13

The Plant/Animal Interface in Models of Grazing Systems

M. Herrero, J. B. Dent, and R. H. Fawcett
University of Edinburgh, Edinburgh, Scotland

I. INTRODUCTION: THE PLANT/ANIMAL INTERFACE IN A SYSTEMS CONCEPT

Grazing systems are one of the main types of agroecological systems for food production in the world. These systems comprise about half of the world's land area (Stuth and Stafford-Smith, 1993), and increased interest exists in improving their management and ensuring sustainability. There is concern to prevent degradation of the resource base and its consequent environmental, social, and economic effects.

A common approach in studying grazing systems has been by way of mathematical modeling (Stuth and Stafford-Smith, 1993). Unfortunately, many scientists have looked at specific and detailed phenomena within a part of the system without taking into account interactions and effects at the whole-system level (Demment et al., 1995). The plant/animal interface is one of many subsystems of a grazing system. It is a key element but is subject to a number of forward and backward interactions with the other subsystems. Consequently, it cannot be fully understood in isolation nor can it be

495

modeled without reference to all relevant components. Only recently have more integrated approaches, linking concepts from different disciplines across a variety of levels of knowledge, been implemented. The integration of various levels exposes enormous complexity within a grazing system. The degree of detail in these levels depends on the purpose for which the model is meant to be used, the users, the level of accuracy required, and the planning horizon (i.e., operational, strategic, or tactical).

This chapter reviews these approaches to obtain an adequate definition of the plant/animal interface in a systems context.

II. MODELING THE FORAGE RESOURCE

A. Modeling Primary Production

A wide range of approaches to modeling the forage resource are found in the literature. These vary widely in degree of complexity, number of species represented, variable and parameter definitions, and simulated output.

Some of the simplest representations are based on the functional form of plant growth curves [see Thornley and Johnson (1990) for a review]. For example, Brougham (1956), Morley (1968), Noy-Meir (1975, 1976, 1978), Christian et al. (1978), and Woodward et al. (1993, 1995) used logistic growth curves to represent pasture growth in their models:

$$\frac{dW}{dt} = mW \left(\frac{W}{W_{max}} \right) \tag{1}$$

where m = the maximum relative growth rate, W = initial plant biomass, W_{max} = the asymptote plant biomass, and t = time. This description assumes that growth is proportional to plant biomass, rate of growth is proportional to amount of substrate, and substrate is finite (Thornley and Johnson, 1990).

Equation (1) is easy to parameterize when smooth experimental data of the dynamics of plant growth are available. The appropriateness of the parameters will depend on the quality of the experimental data and will reflect only the particular conditions in which the plants were growing for that particular data set. Nevertheless, the shape of the curve can be explained physiologically. Exponential growth occurs due to increased irradiance captured by increases in leaf area index (LAI) during early stages of development, while growth progressively decreases to a plateau as respiration losses due to senes-

cence equal photosynthesis. It has the advantage that it is a simple curve with biologically meaningful parameters that can represent changes in the growing environment by modification of m and W_{max}. However, it is limited in that it does not represent the physiological mechanisms (e.g., photosynthesis, LAI development, nitrogen uptake) underlying sward growth and is therefore not flexible enough to represent effects of management interventions. Such models also fail to describe biomass in different botanical fractions (leaves, stems, dead material) or species compositions (grass–legume mixtures or rangelands) and their vertical distribution within the sward, which are important elements in predicting diet selection and/or species succession caused by disturbances (e.g., grazing or fire) in grasslands. The fact that only one sward component is represented [i.e., total herbage dry matter (DM)] implies that diet selection can be studied only by superimposing selectivity coefficients on total DM (Christian et al., 1978).

These limitations have led to the construction of several more detailed grassland models for single pasture species (Johnson and Thornley, 1983, 1985; Thornley and Veberne, 1989; Smith et al., 1985; Lopez-Tirado and Jones, 1991a, 1991b; Doyle et al., 1989; Sheehy et al., 1996; Guerrero et al., 1984; Charles-Edwards et al., 1987; Rodriguez et al., 1990; Murtagh, 1988; Veberne, 1992; van Keulen et al., 1981; Seligman et al., 1992; Herrero, 1995) or multiple species (Gilbert, 1975, Innis, 1978; Parsons et al., 1991; Hanson et al., 1988, 1994; Coughenour, 1984; Coughenour et al., 1984; Hunt et al., 1991; Hacker et al., 1991; Blackburn and Kothmann, 1989; Detling et al., 1979; Lauenroth et al., 1993; Richardson et al., 1991; Moore et al., 1997). The former come mostly from the agricultural sciences, while some of the latter also have a strong ecological background (e.g., Innis, 1978; Coughenour, 1984; Hanson et al., 1988, 1994).

The majority of these models represent plant growth as a function of one or more environmental, soil, and/or management variables. The simplest analyses use only one environmental driving variable (e.g., rainfall or irradiance) to determine sward growth rates. Charles-Edwards et al. (1987) used Monteith's (1972) factorial approach to determine growth rate of a sward, with ample supply of nutrients and water, based on daily irradiance intercepted by the pasture, the efficiency of light utilization by the plant to produce new material, and a partitioning coefficient for above-ground material. Shiyomi et al. (1986) used a similar approach to study energy flows in grasslands in Japan. Guerrero et al. (1984) and Hacker et al. (1991) determined plant growth as a function of rainfall. Due to the large

effects on growth caused by severe water stress in the regions of their studies, they were able to use simple soil water balance budgets as primary predictors of herbage production. In even more complex models (e.g., Hanson et al., 1988, 1994), the basic components of water balance submodels include rainfall, evapotranspiration, transpiration, runoff, and infiltration, and these are modeled using well-recognized principles (van Keulen and Wolf, 1986; Thornley and Johnson, 1990). Moisture indices are derived from these variables to scale the growth rates of forage.

On the other hand, several models estimate biomass production as functions of a number of environmental variables. This usually results in models representing carbon (C) and nitrogen (N) fluxes in grassland ecosystems. The level of detail and empirical representations varies widely between models, although this is usually due to the original objectives of the model or their implicit site-specificity.

