Insect Dietary Needs: Plants as Food for Insects

Spencer T. Behmer
Department of Entomology, Texas A&M University, College Station, Texas, U.S.A.

INTRODUCTION

Insects comprise more than half of all living macroscopic organisms, and about half of all insects feed on plants. Plant-feeding as a lifestyle is, however, found in only 8 of the 30 insect orders—Coleoptera (beetles), Diptera (flies), Hemiptera (sucking bugs), Hymenoptera (sawflies, wasps, ants, and bees), Lepidoptera (butterflies and moths), Orthoptera (grasshoppers, katydids, and crickets), Phasmida (stick and leaf insects) and Thysanoptera (thrips). Like all other animals, plant-feeding insects eat to acquire the nutrients necessary for growth, reproduction, and general maintenance, and while the qualitative nutritional requirements of all insects are generally quite similar, plant-feeding insects do have some special requirements. An additional issue for plant-feeders is that the nutrient content of plants and plant parts are considerably variable. In some instances, plant-feeding insects have developed mutualistic relationships with microorganisms, which has allowed them to feed on plants, or plant tissues, that lack or contain low levels of essential nutrients.

INSECT NUTRITIONAL REQUIREMENTS

Plant-feeding insects, like other insects and animals, have the ability to biosynthesize some nutrients, although most of the nutrients they need are provided by their host-plants. Nutrients that cannot be synthesized endogenously are classified as being essential, while those that can be produced by using other dietary components are termed non-essential. Much of our understanding of nutrition in plant-feeding insects comes from rearing studies using artificial foods. The most common approach is to omit a specific nutrient from the diet and then measure the effect of this deletion on insect growth and/or reproduction. Once essential nutrients have been identified, the effect of replacing these nutrients with analogs can be measured. Finally, radiolabeled precursors can be used to determine which nutrients are generated endogenously.

AMINO ACIDS

Amino acids, the building blocks of protein, are often considered the most limiting nutrients for plant-feeding insects. There are 20 amino acids that are regularly found in plant proteins, and of these 10 are considered essential (Table 1). Plant-feeding insects use amino acids to build proteins, which can be used for structural purposes, as enzymes, for transport and storage, or as receptor molecules. Individual amino acids also serve important physiological functions. For example, tyrosine is essential for hardening of the cuticle, tryptophan is used in the synthesis of visual screening pigments, glutamate operates as a neurotransmitter, and for some plant-feeding insects proline is an important energy source.[1]

Plant proteins are the dominant source of amino acids, although plants also contain a small pool of free amino acids (usually about 5% of the total). An individual plant will contain a range of different proteins, but the value of any particular protein varies depending on its digestibility and amino acid content, particularly the number and balance of essential amino acids. Ribulose bisphosphate carboxylase is likely to be a particularly important dietary protein because it makes up about 50% of the soluble protein in young leaves.[2] Protein composition and quality also vary between and within plant species as a result of genetic and environmental factors, as well as within an individual plant as a result of differences in leaf age (e.g., protein content is usually high in young leaves but tends to be lower in old leaves) or plant part (e.g., nitrogen concentration is lowest in xylem and phloem but highest in flower buds and seeds). In general, the absence of any single essential amino acid from the diet prevents growth, and in some instances non-essential amino acids (e.g., proline for the silkworm, *Bombyx*) may be required.[1] Even though some amino acids are non-essential, optimal growth usually only occurs when there is a good mixture of non-essential amino acids in the diet.

CARBOHYDRATES

Carbohydrates, which contain the elements carbon, hydrogen, and oxygen in a 1 : 2 : 1 ratio, respectively, are the major source of metabolic energy for plant-feeding insects. Carbohydrates are generally split into two groups: sugars (e.g., glucose, fructose, and sucrose) and non-sugars (e.g., starch, dextrin, and cellulose).

