *Anticarsia gemmatilis* Hübner, with less efficiency of nitrogen use in the larvae from pods compared to those from leaves. Lee

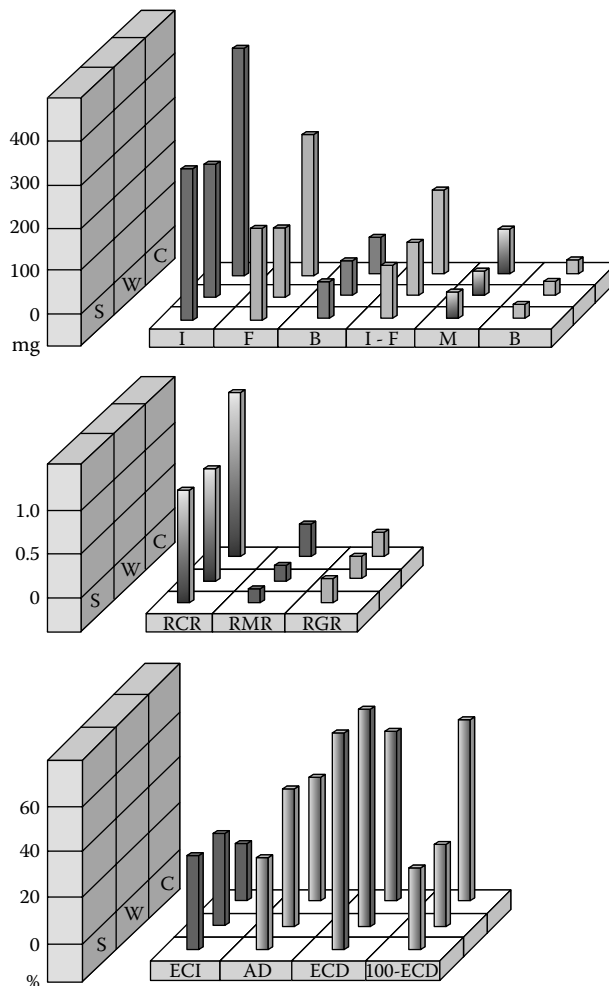


FIGURE 2.3 Means of parameters and nutritional indices obtained for *Spodoptera frugiperda* larvae fed with corn (C), wheat (W), and sorghum (S). Temperature: $25^{\circ}\text{C} \pm 2^{\circ}\text{C}$, relative humidity: $60\% \pm 10\%$, and 14 h photophase. (From Crócomo, W. B., and J. R. P. Parra, *Rev. Bras. Entomol.*, 29, 225–60, 1985.)

et al. (2004) studied the difference between the solitary and gregarious phases of *Spodoptera exempta* (Walker) and observed that the gregarious phase showed greater nitrogen conversion efficiency in a diet with a minimum of protein, and accumulated more lipids per quantity of carbohydrates consumed in a diet deficient in carbohydrate. Thompson and Redak (2005) studied the feeding behavior and nutrient selection in *Manduca sexta* (Cr.), and the alterations induced by parasitism of *Cotesia congregata* (Say). Unparasitized larvae regulate the absorption of proteins and carbohydrates in varying proportions. They consume equal amounts of nutrients independent of the protein:carbohydrate ratio and grow the same. If the level of the nutrient combination is reduced, the caterpillar abandons the regulation and feeds at random. Parasitized caterpillars do not regulate food absorption. Nutrient consumption varies considerably but growth is unaffected. If caterpillars are offered a choice of diet containing equal amounts of casein and sucrose but with variable fat (corn oil), they fail to regulate fat absorption although both the parasitized and the unparasitized caterpillars prefer the diet containing the high fat content.

2.4 Methods Used to Measure Food Intake and Utilization

2.4.1 Direct Method

2.4.1.1 Gravimetric

The gravimetric method is the most used method for measuring food intake and utilization. Although it demands a lot of time, it only needs a balance and a drying oven. It is difficult to measure food use in insects maintained on artificial diets or in situations where they live within the food substrate such as stored product pests, miners, borers, stem and fruit borers, and coprophages (Kogan 1986).

2.4.2 Indirect Methods

With indirect methods, products are added to diets, allowing the determination of consumption and use indirectly. The compound to be added should neither be toxic at the concentrations used nor be metabolized by the insects. Various compounds have been used, including lignin, amide, substances that occur in plant pigments ("chromogens"), coloring agents, iron oxide, barium sulfate, chromic oxide, and radioactive materials.

2.4.2.1 Colorimetric Methods

Dyeing agents are used to determine food consumption and use, such as chromic oxide (McGinnis and Kasting 1964), calco oil red N-1700 (Daum et al. 1969), solvent red 26 and soluble blue (Brewer 1982) and amaranth-acid red 27 (Hori and Endo 1977; Kuramochi and Nishijima 1980), quoted by Kogan (1986).

Among the many dyeing agents used, calco oil red N-1700 and solvent red 26 (Keystone Aniline and Chemical, Chicago, IL) give the best results. This method was developed by Daum et al. (1969) to measure ingestion by adult *Anthonomus grandis* Boh. The procedure is as follows: the dyeing agent is added to the diet at the rate of 100 to 1000 ppm and, in order to facilitate incorporation, it is dissolved in oil (e.g., corn, cotton, or wheat germ oil) (Hendricks and Graham 1970). The marking becomes more visible when the coloring agent is dissolved in corn or cotton oil compared to alcohol or acetone; larvae, prepupae, and pupae are washed with acetone to avoid external contamination by the dyeing agent. The calco oil red concentrated in larvae, pupae, and feces is extracted with tissue macerators and with acetone, the solution filtered, and the concentrations measured in a spectrophotometer, adjusting the wavelength scale to 510 nm (Daum et al. 1969). If necessary, the coloring agent residue on the filter paper used should be extracted in a Soxhlet apparatus. Wilkinson et al. (1972) showed that this coloring agent can be added to diets of *Pieris rapae* (L.), *Helicoverpa zea* (Boddie), and *Trichoplusia ni* (Hübner) larvae, without harming development; this was also observed by Gast and Landin (1966), Lloyd et al. (1968) and Daum et al. (1969) for *A. grandis* and by Hendricks and Graham (1970) and Jones et al. (1975), to *H. virescens* and *H. zea*, respectively. Parra and Kogan (1981) observed that calco oil red, at the rate of 1 g/liter of artificial diet dissolved in wheat germ oil, affected food intake by *P. includens*, reducing it by approximately 50% compared to the control.

The approximate digestibility (AD) can be calculated without collecting the feces or measuring the food consumed, where:

$$AD = \frac{M_F - M_A}{M_F}$$

M_F = concentration of marker in the feces

M_A = concentration of marker in the food

If the weights of the feces or food consumed are known then the weight of food consumed can be calculated = $\frac{MF}{MA} \times \text{wt. of feces}$ or $\text{wt. of feces} = \frac{MA}{MF} \times \text{wt. of food consumed}$.

The chromic oxide method consists of adding a known concentration of chromic oxide to the diet (4%) (dissolved in a basic medium) and determining its concentration in the feces by liquid oxidation of Cr_2O_3 to $\text{Cr}_2\text{O}^{2-}_7$, followed by a colorimetric measurement of the dichromate ion with diphenylcarbazide. Samples are digested with a mixture of perchloric acid–sulfuric acid–sodium molybdate for 30 minutes. The cold material digested is diluted with diphenylcarbazide and the mean absorbance of 540 nm, compared to a control consisting of 9.5 ml of H_2SO_4 0.25 N and 0.5 ml of diphenylcarbazide. This method was described by McGinnis and Kasting (1964) for measuring the approximate digestibility of *Agrotis orthogonia* Morrison (Lepidoptera). According to these authors, this method was faster, more practical, and better than the gravimetric method. However, Daum et al. (1969) consider it an empirical chemical method that is easily influenced by the reaction time and temperature. Further disadvantages include the use of dangerous acids, such as perchloric and sulfuric acids, and the need for someone trained in analytical chemistry. McMillian et al. (1966) showed that chromic oxide inhibited feeding of *H. zea* and *S. frugiperda*. Instead of using colorimetric determinations with diphenylcarbazide, Parra and Kogan (1981) measured chromium directly with atomic absorption spectroscopy. With this method, the following formulae are used: food consumed (F) = (E × %Cr in the feces) + (B × %Cr in the insect), where F = food consumed, B = insect weight gain, and E = feces.

The food consumed is calculated indirectly and the other parameters are measured beforehand. From these values the ECI and the ECD can be calculated. Approximate digestibility (AD) = 1. (% of Cr in the medium/% of Cr in the feces.)

2.4.2.2 Isotope Method

Various isotopes have been used as markers in nutritional studies. Crossley (1966) used cesium 137 to measure the daily consumption of the third instar *Chrysomela knaki* Brow (Coleoptera) larvae feeding on *Salix nigra*. Marked sucrose or cellulose were added to the diet to estimate the food consumption of larval instars (first and fifth) of the lepidopteran, *A. orthogonia* (Kasting and McGinnis 1965), and at the end of the feeding period its feces and CO_2 were measured by radioactivity.

Food consumption by the migratory grasshopper was determined from Na through an abdominal injection (Buscarlet 1974). The CO_2 measured by radioactivity can be very high because in certain diets, mostly in those that are unsatisfactory, it can reach 75% of the total food ingested. Parra and Kogan (1981) observed for the *P. includens* larva, CO_2 equal to 32% of total consumption up to the sixth instar and 37% up to pupation. They used (^{14}C) glucose to measure the consumption and use by *P. includens* in an artificial diet. This glucose was dissolved in acetone and the solution, with an activity of 2.1×10^6 cpm/ml, was added to the artificial medium. Determinations were made during the complete larval development up to pupation with two larvae/rearing recipients. The CO_2 emitted was collected at sites containing 75 ml of carb-sorb. The equipment setup, measurement of the activity in a liquid scintillation counter, and the calculations have been described in detail (Parra and Kogan 1981; Kogan 1986).

