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Insect nutrition

Like other animals, insects also require a balance diet having appropriate amount of proteins, amino acids, carbohydrates, lipids, vitamins, minerals etc. The dietary requirement of the insect is species specific. For the proper development and growth, the insects derived most of the nutrients either by taking food or from the stores inside the body (e.g., fat bodies), or as a result of synthesis (by the insect itself or through associated micro-organisms). Certain moths do not feed as adult, and the food accumulated during larval stages is used for their metabolic processes. All insects are able to synthesise nucleic acids, however only some insects are able to synthesise vitamins, non-essential amino acids.

Amino acids: Amino acids are the building blocks of protein making the tissues and enzymes. Different insects have different requirements, depending upon which amino acids they are capable of synthesizing. Although some 20 amino acids are needed for protein production only ten are essential in the diet, the others can be synthesised from these ten. The ten essential amino acids are arginine, lysine, leucine, isoleucine, tryptophan, histidine, phenylalanine, methionine, valine and threonine. In addition to essential amino acids, few insects need glycine (e.g., flies) or alanine (e.g., Blattella) or proline (e.g., Phorima), however in these cases methionine is not essential.

In general, the absence of any one of these essential acids prevents growth. Although other amino acids are not essential, they are necessary for optimal growth to occur because their synthesis from the essential acids is energy consuming and necessitates the disposal of surplus fragments (Dadd,1973).

Consequently, glutamic acid and aspartic acid are necessary in addition to the essential amino acids for good growth of Bombyx larvae and further improvement is obtained if alanine, glycine or serine are also present. Good growth of *Mysus persicae* depends on the presence of cysteine with glutamic acid, alanine, or serine.

Carbohydrate: Carbohydrate are not considered to be essential nutritive substance for most insects, but they are probably the most common source of chemical energy utilized by insects. However, many insects (e.g., many moths) do, in fact, need them if growth and development are to occur normally. Schistocerca for instance needs at least 20% sugar in an artificial diet for good growth. Tenebrio fails to develop unless carbohydrate constitutes at least 40% of the diet and growth is optimal with 70% carbohydrate. The carbohydrate may be converted to fats for storage or to amino acids. In the diet of Galleria moth, carbohydrate can be entirely replaced by wax and this is also true in many Diptera, such as Musca. Larval Phorima which normally live in necrotic tissues containing little carbohydrate are adversely affected by any carbohydrate in the diet. There may be differences in the ability of larvae and adults to utilize carbohydrates. For instance, the larva of Aedes can use starch and glycogen while the adult cannot.

Lipids: Lipids or fats, like carbohydrates are good sources of chemical energy and are also important in the formation of membranes and synthesis of steroid hormones. Most insects can synthesise lipids from carbohydrates and protein sources. However, some insect species do require certain fatty acids and other lipids in their diets. For example, certain Lepisoptera require linoleic acid for normal larval development.

All insects need a dietary source of sterol (cholesterol, phytosterols or ergosterol) for growth and development. Carotenoids are necessary in the diets of all insects as the visual pigment retinene is derived from the food.

Vitamins: Vitamins are unrelated organic substances that are needed in very small amounts in the diet for the normal functioning of insects as they cannot be synthesised. They provide structural components of coenzymes. Vitamin A (fat soluble) is required for the normal functioning of the compound eye of the mosquito. Insects principally require water soluble vitamins (e.g., B complex vitamins and ascorbic acid). In the absence of ascorbic acid (vitamin C) locusts undergo abortive moults and dies.

Minerals: Like vitamins several minerals are required in traces by insects for normal growth and development, e.g., potassium, phosphorous, magnesium, sodium, calcium, manganese, copper, iron, chlorine, iodine, cobalt, nickel and zinc. The aquatic larvae of mosquitoes are able to absorb mineral ions from the water through the thin cuticle. The nucleic acids: Nucleic acids (DNA and RNA) constitute the genetic material. Like other animals, insects are also able to synthesise them. However, dietary nucleic acids (e.g., RNA) have been shown to have an influence on growth of certain fly larvae.