Inputs to the carbon cycle are usually represented by photosynthesis, and one of the most common methods is to integrate single-leaf photosynthesis over the canopy LAI using Beer's law (Monsi and Saeki, 1953) as the light attenuation factor through the depth of the canopy (Johnson and Thornley, 1983, 1985; Thornley and Veberne, 1989; Hanson et al., 1988, 1994; Sheehy et al., 1996). Single-leaf photosynthesis is commonly represented by rectangular (Innis, 1978; tosynthesis is commonly represented by rectangular (Innis, 1978; Johnson and Thornley, 1983; Doyle et al., 1989) or nonrectangular hyperbolas (Johnson and Thornley, 1985; Thornley and Veberne, 1989; Herrero, 1995). Other authors (Coughenour, 1984; Hunt et al., 1991) also include CO_2 concentrations and stomatal, internal, and leaf boundary layer resistances to account for water use and CO_2 effects on photosynthesis. Temperature and leaf N content (Thornley and Veberne, 1989; Hanson et al., 1994; Herrero, 1995) are used to scale the photosynthetic capacity of the sward. Outputs from the carbon pool are represented by fractions used for new growth, senescence, respiration, and grazing. Recycling of nutrients from senescent tissues also contributes to the carbon cycle.

The approaches to representing the nitrogen cycle of the grazing system are also diverse, but the basic factors are demonstrated in a simple model by Scholefield et al. (1991) (Fig. 1).

Although Scholefield et al.'s (1991) model is empirical, the same processes can receive a mechanistic treatment. However, the complexity of the model and its subsequent validation are increased severalfold (e.g., Veberne, 1992).

Thornley and Veberne (1989) argue that data to validate soil–plant mechanistic models are scarce or incomplete and that experi-
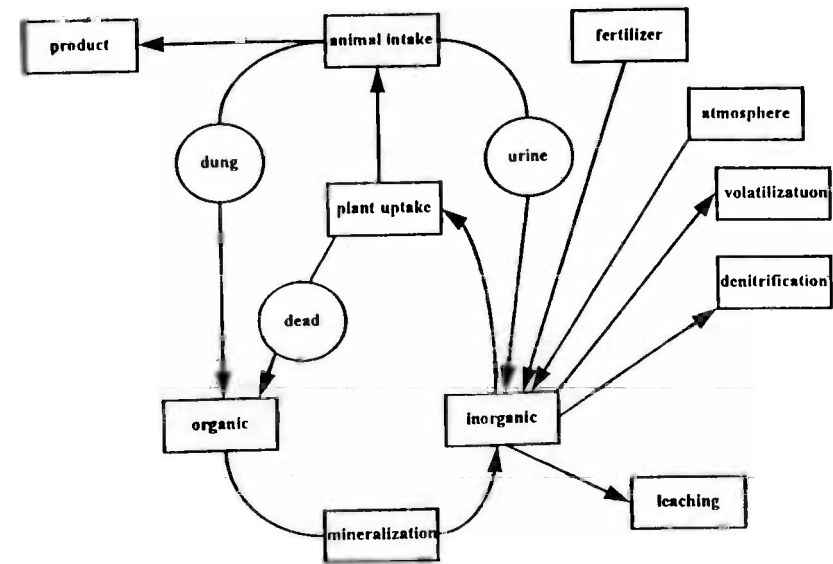

FIGURE 1 Basic nitrogen cycle in pasture ecosystems. [From Scholefield et al. (1991).]

ments are difficult to design, and therefore a subjective assessment on the behavior of the model is sometimes made. While the C cycle is relatively easy to validate due to the wide availability of field methods, there is still a considerable amount of progress to be made in designing soil submodels that are easy to parameterize at field level.

B. Sward Structure and Composition

It is well recognized that apart from herbage availability, sward structure plays an important role in determining the intake of grazing ruminants (Stobbs, 1973; Freer, 1981; Hodgson, 1985; Demment et al., 1995) and that ruminants select preferentially for the leaf component of the sward (Laredo and Minson, 1973; Hendricksen and Minson, 1980; Cowan et al., 1986; Penning et al., 1994). In rangelands (i.e., Coughenour, 1984; Hanson et al., 1994), species composition plays a major role in determining the diet selected by the animal (O'Reagain and Schwartz, 1995), and, depending on animal numbers and environmental conditions or disturbances, this selection modifies the subsequent species composition of the sward (Humphreys, 1991; Hacker

and Richmond, 1994). Therefore, a basic requirement of pasture models, apart from their ability to predict total biomass, is that they should be capable of differentiating between plant parts and their density across the sward's vertical strata and/or species composition in the case of multispecies systems. Table 1 shows some of the main differences in the representation of sward morphology and composition between models. It can be observed from the table that several models do not differentiate between plant parts.

The most common fractionation of morphological composition is between leaf, stem, and dead material, and this is usually linked to age characteristics of the sward. This fractionation occurs partly because the models rely on photosynthesis and require an estimate

of LAI for pasture growth calculations. This is a convenient attribute, since removal of LAI by grazing can link, in a physiological sense, the effect of grazing on total resource capture, pasture growth, and subsequent sward composition (Johnson and Parsons, 1985; Parsons et al., 1994).

The models of Johnson and Thornley (1983, 1985) and Thornley and Veberne (1989) did not represent the vertical distribution and bulk density (bd) within the sward, but they do have a convenient structure to model them. These models divide the leaf and stem structural mass into four distinct age categories, from new material down to senescent. The move from one category to the next is determined by the rates of appearance of these components, therefore making it possible to distribute them, separately, across the height of the sward according to the pasture species modeled. We developed a flexible method to estimate sward structure from these models using the following simple statements (Fig. 2):

1. A sward with a determined total height h and total herbage mass dm can be described as a series of i discrete horizons (h_i) of herbage mass dm_i, where dm_i is composed of variable proportions of leaf and/or stem (L/S) and dead material. The concept of sward horizons or layers in grassland modeling is well recognized and is useful for the representation of grazing processes (Ungar and Noy-Meir, 1988; Ungar et al., 1992; Demment et al., 1995).

2. As h decreases, the amount of dm_i in h_i increases (Fig. 2a), as is commonly observed (Stobbs, 1975; Illius and Gordon, 1987; Mayne et al., 1987).

Table 1 Differences in the Representation of Sward Composition in Some Models

Model	No. of species[a]	Total biomass	Plant parts[b]	Phenology or age of plant parts	Species comp.
Noy-Meir (1975, 1976, 1978)	1	V	—		
Johnson and Thornley (1983, 1985)	1	V	/s/d	V	
Herrero (1995)		V	1/s/d	V	
Parsons et al. (1991)	2	V	1/s/d	V	V
Charles-Edwards et al. (1987)	1	V			
Hunt et al. (1991)	1	V			
Hanson et al. (1988, 1994)	3+	V	g/d/p	V	V
Christian et al. (1978)		V	g/d	V	
Coughenour et al. (1984)	3+	V	b/sh/s/f	V	V
Lauenroth et al. (1993)	3+	V	1/s/d	V	V
Lopez-Tirado and Jones (1991a)	1	V	g/d	—	
Guerrero et al. (1984)	1	V		—	
Rodriguez et al. (1990)	1	V	1/s/d	V	
Woodward et al. (1993, 1995)	1	V			
Doyle et al. (1989)	2	V	1/s/d	V	
Smith et al. (1985)		V	g/d	V	
Hacker et al. (1991)	3+	V	—		V
Seligman et al. (1992)	1	V	1/s/d		—

1 = single species, 2 = grass/legume, 3+ = rangelands.
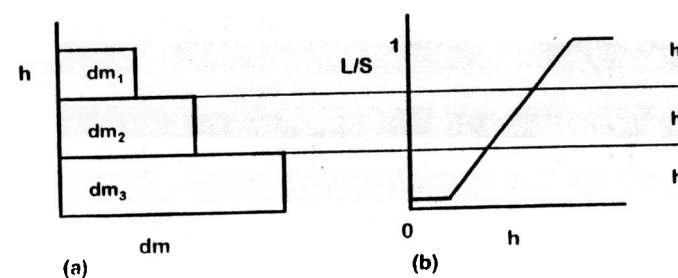1 = leaves, s = stems, d = dead, p = propagules, g = green, sl heats, f flowers.