2.4.2.3 Uric Acid Method

Bhattacharya and Waldbauer (1969a,b, 1970) used the uric acid method (spectrophotometer-enzymatic method) to measure food intake and utilization. This method is indicated when it is difficult to separate

the feces from the medium, such as with stored products pests. The method is based on the fact that uric acid, which has an absorption peak of 292 μm is, in the presence of uricase, oxidized to allantoin, which absorbs less light of the same wavelength. Therefore, the concentration of uric acid can be calculated from the reduction in absorbance after treating with uricase. Extraction is made with an aqueous solution of lithium carbonate and the calculation of mg feces in the mixture is given by the formula:

$$\text{mg feces} = \frac{\text{mg uric acid in mixture}}{\text{mg uric acid per mg feces}} \downarrow + \text{feces wt. of sample}$$

Various authors have used this method to measure the food consumption of insects other than stored products pests. Chou et al. (1973) used it to measure food utilization by *Argyrotaenia velutinana* (Walker) and *H. virescens* and Cohen and Patana (1984) used it for *H. zea*.

2.4.2.4 Trace Element Method

The trace element method is a qualitative method that can, together with quantitative methods, be used in nutritional studies. Rubidium and cesium are used to mark insects in ecological studies (Berry et al. 1972; Stimman 1974; Shepard and Waddill 1976; van Steenwyk et al. 1978; Alverson et al. 1980; Moss and van Steenwyk 1982). These elements are rapidly absorbed by plant tissue and transferred to the insect through feeding. They can be detected by atomic absorption spectroscopy and knowing the concentration of the trace element in the food, insect, and feces, indices can be determined as in the chromic acid method (colorimetric method).

2.4.2.5 Immunological Method

The immunological method was used by Lund and Turpin (1977) to determine the consumption of *Agrotis ipsilon* larvae by carabids, Sousa-Silva (1980) to evaluate consumption of *D. saccharalis* larvae by predators, and Sousa-Silva (1985) in studies with *Deois flavopicta* (Stal) (Homoptera). Calver (1984) revised immunological techniques to identify diets.

2.4.2.6 Calorimetric Method

Food use can be determined based on the caloric equivalent instead of units of mass (Schroeder 1971, 1972, 1973, 1976; Stepien and Rodriguez 1972; Van Hook and Dodson 1974; Bailey and Mukerji 1977; Slansky 1978). Loon (1993), using the calorimetric method observed that *Pieris brassicae* L. (Lepidoptera: Pieridae) reared on artificial diet, developed with a greater metabolic efficiency than when reared on the host plant, *Brassica oleracea*. These differences were not detected when he used the gravimetric method. According to the author, metabolic efficiencies derived from calculations from gravimetric data are subject to random errors that distort the determination of the metabolic efficiency in plant studies. The heat of combustion of larvae, feces, and the medium is determined in a calorimeter using oxygen. This combustion heat is defined as being the energy liberated as heat when a substance is completely oxidized to CO_2 and H_2O . Waldbauer (1968) proposed the following indices:

Coefficient of metabolized energy (CME)

$$\text{CME} = \frac{\text{Gross energy in food consumed} - \text{gross energy in feces}}{\text{Gross energy in food consumed}}$$

Storage efficiency of energy ingested (ESI) (E)

$$\text{ESI (E)} = \frac{\text{Gross energy stored in body}}{\text{Gross energy in food consumed}} \times 100$$

TABLE 2.3Comparison of the Use of Dry Material and Energy by *Bombyx mori*

Up to the End of the Fifth Instar				Up to the Recently Emerged Adult			
Dry Weight (mg)		Energy (cal)		Dry Weight (mg)		Energy (cal.)	
AD	37	CME	42	AD	37	CME	42
ECI	23	ESI (E)	28	ECI	8	ESI (E)	12
ECD	62	ESM (E)	67	ECD	22	ESM (E)	28
Instar		CME		ESI (E)		ESM (E)	
I		52		32		61	
II		49		29		90	
III		42		28		66	
IV		44		29		66	
V		42		28		66	

Source: Hiratsuka, E., *Bull. Seric. Exp. Sta.*, 1, 257–315, 1920; Waldbauer, G. P., *Adv. Insect Physiol.*, 5, 229–88, 1968.

Note: The large quantity of energy stored in the fifth instar is to supply the pupal and adult stages, which do not feed.

Storage efficiency of metabolized energy (ESM) (E)

$$\text{ESM (E)} = \frac{\text{Gross energy stored in body}}{\text{Gross energy in food consumed} - \text{gross energy in feces}} \times 100$$

Although energy use is greater than that of dry matter, both determinations are comparable (Table 2.3).

Slansky (1985) referred that more than 80% of the values for AD (CME), ECI (ESI), and ECD (ESM) calculated using energy values are greater than these indices calculated on the basis of dry weight, based on data from more than 65 species. The greatest values for AD based on energy are due to the large energy content of food and feces and those for ECI and ECD are due to the large energy content of insect biomass in relation to the food assimilated and ingested. The sources of error involved in the conversion of dry weight into energy are discussed (Slansky 1985).

Loon (1993) observed that the ECD calculated by the gravimetric method from feeding by *Pieris brassicae* (L.) was 58.34% and 57.10% in an artificial diet and a natural diet of *Brassica oleraceae*, respectively, with no difference between the values. On the other hand, when the respirometer method (calorimeter) was used, there were differences in the ECD values for the two substrates (9.19% and 11.72%, respectively), showing a limitation of the gravimetric method for studying phytophage food intake and utilization on plants.

Parra and Kogan (unpublished) observed a large quantity of residues of Si and Mn, probably originating from the wire used in this method's combustion process, as well as Mg, Al, and Ca from feces and the artificial medium (Table 2.4). Since the amount of residues was high (4.74% in artificial diet and 9.21% in feces), the variations in AD, ECI, and ECD between the gravimetric and calorimetric methods may be attributed to these residues in the feces and in the artificial diet. These elements were included in the gravimetric method and excluded from the calorimetric analysis. Besides this, there is usually a loss of

TABLE 2.4Residues of the Combustion of Feces and Artificial Diet of *Pseudoplusia includens* Analyzed by Jarrel-Ash Plasma Atomcomp Model 975, Compared with the Wire Used to Measure the Combustion Heat

	Quantity (mg/g)				
	Si	Mg	Al	Mn	Ca
Feces	15.6	14.0	5845	535.7	154.7
Artificial diet	17.7	16.4	5583	618.8	145.2
Wire	23.4	62.6	924	1.7	424.0

Source: Parra and Kogan, unpublished.

TABLE 2.5

Gross Energy (Calories) in Food Consumed, in Feces, and Stored in the Body of the *Pseudoplusia includens* Caterpillar

Stage	Gross Energy in Food Consumed	Gross Energy in Feces	Gross Energy Stored in the Body
I–VI instar	1107.48 ± 119.47	429.80 ± 55.82	398.31 ± 25.65
I–Pupation	1251.98 ± 83.26	516.03 ± 43.59	365.75 ± 37.35

Source: Parra and Kogan, unpublished.

calories corresponding to the loss of lipids during the preparation of the pellets in the calorimetric process. In general, these lipids are not extracted before pelletizing (Schroeder 1972, 1973).

The values for AD, ECI, and ECD in Parra and Kogan's unpublished study based on gravimetric and calorimetric methods decreased when measured until pupation, compared to measurements made until the sixth instar (Table 2.5). The high quantity of stored energy up to the final instar is related to the gross energy stored for the pupal stage. The decrease in total energy was due to pupal metabolic activity that is not compensated by additional food "consumption." However, coinciding with results quoted in the literature, the nutritional indices obtained in the study were superior to those obtained gravimetrically (Table 2.6).

In studies of ecological energetics, some symbols of energy balance are used, based on Klekowski (1970) (cited by Stepien and Rodriguez (1972)). Thus, $C = P + R + U + F = D + F$, $D = P + R + U$, and $A = P + R$ [C = food consumption, P = production (body, exuvia, products from reproduction), R = respiration, U = urine and digestion residues, F = nonabsorbed part of consumption, D = digestion (part of the digested and absorbed food), FU = when difficult to separate F from U (considered together in these cases), A = assimilation (sum of production and respiration, food absorbed less feces)].

An organism's efficiency in using energy is evaluated by the following indices:

$$U^{-1} = \frac{P + R}{C} = \frac{A}{C} = \text{assimilation efficiency};$$

$$K_1 = \frac{P}{C} = \text{efficiency of use of energy consumed for growth (index of efficiency of gross production) and}$$

$$K_2 = \frac{P}{P + R} = \frac{P}{A} = \text{efficiency of use of energy for growth (efficiency index of net production)}.$$

Energy efficiency within and between trophic levels, including the determination of lipids, respiration, and the energy content of biological materials can be very useful for refining details in studies involving nutritional ecology (Slansky 1985). Details of these calorimetric measurements can be found in Petruszewicz and MacFadyen (1970) and Southwood (1978).

TABLE 2.6

Comparison of the Values for AD, ECI, and ECD Determined by the Gravimetric and Calorimetric Methods

<i>Pseudoplusia includens</i>		Indices		
Period	Method	AD	ECI	EDC
I–VI instar	G	56	25	44
	C	61	36	60
I–Pupation	G	52	22	43
	C	59	29	50

Source: Parra and Kogan, unpublished.

Note: G = Gravimetric, C = calorimetric.

According to Waldbauer (1972), the indices used in ecological energetics correspond to those used by insect nutritionists. Thus, U^{-1} is equivalent to AD, K_{-1} to ECI, and $K_{2.10}$ to ECD. The ecologists calculate the caloric values of R (respiration) (using respirometers) from the oxygen consumption of the study organism. This R includes the energy spent in metabolism and activity, and also the energy lost in the urine. R can be determined gravimetrically since it is equivalent to the caloric content of ingested food less the caloric content of the feces (Waldbauer 1972).

2.5 Comparison of Methods

The indirect methods are more sophisticated and are discussed by Waldbauer (1968), Parra (1980), and Kogan (1986). A comparative study between them was done by Parra and Kogan (1981) and Kogan and Parra (1981). A comparison of the precision of the results is shown in Table 2.7 and general characteristics of the different methods in Table 2.8. The time needed to process samples in the indirect methods varied from six (radioisotopes) to 18 times (Cr_2O_3) compared to the gravimetric method. All the indirect methods require a balance as well as other equipment for specific determinations. No greater precision was obtained from indirect methods, and with the calorimetric method where calco oil red was used, it was also observed that this dyeing agent affected insect development when added to the diet. Therefore, based on this study, the gravimetric method is the most suitable and cheapest of those studied. There are specific cases, such as for stored products pests, where indirect methods are preferable, since the separation of feces and food is impractical. In these cases, the uric acid method must be used (Bhattacharya and Waldbauer 1969a,b).