Water: Like all animals, insects require water. Insects fulfil their water requirements from body, by drinking, from absorption through the cuticle (in aquatic forms) or from a by product of metabolism. Insects vary greatly with respect to amounts of water needed. Some, like the rice weevil *(Sitophilus oryzae)* can survive

and reproduce on essentially dry food. Others, for example honey bees and house flies, require large amounts of water for survival. The excrement of the rice weevil is hard and dry with almost all the water absorbed by the insect, while the excrement of bees and house flies contains large amounts of water.

Microbiota and nutrition

Types of micro-organism

The most commonly occurring microorganisms in insects are bacteria or bacterium like forms which are found in Blattoidea, Isoptera, Homoptera, Heteroptera, Anoplura, Coleoptera, Hymenoptera and Diptera. In addition flagellates are found in wood eating cockroaches and termites, yeasts in Homoptera and Coleoptera and an actinomycete in Rhodnius. In many cases the precise nature of the micro-organisms is not known.

Location in the insect body

In some insects the symbionts are free in the gut lumen. This is the case with the flagellates which live in the hindguts of wood eating cockroaches and termites and with the bacteria living in the caeca of the last segment of the midgut in plant sucking Heteroptera. In Rhodnius, Actinomyces lives in crypts between the cells of the anterior midgut. Most microorganisms are intracellular in various parts of the body. The cells housing the symbionts are known as mycetocytes and these may be aggregated together to form organs known as mycetomes. Mycetocytes are large, polyploid cells occurring in many different tissues. Mycetocytes are large, polyploid cells occurring in many different tissues. Normally the microorganisms are incorporated into them when the cells are first differentiated in the embryo,

but sometimes the cells develop for a time before they are invaded. Most commonly the mycetocytes are scattered through the fat body, as they are in cockroaches and coccids, but in *Haematopinus* (Siphunculata) they are scattered cells in the midgut epithelium and in other insects they may be in the ovarioles or free in the haemolymph. The presence of microbes in the gonads ensures the infection of any egg produced thus transferring the microbes in next generation.

The wood eating cockroaches have two sets of symbionts: intestinal flagellates and intracellular bacteroids in the fat body. This situation also occurs in the termites *Mastotermes darwiniensis* but the remainder of the wood eating termites only retain the intestinal fauna.

The association of microbes with the insects may either be casual or constant. The microbes are almost present in food and are ingested by the insects during feeding, e.g., locusts. Such casual association with microbes are important in the nutrition of dung beetles that have fermentation chamber in the hindgut in which decaying food with its content of microbes is retained. The insects may have constant association with the microbes, e.g., insects feeding on wood, dry cereal, feather and hair.

The roles of microorganisms in the insect

It is known that the intestinal flagellates of cockroaches and termites are concerned with the digestion of wood and that they release products which can be utilized by the insect. The yeast of Stegobium (Coleoptera) provides vitamins and sterols, which may be secreted into the gut or released by the digestion of the microorganisms. There is some evidence that the microorganisms particularly those in Homoptera and Heteroptera are concerned with nitrogen metabolism. Some microorganisms contribute to insect nutrition, by providing nutrients or degrading plant material intractable to insect digestion. Resident microorganisms protect their insect hosts against natural enemies, including viruses, bacteria, and parasitoids, by synthesizing toxins or modulating the insect immune system.

What is the role and function of microorganisms?

Microorganisms have several vital roles in ecosystems: decomposition, oxygen production, evolution, and symbiotic relationships. Decomposition is where dead animal or plant matter is broken down into more basic molecules.Oct 28, 2017

Summary Points

1. An insect represents multiple habitats, including the exoskeleton, gut lumen, and cells, that are colonized by microorganisms.

2. The composition and abundance of insect-associated microorganisms are shaped by the physicochemical conditions in the insect habitat, insect immune function, interactions among microorganisms, and transmission mechanisms of the insect.

3. Some microorganisms contribute to insect nutrition, by providing nutrients or degrading plant material intractable to insect digestion.

4. Resident microorganisms protect their insect hosts against natural enemies, including viruses, bacteria, and parasitoids, by synthesizing toxins or modulating the insect immune system.