Figure 2 Representation of the vertical distribution of (a) herbage mass and (b) plant parts within a single-species pasture sward.

3. As h increases, the leaf/stem ratio increases (Fig. 2b). The proportion of dead material decreases, but for simplicity we consider only leaf and stem.

Following the nomenclature in the Thornley papers described above, we divided the dry matter (dm_i) of a sward into three horizons as follows:

$$dm_1 = WL_1 + f_1 Ws \quad (2)$$

$$dm_2 = WL_2 + Wsh_1 + Wsh_2 + f_2 Ws \quad (3)$$

$$dm_3 = WL_3 + WL_4 + Wsh_3 + Wsh_4 + f_3 Ws \quad (4)$$

where WL_j and Wsh_j are the structural weights of leaves and stems of different ages, respectively, where $j = 1$ is new material and $j = 4$ is senescent tissues. In this three-horizon example, note that the first horizon (top of the sward) contains only leaf, which is commonly observed in many pasture species (Hodgson, 1985; Humphreys, 1991). Ws is the storage compartment, and f_i the fraction of Ws associated with the plant material in dm_i. Bulk density can be estimated as

$$bd_i = \frac{dm_i}{h_i} \quad (5)$$

and

$$bd = \frac{dm}{h} \quad (6)$$

where bd_i = bulk density in the ith horizon and bd = total sward bulk density.

The flexibility of the modeling structure presented in this chapter permits representation of a large number of sward structures, since the number of horizons and the type and quantity of plant parts comprising them can be changed without altering the functionality and robustness of the original plant models. At the same time, the structure has useful attributes in modeling intake and diet selection by different methods. The approach has been specifically developed for tropical and temperate monospecific swards, but it can be extended to grass–legume swards.

Separation between green and dead material in other models is mainly for the purpose of determining the sward's nutritive value. For example, to be able to represent diet quality, some models (Christian et al., 1978; Guerrero et al., 1984; Smith et al. 1985) subdivide the

biomass empirically into three or four compartments representing new, mature, senescent, and/or dead material without describing them morphologically and assign quality characteristics (i.e., digestibility, cell wall) within these categories. However, the definition of physiological states without a morphological description presents three problems. First, they are difficult to handle in diet selection studies, where the different components of the diet selected by ruminants are usually identified by botanical fractions (Hendricksen and Minson, 1980; Humphreys, 1991), therefore reflecting morphological differences in the sward (Arnold, 1981; Hodgson, 1985). Physiological state of the sward does not represent its morphological structure. Second, it is difficult to accommodate different diet selection patterns of different animal species. For example, sheep are able to select more leaf than cattle (Arnold, 1981; Forbes and Hodgson, 1985; Penning et al., 1994), and these differences cannot be predicted if the sward is only divided into physiological state compartments. Third, even at a similar chemical composition, botanical fractions have different physical structures (Wilson, 1994), which affect the rates of breakdown from large to smaller particles of forage in the rumen (Kennedy and Murphy, 1988; Wilson and Kennedy, 1996) and therefore affect passage rates and pasture intake. This concept is difficult to model when sward physiological states are used because the botanical composition of each compartment (e.g., new material) is not known. From the diet selection viewpoint, in rangeland models the discrimination between species becomes more important (Baker et al., 1992) than within species, and most rangeland models only discriminate between, rather than within, species to represent sward biomass.

III. GRAZING PROCESSES AND DIET SELECTION

A. Intake and Grazing Processes

Intake prediction is one of the most important elements in grazing systems models because the prediction of animal responses to nutrients (Blaxter, 1989) [see Forbes and France (1993) for reviews] are largely dependent on it. In addition, pasture intake influences the regrowth of the sward (Brougham, 1956; Vickery, 1981; Parsons et al., 1988), the efficiency of fertilizer use (Humphreys, 1991; Herrero, 1995), supplementation strategies (Allden, 1981; Ørskov, 1994; Rook et al., 1994), nutrient cycling (Simpson and Stobbs, 1981; Scholefield et al., 1991), land use practices via the area required to maintain stock

(Olney and Kirk, 1989; Herrero et al., 1996a, 1996b), and the spatial distribution of pasture species in rangeland landscapes (Senft et al., 1987; Demment et al., 1995; O'Reagain and Schwartz, 1995).

A number of methods of simulating intake and grazing processes have been reported, but three distinct approaches can be observed:

1. Prediction of intake from systems of energy requirements
2. Establishment of relations between herbage mass and intake
3. Prediction of intake from grazing behavior measurements

The flexibility of studying different nutritional and management strategies and their effects on the whole system will largely depend on the method chosen to represent intake.

1. Intake as a Function of Energy Requirements

One method used to represent intake assumes that estimates of pasture intake can be derived from the energy requirements of the animal and the energy content of the pasture consumed. This last parameter has been usually derived from in vivo or in vitro digestibility estimates. The energy value of the forage as well as the animal's requirements have been expressed most commonly as digestible energy (DE), metabolizable energy (ME), or net energy (NE) (McDonald et al., 1995).

Two approaches are commonly used. The first is to estimate intake from the "inverse" of the nutrient requirements, and the second is to use regression equations, which are often included in requirements systems. These methods of intake estimation have been widely used in livestock models (Sanders and Cartwright, 1979; Konandreas and Anderson; 1982: Guerrero et al., 1984; Gartner and Hallan, 1984; Olney and Kirk, 1989). However, although it is accepted that nutrient requirements represent one of the most important driving forces of eating, these systems per se [apart from SCA (1990) and NRC (1996)] fail to take into account constraints on intake imposed by herbage availability and sward structure (Hodgson, 1985). This has already been discussed by Whelan et al. (1984). However, the following points should also be considered.