Kogan & Parra (1981) indicated the main sources of variation in these types of experiments: (1) individual insect variability in a population, (2) variations in diet humidities, (3) behavioral feeding

TABLE 2.7

Precision of Measurements of ECI and ECD for *Pseudoplusia includens* Reared on Artificial Diets by Five Methods^a

Method	Precision (%)	
	ECI	ECD
Gravimetric	85.7	85.7
Colorimetric (Calco oil red) (COR)	33.3	34.7
Colorimetric ^b (Cr_2O_3)	80.0	82.1
Radioisotope	60.0	19.4
Calorimetric	88.9	80.0

Source: Parra, J. R. P., and M. Kogan, *Entomol. Exp. Appl.*, 30, 45–57, 1981.

^a Precision = $(1 - \text{standard deviation/mean}) \times 100$.

^b Done by atomic absorption.

TABLE 2.8

General Characteristics and Costs of Five Methods for Measuring the Food Intake and Utilization (of Artificial Diet) by *Pseudoplusia includens*

Method	Specimen	CO ₂	Diet	Cost	
				Equipment (U.S. \$)	Time
Gravimetric	Live or dead	No	Natural or artificial	\$1,300.00	5 min/individual
COR	Dead	No	Artificial	\$1,500.00	1 hour/individual
Cr_2O_3	Dead	No	Artificial	\$7,000.00	1.5 hour/individual
Radioisotope	Dead	Yes	Natural or artificial	\$10,000.00	30 min/individual
Calorimetric	Dead	No	Natural or artificial	\$5,000.00	1 hour/individual

Source: Parra, J. R. P., and M. Kogan, *Entomol. Exp. Appl.*, 30, 45–57, 1981.

differences resulting from adding components (coloring agents, chemical substances) to diets, (4) differences in diet utilization after ingestion, and (5) differences in sample handling.

Studies on food consumption and use based on nutritional indices conducted in Brazil are listed (Table 2.9). They include comparison of food substrates (natural and artificial), effect of pathogens or natural enemies on quantitative nutrition, and effect of different temperatures on nutrition and feeding behavior in a host.

TABLE 2.9

Some Studies Carried Out in Brazil Regarding Insect Food Intake and Utilization with the Indices That Were Determined

Insect	Host	Indices						Reference
		RCR	RMR	RGR	AD	ECI	ECD	
<i>Eacles imperialis magnifica</i>	Coffee	x	—	x	x	x	x	Crócomo and Parra (1979)
<i>Spodoptera latifascia</i>	Cotton, lettuce, soybeans	—	—	—	x	—	—	Habib et al. (1983)
<i>Spodoptera frugiperda</i>	Artificial diets	x	—	x	x	x	x	Susi et al. (1980)
<i>Anticarsia gemmatilis</i>	Artificial diets	x	—	x	x	x	x	Silva and Parra (1983)
<i>Agrotis subterranea</i>	Kale	x	—	x	x	x	x	Vendramim et al. (1983)
<i>Alabama argillacea</i>	Cotton	x	—	x	x	x	x	Carvalho and Parra (1983)
<i>Lonomia circumstans</i>	Coffee	x	—	x	x	x	x	D'Antonio and Parra (1984)
<i>Heliothis virescens</i>	Artificial diets	—	—	—	x	x	x	Mishfeldt et al. (1984)
<i>H. virescens</i>	Cotton	x	—	x	x	x	x	Precetti and Parra (1984)
<i>S. frugiperda</i>	Artificial diets	—	—	—	x	x	x	Parra and Carvalho (1984)
<i>Erinyis ello ello</i>	Rubber	x	—	x	x	x	x	Reis F° (1984)
<i>S. frugiperda</i>	Corn, wheat, sorghum	x	x	x	x	x	x	Crócomo and Parra (1985)
<i>Diatraea saccharalis</i>	Artificial diets	—	—	—	x	x	x	Mishfeldt and Parra (1986)
<i>D. saccharalis</i>	Artificial diets	—	—	—	x	x	x	Martins et al. (1986)
<i>S. frugiperda</i>	Artificial diets	x	—	x	x	x	x	Genthon et al. (1986)
<i>Apanteles flavipes</i>	<i>D. saccharalis</i>	—	—	—	x	x	x	Pádua (1986)
<i>S. eridania</i>	Sweet potato and <i>Mimosa scabrella</i>	x	x	x	x	x	x	Matana (1986)
<i>D. saccharalis</i>	Artificial diets	x	—	x	x	x	x	Almeida (1986)
<i>Pseudaletia seauax</i>	Artificial diets	x	—	x	x	x	x	Salvadori (1987)
<i>A. gemmatilis</i>	Soybeans	x	x	x	x	x	x	Zonta (1987)
<i>S. frugiperda</i>	Corn	x	x	x	x	x	x	Oliveira (1987)
<i>A. gemmatilis</i>	Soybeans	x	x	x	x	x	x	Gamundi (1986)
<i>S. frugiperda</i>	Corn	x	x	x	x	x	x	Nalim (1991)
<i>D. saccharalis</i> , <i>H. virescens</i> and <i>S. frugiperda</i>	Artificial diets				x	x	x	Souza et al. (2001)
<i>S. frugiperda</i>	Corn	—	—	—	x	x	x	Fernandes (2003)

Note: x = determined, — = not determined.

2.6 Interpretation of Nutritional Indices Values

The interpretation of results from quantitative nutritional research based simply on nutritional indices is not easy. In general, the highest indices indicate a greater nutritional suitability but the presence of allelochemicals, or even the interaction between nutrients and allelochemicals, can lead to erroneous results or interpretations. Sometimes, certain factors can cause lower digestibility that can result in the food being consumed in large quantities but with low growth rates. Besides this, the insect often shows a capacity to compensate a low consumption through greater use of the food. All these factors can alter the values of the nutritional indices cited and make their interpretation difficult. Thus, it is often necessary to associate the index values obtained with biological data from different food substrates or even based on data on insect behavior. In this case, other methods, such as cluster analysis, should be used (Kogan 1972; Parra and Carvalho 1984; Precetti and Parra 1984). Obviously, there are rare cases in which a simple analysis involving a test to compare means is sufficient to arrive at a satisfactory conclusion. The analyses done for the indices are based on the supposition that there is an isometric relationship between the variables in the numerator and the denominator, which does not always occur in biology. Raubenheimer and Simpson (1992) proved that when the relationship between the numerator and denominator of a nutritional index is not linear, the statistic *F* and its level of significance are altered, which can compromise the conclusion of a nutritional study. Another consequence of this fact is that the statistical power of the Tukey test to detect small treatment differences is much reduced using the indices. Since the interactive effect of the denominator and treatment are not measured in the analysis of the indices, the conclusions about the treatment effects are compromised. In spite of the advance of research on nutritional ecology (Slansky and Rodriguez 1987a), many conclusions are speculative today and need further studies to be properly supported.

Raubenheimer and Simpson (1992) presented a covariance analysis as an alternative for comparing treatments, considering one of the nutritional food intake and utilization indices (RCR, RGR, ECI, AD, and ECD) and indicated the RCR as the ideal index. The analysis of covariance (ANCOVA) better satisfies the statistical demands, supplying important information about data that is neglected by using a conventional form of analysis of variance that can lead to errors in evolutionary biology, morphometry, systematics, physiology, and plant ecology. Horton and Redak (1993) discuss the care that has to be exercised when using the ANCOVA. They further suggest that the ANCOVA could be used to evaluate the effect of the larval diet on adult fecundity after adjustments for larval consumption, the effects of the adult diet on fecundity after adjustments for food consumption, or the effects of the larval diet on adult size after adjustments for consumption in the larval stage. The ANCOVA has many advantages when using indices in biological data, including increased power of tests of hypotheses, more information on data groups, greater reductions in the error of the dependent variable, and greater reduction in the incidence of untrue treatment effects. Besides this, it analyzes the interaction of the dependent variable and treatments.

An example of the values of RGR, RCR, AD, ECI, and ECD of a hypothetical consumption of a noctuid lepidopteran on two artificial diets is shown in Table 2.10. Considering the RCR index in the tables referred to from the conventional analysis of variance and from the ANCOVA. From these results, diets A and B differ statistically ($P = 0.0096$) when the ANCOVA is used and do not differ ($P = 0.1280$) when analyzed using Tukey's *t*-test. The SAS program for covariance analysis is presented following Table 2.10.

2.7 Food Consumption and Use for Growth in the Larval Phase

Immatures tend to choose an appropriate food to consume it in balanced proportions to promote optimum growth and development, making originating adults reproductively competitive. This choice involves adaptations and strategies for each species including capacity to compensate for unsuitable conditions.

TABLE 2.10

Values of AD, ECI and ECD, RCR, RGR, Independent Variable Y and Covariance (X) of a Hypothetical Noctuid Lepidopteran on Two Artificial Diets (A and B), with the Respective Analyses of Covariance and Variance for RCR

Diet A						
AD%	ECI%	ECD%	RCR	RGR	Y	COV (X)
42.59	16.91	39.71	0.5914	0.1	0.7333	1.2400
40.03	16.72	41.77	0.5981	0.1	0.8822	1.4750
39.63	16.14	40.73	0.6196	0.1	0.8365	1.3500
43.19	20.09	46.52	0.4978	0.1	0.8536	1.7150
43.78	18.99	43.39	0.5265	0.1	0.7897	1.5000
53.03	16.67	31.44	0.5998	0.1	0.6898	1.1500
50.54	15.08	29.84	0.6631	0.1	0.9483	1.4300
47.53	28.97	60.96	0.3451	0.1	0.6385	1.8500
43.86	18.42	42.00	0.5428	0.1	0.6947	1.2800
42.30	17.14	40.52	0.5835	0.1	0.8752	1.5000
42.42	18.45	43.49	0.5421	0.1	0.9378	1.7300
49.40	17.05	34.51	0.5866	0.1	0.7332	1.2500
63.34	28.00	44.22	0.3571	0.1	0.5428	1.5200
41.28	19.52	47.29	0.5123	0.1	0.5943	1.1600
41.17	21.32	51.79	0.4691	0.1	0.6051	1.2900

Y = independent variable = portion of food ingested by insect = numerator of RCR.

Covariable (X) = (dry weight of insect/2) * experimental time = denominator of RCR.