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Table 1 Essential and non-essential amino acids for plant-feeding insects. Amino acids that cannot be synthesized by insects are called essential, and these must be obtained from the diet or generated from non-essential amino acids by endosymbionts

Essential	Non-essential
Arginine	Alanine
Histidine	Asparagine
Isoleucine	Aspartate
Leucine	Cystine
Lysine	Glutamate
Methionine	Glycine
Phenylalanine	Histidine
Threonine	Proline
Tryptophan	Serine
Valine	Tyrosine

The ability of a plant-feeding insect to use a particular carbohydrate depends upon the type of digestive enzymes present in the salivary glands and midgut. Most plant-feeding insects can use sugars, starch, and dextrin, but not cellulose.[3]

Strictly speaking, carbohydrates are not essential nutrients because insects can convert fats and amino acids to carbohydrates via gluconeogenesis. Nonetheless, carbohydrates are considered important, and growth is enhanced when they are provided in the diet. For example, the desert locust, *Schistocerca*, grows best on a diet containing 20% digestible carbohydrates, while the flour beetle, *Tenebrio*, exhibits optimal growth on diets containing 70% carbohydrate.[1] *Tenebrio* fails to develop, however, if the carbohydrate concentrations drop below 40%.

LIPIDS, VITAMINS, AND MINERALS

Lipids are found in both plants and animals, where they operate as electron carriers, substrate carriers in enzymatic reactions, components of biological membranes, and sources and stores of energy, and their common property is insolubility in water. Sterols, fatty acids, fat-soluble vitamins, and carotenoids are examples of lipids that are either essential or considered important for plant-feeding insects.

Sterols serve as structural components in cellular membranes and as precursors for steroid hormones (e.g., molting hormone), and are essential nutrients for all insects, in fact all arthropods. Cholesterol (Fig. 1) tends to be the dominant tissue sterol in plant-feeding insects despite the fact that plants rarely contain it at appreciable levels. To date hundreds of different sterols have been identified in plants, with

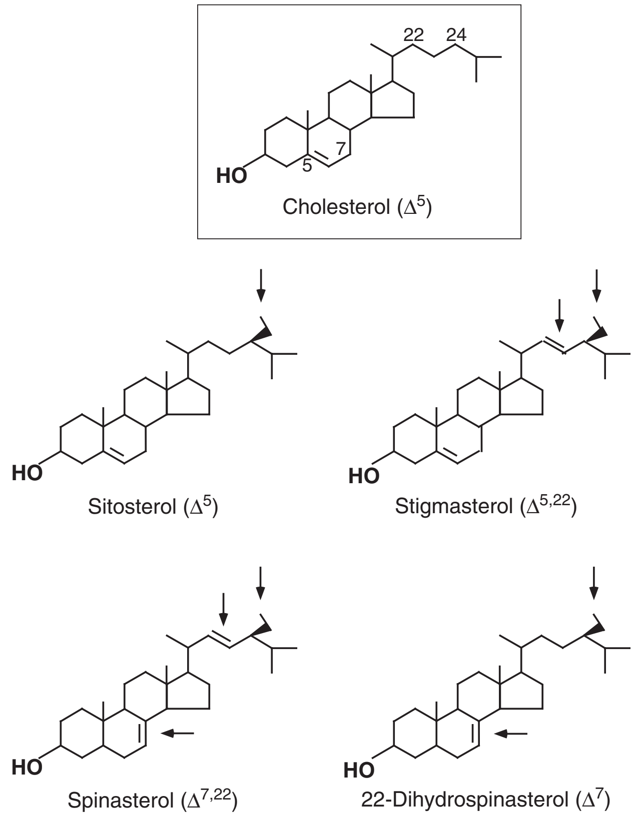

Fig. 1 All plant-feeding insects require a dietary source of sterol, and cholesterol, with a double bond at position 5 (Δ^5), is the dominant tissue sterol found in insects. Plants, however, rarely contain cholesterol at appreciable levels. The arrows on the four plant sterols indicate structural differences from cholesterol. Of the four plant sterols shown, only sitosterol supports normal growth and development in grasshoppers.

