

carbohydrate were those with endosymbiotic bacteria which presumably contribute to nitrogen metabolism. Use of a geometric framework to investigate performance of newborn pea aphids, *A. pisum* (Homoptera, Aphididae), demonstrated an intake target based on an 8:1 ratio of sucrose to amino acids (Abisgold *et al.* 1994).

The best direct evidence that mycetocyte symbionts are important to nitrogen balance comes from aphids. The amino acid composition of phloem sap is unbalanced, and essential amino acids are synthesized by symbiotic bacteria of the genus *Buchnera* (Febvay *et al.* 1999; Douglas *et al.* 2001). These bacteria live inside the host mycetocytes (occupying most of the cell volume) and are transmitted vertically from a female to her progeny. The symbionts convert non-essential to essential amino acids, and also use dietary sucrose extensively in the synthesis of essential amino acids (Fig. 2.12), even when the diet resembles aphid tissues (and not phloem sap) in composition (Febvay *et al.* 1999). Aposymbiotic insects, in which heat or antibiotic treatment is used to eliminate the intracellular microorganisms, have been widely used to investigate interactions between partners. Aphid performance is dramatically reduced after treatment with antibiotics, especially when the insects are reared on diets from which individual amino acids have been omitted (Douglas *et al.* 2001). It has been suggested that symbionts of the silverleaf whitefly *B. tabaci* (Aleyrodidae) are responsible for production of trehalulose (Davidson

et al. 1994), although oligosaccharide synthesis is unchanged in aposymbiotic pea aphids (Wilkinson *et al.* 1997). Yeast-like endosymbionts in the brown planthopper *Nilaparvata lugens* (Delphacidae), a major pest of rice, have high uricase activity and may be recycling nitrogen (Sasaki *et al.* 1996).

Nitrogen recycling also occurs in cockroaches, but here the microbiology is more complicated because they have both a complex hindgut microflora and bacterial endosymbionts, which mobilize urate deposits in the fat body on low-nitrogen diets and convert them to essential amino acids. Nitrogen is often limiting in the diets of these opportunistic scavengers (Kells *et al.* 1999). Termites survive on diets with very high C:N ratios, but possess hindgut bacteria which contribute significantly to the nitrogen economy of their hosts by recycling uric acid nitrogen and by fixing atmospheric nitrogen (Breznak 2000). Nardi *et al.* (2002) have recently drawn attention to the substantial contribution that microbes in the guts of arthropod detritivores may be making to nitrogen fixation in terrestrial ecosystems. Molecular techniques have made it possible to study gut microbes and identify their nitrogenase enzymes without the necessity of culturing difficult organisms, which has hindered such studies in the past (Breznak 2000).

2.4.3 Secondary plant compounds

The molecular structure of secondary plant compounds is far better known than their modes of

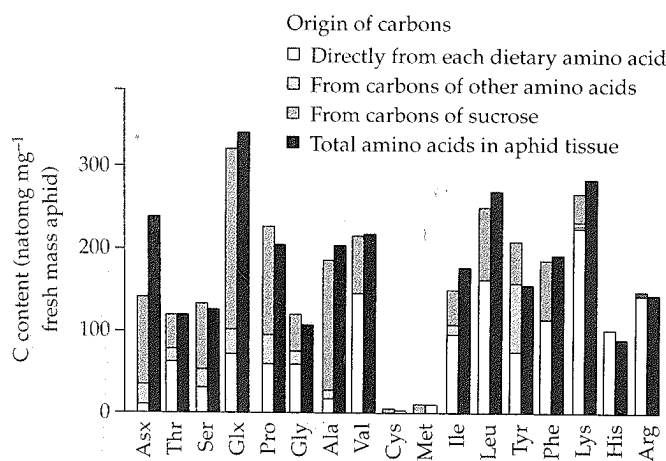


Figure 2.12 Origin of the carbons of each amino acid in the pea aphid, *Acyrthosiphon pisum*, reared on an artificial diet with balanced amino acid composition as in aphid tissue.

Note: Carbons are derived from amino acids in the food, from other dietary amino acids after conversion, or from dietary sucrose. For each amino acid, the sum of the carbons from different sources is roughly the same as the amount recovered in aphid tissues (black bars).

Source: Febvay *et al.* (1999).

action, and is especially in t...
mists have f...
Firn 1991). In...
three primary...
angiosperms,...
chemistry. Ch...
according to...
(discussed by...
a distinction...
(produced in s...
plants) and di...
(‘quantitative’...
large quantities...
Mattson (1980)...
are associated...
legumes, and...
based (e.g. a...
non-protein am...
glycosides) are...
proteinase inhi...
toxic. Digestibil...
other hand, ten...
nitrogen enviro...
carbon-based (...
the carbon-nut...
et al. (1983), the...
plants and inv...
and defence. N...
concentration w...
increases, whil...
defences decrea...
ally, Haukioja...
protein synthes...
phenylalanine,...
dense tannins...
tests of the ca...
(Hamilton *et al.*...
generated to ex...
see Cipollini *et al.*...
measurement o...
thorough study...
The distinction...
allelochemicals...
uses the term ‘a...
which reduce...
(Felton and Gate...
availability may