5. Microorganisms have been implicated in the detoxification of dietary compounds and insecticides, and as the source of signals and cues important to insect communication, but the incidence and general significance of these functions are largely unexplored.

6. The resident microbiota of insects has great potential in promoting effective management of insect pests, as biomarkers for insect traits, as modulators of insect vector competence, and as targets for novel strategies to control pests and manipulate their traits.

Nutrition

Many insect-associated microorganisms promote insect capacity to utilize diets of low or unbalanced nutritional content by providing specific nutrients that the insect cannot synthesize, including essential amino acids and B vitamins and sterols and, for insects feeding on diets rich in plant fiber, by degrading complex plant polysaccharides.

The role of microorganisms in provisioning essential amino acids has been demonstrated most conclusively in hemipteran insects feeding on plant phloem sap. The principal sources of nitrogen in phloem sap are the free amino acids of unbalanced composition, with <20% essential amino acids (the 9/10 of 20 amino acids that contribute to protein that cannot be synthesized by animals) (36). The key evidence that the primary symbiont, *Buchnera aphidicola*, in aphids synthesizes and releases essential amino acids is threefold: (*a*) Aphids have no dietary requirement for essential amino acids (unlike most animals) and can synthesize essential amino acids de novo, but they lose these capabilities when the *Buchnera* bacteria are eliminated by antibiotic treatment (39, 44); (*b*) isolated *Buchnera* bacteria release essential amino acids at linear rates for an hour or more (93); and (*c*) the *Buchnera* genome has retained the genetic capacity for essential amino acid synthesis, despite massive genome reduction (106). Microbial involvement in essential amino acid provisioning in other plant sap–feeding insects is indicated by the apparently universal incidence of symbioses in these insects (16) and by the retention of essential amino acid biosynthesis genes in all symbionts tested (76). Microbial symbionts have also been implicated in essential amino acid provisioning in ants (45), cockroaches (95), and some wood roaches (113).

Microorganisms associated with insects can gain access to nitrogenous precursors from dietary nitrogen, insect waste nitrogen, and nitrogen fixation. Insect nitrogenous waste is recycled to essential amino acids in the ant-*Blochmannia* symbiosis, in planthopper (*Nilaparvata lugens*)-yeast associations, and in cockroaches and termites ([45](#), [90](#), [95](#), [98](#)) but apparently not in the aphid-*Buchnera* symbiosis ([72](#)). Persuasive evidence for nitrogen fixation by insect-associated bacteria has been obtained for some termites ([87](#)). The microbiota in various other insects includes taxa with the genetic capacity to fix nitrogen and, in some instances, with demonstrable nitrogen fixation or acetylene reduction (which is a valid proxy for nitrogen fixation) ([3](#), [7](#), [79](#), [82](#), [94](#)), but the quantitative contribution of this capability to the nitrogen economy of the insects is largely unexplored.

B vitamins have been inferred to be provided by resident microorganisms, especially in insects feeding throughout the life cycle on vertebrate blood (e.g., the tsetse flies and other Diptera Pupipara, Cimicidae bed bugs, anopluran lice) and some phytophagous and xylophagous insects, including plant sap–feeding hemipterans, and various Coleoptera spp. of the families Anobiidae and Curculionidae ([4](#), [16](#), [35](#), [75](#), [106](#)). Contributions of microbiota to insect sterol nutrition relate exclusively to eukaryotic, particularly yeast, symbionts, because bacteria lack the capacity for sterol synthesis. A fungal source of insect sterols is indicated by the fungal sterol ergosterol and related compounds in the sterol profile of anobiid beetles (Coleoptera, Anobiidae) and planthoppers with yeast symbionts ([83](#), [86](#)). However, sterol analysis of the wood wasp *Sirex*

noctilio suggests that this xylophage derives its sterols from the diet and not the fungal symbiont ([112]).

