CHAPTER 2

Nutritional physiology and ecology

> An understanding of insect ecology has been hampered by an inadequate knowledge of nutritional physiology.
>
> Scriber and Slansky (1981)

Diverse insect diets are associated with entirely different constraints: liquid diets come with a weight or volume problem, solid diets require mechanical breakdown without damage to the gut, plant diets are poor in nutrients, and animal meals are unpredictable in time and space (Dow 1986). Most species of holometabolous insect could be represented in Fig. 2.1 by two linked circles, as a result of vastly different diets in the larval and adult stages. Folivory necessitates an increase in mass of the gut and its contents, with longer retention time, which is incompatible with flight (Dudley and Vermeij 1992). Although this applies to relatively sessile caterpillars, they metamorphose into nectar-feeding adults. About half of known insects are phytophagous, and among these some feeding guilds have been relatively well studied, in particular the leaf-chewers, which are mostly larvae. The nutritional ecology of immature insects was the subject of a classic review by Scriber and Slansky (1981). The present chapter is inevitably biased towards grasshoppers and caterpillars and, to a lesser extent, cockroaches and various fluid feeders. Recent technical advances and the advent of molecular biology have made it possible to study in some depth the nutrition of aphids, another group of agricultural pests, and their simpler diet means that synthetic diets are closer to the real thing. We consider the physiological constraints on feeding behaviour and the physiology of digestion and absorption, before turning to the difficulties of plant feeding and the longer-term consequences of feeding for growth, development, and the life histories of insects.

A major theme of this chapter is compensatory feeding. In spite of the enormous variation in the quality of plant food, insects obtain their requirements by means of flexible feeding behaviour and nutrient utilization (Slansky 1993). There are three basic categories of compensatory responses shown by phytophagous insects (Simpson and Simpson 1990): *increased consumption* in order to obtain more of a limiting nutrient such as nitrogen, *dietary selection* of a different food to complement a limiting nutrient, or *increased digestive efficiency* to make the best use of a nutrient. The mechanisms of compensatory feeding have been studied in some detail for the major nutrients, proteins and carbohydrates. To avoid difficulties in interpreting experiments, the use of artificial diets is essential, in spite of their ecological limitations (Simpson and Simpson 1990). Another pervasive theme is nitrogen limitation. Insect herbivores tend to be limited by nitrogen because their C:N ratio is so much lower than that of the plants they eat (Mattson 1980).

It is feeding that makes insects into agricultural pests and disease vectors, although the choice of species and problems for research has often been very selective as a result (Stoffolano 1995). Knowledge of food consumption and utilization is of great importance in managing problem insects, and consequently there is an enormous literature on basic and applied insect nutrition and nutritional ecology. As examples of major reviews, the more