Diet B						
AD%	ECI%	ECD%	RCR	RGR	Y	COV (X)
99.03	37.65	38.02	0.2656	0.1	0.1859	0.7000
41.76	46.84	112.16	0.2135	0.1	0.7899	3.7000
41.16	16.00	38.87	0.6250	0.1	0.7563	1.2100
34.52	14.50	41.99	0.6898	0.1	0.8140	1.1800
43.94	16.23	36.94	0.6160	0.1	0.7885	1.2800
44.21	16.21	36.66	0.6170	0.1	0.7528	1.2200
40.66	16.46	40.48	0.6075	0.1	0.6926	1.1400
81.70	14.23	17.42	0.7026	0.1	0.6393	0.9100
60.33	11.97	19.83	0.8357	0.1	0.3050	0.3650
51.01	17.25	33.81	0.5798	0.1	0.7654	1.3200
85.35	16.79	19.67	0.5955	0.1	0.6074	1.0200
51.15	10.67	20.86	0.9372	0.1	0.2109	0.2250
96.22	11.20	11.64	0.8931	0.1	0.2590	0.2900

Y = independent variable = portion of food ingested by insect = numerator of RCR.

Covariable (X) = (dry weight of insect/2) * experimental time = denominator of RCR.

Analysis of variance and Tukey test for data on nutritional index RCR for diets A and B.

Causes of Variation	GL	Sum of Squares	Mean Squares	F-Test	Pr > F
Diet	1	0.06080541	0.06080541	2.47	0.1280
Residual	26	0.63968088	0.02460311		
Total	27	0.70048629			

(continued)

TABLE 2.10 (Continued)

Values of AD, ECI and ECD, RCR, RGR, Independent Variable Y and Covariance (X) of a Hypothetical Noctuid Lepidopteran on Two Artificial Diets (A and B), with the Respective Analyses of Covariance and Variance for RCR

Groups	Mean	N	Diet
A	0.62910	13	B
A	0.53566	15	A

Means followed by the same letter do not differ statistically ($P \leq 0.05$)

Analysis of Covariance (ANCOVA) for the data of the nutritional index RCR for the diets A and B.

Causes of Variation	GL	Type I Error	Mean Squares	F-Test	Pr > F
Treatments (Diets)	1	0.21309866	0.21309866	7.92	0.0096
COV (X)	1	0.31338411	0.31338411	11.65	0.0023
COV*DIET	1	0.00017631	0.00017631	0.01	0.9362

SAS Program (9.1) for Analysis of Covariance (ANCOVA) of nutritional indices

```
data ENTO;
input TREAT $ NU CO;
datalines;
DA 0.73333 1.24
DA 0.8822 1.4750
DA 0.8365 1.35
DA 0.8536 1.715
DA 0.7897 1.5
DA 0.6898 1.15
DA 0.9483 1.43
DA 0.6385 1.85
DA 0.6947 1.28
DA 0.8752 1.5
DA 0.9378 1.73
DA 0.7332 1.25
DA 0.5428 1.52
DA 0.5943 1.16
DA 0.6051 1.29
DB 0.1859 0.7
DB 0.7899 3.7
DB 0.7563 1.21
DB 0.8140 1.18
DB 0.7885 1.28
DB 0.7528 1.22
DB 0.6926 1.14
DB 0.6393 0.91
DB 0.3050 0.365
DB 0.7654 1.32
DB 0.6074 1.02
DB 0.2109 0.225
DB 0.2590 0.29
;proc print;
run;
ods html;
ods graphics on;
proc glm data=ENTO;
```

(continued)

TABLE 2.10 (Continued)

Values of AD, ECI and ECD, RCR, RGR, Independent Variable Y and Covariance (X) of a Hypothetical Noctuid Lepidopteran on Two Artificial Diets (A and B), with the Respective Analyses of Covariance and Variance for RCR

```
class TRAT;
model NU=TRAT CO TRAT*CO;
lsmeans TRAT/adjust=tukey pdiff;
run;
ods graphics off;
ods html close;
```

Where:

NUN = numerator of RCR or independent variable Y

CO = denominator of RCR or covariable (X)

TREAT = treatment, in this case diet A and diet B

2.7.1 Number of Instars

The number of instars is constant and varies in most insects from four to eight. However, there are some Odonata that have 10 to 12 ecdyses and some Ephemeroptera that have 20 or more (Table 2.11). There are various rules that try to forecast the degree of insect growth, such as from Dyar's rule (Dyar 1890; the cephalic capsule of Lepidoptera larvae grows in geometric progression, increasing in width at each ecdysis, at a constant rate for a certain species and on average 1.4), which is valid for many Lepidoptera, Archaeognata, Hymenoptera, Coleoptera, and Hemiptera. Other rules, such as from Przibram (Batista 1972), are postulated originating from the supposition that insect growth is harmonic. Since this growth is generally nonharmonic, heterogenic, or allometric, this rule is not applicable because according to it, "at each ecdysis there should be an increase of each body part in the same proportion as the whole body." In studies done with 105 insect species, Cole (1980) showed that at each ecdysis all the linear dimensions are increased by 1.52 and 1.27 times, respectively, for holometabolic and hemimetabolic insects. There are various factors besides those intrinsic to the species, which cause a variation in the number of instars, such as hereditary factors (Albrecht 1955; Moreti and Parra 1983) (Table 2.12), rearing method (crowded or isolated) (Long 1953; Peters and Barbosa 1977), temperature (Ferraz et al. 1983; Kasten and Parra 1984) (Table 2.13), nutrition (Parra et al. 1977; Reis 1984; Matana 1986) (Table 2.14), sex (Roe et al. 1982), and parasitism (Reynolds et al. 1984; Orr and Boethel 1985).

There is no direct correlation between the duration of the life cycle and instar number (Slansky and Scriber 1985), and depending on the insect's habits a change in instar may be necessary. Thus, an insect that wears down its mandibles when feeding may need a more constant change (Slansky and Rodriguez 1987b) compared to another one that feeds on more tender food. An insect that needs to maintain its agility in each instar cannot increase its weight very much. Thus, in order not to follow the normal sequence of weight gain during the instar (Figure 2.4), the insect tends to have ecdyses at shorter intervals (Daly 1985). In unfavorable conditions, an insect tends to have more instars (Roe et al. 1982; Nealis 1987; Parra et al. 1988).

Females, due to their reproductive activity, are generally bigger, with a longer development time, and therefore may have an additional instar (Slansky and Scriber 1985). Besides this, males tend to be born beforehand in order to facilitate mating (protandry). Larger size differences are observed between the sexes in those species whose adults do not feed. Weight is at least doubled at each instar and those larvae that are not mobile (Lepidoptera larvae) have larger increments than those that have to move around to find food (e.g., certain beetles, cockroaches) (Capinera 1978; Vendramim et al. 1983).

TABLE 2.11

Number of Larval Instars for Different Insect Orders

Insect Order	Number of Instars
Archaeognata	10–14
Zygentoma (or Thysanura)	9–14
Ephemeroptera	20–40
Odonata	10–12
Blattaria	(3) 6–10 (8)
Mantodea	5–9
Grylloblattodea	8
Orthoptera	5–11
Phasmida	8–12
Isoptera	5–11
Dermaptera	4–6
Embioptera	4–7
Plecoptera	22–33
Zoraptera	–
Heteroptera	(4) 5 (9)
Homoptera	3–5
Thysanoptera	5–6
Psocoptera	6
Phthiraptera	3–4
Strepsiptera	7
Coleoptera	3–5 (10)
Raphidioptera	3–4
Megaloptera	10
Neuroptera	3–5
Mecoptera	4
Siphonaptera	3
Diptera	3–6
Trichoptera	5–7
Lepidoptera	(3) 5–6 (11)
Hymenoptera	3–6

Source: Sehna, F., In *Comprehensive Insect Physiology Biochemistry and Pharmacology*, ed. G. A. Kerkut, and L. I. Gilbert, 1–86, v. 2, Pergamon Press, Oxford, UK, 1985.

TABLE 2.12

Percentage of Larvae of *Heliothis virescens* That Reached the Sixth Larval Instar, Reared on Cotton Leaves (IAC-17) for Four Successive Generations

Generation	Male (%)	Female (%)
F ₁	63.0	33.3
F ₂	95.0	95.0
F ₃	100.0	88.9
F ₄	100.0	100.0

Source: Moreti, A. C. C., and J. R. P. Parra, *Arq. Inst. Biol.*, 50, 7–15, 1983.

Note: Temperature = 24°C ± 2°C, relative humidity = 65% ± 5%, 14 h photophase.

TABLE 2.13

Effect of Temperature on the Number of Insect Instars

Species	Temperature				Reference
	20°C	25°C	30°C	35°C	
<i>Spodoptera frugiperda</i>	7	6	6	6	Ferraz et al. (1983)
<i>Alabama argillacea</i>	6	6	5	5	Kasten and Parra (1984)

TABLE 2.14

Effect of Nutrition on the Number of Instars in Two Lepidopteran Species

Species	Host		Reference
<i>Spodoptera eridania</i>	Cotton	Soybeans	Parra et al. (1977)
Number of instars	6	7	
<i>Spodoptera eridania</i>	Sweet potato	<i>Mimosa scabrella</i>	Matana (1986)
Number of instars	6	7	

2.7.2 The Cost of Ecdysis

The molting process has a high energy cost and the caloric and nutritional content of a molted cuticle may represent >20% of total larval biomass production. The insect often compensates for this loss by reabsorbing the internal layers of the old cuticle before ecdysis and consuming (and even digesting) parts of the cuticle. About 33% of the lipids accumulated by the penultimate nymphal instar of *Acheta domesticus* (L.) (Orthoptera) are metabolized at ecdysis to the last instar and these lipids are only reconstructed on the second day after molting. From 19% to 34% of existing lipids in the “premolts” are used in the four ecdyses of *B. mori*, as well as 65% to 73% of carbohydrates existing in the premolts are used during ecdyses (Hiratsuka 1920). Therefore, to grow, increase weight, and accumulate energy reserves, insects need to alter body composition or make better use of food.

2.7.3 Food Intake and Utilization through Instars

The rates of consumption, metabolism, and growth tend to reach a peak at the beginning or near the middle of the instar, and efficiencies tend to decrease (Waldbauer 1968; Scriber and Slansky 1981; Crócomo and Parra 1985). There is a tendency to accumulate lipids from the first to the last instars, especially in the Holometabola that use energy to produce the cocoons. About 30% of the energetic content of the last larval instar of *B. mori* is used to make the cocoon (Hiratsuka 1920). Lipid accumulation also occurs in the Hemimetabola but in this case, instead of the accumulation happening via cocoon as in the Holometabola, it occurs in the last larval instar. There are cases of lipid accumulation that are not governed by this general rule when the insect enters diapause.