sitosterol being the most common; so plant-feeding insects produce cholesterol by metabolizing the sterols found in their host-plants.[4] Some plant-feeding insects, however, have strict limitations on which plant sterols can be metabolized to cholesterol. Grasshoppers, for example, cannot use sterols with double bonds in certain positions (Fig. 1).[4] Some plant-feeding insects, such as the cactus fly, *Drosophila pachea*, can only use the phytosterols found in the plants on which they specialize.[5]

Most plant-feeding insects also have a dietary requirement for polyunsaturated fatty acids. Generally plant-feeding insects grow well when linoleic or linolenic acid is present in the diet (Fig. 2).[3] The effect of omitting fatty acids from the diet varies from species to species. For example, in the Lepidoptera and Hymenoptera, adults fail to develop properly if linolenic acid is omitted from their larval diet,[1] although this does not appear to be the case for the caterpillar *Heliothis subflexa*.[6] Fatty acids also seem to play a role in

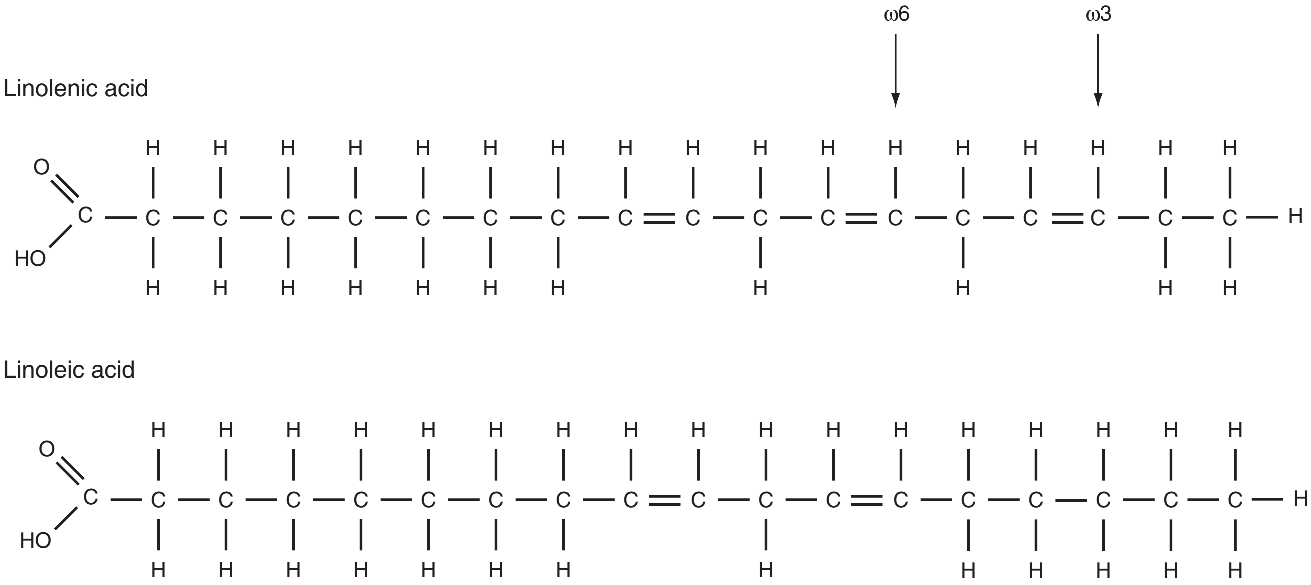

Fig. 2 Most plant-feeding insects require a dietary source of polyunsaturated fatty acids with double bonds in the 3 and/or 6 position. Linoleic and linolenic acid each have a chain length of 18 carbons, but they differ in the number of double bonds contained within the chain (2 and 3, respectively).

reproduction because some beetles suffer reduced fecundity and produce slow growing larvae when it is omitted from the diet. The Diptera, with the exception of mosquitoes, do not seem to require polyunsaturated fatty acids.[1]

