herbivores are 5–10-fold lower than those of foliage. Phosphorus content is inversely related to body mass in insects, and more recently derived orders tend to have lower nitrogen and phosphorus contents (Fagan *et al.* 2002; Woods *et al.* 2004).

Nitrogen is a general indicator of host plant quality, but because other phytochemicals and water vary simultaneously with nitrogen, causality is difficult to prove (Kytö *et al.* 1996; Speight *et al.* 1999; Karley *et al.* 2002). An exception is found in phloem feeders, whose relatively simple but nutritionally unbalanced food provides an excellent opportunity for testing mechanistic relationships between plant quality and insect performance. Nitrogen quality is also important, and this is measured as the concentrations of individual amino acids in phloem sap. Silverleaf whiteflies *Bemisia tabaci* (Aleyrodidae) feeding on cotton plants with and without fertilizer treatment differ greatly in free amino acid pools, especially the proportion of the non-essential amino acid glutamine (Crafts-Brandner 2002). Another rapid adjustment was in amino nitrogen excretion (but not honeydew production), which essentially stopped for whiteflies fed on low-nitrogen plants. Aphids are serious pests of potato crops, and Karley *et al.* (2002) compared several performance parameters of *Myzus persicae* and *Macrosiphum euphorbiae* on young and old potato plants, and on artificial diets mimicking their phloem sap. Decreased performance on older plants is due to changes in the amino acid profile of the phloem sap, especially a dramatic decline in glutamine levels. It is interesting that there was no significant correlation between the C : N ratio of plant tissue and the phloem sap sucrose:amino acid ratio (Karley *et al.* 2002). Incidentally, carbon is even more scarce than nitrogen in a xylem diet, and carbon retention by three species of leafhoppers (Homoptera, Cicadellidae) far exceeds nitrogen retention, excess nitrogen being excreted as ammonia (Brodbeck *et al.* 1993).

Bernays (1986*b*) compared the utilization of a wheat diet in a grasshopper and a caterpillar of similar size, reared under identical conditions. Values of AD were similar, but ECD was lower in the grasshoppers, and this was attributed to their large investment in cuticle mass. Cuticle consists mostly of protein and chitin, which are 16 and 7 per cent nitrogen by mass, respectively. Using rain forest beetles in Borneo, Rees (1986) found that adult Chrysomelidae carried significantly less exoskeleton in proportion to body mass than did representatives of several other beetle families, and attributed this to a shortage of nitrogen in their plant diet. However, this conclusion may be biased by phylogenetic relatedness and allometric considerations: the fraction of body mass in the skeleton increases with increasing body size (Schmidt-Nielsen 1984). The importance of recycling cuticular nitrogen was demonstrated recently in cockroaches eating and digesting their own exuviae (Mira 2000). This behaviour was more common in females, in insects reared on a low-protein diet, and in those deprived of their endosymbiotic bacteria. Mira also speculated that acquiring particular amino acids might be important, rather than nitrogen in general: phenyalanine is abundant in cuticle but scarce in plant tissues, and is selected by grasshoppers (Behmer and Joern 1993). Pea aphids (*A. pisum*) lose in their exuviae about 10 per cent of the total amino acids in the tissues of the adult aphid (Febvay *et al.* 1999).

Contribution of symbionts to nitrogen balance

Many insects possess microbial symbionts which assist with apparently unpromising or deficient diets. Their contributions are diverse and hold much potential in the area of pest management (Douglas 1998). The symbionts may be extracellular, like those in the gut lumen of termites, or intracellular, confined to large cells known as mycetocytes. Mycetocyte symbiosis is best known in Blattaria, Homoptera, Phthiraptera, and Coleoptera living on nutritionally poor diets such as wood, plant sap, or vertebrate blood. Nutritional benefits to the host are often assumed to involve nitrogen, but blood-feeding tsetse flies are provided with missing B vitamins and other insects with sterols (for review see Douglas 1989). Simpson and Raubenheimer (1993*a*) presented a phylogenetic analysis of the effect of mycetocyte symbionts on the ratio of protein to digestible carbohydrate required in insect diets, using data from an extensive literature on artificial diets. Insects with the lowest protein requirements in relation to