

higher (Fig. 2.7), most amino acid absorption is  $K^+$ -dependent (Sacchi and Wolfersberger 1996). Transport of neutral amino acids has received the most attention, and this model seems to be generally applicable to other lepidopteran larvae. Neutral amino acid- $K^+$  symport is effective over most of the pH range found in *M. sexta* midgut, but occurs mostly in the posterior third of the midgut where luminal pH is less extreme (Sacchi and Wolfersberger 1996). The latter review of amino acid absorption in insect midgut was updated by Wolfersberger (2000), including molecular studies of the symporters involved. The literature remains unbalanced in favour of large caterpillars, but the focus has shifted from *P. cynthia* to *Bombyx mori* and *M. sexta*, which can be reared throughout the year on artificial diets. Several absorption mechanisms are evident in midguts of larval *B. mori*: the neutral amino acid- $K^+$  symport described above, and a less selective uniport system which facilitates diffusion of amino acids (Giordana *et al.* 1998; Leonardi *et al.* 1998). Another uniport system transports the dibasic amino acids arginine and lysine (Casartelli *et al.* 2001). The cDNA encoding a  $K^+$ -amino acid symporter from *M. sexta* midgut has been isolated and cloned, and the deduced amino acid sequence shows homology to mammalian amino acid transporters (Castagna *et al.* 1998).

Absorption of lipids requires solubilization in the layer of water adjacent to the absorptive cells, but the details are poorly understood in insects (Turunen and Crailsheim 1996). Nothing is known about the possible role of fatty acid transporters in the apical membrane of midgut cells (Arrese *et al.* 2001). After absorption, fatty acids are converted to diacylglycerols in midgut cells and released to a haemolymph lipoprotein called lipophorin: this is a transport protein which acts as a reusable shuttle and delivers diacylglycerols and other lipids to various tissues (Arrese *et al.* 2001). In the fat body the diacylglycerols are converted to triacylglycerols for storage, and in the larva of *M. sexta* they can be 30 per cent of the wet mass of this tissue. Lipophorin also transports diacylglycerols from fat body to flight muscles during sustained flight. Ryan and van der Horst (2000) recently reviewed lipid mobilization (in response to adipokinetic

hormone) and lipid transport in relation to flight. These aspects of lipid biochemistry in insects, which are being used as a model system for comparison with vertebrates, seem to be better known than digestion and absorption.

Glucose transporters such as the well known  $Na^+$ -glucose cotransporters have been intensively studied in vertebrates, although little is known about their equivalents in insects (but see Andersson Escher and Rasmuson-Lestander 1999). Evidence summarized by Turunen and Crailsheim (1996) suggests that glucose transport is passive in most insects: transport is unaffected by metabolic inhibitors, depends on concentration gradient, and fructose and unmetabolized 3-O-methylglucose are transported at the same rate as glucose. Crailsheim (1988) found that 3-O-methylglucose injected into the haemolymph of honeybees became equally distributed between midgut lumen and haemolymph in 30 min. It is assumed that fructose transport across the gut wall is also passive, and fructose is then converted to glucose by hexokinase and phosphoglucosomerase (Bailey 1975). In the fat body, trehalose is synthesized from glucose via hexose phosphates (also intermediates in glycogen synthesis). Like the transport disaccharide of plants (sucrose), it is a non-reducing sugar and less reactive than glucose (Candy *et al.* 1997). Treherne (1958) first showed the conversion of labelled glucose and fructose to trehalose, and pointed out its significance in maintaining a steep concentration gradient for absorption of monosaccharides. Water absorption from the midgut would also increase this concentration gradient (Turunen and Crailsheim 1996). Absorption of sugars is fast and complete. For example, female mosquitoes that have been flown to exhaustion will resume continuous flight within a minute of starting to feed on glucose solution (Nayar and Van Handel 1971). Unfed honeybees given labelled glucose incorporate it into trehalose within 2 min of feeding and there is no loss of label in the excreta (Gmeinbauer and Crailsheim 1993).

These last examples concern insects with initially empty crops. Crop-emptying is in fact, the limiting process for absorption of monosaccharides in insects, and its control has been attributed variously to the osmolality or sugar concentrations

of food or haemolymph concentration. In honeybees, crop-emptying is unrestrained by amounts of sucrose in the crop (Blatt and Roeser 1996). In some species, crop-emptying is inversely related to sugar concentration. Conversion to sucrose left the crop empty, and the concentration of food concentration with the metabolic rate. It is well known that the rate of food intake depends on the concentration of food (Moffat and Núñez 1996). Haemolymph sugar concentration under all conditions of food and a high temperature (cold); haemolymph sugar concentration decreased. Crop-emptying is the energy demand for trehalose concentration. We conclude that the rate of food intake by considering the rate of food intake there are reversible changes in absorption capacity, which have been demonstrated (Weiss *et al.* 1998). The rate of food intake compensates for reduced food intake (Yang and Joern 1996). Low protein diet and although they still feed, Woods and Chambers (1996) found transport in the posterior midgut. They found no response to flat salinity. They used flat salinity, asymmetrical salinity conditions, and not L-proline, which was in the haemolymph 15 times in the same direction. However, the border membrane of *B. mori* (Lepidoptera) starved larvae (Leonardi *et al.* 2000) data from vertebrates showing upregulation of responses to increased substrate concentrations describe