For the adult insect to be reproductively competitive, there are two larval characteristics that must be satisfied: the size, which can influence the choice for mating and its success as well as the capacity to disperse, and the weight, which is indicative of the nutrients and energy stored, and that influence the search for mating, dispersal flights, and fecundity. The minimum size and weight depend on the species lifestyle, environmental conditions, food availability, and neurohormonal control. A list of minimum weights that permit the pupation of different species includes values for Lepidoptera, from 13% to 26% (in dry weight matter) and from 25% to 60% (in fresh weight matter), in relation to the normal species weight (Slansky and Scriber 1985).

Food consumption of the last two instars is at least 75% of total (Waldbauer 1968) (Table 2.1). In this way, given the difficulties of separating the feces and even detecting the weight gain or food consumed (depending on the insect size) in the first instars, it can be said that the determination of nutritional indices only in these instars is sufficient for many types of study. In general, the relative indices tend to decrease from the first to the last instars due to the lipid reserves (less metabolic activity). Since females

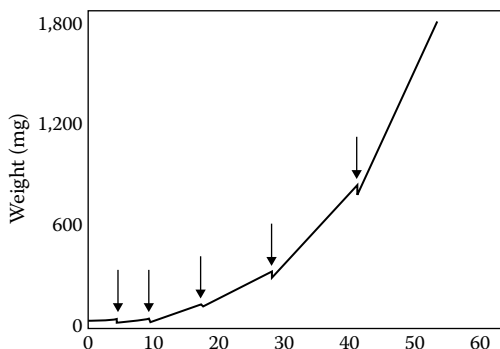


FIGURE 2.4 Standard weight increases in grasshoppers of the *Locusta* genus. (From Chapman, R. F., *The Insects: Structure and Function*, Harvard University Press, Cambridge, MA, 1982.)

are generally bigger, they consume more food to accumulate eggs and also because they have a longer development time, and in many cases, an extra instar. Despite this, the differences between the sexes in the efficiency of food use are small (Slansky and Scriber 1985).

2.8 Adult Food Consumption and Use for Reproduction and Dispersal

The main function of the adult is reproduction, and in many cases, dispersal. These functions depend on the interaction and integration of physiological processes and behaviors that are intimately correlated with food consumption and utilization. The production of eggs or progeny involves energy and nutrient accumulation by the female, which makes her consume more and gain more weight than the males. Egg production is affected by biotic and abiotic factors acting directly on adult performance and indirectly on larval development. Some components of the reproductive process and its relationship with food consumption and utilization are discussed by Slansky and Scriber (1985). Mating attraction and acceptance can depend on pheromone production that can be influenced by the absorption of pheromone precursors. Mating access and acceptance, which depend on body size, can be influenced by food in the larval stage and food quality can also affect this acceptance. In mating, the male can contribute nutritionally through secretions of accessory glands and spermatophores. For ovogenesis and oviposition, nutrient accumulation by larvae, food quality and quantity in the adults, the amount of nutrient deposited by the female in each egg, and the presence of suitable larval food as a stimulant for oviposition, can all be important.

2.8.1 Food Quality

Food quality depends on physical attributes (e.g., hardness, surface hairiness, shape) that influence insect capacity to consume and digest the food as well as allelochemicals and nutritional components. Allelochemicals, such as alkaloids, cyanogenic glycosides, glucosinolates, lignins, protein inhibitors, tannins, terpenoids, lipids and toxic amino acids, and hormones and antihormones, can act as food attractants and stimulants or as deterrents and repellents (Kogan 1977; Norris and Kogan 1980; Berenbaum 1985; Ishaaya 1986). The nutrients have already been fully discussed and in order to obtain nutrients in balanced proportions for optimal growth and development, the insect makes interconversions or syntheses, excretions, and selective concentrations or often counts on the fundamental help of microorganisms. The impact of the different aspects of food quality varies within and between different food categories (guilds). The amounts of water and nitrogen are fundamental for evaluating this behavior. Chewing insects show the best performance for food with high values of nitrogen (N) and water. Mattson (1980) (cited by Hagen et al. 1984), on correlating the ECI with N concentration for many herbivores found that this efficiency varied from 0.3% to 58%. The lowest values (1%) are associated with aquatic insects or terrestrial insects that feed on wood poor in N, litter, and detritus. The highest values (40% to 50%) were for those insects that feed on seeds, phloem sap, pollen, and nectar. The biggest conversion (more than 50%) was registered for

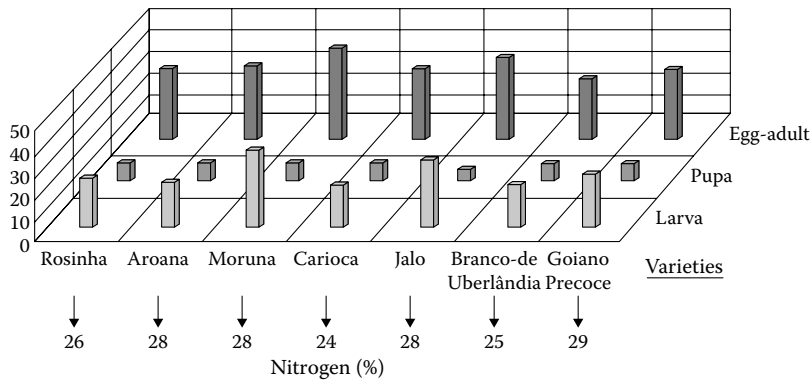


FIGURE 2.5 Duration of the larval, pupal, and total life cycle phases (egg, adult) of the lepidopteran, *Spodoptera frugiperda*, in seven artificial media and the respective percentages of nitrogen per variety used, temperature: 25°C ± 1°C, relative humidity: 70% ± 10%, 14h photophase. (From Parra, J. R. P., and S. M. Carvalho, *An. Soc. Entomol. Brasil*, 13, 305–19, 1984.)

parasitoids and predators. This author concludes that organisms feeding on nitrogen-poor diets consume more food than those who feed on nitrogen-rich diets. It is the amount of available N that limits insect growth, development, and fecundity. Thus, Parra and Carvalho (1984) observed that there was no correlation between *S. frugiperda* development and the total existing protein in dry bean varieties used in its artificial diet. The insect developed better on the diet in which N was supposedly more available (Figure 2.5). A list of the N content of different insect foods was compiled by Slansky and Scriber (1985). This N is variable in quantity and quality depending on the nutritional source (e.g., leaf, fruit, nectar, pollen, wood, and detritus). The content varies from 0.08% to 7% (in dry weight) depending on the plant part and the phase of the plant cycle. The highest concentrations are registered in new growing tissues and in propagules such as seeds and bulbs. N concentration tends to diminish according to leaf age, down to 0.5% at abscission. There is more N in the phloem than the xylem although the sap has low N levels (0.0002%–0.6%). The nitrogen fixers (legumes and nonlegumes) show variations of 2% to 5% (in dry weight). Gymnosperms have half the N of angiosperms, that is, 1% to 2% and 2% to 4%, respectively. Pollen and nectar are rich sources of N.

The limits between food quality categories are not so distinct. Thus, the amino acid L-canavanine is toxic to some insects, and therefore functions as an allelochemical. However, for other insects it is a source of N (Rosenthal et al. 1982). This explanation is valid for many phenols (Bernays and Woodhead 1982), and it is evident that these relationships depend on the quantities of these allelochemicals present in the food and on their persistence during use.

Insect performance can be affected by biotic and abiotic factors. For herbivores, plant quality varies with leaf age, the plant's growth conditions (temperature, soil fertility), disease and parasitoid infection, previous damage by other insects, and even chemical action. The influence of pathogens on food consumption and use is discussed by Mohamed et al. (1982) and Sareen et al. (1983), and for parasitoids by Slansky (1978),

TABLE 2.15

Effect of Parasitism by *Cotesia flavipes* on the Consumption and Use by Larvae of *Diatraea saccharalis* Reared on Artificial Diet

Caterpillars	Nutritional Indices		
	AD	ECI	ECD
Not parasitized	82.42a	13.47a	16.38b
Parasitized	70.28b	14.10a	20.74a

Source: Pádua, L. E. M., Ph.D. Thesis, University of São Paulo, Piracicaba, Brazil, 1986.

Note: Temperature = 25°C, relative humidity = 70% ± 10%, photophase = 14 h. Means followed by the same letter on the same column do not differ significantly, based on the Tukey test ($P \geq 0.05$), for parasitized and not parasitized *D. saccharalis* by *C. flavipes*.

Brewer and King (1980, 1982), Slansky (1986), and Pádua (1986) (Table 2.15). The effect of temperature on nutritional indices has also been reported (Bhat and Bhattacharya 1978; Almeida and Parra 1988), the influence of fertility on consumption and use (Al-Zubaidi and Capinera 1984; Oliveira 1987), the effect of physiological stress on the quantitative nutrition of *Agrotis ipsilon* (Hufnagel) (Schmidt and Reese 1988), and the effect of diflubenzuron and its analogue, triflurion, on *Spodoptera littoralis* (Boisduval) (Radwan et al. 1986).

2.8.2 Food Selection and Acceptance

The semiochemicals (intra- or interspecific) are involved in the physiological or behavioral interactions between organisms. Among the numerous semiochemicals that insects respond to, many are associated with plants, and Fraenkel (1953) called attention to the secondary substances (allelochemicals). Thus, certain allelochemicals (alomones) protect plants from herbivores or pathogens, avoiding oviposition, reducing feeding and digestive processes and modifying food assimilation. Kairomones, on the other hand, favor insects, attracting them, stimulating them to oviposit and feed, and to use such compounds as precursors for hormones, pheromones, and alomones. An allelochemical may be a deterrent for one species and phagostimulant for another species. Thus, a substance that is a deterrent for an insect generalist can be a stimulant for a specialist. The main chemoreceptors responsible for food rejection or acceptance are located in the maxillary palps. Food characteristics are taken into consideration at feeding (e.g., color, shape, size, sound, temperature, texture, hardness) and chemical aspects (e.g., smell and taste) (Maxwell and Jennings 1980). The insect feeds on variable quantities of food to obtain different nutrients and also digests and assimilates this food with variable efficiencies. According to Slansky and Scriber (1985) the rate of relative consumption is variable [$0.002\text{--}6.90\text{ mg (day} \times \text{mg)}$] with higher values for the Lepidoptera. It is difficult to remove water from some foods, and in this case, as in stored products pests, the insect drinks free water or absorbs water from water vapor or may produce metabolic water. In other cases, the insect avoids water loss by building a cocoon or wrapping itself in leaves or even lowering cuticle permeability. Often, essential nutrients are unavailable and the insect adapts and obtains them through various processes (Slansky and Rodriguez 1987b).