Microorganisms make a critical contribution to the degradation of plant cell wall material in insects that feed on sound wood and other plant products with a high lignocellulose content (e.g., termites, wood roaches, scarab beetle larvae). The microorganisms are located in a hindgut fermentation chamber, where they mediate the slow enzymatic degradation of the cellulose and hemicellulose components of the diet to sugars, which are then fermented to short-chain fatty acids and made available to the insect ([17]). Insects that feed on living plant material are largely independent of microbially mediated degradation of plant cell wall material because they subsist on the soluble carbohydrates and proteins in the plant cell contents and produce midgut glucosyl hydrolases capable of degrading plant cellulose and other plant cell wall polysaccharides ([8], [17]).

Protection Against Natural Enemies

Resident microorganisms can protect their insect hosts against pathogens and other natural enemies by multiple mechanisms that are not mutually exclusive, including competition for nutrients or space, production of toxins active against the invader, and activation of insect immune system functions that are more deleterious to the invader than the resident. Some of these mechanisms are equivalent to traits of environmental microorganisms that protect a resource patch, for example in soil or the water column, with the implication that protective traits of insect-associated microorganisms are not necessarily specific adaptations to the insect habitat. Microorganisms may defend their insect habitat against competing microorganisms

that happen to include insect pathogens. Nevertheless, many protective functions of insect microbiota likely involve adaptations specific to the insect habitat, such as novel microbial chemistries against parasitoids. Coevolutionary interactions between insects and their microbiota are also expected and would lead to selection for reduced toxicity of the microbial agents against the host and coordination of the timing and magnitude of microbial toxin production to optimize protection of particularly vulnerable insect life stages or tissues.

There is now persuasive evidence that resident microorganisms can dictate the outcome of insect interactions with natural enemies, but understanding of the underlying mechanisms is fragmentary. The secondary symbiont *Hamiltonella defensa* confers pea aphid resistance to the parasitoid *Aphidius ervi* ([88]), but not all *Hamiltonella* spp. are protective. Function has been correlated with a bacteriophage in the *Hamiltonella* spp., and specifically with phage-encoded genes for toxins, such as Shiga-like toxin, cytolethal distending toxin, and YD-repeat toxins ([31]). A different group of toxins, polyketides, has been implicated in the *Pseudomonas*-mediated protection of *Paederus* rove beetles against predators ([89]) and in an undefined protective role of *Profftella armatura,* localized in the bacteriocytes of Asian citrus psyllid *Diaphorina citri* ([81]). ROS produced in the insect gut by either

microorganisms or the insect gut epithelium can have strong antimicrobial effects. ROS production by prevalent gut bacteria *Enterobacter* spp. in anopheline mosquitoes inhibits the development of *Plasmodium* ookinetes into oocysts ([22]), and *Leishmania* parasites are sensitive to ROS induced by some members of the gut microbiota in their phlebotomine sand fly vector (*Lutzomyia longipalpis*) ([32]).

Antimicrobial compounds are of particular importance to insects living in enclosed, humid environments, where opportunistic fungal or bacterial infections can develop

rapidly. Adult females of the solitary digger wasp *Philanthus triangulum* smear the ceiling of each subterranean brood cell with an antennal secretion containing antibiotic-producing *Streptomyces* spp. (Figure 1a); and the larva subsequently transfers the secretion to the surface of the cocoon. Survival is reduced from 80% to 10% if the *Streptomyces* bacteria are removed (60). Similarly, adults of the spruce bark beetle *Dendroctonus rufipennis* smear oral secretions containing bacteria onto the gallery walls of the trees they infest, likely conferring protection against antagonistic fungi, such as *Aspergillus* spp. (19).

From an evolutionary perspective, these beneficial effects of resident microorganisms in insects challenged by natural enemies can be attributed to strong selective overlap between the micro-biota and their insect host: Persistence of the insect habitat is advantageous to the microbiota. Some microbial partners may, however, respond to pathogen/parasitoid-mediated reduction in insect fitness by increased proliferation and dissemination from the failing insect. These microbial residents of insects are opportunistic pathogens. One possible instance of this response comes from the reduced virulence of baculovirus infecting *Spodoptera*

exigua treated with antibiotic to eliminate the gut microbiota, relative to untreated caterpillars (59).