1. Classic work by Conrad et al. (1964) demonstrated that intake was proportional to energy requirements when the digestibility of the diet was higher than 67%. Below this threshold, intake was constrained by physical limitations of the reticulorumen. Therefore, for low digestibilities, when

the "reverse" calculation of intake from requirements is applied, intake is usually overestimated because animals are not physically able to eat sufficient quantities of forage. More recently, Forbes (1993) suggested that, for cows, this digestibility threshold may be higher depending on the level of production. In view of these problems, several models have incorporated static physical fill limitation constraints on intake (Forbes, 1977; Kahn and Spedding, 1984; Mertens, 1987; Finlayson et al., 1995).

2. Maintenance energy requirements scale with metabolic weight (Brody, 1945), but rumen size scales with body weight (Demment and van Soest, 1985; Illius and Gordon, 1991), thus partly explaining why digestibility, which is a crucial parameter in requirements systems, is not a good predictor of intake for low quality forages (Laredo and Minson, 1973; Poppi et al., 1981; Kibon and Ørskov, 1993). In the trial of Laredo and Minson (1973), sheep consumed more leaf than stem with both plant fractions having the same digestibility, suggesting that other factors, such as the physical structure of plant parts, which influence particle breakdown and passage rates (Poppi et al., 1981, Kennedy and Murphy, 1988; McLeod et al., 1990) play an important role in the control of feed intake and also that dynamic models of digestion that consider these factors may yield better estimates of potential intake.

2. Empirical Relations Between Herbage Mass and Intake

A variety of models have simulated the effect of herbage availability on intake using empirical relations (Freer et al., 1970; Noy-Meir, 1975, 1976; Arnold et al., 1977; Vera et al., 1977; Edelsten and Newton, 1975, 1977; Christian et al., 1978; Sibbald et al., 1979; White et al., 1983; McCall, 1984; Johnson and Parsons, 1985; Thornley and Veberne, 1989; Rodriguez et al., 1990; Blackburn and Kothmann, 1991; Richardson et al., 1991; Seman et al., 1991; Finlayson et al., 1995). These models use three basic steps for the calculation of intake at grazing.

Step 1 Estimate potential intake of the animal. Potential intake is usually defined as the intake of herbage without the constraints imposed by herbage availability, as a function of animal and plant characteristics. It is usually an input (Johnson and Parsons, 1985; Thornley and Veberne, 1989) or calculated in another submodel from the knowledge of body weight, the energy requirements of the ani-

mal, and the digestibility or metabolizability of the diet (Arnold et al., 1977; Christian et al., 1978; Richardson et al., 1991) and physical fill limitations (Kahn and Spedding, 1984; Doyle et al., 1989; Finlayson et al., 1995).

Step 2 Calculate the constraints on intake imposed by herbage availability. This is usually done by estimating "scaling factors" with empirical functions and leads to a term often called relative intake. Table 2 summarizes the functions used in different models to scale intake on the basis of different measures of herbage availability.

Common features of these scaling factors are their general shape, often expressed as Michaelis–Menten equations (Noy-Meir, 1975, 1976; Johnson and Parsons, 1985; Blackburn and Kothmann, 1991) and exponential or quadratic functions (see Table 2). However, large discrepancies occur between authors in the slopes of these functions (Fig. 3), which are caused by the animal and sward characteristics for which the equations were derived. Nevertheless, marked decreases in intake appear to occur if less than 1000–1500 kg/ha DM is available.

Herbage availability is described in different ways by different authors. The most common relationship between intake and herbage availability is derived from herbage mass per unit of area, while others derive functions on the basis of herbage available per animal (Zemmelink, 1980; Loewer et al., 1987) and yet others use both measures (McCall, 1984). An exception is the function of Johnson and Parsons (1985), which uses LAI to estimate relative intake. This is an interesting concept, since LAI provides an appropriate physiological interface between pasture removal (grazing) and regrowth (resource capture by photosynthesis). However, under most practical circumstances LAI is not measured, and some types of animals (e.g., cattle) remove not only LAI, which is associated with the leaf components of the sward only, but also the stem fraction. We have adapted this function and expressed it on the basis of leaf or total herbage mass while at the same time keeping the physiological relationship with LAI. This can be done with the knowledge of three easily measured parameters: the specific leaf area (SLA) of leaves, the leaf mass (LM), and the leaf-to-stem ratio of the sward being grazed (pL). The adaptation can be done in two simple steps. First,

$$LAI = LM*SLA \qquad (7)$$

Table 2 Functions to Estimate the Effect of Herbage Availability on Dry Matter Intake of Grazing Ruminants

Source	Function to estimate relative intake (RI)[a]
Freer et al. (1970); Arnold et al. (1977)	RI = 1 − exp(−0.001*DM)
Noy-Meir (1975, 1976); Blackburn and Kothmann (1991); Woodward et al. (1993, 1995)	RI = [imax*(DM/(DM + X))]/imax
Vera et al. (1977)	RI = 1 − exp(−0.002503*DM)
Edelsten and Newton (1975, 1977)	RI = 1 − exp(−2.4*10⁻⁷*DM²)
Christian et al. (1978)	RI = 1 − exp(−0.000008*DM²)
Sibbald et al. (1979)	RI = DM/(DM + 250)
White et al. (1983); Bowman et al. (1989)	RI = 1 − exp(−0.000002*DM²)
Zemmelink (1980); Konandreas and Anderson (1982); Doyle et al. (1989)	RI = [imax*(1 − exp(−DMH/imax)¹·²³)⁽¹/¹·²³⁾]/imax
Johnson and Parsons (1985); Thornley and Veberne (1989); Parsons et al. (1991); Richardson et al. (1991)	RI = [imax*(LAI/K)^Q/(1 + (LAI/K)^Q)]/imax, where RI = imax/2 for LAI = K; K = 1 and Q = 3 for sheep grazing ryegrass
Loewer et al. (1987); Rodriguez et al. (1990)	RI = 2*FA/B − FA²/B², where B = 750
Seman et al. (1991)	RI = 1 − ((1 − 0.1)/(HI − LOW)²)*(HI − SH)², where HI = 20 and LOW = 5
McCall (1984); Finlayson et al. (1995)	RI = θ* exp[−1.016* exp(−1.038*A)], where A = (DM/imax)*(area/animals); θ = 1 − 1.42* exp(−0.00198*DM)