The synchrony of the life cycle stage with periods when nutrients are more available is one of these processes. Thus, chewing insects feed on new leaves that are nutrient-rich, sucking insects are in synchrony with the emission of plant buds or fruiting, parasitoids are synchronous with their hosts, the activities of bees are in synchrony with flower phenology, and so on. There is a harmony between these synchronisms with photoperiod, temperature, and host hormones. Another process is the modification of food quality. Gall-forming insects (see Chapter 16) alter plant tissue content by forming galls and this often results in an increase, for example, of lipids, influencing plant hormone production, and there are cerambycids that kill off the branches to interrupt nutrient flow and parasitoids that increase the available nutrients of the host hemolymph that stimulates consumption by the host.

There are special conditions of the digestive tract that permit the separation of usually indigestible complexes. Thus, insects that consume tissues with tannins can have an alkaline mesenterum that reduces the formation of indigestible protein/tannin complexes. The gut pH can be important for symbiotic microorganism growth. The cerambycids degrade all classes of structural polysaccharides and for this reason constitute the largest insect family that feeds on wood. On the other hand, the Lyctidae, which do not have the capacity to degrade cell walls, have a much smaller number of species. The synthesis of cellulose (by insects that feed on wood) and keratinase (by insects that feed on keratin-rich compounds) permit the use of unavailable substances. In *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae), amylase activity is greater than in *S. granarius* (L.); for this reason, the first species uses more amide and grows more. Many bruchids have potent amylases and some species use trypsin inhibitors in the seeds as a nitrogen source. Other species leave the proteases of the gut and use free amino acids, thus avoiding the effects of trypsin inhibitors. Another specialization shown by insects is the time food takes to pass through the gut. A longer stay can facilitate nutrient extraction. Wood-feeding termites maintain the food in the gut for 13 to 15 h compared to the 4 to 5 h for a fungus-feeding termite (Slansky and Scriber 1985).

Alternating food is another adaptation shown by insects to obtain a balanced nutrition. There are a small number of species that alternate between unsuitable and suitable foods (Chang et al. 1987). This is the case with aphids, which alternate between herbaceous hosts and trees. This phenomenon also occurs

in seed-sucking insects, termites, and soil arthropods. Also, the microorganisms can play an important role acting externally with their own chemical action or supplying more easily digested nutrients concentrated in their own biomass.

Nutrient conservation may also occur. The food assimilated is conserved by the insect digesting and absorbing the internal part of the cuticle, before ecdysis, or even consuming the chorion and the exoskeleton left behind in this process. From 3% to 27% of larval biomass (energy and N) can be lost with cuticle separation. However, digestive enzymes can be absorbed by the digestive tract during metamorphosis. Other types of nutrient conservation involve uric acid metabolism and the use of nutrients that have an allelochemical function. Coprophagy can allow a more complete nutrient use as well as facilitate the consumption of nutrient-rich bacteria.

Another adaptation is the transfer of nutrients between stages of the life cycle. The performance of each life stage basically depends on the success of the previous stage in obtaining, synthesizing, and accumulating nutritional substances in appropriate quantities. This is more evident for stages that do not feed (egg, pupae, and some adults), but the influence of previous stages is also significant in insects that feed. Females of *Aedes aegypti* L. can complete the previtellogenic phase of the ovarian cycle without feeding if they have not been reared in superpopulated conditions as larvae. However, if reared under very crowded conditions, they need blood or sugar to complete this phase (Slansky and Scriber 1985). In some species in which the adult normally feeds during the stage before egg production, a limited number of eggs can be laid if the females do not feed, depending on the micronutrients transferred during metamorphosis. Often, the micronutrients transferred by the egg phase are sufficient to satisfy the needs of the subsequent phases of the life cycle, at least for one generation. Therefore, nutritional studies should be carried out for successive generations. Finally, nutrient transfer between individuals may occur. Included in this category are cannibals (including autoparasitism), the production and consumption of nonfertilized eggs, specialized glandular secretions (e.g., a female consuming, digesting, and absorbing internally the spermatophore and seminal fluid). Trophallaxy in social insects and coprophagy can be considered. These exchanges allow not only exchanges of nutrients but also of symbionts and chemical products associated with caste regulation in social insects.

2.8.3 The Role of Allelochemicals

Allelochemicals play an important role in host selection and are very important in the tropics because this number tends to be higher than in temperate regions (Edwards and Wratten 1981) due to insect pressure throughout the year. However, insects have developed mechanisms to avoid them. Thus, seed-sucking insects avoid the toxins in the seed coat, perforating them with the stylets and feeding only on the cotyledons. Insects that suck the xylem and phloem can avoid allelochemicals in the same way. The coccinellid, *Epilachna tredecimnotata* (Latreille), makes circular holes in the plant in order to avoid deterrent substances produced when the leaf is damaged (Slansky and Scriber 1985).

Enzymatic desintoxication is also used by many arthropods to metabolize allelochemicals and thus avoid their toxicity. Many plant-sucking insects inject detoxifying phenolases with the saliva. Besides this, some insects avoid allelochemicals by producing surfactants or making the digestive tract alkaline or even through rapid excretion. Insects avoid photoactive compounds by feeding at night or even inside the leaves that they roll up (Slansky and Scriber 1985). Fungus-eating insects have certain species of microorganisms whose function is to detoxify allelochemicals. The interaction of nutrients and allelochemicals can affect food suitability. The tannins can block protein availability, forming complexes. Fox and Macauley (1977) found high levels of condensed tannin in some *Eucalyptus* species and low levels in others. The ECI values for *Paropsis atomaria* Olivier (Coleoptera) were similar when the insect fed on different plant species and the authors concluded that tannins and other phenols did not affect nutritional physiology. In some grasshoppers, hydrolyzed tannin is damaging when it passes through the peritrophic membrane but there are no damaging effects in other species (Bernays 1978). To pass through the gut, nutrients must be in a suitable form. Thus, the proteins are broken up into amino acids, due to the proteases that are produced which reduce protein availability. The plants can produce higher levels of these inhibiting enzymes after being attacked by insects and then transfer them to other parts. Green and Ryan (1972) describe this for the coleopteran, *Leptinotarsa decemlineata* (Say).

The allelochemicals, with the dehydroxy-ortho group in the aromatic ring, can quellate essential minerals. Gossypol reduces assimilation of *H. zea* larvae although it has no effect on *H. virescens*. Sinigrine reduces assimilation of *Papilio polyxenes* Fabr. (Lepidoptera) and many other allelochemicals reduce insect growth (Beck and Reese 1976; Berenbaum 1978). Studies on antihormones extracted from plants such as *Ageratum houstonianum* (Bowers et al. 1976), which act in the early stages or in adults, and of juvenile hormone analogues, which act in the last stages of metamorphosis, show an ecological function for these components (Harborne 1982).

Insects can compensate the low nutritional quality by consuming more food (Crócomo and Parra 1985; Simpson and Abisgold 1985) or altering the efficiency of use. Slansky and Wheeler (1992) observed that this attempt to compensate can lead to ingestion of higher doses of allelochemicals for example. Thus, *Anticarsia gemmatilis* Hub. tends to eat more on poor diets and eat more on diets that contain an allelochemical such as caffeine, and there will be changes in food use, growth, and survival. A similar effect was found by Lee et al. (2004) in an unbalanced diet with regard to the ingestion of cellulose by a generalist lepidopteran. Pompermayer et al. (2001) also observed that diet composition is important for the effect of proteinase inhibitors and for *D. saccharalis*, supporting what Broadway and Duffey (1986) and Jongsma and Bolter (1997) had observed previously. Warbrick-Smith et al. (2006) observed that *Plutella xylostella* L. reared for successive generations on a carbohydrate-rich diet progressively developed the ability to eat excess carbohydrate without converting it into fat, showing that the excess storage of fat has an adaptive cost. These studies always need considerable care because the insect can adapt physiologically to the proteinase inhibitors, as seen in *S. frugiperda*, which alters the complement of proteolytic enzymes of the mesenteron (Paulillo et al. 2000); the same happens with *H. virescens* (Brito et al. 2001) and with *S. frugiperda* and *D. saccharalis* (Ferreira et al. 1996).

Chang et al. (2000) demonstrated that a cysteine proteinase from corn plants caused a reduction in the efficiency of digestion and absorption of *S. frugiperda* feeding on a natural diet and also on an artificial diet containing this substance; this lower efficiency is due to damage to the peritrophic membrane caused by the enzyme in corn (Pechan et al. 2002). At other times, when the food supply is limited, the insect must search more, increasing its dispersal capacity and even increasing the range of food used. After fasting, enzymatic action is reduced due to a lower metabolic activity. With total fasting, oviposition can cease. When food is limited, the adult can reduce the rate of oviposition (reducing embryogenesis or resorbing eggs). When starving is total, there is an early transformation into pupae, which weigh less. In many cases, the consumption rate can return to normal and a normal insect can result if food is offered after starving. Often the insect promotes changes associated with feeding, such as morphological adaptations (e.g., mouth parts, legs, spine formation), changes in the number of sensors (e.g., number of coeloconic sensilla on the palps), changes in the size of the gut or even internal structures, as in cockroaches, which facilitates the establishment of microorganism colonies. However, the insect shows adaptive strategies that include specializations, suitable development and size, defense, and responses to environmental variations (abiotic factors, starving, food quality, endoparasitism, density and competition, migration) (see Scriber 1984 and Slansky and Scriber 1985 for more details).