Vitamins are organic compounds, and plant-feeding insects, like other animals, need them in small amounts. Typically, vitamins are split into two groups based on their solubility in water. The B vitamins, including thiamine, riboflavin, nicotinic acid, pyridoxine, pantothenic acid, folic acid, and biotin, are water soluble. Primarily, they function as cofactors of the enzymes catalyzing metabolic transformations, but they also serve additional roles (e.g., biotin is part of the enzyme pyruvate carboxylase, and folic acid is necessary for nucleic acid biosynthesis).[3] *Myo*-inositol and choline are components of some phospholipids and are usually required in larger quantities than vitamins. Choline can be produced from methionine, though, so the amount of choline a plant-feeding insect needs will vary depending on the levels of methionine in the diet.[1] Ascorbic acid, which is also known as vitamin C, is required by most plant-feeding insects.

Plant-feeding insects also require two fat-soluble vitamins. The first of these, β-carotene (provitamin A), is a functional component of visual pigments and is involved in the normal pigmentation of plant-feeding insects. It is, however, produced only by plants and microorganisms, and when carotenoids are absent from the diet, insects often appear rather drab and dull, and melanization is reduced.[1] Vitamin E (α-tocopherol) is the other lipid-soluble vitamin needed by most plant-feeding insects. Its presence boosts fecundity, while its absence negatively affects sperm production.[1]

Mineral elements are found in most plant-feeding insects because they are constituents of plants. However, sodium, potassium, calcium, magnesium, chloride, and phosphate are considered essential because they each play an important role in metabolic processes. As with other animals, plant-feeding insects require iron because it is the central element in cytochromes.[1] Zinc and manganese are also required because they play a part in hardening the cuticle of mandibles.[3]

NUTRIENT POOR FOODS AND ENDOSYMBIONTS

While most plant-feeding insects eat leaves, those in the order Hemiptera have specialized mouthparts that enable them to feed from individual plant cells. For example, some treehoppers (Membracidae) feed from leaf mesophyll, aphids (Aphididae) and planthoppers (Fulgoridae) feed on phloem, and spittlebugs (Cercopidae) feed on xylem. Some plant-feeding insects have also become specialists on wood (e.g., beetles in the family Bostrycidae), while others specialize on detritus (e.g., crickets). Generally speaking, sap, wood, and detritus are not particularly nutritious, so insects feeding on these substrates use endosymbionts, which reside in the alimentary canal and/or intracellularly, to overcome nutritional deficits.[7] The majority of the endosymbionts in plant-feeding insects are bacteria, although yeast is found in planthoppers and in some wood-boring beetles.[1,7] The endosymbionts of aphids and wood-boring beetles produce essential amino acids from non-essential amino acids, while the endosymbionts of wood-feeding insects digest and metabolize cellulose. Endosymbionts, particularly yeast, may also supply sterols.[3]

CONCLUSIONS

Much of the success of insects as a group has been attributed to their ability to feed on a wide range of foods, and this certainly seems the case for plant-feeding insects because they are found on every plant and virtually every plant part (leaves, stems, flowers, roots, vascular tissues, etc.). Compared to their predaceous relatives, however, the food of plant-feeding insects is nutritionally poor. For example, it has a much lower protein/carbohydrate ratio and is generally lower in sodium. Additionally, many plants contain defensive compounds that are toxic or interfere with digestion.[2] Nonetheless, plant-feeding insects are quite adept at regulating the intake of important nutrients,[8] and they employ a range of pre- and post-ingestive mechanisms to reduce the intake of harmful chemicals and their toxicity, respectively.[2,8] Nutrient regulation is a critical component in determining the individual success of any insect, including economically important pest species, and a more comprehensive understanding of insect nutrition might lead to the development of novel control methods that exploit insect nutritional requirements. Such an approach would be advantageous because it would be target specific and environmentally friendly.

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