[a]imax = potential intake [kg/(animal·day)], DM = pasture dry matter (kg/ha); X = Michaelis constant for consumption (g/m²); LAI = leaf area index (m² leaf/m² soil); K = half-maximal response of LAI; Q = constant; DMH = available dry matter/animal [kg/(animal·day)]; FA = forage available/kg bodyweight (g DM/kg BW); B = threshold level of forage availability (g DM/kg BW); HI = height above which additional increases in sward height do not affect intake (cm); LOW = height below which forage is unavailable for grazing (cm); SH = total sward height (cm) area = grazing area (ha); animals = number of animals.
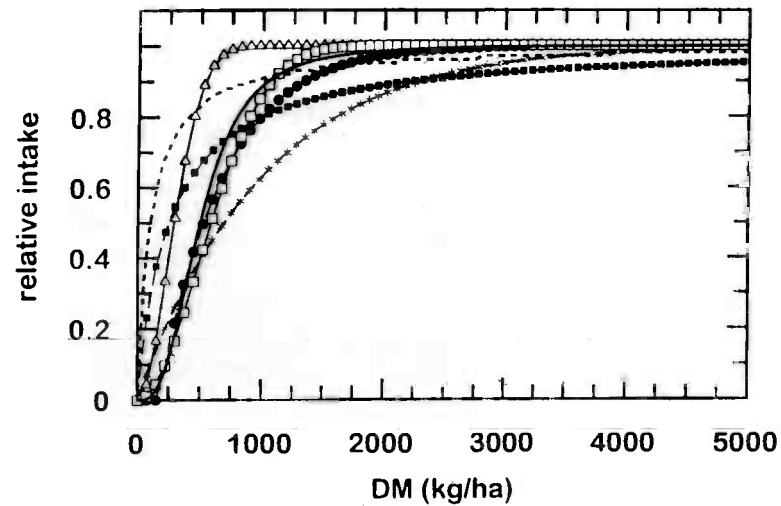
—+— Freer et al. (1970), Arnold et al. (1977)

—△— Christian et al. (1978)

—●— McCall (1984), Finlayson et al. (1995)

—■— Sibbald et al. (1979)

—□— White et al. (1983), Bowman et al. (1989)

Johnson and Parsons (1985),Thornley and Veberne (1989), Richardson et al. (1991)

- - - - Noy-Meir (1975, 1976)

FIGURE 3   The relationship between herbage availability and intake at grazing in different models.

where LM = leaf mass in the sward (g/m^2) and SLA = specific leaf area $(m^2/kg$ leaf). The total dry matter of the sward is then

$$DM = \frac{LM}{pL} \qquad (8)$$

where pL = proportion of leaf in the sward.

The analysis provided here is more flexible than that offered by other authors (e.g., Johnson and Parsons, 1985). It can be linked to previously validated pasture growth models, and it can be extended for different horizons within the sward by obtaining the above-mentioned parameters on a horizon basis. The functional responses can be estimated on the basis of LAI, leaf mass, or total herbage mass, and the model is sensitive to changes in leaf-to-stem ratio, therefore representing the effect of morphological changes in the grazed sward (Fig. 4).

The functional response to pasture availability should also be modified by animal size, because animals of different sizes have different abilities to harvest forage under different sward conditions (Stephens and Krebs, 1986; Belovsky, 1987; Illius and Gordon, 1987; Ungar and Noy-Meir, 1988). For example, smaller ruminants can
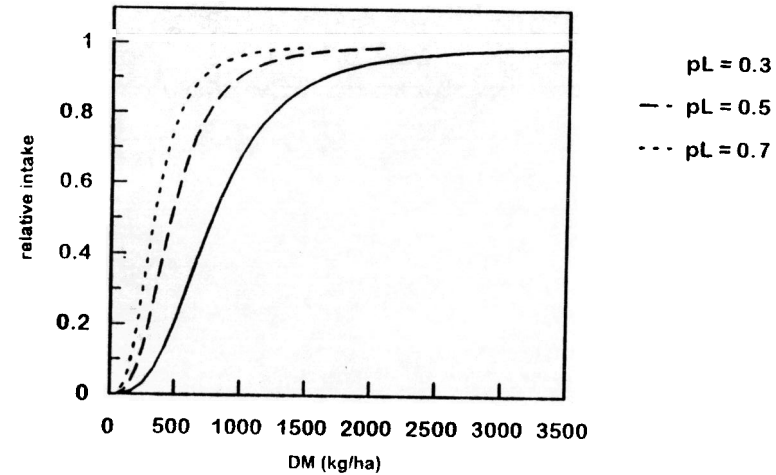

FIGURE 4   Effect of changes in the proportion of leaf on the functional response between herbage availability and intake at grazing.(——) pL = 0.3; (— — —) pL = 0.5; (---) pL = 0.7.

graze shorter swards more efficiently, and therefore swards can reach lower herbage masses before intake is reduced (Illius and Gordon, 1987). Although all models modify potential intake largely on the basis of body weight or a function of it, few models (Zemmelink, 1980; McCall, 1984) modify explicitly the functional response according to body size. Johnson and Parsons (1985) claim a value of $K = 1$ for ewes (i.e., 80 kg body weight) grazing ryegrass while a value of $K = 2$ provides a suitable relation for mature dairy cattle (i.e., 600 kg body weight) (Parsons, personal communication). However, they do not provide a specific relation of this parameter with body weight. We scaled parameter K to body weight using an allometric relationship derived from Illius and Gordon (1987), who claim that differences in the ability of animals of different sizes to graze are caused by differences in incisor breadth, hence mouth size. The relationship between parameter K and body weight then becomes

$$K = 0.229 \, BW^{0.36} \tag{9}$$

Figure 5 shows this relation for three body sizes.

Step 3 The third and final step in calculating intake in these models is to multiply potential intake by the relative intake factor and by the number of grazing animals. This approach is probably the most commonly used to represent the effect of herbage availability on intake because of its simplicity and the ease of obtaining appropriate data for validation. However, these systems fail to represent the mechanics of grazing and therefore fail to provide full understanding about the sward variables affecting intake. Therefore, for some purposes, more detailed models, usually based on grazing behavior measurements, are used to represent these relations.

3. Prediction of Intake from Grazing Behavior Measurements

The prediction of intake from grazing behavior measurements [for recent reviews see Hodgson et al. (1994), Demment et al. (1995), and Laca and Demment (1996)] has been largely based on the early work of Allden (1962), Arnold and Dudzinski (1967a, 1967b), Allden and Whittaker (1970), Stobbs (1970, 1973, 1974), and Chacon and Stobbs (1976). Allden and Whittaker (1970) postulated that intake at grazing could be predicted as

$$Intake = IB \cdot RB \cdot GT \tag{10}$$

where IB = bite size, RB = biting rate, and GT = grazing time.