Many nutritional studies are done with artificial diets, which show comparable results to those obtained for natural diets. Diets are suitable for certain types of research, such as the evaluation of specific nutrients, their concentrations, and the determination of the concentrations of allelochemicals that affect the insect/plant relationship (Giustolin et al. 1995). However, some care is necessary in these studies because many diets require cellulose (Vendramin et al. 1982), which can change the approximate digestibility. Besides this, the allelochemicals added to diets can interact in a different way with the nutrients in relation to natural food. Thus, artificial diets should not have phytoalexin induction in damaged tissue as happens in nature. The anticontaminants added to the diets (Greenberg 1970; Sikorowski et al. 1980; Funke 1983; King and Leppla 1984; Reinecke 1985) can affect the existing symbionts and even interfere in enzyme detoxification. In other types of studies of insect/plant relationships, plant extracts added to artificial diets are used. In these cases, there is a possibility that chemical resistance may be destroyed in the preparation of the extract and even undue dilution of the responsible chemical substance for the insect response. However, these studies with plant extracts can give good results (Martins et al. 1986). These authors, studying resistance in rice varieties to *D. saccharalis*, used plant extracts in artificial diets, eliminated the physical factor of the resistance, and through chemical analysis detected possible sources of resistance to this insect.

Whenever artificial diets are used as vehicles to test antinutrients and toxins, there must be some characteristics present for the results to be reliable, including (1) the substance to be tested, whether it be an allelochemical, a protein crystal, or a virus, should not be chemically affected (changed) by the diet; (2) the substance should not affect the palatability and/or attractivity of the diet; (3) it should not be avoided by specialized feeding mechanisms (such as extra oral digestion); (4) the formulation ingredients of the basic diet cannot mask or change the effects of the substance that is being tested; and (5) the diet should be totally suitable for offering and maintain healthy characteristics (no microorganisms) (Cohen 2004).

2.9 Final Considerations

Nutritional quality requirements in insects are similar, independent of their systematic position and feeding habits (identity rule). However, the proportions of the nutrients needed vary significantly between insect species (principle of nutritional proportionality), which results in a very diverse set of feeding habits. Also, food choice is not only determined by the nutritional components but also by the physical characteristics and by allelochemicals in the diets. Thus, the way foodstuff is ingested, digested, assimilated, and converted into growth tissues depends on these components within an ecological and evolutionary context (nutritional ecology). These nutritional analyses involving interactions at the different trophic levels require mostly the determination of nutritional indices discussed in this chapter, which demand meticulous studies and which, depending on insect type and size, can lead to mistakes, especially for determinations done with the first instars.

These types of studies evolved considerably during the 1970s and 1980s, as supported by the 347 citations on food consumption and use mentioned by Slansky and Scriber (1982, 1985). This evolution did not stop the continuation of many problems in their determination (sources of variation) and in the interpretation of the values obtained (see Section 2.6). At some trophic levels, more research is needed on physiology, nutrition, genetics, and behavior, especially for host/parasitoid relationships. There are innumerable aspects of mating, adult feeding, oviposition, development of immature forms and diapause (in colder regions) that need to be researched and discovered (Thompson 1986). In these cases, the attempt to rear the natural enemy *in vitro* is still a challenge. It is expected that with new techniques in molecular biology, these challenges will be overcome. In Brazil, where research with these nutritional indices began at the end of the 1970s (Crócomo and Parra 1979) and where there are few research groups directly involved, the problems are still greater. In general, the research is limited to the determination of nutritional indices and an unbiased analysis of the results obtained, which does not reach the expected level of detail. It is suggested that there be more interaction, principally of entomologists and biochemists, since through this association many of the complicated mechanisms that involve insect/plant relationships can be evaluated. In the last few years, new analytical methods of data (use of covariant analysis; see Table 2.10), studies with transgenic plants (Fernandes 2003) (Table 2.16), and even nutrigenomics development will be able to elucidate the intricate mechanisms of insect nutrition.

TABLE 2.16

Consumption of Leaf Area by *Spodoptera frugiperda* in Conventional and Transgenic (MON810) Corn during Three Laboratory Generations

	Generations		
	F ₁	F ₂	F ₃
Treatment	Leaf Consumption (cm ²)		
Conventional corn	201.44 ± 5.12 a A*	215.58 ± 6.10 a A	214.98 ± 6.24 a A
MON810	164.67 ± 4.44 b A	171.50 ± 7.15 b A	177.48 ± 5.38 b A

Source: Fernandes, O. D., Ph.D. Thesis, University of São Paulo, Piracicaba, Brazil, 2003.

Note: Temperature = 28°C ± 1°C, relative humidity = 60% ± 10%, 14h photophase.

* Means followed by the same small letter in the columns and large letter in the rows are not different between themselves by the Tukey test ($P < 0.05$).

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3

The Evolution of Artificial Diets and Their Interactions in Science and Technology

José R. P. Parra

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3.1 The Importance of Rearing Insects in the Laboratory

The rearing of insects in the laboratory is of fundamental importance for solving problems of pure or applied entomology (Kogan 1980). The advance of research in modern entomology depends on insect availability in the laboratory so that studies do not suffer from lack of continuity or depend on the natural occurrence of the study insect, especially agricultural pests.

There are insects that can be easily reared in the laboratory and maintained at high populations. This is the case of *Drosophila*, which has been easily reared for many years and has been the main organism used in genetic research. In the same way, the silkworm, *Bombyx mori* L., has given rise to one of the largest industries in the world since 2000 B.C. in Asia (Cohen 2004), and the rearing of *Apis mellifera* L. since ancient Egypt (Cohen 2004) has increased agricultural yield by pollinating various crops important in human consumption. However, many insects, especially phytophages, require detailed study for mass rearing.

There have been revisions of insect nutrition and feeding habits since the beginning of the last century, such as those of Uvarov (1928) and Brues (1946), but the big advance occurred with the studies of G. Fraenkel of the University of Illinois, after the 1940s, in his research on the nutritional needs of stored products pests.

The big advances in rearing techniques on artificial media occurred in the 1960s, 1970s, and 1980s, especially in the developed countries. In the bibliographic compilation done by Singh (1985), artificial diets for more than 1,300 insect species belonging to most of the orders of agricultural importance were described (Table 3.1). Dickerson et al. (1980) listed around 1,000 insect colonies corresponding to 480 species (representing 109 families) maintained in 200 laboratories in the United States and other countries. Edwards et al. (1987) brought this list up to date and included a further 693 species reared in 263 facilities.

TABLE 3.1

Artificial Diets for Different Orders of Agricultural Importance

Order	Number of Species
Lepidoptera	556
Coleoptera	284
Diptera	279
Hemiptera	93
Hymenoptera	67
Orthoptera	24
Isoptera	5

Source: Singh, P., In *Handbook on Insect Rearing*, Vol. I, ed. P. Singh, and R. F. Moore, 19–44, Elsevier Amsterdam, the Netherlands, 1985.

The first phytophagous insect to be reared in Brazil on an artificial diet was *Diatraea saccharalis* (Fabr.), the sugarcane borer, in 1969, using the artificial diet developed by Hensley and Hammond (1968), at Piracicaba, São Paulo, in research on biological control developed by Domingos Gallo, then head of the Department of Entomology (ESALQ/USP).

The validity and/or importance of rearing insects in the laboratory is clear. Knipling (1979) declared that one of the most important advances in entomology was the progress made by scientists in managing to rear an almost unlimited number of insects at a reasonable cost. The theme “insect rearing” is one of the most relevant since this topic has become a major part of the modern science of entomology (Leppla and Adams 1987; Cohen 2004; Schneider 2009).

The publication of Smith's (1966) classic book encouraged innumerable studies, such as those by Rodrigues (1972), Singh (1977), Leppla and Ashley (1978), Dickerson et al. (1980), Dadd (1985), Edwards et al. (1987), King and Leppla (1984), Singh and Moore (1985), Reinecke (1985), Ashby and Singh (1987), Parra (1991), Anderson and Leppla (1992), Thompson and Hagen (1999), Parra (2007, 2008), and Parra et al. (2002), which developed this area of entomology. After this, specific books on the subject became less common, perhaps due to the apparent failure to rear parasitoids and predators *in vitro*. In 2004, Cohen published the book *Insect Diets—Science and Technology*, covering basic aspects but also the technology involving knowledge of food science, including chemistry, physics, and microbiology, and the effect of the components on the manufacturing of the artificial diet during the processing. Although the advances in diets for parasitoids (Cônsoi and Parra 2002; Cônsoi and Grenier 2010) and predators (Cohen 2004), there is no doubt that 85% of artificial diets are concentrated on phytophages of the orders Lepidoptera, Coleoptera, and Diptera.

Depending on the study area, it is evident that insect field populations can be manipulated or insects can be kept in natural hosts in laboratories, insectaries (mesh screens), or in incubators. However, owing to the development of artificial media, it became possible to rear large number of insects necessary for studies in integrated pest management (IPM) programs, with total control over populations. Thus, it was possible to obtain significant advances in basic areas such as nutrition, toxicology, production of recombinant proteins and drugs, transgenic plants, biochemistry (enzyme studies), biotechnology, endocrinology, genetics, behavior, ecology, and taxonomy. With the development of insect mass rearing, applied research on biological control, plant resistance, insect pathology, genetic control (male sterilization and the use of lethal genes), disease vectors, the production of pheromones and kairomones (behavioral control methods), and chemical control, has been developed. This advance happened over the last 30 years, since Singh (1977) listed 154 publications on artificial diets from 1908 to 1950, and 1,807 from 1951 to 1976. From 1976 to 2010, there were few publications containing new knowledge on artificial diets, especially for phytophages.

In 1974, an international newsletter titled *Frass (Insect Rearing Group Newsletter)* was started in the United States to improve communication and cooperation as well as to solve the problems of scientists concerned with insect rearing. It has information on new diets, ingredient prices, the addresses of researchers working with different species, health and laboratory models, quarantine, and quality control (Dickerson and Leppla 1992).

A layout of the relationships between insect rearing and the diverse areas of entomology, focusing on pest management and sustainable agriculture, was drawn up by Parra (2008) (Figure 3.1). The maintenance of insect colonies in the laboratory is indispensable to modern strategies of pest management since in both basic and applied research programs, a continuous supply of insects is needed.

When the objective is research, insect colonies can be kept on natural media because large populations are not always necessary. However, whether on natural or artificial media, basic biological and behavioral information are fundamental for developing research that will support the different control methods (Parra 2000). In other cases, when the colonies are used for actual control, the number of insects to be used should be large, and in this case, artificial diets are mostly used. This gives rise to mass rearing, which has a series of peculiarities with not only entomological problems but also those related to a real factory involving the production of millions of insects.