Detoxification of Toxins: Plant Allelochemicals and Insecticides

Most described instances of detoxification in insects are intrinsic. They are mediated by capabilities encoded by the insect genome, including cytochrome P450 monooxygenases, glutathione S-transferases, and esterases. Resident microorganisms have, however, been implicated in a few systems. Elimination of the yeast-like symbiont *Symbiotaphrina kochi* from *Lasioderma serricorne* beetles depresses larval development on diets containing allelochemicals that cultured *S. kochi* can degrade (40, 104). The capacity of the mountain pine beetle *Dendroctonus*

ponderosae to utilize terpene-rich trees may be facilitated by species of *Pseudomonas*, *Rahnella*, and other resident gut bacteria that have the genetic capacity to degrade terpenes ([1](#)). A laccase enzyme produced by the fungal symbiont of attine ants also mediates the detoxification of plant material brought to the nest by the worker ants ([30](#)).

Resident microorganisms have repeatedly been proposed as a source of insecticide resistance, but most claims lack proper validation. Exceptionally, the resistance of the alydid stink bug *Riptortus pedestris* to the organophosphate fenitrothion is mediated by fenitrothion-degrading *Burkholderia* bacteria that are acquired from the soil by the insects ([63](#)). Further research is required to establish whether other insects benefit from microorganisms that can utilize both the insect habitat and the wider environment in this way.

A Source of Cues and Signals

Microorganisms associated with insects have been invoked as the source of chemicals that alter the behavior of conspecifics or other organisms ([43](#)), to the benefit or disadvantage of the insect host. To illustrate: The phenolic guaiacol in the aggregation pheromone of the desert locust *Schistocerca gregaria* is synthesized by *Pantoea agglomerans* and other *Enterobacteriaceae* in the insect gut ([33](#)); *Drosophila* prefer to mate with conspecifics that have a similar gut microbiota, and this preference is probably linked to microbiota-dependent variation in the

cuticle hydrocarbon profile ([103](#)); and parasitic wasps of the bark beetle *Dendroctonus ponderosae* are attracted to logs containing the fungal partners (*Grosmannia clavigera* and *Ophiostoma montium*) of the beetle, suggesting that these para-sitoids use fungal volatiles as cues to locate beetle larvae and pupae ([2](#)). Most experimental studies, however, lack definitive evidence ([38](#)), and establishing

precisely the role of the microorganisms in the synthesis of insect semiochemicals is a priority for future research in insect chemical ecology.

Resident Microorganisms in Economically Important Insects

The resident microbiota offers great potential for improved methods to manage economically important insects. Three primary opportunities are to predict the traits of insect pests, and hence efficacy of control strategies, from the composition of the microbiota, to target the microbiota for insect pest control, and to manipulate the microbiota to depress the vector competence of insects.

Predictor of Insect Pest Traits

Traits crucial to the management of certain insect pests are dictated by their possession of particular microorganisms. Examples include the secondary symbionts that determine the resistance of aphids to parasitoids and fungal pathogens used as biological control agents ([88], [99]); the pesticide-resistant *Burkholderia* strains that confer pesticide resistance to *Riptortus pedestris* ([63]); and bacteria that enable *Megacopta* stink bugs to utilize soybean crops ([53]). In these systems, the prevalence of the critical microorganisms in insect populations can be used to monitor the pest status and identify preferred control strategies. Regular monitoring would be required because the micro-biota in insect populations can change rapidly ([52], [58]). Monitoring may be particularly valuable for exotic insect species, whose invasiveness can depend on interactions with microorganisms in the introduced range. For example, the US turpentine beetle *Dendroctonus*

valens (Scolytinae) is a minor forestry pest in its native range, but it has been causing high mortality to Chinese pines since its introduction to China in the 1980s ([108]), partly because of its acquisition of fungi from local Chinese Scolytinae ([109]). By contrast, *Megacopta cribraria*, introduced from eastern Asia to the eastern United

States in 2009, appears to have retained the ancestral *Ishikawaella* symbiont; and its rapid transfer to soybean crops in the United States is not linked to symbiont switching ([12](#)).