Intake per bite is the variable most sensitive to sward characteristics, while biting rate and grazing time are partly dependent on
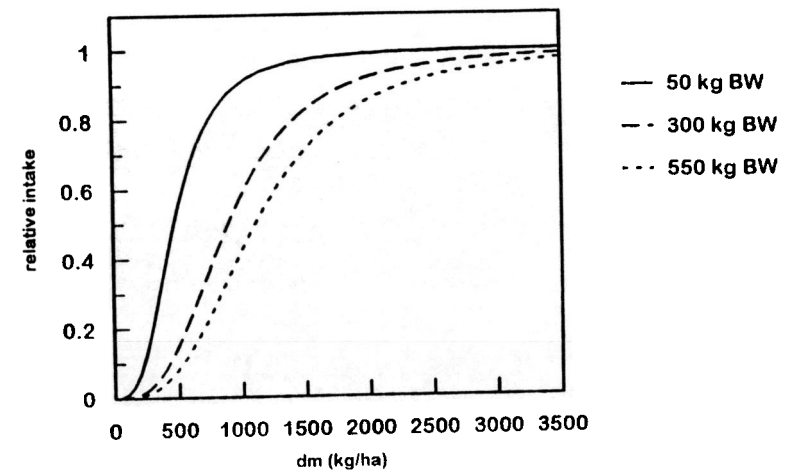

FIGURE 5 Effect of different body weights on the shape of the functional response between herbage mass and intake. (——) 50 kg BW; (– – –) 300 kg BW; (---) 550 kg BW.

bite size and act as compensatory mechanisms when bite size is too small to obtain the desired intake level (Hodgson, 1981). Chambers et al. (1981) and Newman et al. (1994a) suggested that biting rate declines at high bite sizes because of an increase in the ratio of manipulative to biting jaw movements and therefore it is also partly dependent on sward characteristics. This subject has been clearly depicted by Laca et al. (1994), who found that time per bite (TB) was linearly associated with the total number of jaw movements per bite (JM) (Fig. 6a):

$$TB = 0.43 + 0.682 \, JM, \qquad r^2 = 0.96 \tag{11}$$

The proportion of total manipulative jaw movements that performed manipulation and mastication (MJM) increased asymptotically with bite size (Fig. 6b) according to the relation

$$MJM = \frac{1.028 \, IB - 0.246}{0.234 + IB}, \qquad r^2 = 0.69 \tag{12}$$

As bite size decreases, biting rate and/or grazing time increase to compensate for this reduction. However, this compensation is sometimes partial (Allden and Whittaker, 1970; Stobbs, 1973; Jamieson and Hodgson, 1979; Hendricksen and Minson, 1980; Hodgson, 1981); thus
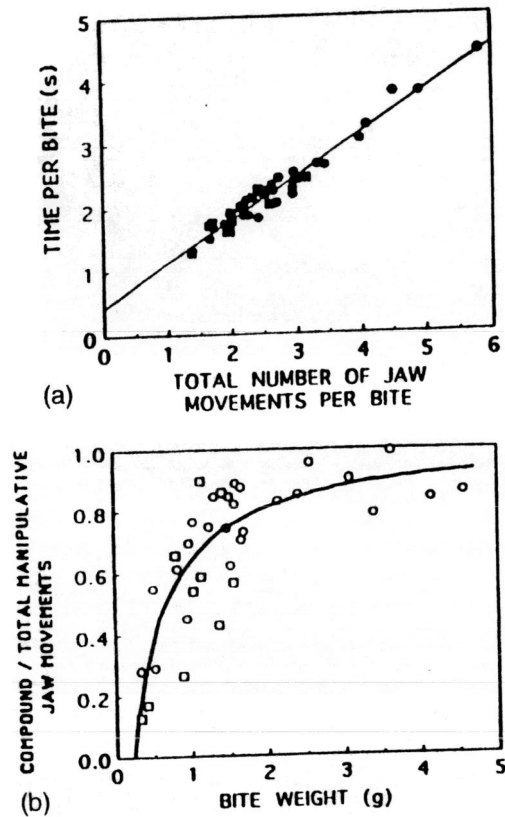
FIGURE 6   (a) Relationship between time per bite and total number of jaw movements per bite. (b) Relationship between bite size (IB) and the proportion of manipulative jaw movements relative to total jaw movements. [From Laca et al. (1994).]

potential intake cannot be attained. Hodgson (1986) claims that this is the reason variations in daily herbage intake frequently reflect closely the observed variations in bite size.

In most modeling studies, maximum values of biting rate and grazing time obtained from experimental studies are often used as behavioral limits of the grazing process, while most efforts are concentrated on modeling bite dimensions. Maximum biting rate is close to 36,000–40,000 bites/day (Stobbs, 1973; Chacon and Stobbs, 1976; Jamieson and Hodgson, 1979), while maximum grazing time is about

12–13 h/day (Fig. 7) (Arnold, 1981). These values are similar for cattle and sheep (Hodgson, 1982, 1985; Forbes, 1988; Demment et al., 1995).

Bite size is positively related to herbage mass or sward height (Black and Kenney, 1984; Hodgson, 1985; Forbes, 1988; Burlison et al., 1991). Burlison et al. (1991), working in swards ranging from 5 to 55 cm in height, explained 78% of the variation in IB of sheep with the relation

$$IB = 33 + 5.2H \tag{13}$$

where H = sward height.

The slope of this relationship was similar to those reported by Hodgson (1981) and Forbes (1982) when expressed on the basis of bite size per kilogram body weight. Burlison et al. (1991) also argued that due to the bias caused by changes in bulk density across grazed horizons, the responses often found were asymptotic, thus confirming the results of other authors (Penning, 1986; Ungar and Noy-Meir, 1988; Baker et al., 1992).

A better understanding of how changes in sward characteristics affect bite size can be achieved by describing this variable at a lower, more detailed, level of aggregation. Burlison et al. (1991) describe the components of bite size in Fig. 8.

Bite depth is generally proportional to sward height (Milne et al., 1982; Wade et al., 1989; Laca et al., 1992; Ungar et al., 1992; Demment et al., 1995), but it may decrease depending on the relative height of stem material in the grazed horizons (Barthram and Grant, 1984; Forbes, 1988; Flores et al., 1993). Burlison et al. (1991) found that the following relation for sheep explained 93% of the variation in bite depth:

$$Bite\ depth = -1.0 + 0.37H \tag{14}$$

Since sward height is a good predictor of LAI (Parsons et al., 1994), which in turn reflects leaf mass [see Eq. (7)], these results are in close agreement with the relation between leafiness and bite size found in several pastures (Stobbs, 1975; Chacon and Stobbs, 1976; Hendricksen, and Minson, 1980; Hodgson, 1986).

