



Figure 2.9 Rates of proline transport by posterior midguts of *Manduca sexta* caterpillars (fifth instar) reared on high or low protein diets and then transferred to high or low protein diets for 24 h. Mean \pm SE of 6–7 midguts.

Note: The four high traces are fluxes from lumen to haemolymph, and the four low traces are fluxes in the other direction. Lower values at 15 min are due to equilibration of labelled proline. There was no effect of rearing or test diets.

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of monosaccharides in insect midgut is less likely to be modulated in response to dietary change. Whether the paracellular route is involved in nutrient absorption in insects has apparently not been considered.

2.4 Overcoming problems with plant feeding

Half of all insect species feed on living plants. Although few orders have overcome the evolutionary hurdles of plant feeding, those few (especially Orthoptera, Hemiptera, and Lepidoptera) have been extremely successful (Southwood 1972; Farrell 1998). Apart from mechanical obstacles to feeding, herbivores must contend with indigestible cellulose, nutrient deficiencies (especially low nitrogen), and allelochemicals. Often, maximizing nutrient intake while minimizing secondary compound intake requires complex foraging decisions and can prevent the insect from reaching its intake target (Behmer *et al.* 2002). Many of the solutions involve interactions with microorganisms. There is a vast literature in this area and our treatment is highly selective.

2.4.1 Cellulose digestion: endogenous or microbial?

Caterpillars and most other insect folivores are unable to use the huge proportion of plant energy locked up in cellulose. Martin (1991), in reviewing the evolutionary ecology of cellulose digestion, suggests that it is rare because insect herbivores are usually limited by nitrogen or water and not by carbon, so they would derive no particular benefit from exploiting the energy in cellulose. Cellulose digestion is much more likely in wood-feeding (xylophagous) insects or omnivorous scavengers with nutritionally poor diets, especially those whose guts are colonized by microorganisms. The best known cellulose-digesting insects are termites and the closely related cockroaches.

The traditional assumption is that cellulose-digesting enzymes are derived from protozoa or bacteria residing in the hindgut, or fungi ingested with the diet; this assumption is consistent with the independent evolution of the capacity in different taxa (Martin 1991). However, the contribution of endogenous enzymes has been strongly debated (Slaytor 1992). Because insects are almost universally associated with microorganisms, it has been difficult to refute the long-standing hypothesis of derived enzymes, even though most symbionts are located in the hindgut, endogenous cellulase is present in salivary glands and midgut, and cockroaches have far smaller symbiont populations than do termites. Lower termites appear to utilize both endogenous and protozoal cellulases; their specialized hindgut has chambers containing large populations of protozoa, which break down cellulose to glucose and ferment it to short-chain fatty acids, mainly acetate, propionate and butyrate. Higher termites (the majority of termite species) lack hindgut protozoa and appear to utilize endogenous enzymes, except for fungus-growing species in the subfamily Macrotermitinae which acquire additional cellulases from the fungus (*Termitomyces* sp.) that they cultivate and consume.

Cellulase is an enzyme complex capable of converting crystalline cellulose to glucose (Slaytor 1992). In termites and cockroaches its main components are endo- β -1,4-glucanases, which cleave glucosidic bonds along a cellulose chain, and

β -1,4-glucosidases. Insects are active against cellulose but their endogenous cellulase activity and as in *Panesthia* which feeds on rotting wood (1994). An endogenous 4-glucanase from *Termitomyces* (Rhino Watanabe *et al.* (1994) glands, along with glucose from cellulose is then for the high e mentioned by M

The Macrotermitinae on combs consume and consume food. Besides enzymes, because of structural carbohydrates in newly formed comb with spore foragers (Johnson have recently been histories of fungus beetles (see Muel has evolved several origins are evident cerambycid larvae ants and termites cellulose digestion and the Macro herbivores and c and fungus-growing pests. The emphasis cellulose digestion leaf-cutting ants (2002). Other potential leaf-cutting ants possess the enzyme xylan and laminar *et al.* 2002). While large proportion of extracellular degradation enzymes of fungus