even beetles preferring the very coarse dung of elephant or rhino are essentially liquid feeders which benefit from microbial protein.

2.4.2 Nitrogen as a limiting nutrient

Because animals consist mainly of protein but plants are mainly carbohydrate, it follows that nitrogen is a limiting nutrient for many herbivores (for a major review see Mattson 1980). Nitrogen in plant tissue ranges from 0.03 to 7.0 per cent dry mass, the highest concentrations occurring in actively growing or storage tissues. Assessment of the importance of nitrogen is complicated by the fact that nitrogen and water contents of foliage vary enormously and tend to vary together, especially when the proportion of structural carbohydrates increases in maturing leaves (Slansky and Scriber 1985). Performance indices of many insect-feeding guilds are strongly correlated with both nitrogen and water contents of the food, which is why larval feeding often occurs early in the growing season (Slansky and Scriber 1985). Insects respond to low nitrogen content by increasing food consumption or the efficiency of nitrogen use (=N gained/N ingested) (Slansky and Feeny 1977; Tabashnik 1982). Both responses are shown in Fig. 2.11 for larvae of *Pieris rapae* (Lepidoptera, Pieridae) feeding on a variety of wild and cultivated plants, mostly Cruciferae (Slansky and Feeny 1977). Much of the research on nitrogen limitation has concerned caterpillars, which accumulate nitrogen for adult reproduction (see Section 2.5.2), but positive responses to nitrogen in larvae may not always benefit pupal and adult stages of a species. For example, increased dietary nitrogen (via fertilizer treatment of food plants) decreases development time of *Lycaena tityrus* (Lepidoptera, Lycaenidae), but also increases pupal mortality and reduces adult size (Fischer and Fiedler 2000). Results from larval stages only should be treated with caution. Climate change has stimulated research on insect herbivory, although many contradictions remain. Plants grown in high CO_2 levels generally have lower foliar nitrogen concentrations (Watt *et al.* 1995), and negative effects on insect herbivores have been ascribed to dilution of plant nitrogen levels by cellulose and other carbon-based

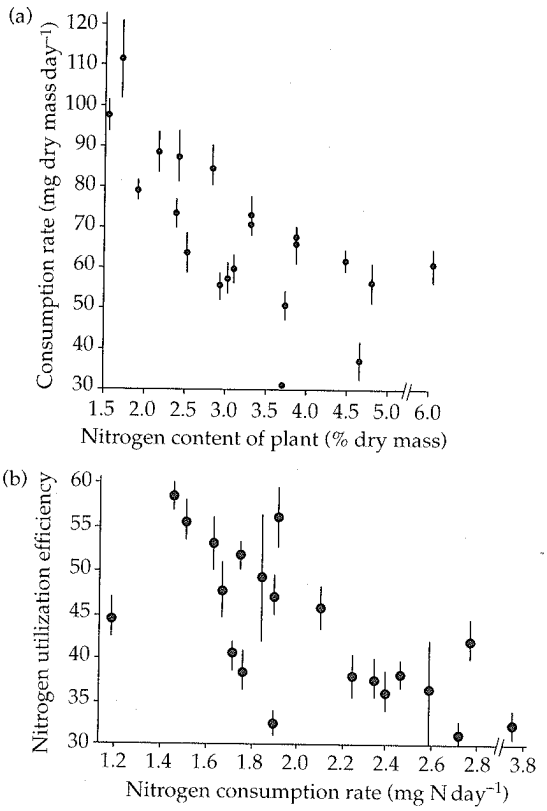

Figure 2.11 Responses of fifth instar *Pieris rapae* larvae to variation in nitrogen content of their food plants (mainly Cruciferae). (a) Rate of consumption (mg dry mass per day) as a function of plant nitrogen content (% dry mass). (b) Nitrogen utilization efficiency as a function of the rate of consumption of nitrogen (mg N per day).

Note: Data are means ± SEs, based on two experiments with various food plants and a nitrogen fertilization experiment.

Source: Slansky and Feeny (1977).

compounds, so that insects must compensate by eating more and their development is prolonged. The situation is more complex because allelochemicals may be affected, more carbon being available for allocation to defensive compounds (Coviella *et al.* 2002).

Although the focus has been on nitrogen as a limiting nutrient in terrestrial systems, Elser *et al.* (2000) have recently demonstrated that terrestrial plants are also poor in phosphorus. Stoichiometric analyses provide a more quantitative way of thinking about the differences between trophic levels, and the C:N and C:P ratios of terrestrial