Bite area increases with sward height (Burlison et al., 1991; Laca et al., 1992). However, it also increases with decreasing bulk density (Burlison, 1987), especially on higher swards (Laca et al., 1992), which might be explained by the limitations posed by the shearing strength required to harvest a bite (Hodgson, 1985). Nevertheless, bite area is less sensitive to sward characteristics than bite depth (Hodgson, 1986)
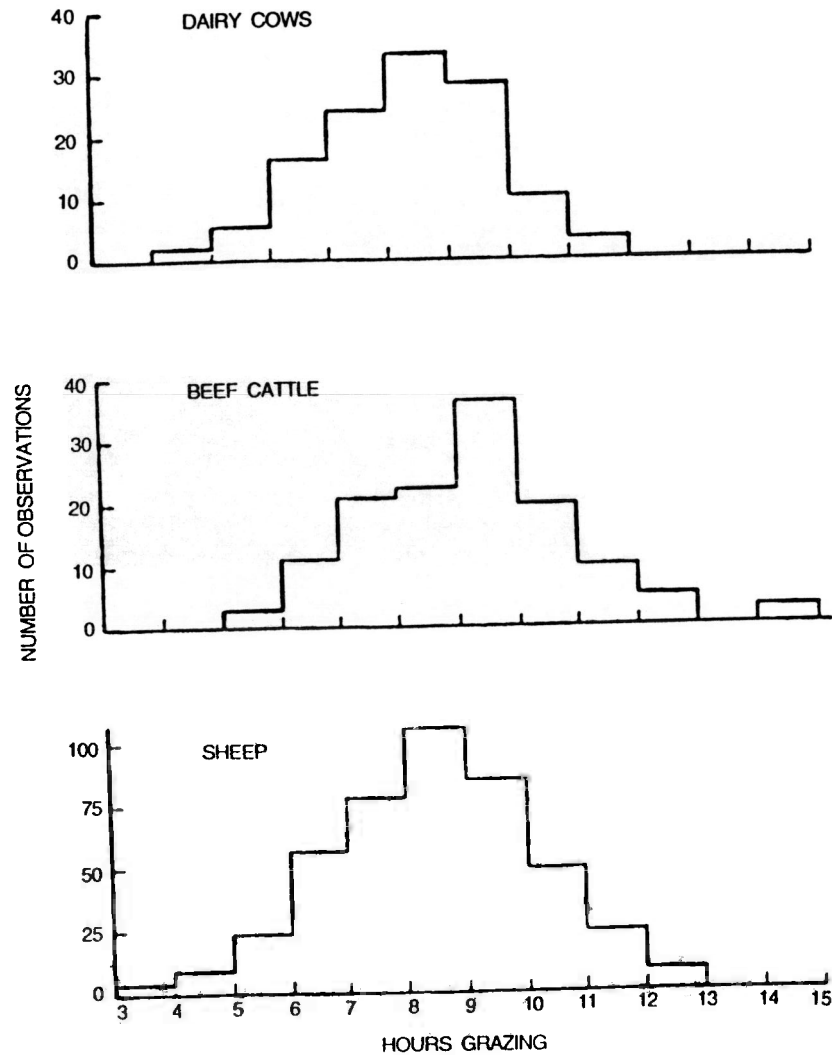
FIGURE 7 Distribution of grazing times of cattle and sheep. [From Arnold (1981.)]
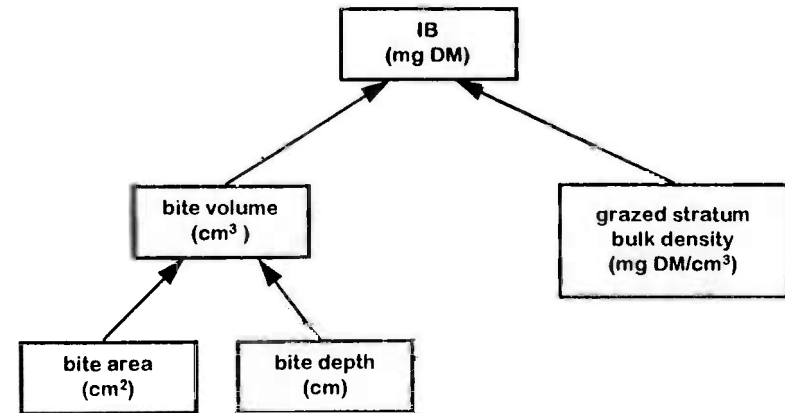
FIGURE 8 The components of bite size. [From Burlison et al. (1991.)]

and has been considered constant for a given body weight in some models (Parsons et al., 1994).

Bite volume is also positively related to sward height (Ungar and Noy-Meir, 1988). Burlison et al. (1991) obtained the following relationship for sheep, thus explaining 83% of the variation in bite volume:

$$\text{Bite volume} = -32 + 8.0H \tag{15}$$

There are some factors unrelated to sward structure that affect grazing behavior, mainly grazing time. For example, Brumby (1959) and Journet and Demarquilly (1979) showed that cows increased their grazing time by 5 min/kg milk between yields of 5 and 25 kg of milk, and by 12 min/kg milk between 20 and 35 kg of milk. Similarly, Arnold and Duzinski (1967a) and Arnold (1975) found increases of 7–12% in grazing time during early lactation of sheep. Dougherty et al. (1988) found no difference in biting rate, bite size, and grazing time when cattle were supplemented with ground corn at levels up to 4.5 kg/animal. However, other authors (Holder, 1962; Marsh et al., 1971; Leaver, 1986; Mayne and Wright, 1988; Rook et al., 1994) suggest that grazing time is reduced with supplementation, with the level of reduction being dependent on the type and level of supplementation. For example, Marsh et al. (1971) found reductions in grazing time of 22 min/kg concentrate fed, while Mayne and Wright (1988) found reductions of 43 min/kg when silage was fed. The type of supplement and its interactive effects with the basal diet might be the reason

why Dougherty et al. (1988) could not find differences in grazing time at various levels of supplementation. In temperate regions, the largest proportion (70–90%) of grazing time occurs during daylight (Penning et al., 1991; Rook et al., 1994); however, in the tropics night grazing is frequently observed due to high ambient temperatures during the day (Humphreys, 1991). The largest proportion of rumination time also occurs during daylight (Rook et al., 1994). Mastication and rumination increase with increased neutral detergent fiber (NDF) concentration in forages (Demment and Greenwood, 1988) or reduced digestibility (Arnold, 1981), in order to reduce particle sizes of the forage consumed for passage through the gastrointestinal tract. Fasting increases grazing time and reduces rumination time (Greenwood and Demment, 1988).

Comparison of predicted intakes from grazing behavior measurements with limited experimental data has shown close agreement (Gordon, 1995). However, these models still require considerable effort to be widely validated; thus their range of application has been limited mostly to research purposes. Nevertheless, they have provided a significant contribution to the understanding of intake from grazed grasslands in the past two decades and have given valuable insight to assist design of appropriate management strategies in some grazing systems.

