tubules (Snyder *et al.* 1994). Rapid and reversible induction of nicotine metabolism, and the efficient active transport system in the tubules, are major adaptations of *M. sexta* to high levels of this active alkaloid. The reversibility of the response suggests that detoxification might be costly, but in *M. sexta* larvae the processing of nicotine does not impose a significant metabolic cost, nor does the processing of toxins from non-host plants, although the latter do have other adverse effects (Appel and Martin 1992).

According to coevolutionary theory, certain insect species have been successful in counteracting plant defences and those defences may then be used as unique feeding stimulants for species which specialize on the plant. Meanwhile the toxic or deterrent effect still works for other, generalist herbivores (for many fascinating examples see Harborne 1993). In such specialist feeders, allelochemicals may be sequestered for chemical protection, as in insects which sequester cardiac glycosides from milkweeds (Asclepiadaceae). Moreover, the allelochemicals become feeding attractants and oviposition stimulants, contributing to the evolution of close insect–plant associations and the enormous diversity of angiosperm feeders (Farrell 1998). Molecular phylogenies of *Blepharida* (Coleoptera, Chrysomelidae), many of which are monophagous, and *Bursera* species, which are rich in terpenes, show that host shifts have been strongly influenced by host plant chemistry (Becerra 1997). The role of chemistry in plant–animal interactions is beautifully illustrated by the cactus–microorganism–*Drosophila* system of the Sonoran desert (reviewed by Fogleman and Danielson 2001). Four species of *Drosophila* feed and reproduce in the necrotic tissue of five species of columnar cacti, each fly on a specific cactus, the specificity being due to the allelochemistry of the cacti (the presence or absence of certain sterols, alkaloids and terpenoids) and the volatile cues resulting from microbial action. Molecular ecological studies are now focusing on the evolution of the multiple cytochrome P-450 enzymes involved in these *Drosophila*–cactus relationships.

Host-plant specificity

There are two main benefits to feeding on a mixture of plants: selection of a suitable balance of nutrients, and dilution of allelochemicals, so that levels of particular compounds remain below critical values. Grasshoppers are highly mobile compared to other phytophagous insects and generally polyphagous, and they have exploited the fact that grasses have minimal chemical defence (Joern 1979; Harborne 1993). Increased locomotion presents more opportunities for diet mixing. However, different populations of an oligophagous species may be regional specialists, and individual insects may be more specialized than the population as a whole. This variation may be a function of both plant resistance and insect preference (Singer and Parmesan 1993). The latter hypotheses are not supported by Joern's (1979) study of two arid grassland communities in Texas, in which niche breadths for 12 grasshopper species common to both study sites were strikingly similar, or by close field observations of feeding in the polyphagous grasshopper *Taeniopoda eques*, in which single meals of individual females included up to 11 food items (Raubenheimer and Bernays 1993). The more phylogenetically derived insect orders (with more sedentary larvae) have tended towards diet specialization, which suggests greater efficiency than polyphagy, but there is not much supporting evidence for the idea that increased performance on one plant species is correlated with reduced performance on others, or that there is a physiological advantage to be gained from feeding specialization (Jaenike 1990). In a detailed comparison of 20 species of Lepidoptera larvae of varying degrees of specialization, the feeding generalists had slower consumption and growth rates, but this was mainly because they tended to be tree-feeders (Scriber and Feeny 1979). The advantages may be more ecological than physiological (as when a specialized insect becomes adapted to detoxify that plant's allelochemicals, and may even sequester and use the toxins for its own defence). For a readable account of the complexities of host plant specificity see Schoonhoven *et al.* (1998). It is also becoming clear that the study of tritrophic interactions may be necessary to explain host plant selection of some insect herbivores that select plants that are apparently suboptimal in nutritional quality (Singer and Stireman 2003).