A Target of Novel Insect-Pest-Control Strategies

The potential of insect pest control with the microbiota as the primary target is greatest for insects dependent on vertically transmitted microorganisms because the insect has no opportunity to acquire equivalent microorganisms from the environment. Many insects with vertically transmitted bacteriocyte symbioses ([Table 1](#)) are agricultural or medically important pests: aphids (super-family Aphidoidea), whiteflies (family Aleyrodidae), planthoppers (infraorder Fulgoroidea), and sharpshooters (tribe Proconiini of the family Cicadellidae)feeding on plant sap; anopluran lice (suborder Anoplura), bed bugs (family Cimicidae), and tsetse flies (family Glossinidae) feeding on vertebrate blood; pests of stored products and timber (e.g., various beetles of the families Curculionidae and Anobiidae); and cockroaches (order Blattodea). The population increase of these insects is abrogated by antibiotics that eliminate the microbial symbionts. The key priority is to identify alternatives to antibiotics that are cost-effective and specific. Recent advances in understanding the cellular processes underlying vertical transmission ([66](#)) and nutrient translocation between the insect and microbial partners ([91](#), [93](#)) are providing candidate molecular targets for disruption of these symbioses.

Microbially Mediated Manipulation of Insect Traits

The insects of greatest interest for microbially mediated manipulation are vectors of disease agents, especially mosquitoes. The goal is to introduce microorganisms that both suppress vector competence and promote their own dissemination through the insect population.

Bacteria of the genus *Wolbachia* have long been identified as candidate microorganisms for this application. Most mosquito vector species are not infected with *Wolbachia* naturally, and the stable introductions of *Wolbachia* from *Drosophila* into *Aedes aegypti* ([77](#)) and *Anopheles stephensi* ([9](#)) are major breakthroughs. The insects bearing *Wolbachia* display enhanced resistance to dengue and chikungunya viruses and *Plasmodium* parasites, probably through heightened immunological function ([9](#), [55](#), [62](#), [118](#)). Field trials are investigating the fate of introduced *Wolbachia*-infected mosquitoes, with the long-term goal to release these insects to reduce disease transmission.

An alternative route for microbial manipulation of insect pests is to exploit members of the native microbiota of the insect vector by introducing gene(s) deleterious to the disease agent into a bacterial symbiont. Proof of principle has been obtained for *Trypanosoma cruzi*, the agent of Chagas disease, vectored by *Rhodnius prolixus*; when the gut symbiont, *Rhodococcus rhodnii*, was genetically modified to express the antimicrobial peptide cecropin A and then introduced to *R. prolixus*, transmission of *T. cruzi* was suppressed ([41](#)). Furthermore, *R. prolixus* populations in domestic environments are readily infected when they feed on mock fecal pellets containing the genetically modified bacteria, a formulation that has been developed as Cruzigard. Analogous approaches are under development to suppress transmission of the *Leishmania* parasite by sand flies *Phlebotomus argentipes* ([57](#)).

In principle, multiple opportunities are available to modify the pest status of insects by promoting members of the insect's native microbiota that influence vector competence or other traits of interest (e.g., plant range of crop pests, capacity for dispersal, mate choice, oviposition preference). Effective manipulation of native microbiota in pest management, however, depends on a detailed understanding of the function of insect-associated microorganisms and the interplay of factors that

shape their abundance within an insect and dissemination through insect populations.

Perspectives and Future Directions

Microorganisms are ubiquitous in insects and have pervasive impacts on multiple aspects of insect biology. Consequently, microorganisms should be included as candidate factors affecting virtually any aspect of insect biology. Fortunately, the tools to study these associations are increasingly available, including methods to identify and quantify microorganisms and their functions, to manipulate the composition of the microbiota, and to investigate their interactions with the nutrition, immunity, and other physiological systems of the insect.

Some aspects of insect-microbe interactions now have a firm experimental foundation, but others remain contentious. Of particular interest for future research are the mechanisms by which resident microorganisms influence insect susceptibility to pathogens, insect capacity to degrade phytotoxins, and insect capacity to vector plant viruses and medically important disease agents. Careful experimental analyses are required to assess the generality of microorganisms as determinants of insect communication (38), plant range (50), resistance to insecticides (63), and insect speciation events (13).