In general, insect rearing is necessary for studies on insect plant resistance, insecticide trials (biological products, pathogens, growth regulators, new agrochemical groups), small-scale production of natural enemies (parasitoids, predators, and pathogens), studies on nutritional needs, mass production of natural

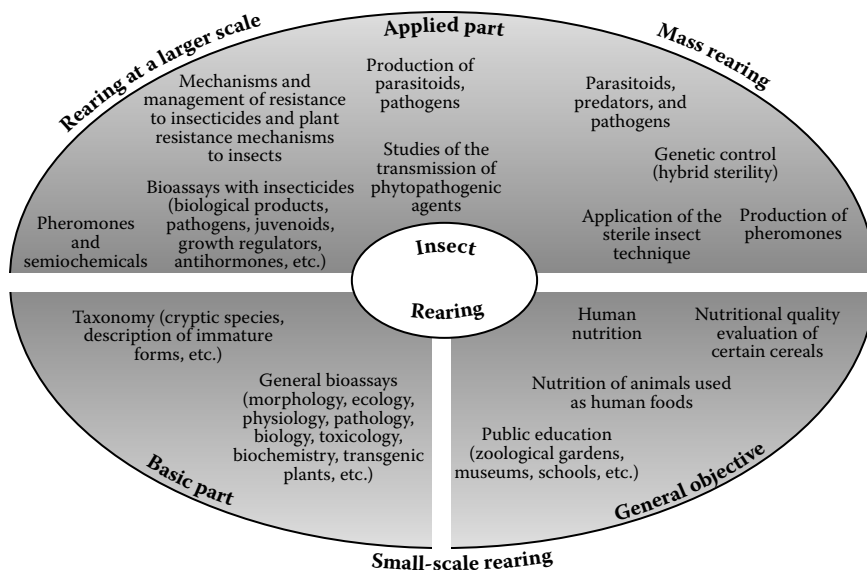


FIGURE 3.1 Relationships between insect rearing and various areas of entomology. (Modified from Parra, J. R. P., in *Encyclopedia of Entomology*, 2nd Edition, Vol. 3, ed. J. L. Capinera, 2301–05, Springer, 2008.)

enemies (parasitoids, predators, and pathogens), mass production for sterility programs, mass production for genetic control (hybrid sterility), evaluation of the nutritional quality of cereals (more economically than with other animal tests), nutrition of animals used in human feeding (fish, birds, and frogs), bioassays (morphology, biochemistry, physiology, pathology, biology, toxicology, ecology), studies on pheromones and semiochemicals, studies on taxonomy (cryptic species, description of immature forms), studies on insect and insecticide resistance (resistance mechanisms and management), studies on insect transmission of phytopathogenic agents, bioassays in biotechnology and molecular biology (especially for evaluation of transgenic plants), drugs, symbionts, enzymes, and other biochemical aspects. Insect colonies are also used in public education (zoos, museums, and schools) and as human food, since they represent important protein sources (Table 3.2) (Parra 2007, 2008).

TABLE 3.2

Relative Nutritional Value of Some Types of Insects

Insect	Protein %	Fat
<i>Isoptera (termites)</i>		
A live sample	23.2	28.3
A fried sample	36.0	44.4
<i>Orthoptera (grasshoppers)</i>		
12 dry samples	60.0	6.0
<i>Diptera</i>		
Three domestic fly pupae	63.1	15.5
<i>Hymenoptera (ants)</i>		
Adults		
Females	7.4	23.8
Males	25.2	3.3

3.2 History of Artificial Diets

The first insect to be reared axenically from egg to adult in an artificial diet (composed of peptone, meat extract, amide, and minerals) was *Calliphora vomitoria* (L.), by Bogdanov in 1908. In 1915, Loeb reared *Drosophila* sp. for five generations on a diet composed of grape sugar, sugar from sugarcane, ammonium tartarate, citric acid, potassium monoacid phosphate, magnesium sulfate, and water. Guyénot (1917) maintained *Drosophila ampelophila* Loew colonies with good results on an exclusively artificial diet. The cockroach species, *Periplaneta orientalis* (L.) and *Blatella germanica* (L.), were successfully reared by Zabinski (1926–1928) in a medium composed of egg albumin, amide, sucrose, agar, and a mixture of salts. In the 1940s, Fraenkel and his collaborators reared a large number of insects and stored products pests on a casein-based diet (Singh 1977).

The first attempt to rear a phytophagous insect on an artificial medium was made by Bottger (1942), who used a diet for *Ostrinia nubilalis* (Hübner) consisting of casein, sugars, fats, salts, vitamins, cellulose, agar, and water. Later, Beck et al. (1949) developed a diet for *O. nubilalis* composed of highly purified natural pure chemical products, also including an extract from corn leaves for supplying an unidentified growth factor (later identified as ascorbic acid by Chippendale and Beck (1964)). In 1949, House started a series of classic studies on applied aspects of insect nutrition. In 1950, K. Hagen, in Berkeley, California, launched the basis of parasitoid and predator nutrition and diets. Ishii (1952) and Matsumoto (1954) used diets that contained extracts of the host plants for *Chilo suppressalis* (Walker) and *Grapholita molesta* (Busck). Vanderzant and Reiser (1956) reared the pink bollworm, *Pectinophora gossypiella* (Saunders), on a diet that did not contain plant extracts. From these initial experiments, a large number of insects have been reared on diets that consist entirely of pure chemical products and nutritional substances that are completely strange to the insect's natural food. In 1959, Fraenkel includes the concept of "secondary substances" to understand insects' feeding mechanisms. Ito (1960) in Japan began classic nutritional studies with *Bombyx mori* (L.).

The rearing of Hemiptera on artificial substrates was done by Schell et al. (1957), with the species *Oncopeltus fasciatus* (Dallas) and *Euschistus variolarius* (Palisot de Beauvois). The rearing techniques for aphids in the laboratory were developed in parallel in the United States and Canada by two research groups. Thus, Mittler and Dadd (1962) succeeded with *Myzus persicae* (Sulzer) in the United States and Auclair and Cartier (1963) with *Acyrtosiphon pisum* (Harris) in Canada. Mittler (1967) developed studies on the biochemistry, biophysics, and behavior of aphid nutrition. Gordon (1968) stated the principle of quantitative nutrition in insects, and Waldbauer (1968) standardized the indices for studying insect quantitative nutrition. The first references to rearing parasitoids in the laboratory on artificial media were made by Yazgan and House (1970) and Yasgan (1972) with the species *Itopectis conquisitor* (Say) (Hymenoptera, Ichneumonidae).

One of the biggest advances in rearing techniques for Lepidoptera and other phytophages in the laboratory was due to the introduction of wheat germ in the diet formulations for *P. gossypiella* (Adkisson et al. 1960) and for *Heliothis virescens* (Fabr.) (Berger 1963). With some modifications, the formulations of these two authors constitute the basis for many insect diets. Such revisions of the history of artificial diets are based on Singh (1977), Singh and Moore (1985), and Cohen (2004).

A list of insect species reared is shown in Table 3.3. Revisions of the rearing of natural enemies were also done by Waage et al. (1985). In the last 30 years, research on artificial diets for parasitoids and predators *in vitro* has intensified and revisions on this subject have been made by Thompson (1986), Thompson and Hagen (1999), Cônsoli and Parra (2002), and Cônsoli and Grenier (2010). One of the few cases of successful rearing of a parasitoid *in vitro* is the production of *Trichogramma* by the Chinese in artificial eggs with a polyethylene chorion (Li Li Ying et al. 1986). The artificial medium is composed of the pupal hemolymph of *Antheraea pernyi* (Guérin-Ménéville) [or *Philosamia cynthia ricini* (Boisd.)], chicken egg yolk, malt, and Neisenheimer salts (these are oviposition attractants). This medium can be used to rear various *Trichogramma* species if necessary, and using various thicknesses of plastic owing to the ovipositor size of the species being reared. The parasitoids are produced on plastic rings or cards that contain a large number of parasitoids. The Chinese now have computerized machines to produce thousands of *Trichogramma in vitro* per day for field liberation

TABLE 3.3

Taxonomic Distribution of Species Reared on Artificial Diets

Order/Family	Number of Species Reared
<i>Coleoptera</i>	284
Anobiidae	4
Bostrychidae	3
Buprestidae	1
Bruchidae	1
Cerambycidae	69
Chrysomelidae	11
Coccinellidae	69
Cucujidae	3
Curculionidae	28
Dermestidae	18
Elateridae	5
Lyctidae	2
Meloidae	5
Nitidulidae	5
Pythidae	1
Ptinidae	1
Scarabaeidae	17
Scolytidae	33
Tenebrionidae	7
Trogositidae	1
<i>Dermaptera</i>	1
Labiduridae	1
<i>Dictyoptera</i>	5
Blattellidae	4
Blattidae	1
<i>Diptera</i>	279
Anthomyiidae	10
Calliphoridae	19
Ceratopogonidae	19
Chironomidae	14
Chloropidae	4
Culicidae	61
Cuterebridae	1
Dolichopodidae	1
Drosophilidae	34
Glossinidae	1
Muscidae	16
Mycetophilidae	1
Mystacinobiidae	1
Oestridae	1
Phoridae	3
Piophilidae	1
Psilidae	1
Psychodidae	18
Sarcophagidae	8
Scatopsidae	1
Sciaridae	22

(continued)

TABLE 3.3 (Continued)

Taxonomic Distribution of Species Reared on Artificial Diets

Order/Family	Number of Species Reared
Sciomyzidae	1
Simuliidae	8
Sphaeroceridae	2
Syrphidae	3
Tabanidae	5
Tachinidae	4
Tephritidae	18
Tipulidae	1
<i>Hemiptera</i>	93
<i>A. Heteroptera</i>	22
Alydidae	1
Anthocoridae	6
Lygaeidae	1
Miridae	4
Nabidae	1
Pentatomidae	3
Reduviidae	5
Scutelleridae	1
<i>B. Homoptera</i>	71
Aphididae	50
Cercopidae	1
Cicadellidae	8
Coccidae	3
Delphacidae	7
Pseudococcidae	2
<i>Hymenoptera</i>	67
ApheLinidae	1
Apidae	4
Bethylidae	1
Braconidae	4
Cephidae	1
Chalcididae	2
Encyrtidae	1
<i>Lepidoptera</i>	556
Arctiidae	15
Bombycidae	2
Carposinidae	1
Cochylidae	1
Cossidae	2
Gelechiidae	10
Geometridae	32
Heliconiidae	1
Hepialidae	2
Hesperiidae	7
Lasiocampidae	6
Limacodidae	1
Liparidae	3
Lycaenidae	12

(continued)