from cell-to-cell, selection in the model was ultimately for the area represented by each grid cell (*see below*). But, the selectivity of animals for each cell was determined at the finer spatial scale of plant part density, with assessment of larger areas being based simply on mean accumulated resource profitability.

A daily iteration was chosen for the model. Although quicker processes are modelled (*e.g.*, animal movement between cells), energy fluxes were tallied at the end of each simulated day. Thus, a smaller temporal scale would not have enabled any more precision, whereas a longer iteration period (not just summation across days) would have denied investigation of daily foraging bouts (including animal digestive constraints, see below). The SAVANNA model (Coughenour 1993) employed a weekly time step, but the model aggregated daily rates and then merely reapportioned animal foraging days per grid cell according to a preference score. It is possible that a longer time step for the current model would have reduced simulation time.

3.13.4 Energy intake

Herbivores select their diets from a wide range of plants. The size of the animal typically determines their feeding behaviour (Illius & Gordon 1987). Buccal characteristics scale allometrically with body mass, the smaller animal having a narrower snout, which can be used to probe plant morphology (Gordon & Illius 1988). Therefore, depending on body size, the animal is able to select parts from within each plant. The reason for doing this is because plant parts differ in their nutritional value, which is related to a part's digestibility, a function of its nitrogen content (Illius *et al.* 1996a). Hence, upon maturation of plant parts, replacement of the nitrogen-rich cell contents by plant secondary thickening carries with it an associated reduction in digestibility (Illius *et al.* 1996a).

Digestibility is an important factor in energy intake. The digestible portion of consumed forage is that part that can be absorbed by the animal and is not excreted as fæces. Increased digestibility means less rumen fill, higher throughput and, therefore, more

total intake by reduction of digestive constraints on intake (McDonald *et al.* 1977). The maximum intake of food was predicted with respect to its digestibility and animal size (Illius & Gordon 1991, 1992). Constant digestibility values for each plant part were included in the model. As the animals were able to select from a mixture of dietary components, the daily digestibility was an average of the plant part digestibilities weighted according to their contribution to daily intake (Fig. 3.4, see Section 3.13.12 for parameter values).

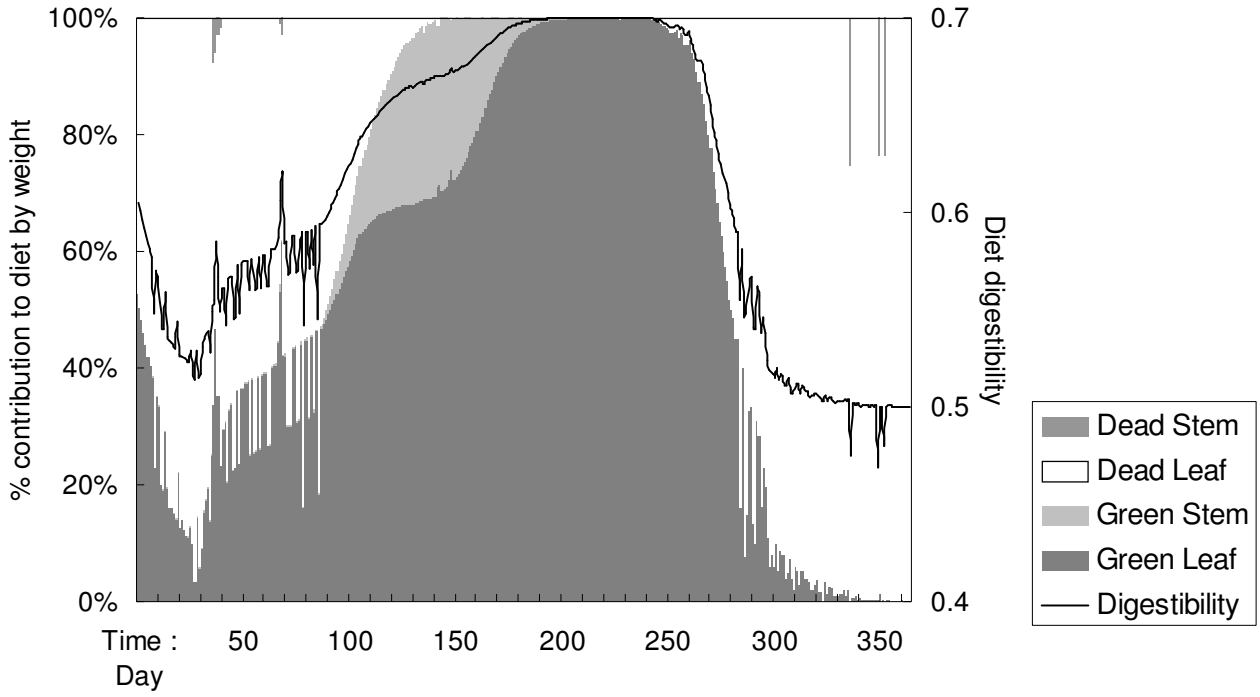

Fig. 3.4: Typical annual seasonal change in modelled herbaceous diet composition and the resulting digestibility for goats selecting parts of a perennial grass. *Dead stem* appears as the thin drop-down bars at the top of the figure.

~~3.13.5 Spatial foraging~~

~~Field observations and modelling exercises have shown that the maximization of daily energy gain is the rationale for optimal foraging strategies (Fryxell *et al.* 2001) and the~~