action, and is characterized by great diversity—especially in those plant taxa on which phytochemists have focused their attention (Jones and Firn 1991). In fact, Harborne (1993) considers the three primary areas of biological diversity to be angiosperms, insects, and secondary compound chemistry. Chemical defences have been classified according to various plant–herbivore theories (discussed by Speight *et al.* 1999). In broad terms, a distinction has been made between toxins (produced in small quantities by rare or ephemeral plants) and digestibility-reducing allelochemicals ('quantitative' or deterrent defences, produced in large quantities by long-lived or apparent plants). Mattson (1980) pointed out that toxic compounds are associated with nitrogen-rich plants such as legumes, and many of the toxins are nitrogen-based (e.g. alkaloids, cyanogenic glycosides, non-protein amino acids), although others (cardiac glycosides) are not (Harborne 1993). Moreover, proteinase inhibitors are nitrogen-based but not toxic. Digestibility-reducing allelochemicals, on the other hand, tend to occur in plants adapted to low nitrogen environments (such as *Eucalyptus*) and are carbon-based (tannins, terpenoids). According to the carbon–nutrient balance hypothesis of Bryant *et al.* (1983), the production of defences is costly to plants and involves a trade-off between growth and defence. Nitrogen-based defences increase in concentration when nitrogen availability to plants increases, while concentrations of carbon-based defences decrease (Kytö *et al.* 1996). More specifically, Haukioja *et al.* (1998) have proposed that protein synthesis, because of the requirement for phenylalanine, competes with synthesis of condensed tannins. Conflicting results are common in tests of the carbon–nutrient balance hypothesis (Hamilton *et al.* 2001) and other hypotheses generated to explain patterns in plant defences: see Cipollini *et al.* (2002) for an example involving measurement of many different variables in a thorough study of leaf chemistry and herbivory. The distinction between toxic and deterrent plant allelochemicals can be misleading: a recent review uses the term 'antinutrients' for natural products which reduce nutrient availability to insects (Felton and Gatehouse 1996). Reduction of nutrient availability may involve chemical modification of the nutrient, formation of complexes with it, or interference with its digestion or absorption, and the effect of antinutrients can be overcome by providing the insects with supplemental nutrients.

Tannins and other phenolics

Feeding experiments involving these aromatic compounds require careful design and have shown some complex effects. For example, Raubenheimer and Simpson (1990) found no interactive effects of tannic acid and protein–carbohydrate ratios in *Locusta*, which is a grass-feeding oligophage, and *Schistocerca*, which is polyphagous and receives greater exposure to tannins in its diet. In the short term, tannic acid had a phagostimulatory effect on *Schistocerca*, and this must be distinguished from compensatory consumption of an inferior diet. More recent use of the geometric approach has shown that tannic acid is more effective as a feeding deterrent in *Locusta* than as a post-ingestive toxin, but its effect is markedly influenced by the proportions of protein and carbohydrate in the food (Behmer *et al.* 2002). Tannic acid has a stronger deterrent effect when foods contain a large excess of carbohydrate relative to protein, whereas locusts are willing to consume relatively large amounts of tannic acid included in protein-rich diets. These authors suggest that this is another factor favouring carbon-based defences in resource-poor habitats.

Eucalyptus species contain very high concentrations of phenols and essential oils (mixtures of terpenoids), yet these do not seem to affect feeding by chrysomelid beetles, which are far more constrained by the low nitrogen content of *Eucalyptus* foliage (Fox and Macauley 1977; Morrow and Fox 1980). This explains the apparent paradox of heavy grazing in spite of these quantitative chemical defences. Phenolics have varied effects, both inhibitory and stimulatory, on the performance of insects (Bernays 1981) and negative effects on feeding and growth may involve a variety of mechanisms, including oxidative stress. Felton and Gatehouse (1996) exclude tannins from their review of plant antinutrients.

Caterpillars maintain strongly alkaline midguts, and Berenbaum's (1980) survey of published gut pH values for 60 species showed that those feeding