



Figure 2.3 Utilization plots of nutrient output versus intake. (a) Hypothetical plot in which the dotted line represents total elimination of a nutrient, while the solid line shows its utilization up to a certain level, with elimination occurring beyond this level. (b) Utilization plot for nitrogen in fifth instar *Locusta migratoria* fed four different diets (7:7 indicates a diet containing 7% protein and 7% digestible carbohydrate). When nitrogen consumption exceeded 30 mg, uric acid excretion was used to remove the excess.

Source (a): *Regulatory Mechanisms in Insect Feeding*, 1995, Simpson *et al.*, pp. 251–278. With kind permission of Kluwer Academic Publishers. Source (b): Zanotto *et al.* (1993). *Physiological Entomology* **18**, 425–434, Blackwell Publishing.

are the geometrical representation of analysis of covariance (ANCOVA) designs and are statistically preferable to the widely used ratio-based indices (Raubenheimer 1995). Specific examples of both behavioural regulation of food intake and physiological regulation of its utilization are described in Section 2.2.3 below.

Some studies have used both old and new methods, represented by nutritional indices and bicoordinate plots, to assess nutritional performance (Chown and Block 1997; Ojeda-Avila *et al.* 2003). A plot of growth rate against consumption rate gives a visual assessment of ECI, while growth against absorption gives ECD.

2.2 Physiological aspects of feeding behaviour

Regulatory mechanisms involved in insect feeding were comprehensively reviewed by Chapman and de Boer (1995). We will briefly examine the

inter-relationships between feeding and digestion in caterpillars, the regulation of meal size in fluid feeders, and finally the regulation, especially in locusts, of intake of protein and digestible carbohydrate. These are all relatively short-term aspects, whereas diet switching, as defined by Waldbauer and Friedman (1991), refers to long-term changes in diet that occur between larva and adult or between instars in some herbivores.

2.2.1 Optimal feeding in caterpillars

Inter-relationships between consumption and digestion have been explored in detail in caterpillars (for excellent reviews see Reynolds 1990; Woods and Kingsolver 1999). The experimental caterpillar is commonly the fifth instar of the tobacco hornworm *M. sexta* (Lepidoptera, Sphingidae); appropriately, *Manduca* means 'the chewer'. During its last instar this species increases in mass at the rate of 2.7 g per day, which is faster than the growth rates of

similar-sized out the bene 1985). The gu of the mass of ing period of of leaf protei rapid growth and Kingsolv digestion of amino acids, a midgut epith The last three influence, and consumption.

In the cont caterpillar, gut consumption. between fast p Woods and K reactor model of proteins an the midgut, a sumpstion rate Reynolds (1990 a model of o 1986): AD is a time, which th tion. Caterpill to an optimal nutrient uptake *et al.* 1985). Fr rates, midgut d lumen (V_{max}), a half-maximal i (1999) predicted the anterior mi products may Reynolds (1990 amino acids in suggest post-a constraints on emphasize cate proteins differ undigested pro further along t 1999). Most cate mandibles have and few of the