A recognized criticism of this approach is that a large part of grazing behavior is caused by the animals' need for nutrient supply (Ungar and Noy-Meir, 1988). Most models do not integrate the two processes, and those that do have not integrated mechanistic models of digestion and metabolism at the same level of aggregation as they treat grazing behavior. Considerable research needs to be done to address these issues.

B. Diet Selection

Diet selection is one of the crucial elements in grazing systems models for appropriate prediction of animal performance (see above). The two basic distinctions that are made are (1) selection within pasture species and (2) selection between plant species. Following Thornley et al. (1994), it is possible to describe the approaches for modeling diet selection as (1) empirical (descriptive), (2) goal-oriented (teleonomic), and (3) mechanistic (reductionist). The application of a particular approach is dependent on the type of pasture and animal models used.

There is general agreement that ruminants prefer to eat leaf instead of stem or dead material and that the material eaten is usually

of a higher nutritive value than the material on offer. Ruminants also tend to avoid plants with antinutritional compounds (e.g., tannins, alkaloids). In rangelands, abundance, nutritive value, and spatial distribution are interrelated. For example, plants of a higher nutritive value are less abundant than low quality ones (Belovsky, 1987). Management practices and the spatial distribution of plant species create grazing routes that animals follow and thus have an influence on the diet selected. Animals also tend to graze closer to the water source in arid and semiarid environments (Arnold, 1981). Even when some basic empirical rules, such as those previously mentioned, appear to exist, the mechanisms used by animals to select their diet have not been fully elucidated.

Empirical representations of diet selection are the most common in grazing models, and in general they use the basic principles described above. Examples of these can be found in Christian et al. (1978), Illius (1986), Blackburn and Kothmann (1991), Baker et al. (1992), and Freer et al. (1997). These models assign "selectivity coefficients" on the basis of digestibility or palatability of different morphological units (Illius, 1986; Blackburn and Kothmann, 1991) or physiological states (e.g., Freer et al., 1997). A problem that arises with assigning these types of coefficients on a plant species basis is that they are modified according to the species composition of the patch and therefore may modify diet selection. For example, in terms of acceptability for an animal, the selectivity coefficient of the species depends on the other species present. Arnold (1981) argues that little progress is going to be made in understanding diet selection as long as nutritive value is expressed with traditional analyses (e.g., digestibility, cell wall constituents, nitrogen), because these cannot be described at a molecular level and therefore the substances determining "palatability" cannot be fully determined.

Goal-seeking diet selection models are based on foraging theory (Stephens and Krebs, 1986). The general principle behind them is optimization of the diet selected using the predator–prey concept. The ruminant (predator) will try to maximize its *benefits* (e.g., energy retention in most cases) relative to the *costs* of obtaining them (e.g., energy expenditure due to searching, handling, and walking) by optimally selecting between plant species and/or plant parts (prey). These models are used mostly for ecological research (Belovsky, 1987; Thornley et al., 1994; Newman et al., 1994b).

Few mechanistic models of diet selection are available (Parsons et al., 1994), and it is recognized that a mechanistic representation is still far from complete due to the lack of knowledge to describe mech-

anistically some of the factors affecting diet selection. Certainly, this is an area that requires more research to improve understanding of the mechanisms involved and to make better predictions of the diets selected by grazing ruminants.

IV. MODELING ANIMAL PERFORMANCE

From the viewpoint of whole grazing systems, it is now clear that the plant/animal interface is not completely represented if the consequences of grazing and other nutritional management practices (e.g., production) on the animal are not modeled. A series of papers and books relate to the subject (e.g., Forbes and France, 1993; van Soest, 1994; Journet et al., 1995), but there appears to be no consensus on the best approaches to modeling these processes. Nevertheless, those discussed in the following subsections represent, broadly, the most common approaches.

A. Empirical Relations Between Stocking Rate and Animal Production

It is widely recognized that stocking rate (SR) is one of the major determinants of animal production from pastures and the sustainability of the grazing system. There have been a number of mathematical descriptions of the relationship between SR and animal performance (e.g., Mott, 1961; Petersen et al., 1965; Edye et al., 1978), but the one most commonly used was derived by Jones and Sandland (1974), who suggested that (1) the relation between animal performance per head (kg/hd) and SR could be described by a linear regression and (2) the relation between animal production per hectare (kg/ha) and SR was quadratic.

Apart from SR, other authors have used different statistical relations between animal performance and herbage availability [see Humphreys (1991)], level of N fertilization (Karnezos et al., 1988), rainfall (Bransby, 1984), pasture species (McCaskill and McIvor, 1993; McIvor and Monypenny, 1995), and others. These relationships will not be considered further, since we believe they are not appropriate for use in grazing systems models because they are statistical relationships of specific datasets and as such represent only the data from which they are derived (slopes and intercepts vary significantly between studies); they do not provide an understanding of the factors influencing animal performance, and they do not have the flexibility to represent changes in management practices within the system.

Therefore they are not suitable to test alternative strategies on the behavior of the system and its parts. However, for a full explanation of these types of relationships see Humphreys (1991).

B. Systems of Nutritional Requirements

The energy requirements of ruminants have been estimated with reasonable accuracy, and differences between the systems used in different countries (i.e., Jarrige, 1989; NRC, 1989, 1996; SCA, 1990; AFRC, 1993) seem to be small (McDonald et al., 1995). Traditional "requirements systems" were not designed to predict intake but to assess the nutritional and productive consequences of different feedstuffs for the animal once their intake was known. Therefore, a criticism that often arises is that the effective calculation of nutrient supply to the animal, and hence the quality of the predictions of animal performance, are largely dependent on the accuracy of the intake estimate used for the calculations. Hence the importance of the representation of intake prediction in grazing systems models.

Several models of grazing systems, whether designed for sheep or beef or dairy cattle, rely on one form or another of an energy requirements system to represent animal performance (Vera et al., 1977; Christian et al., 1978; Sibbald et al., 1979; Konandreas and Anderson, 1982; White et al., 1983; Doyle et al., 1989; Walker et al., 1989; Richardson et al., 1991; Seman et al., 1991; Hanson et al., 1994; Thornley et al., 1994; Freer et al., 1997). However, from the nutritional management viewpoint, these systems per se present some inadequacies that need to be addressed by other mechanisms to improve their flexibility.

1. These systems are static, and digestibility estimates are central to the calculation of energy in feedstuffs in the appropriate units (e.g., DE, ME, NE). In requirements systems, these estimates are an input and are fixed for a particular feedstuff. However, effective digestibility is a consequence of degradation and passage through the gut, and therefore it is dependent on plant and animal characteristics (Demment and Greenwood, 1988; Illius and Gordon, 1991). Due to the inherent selection by grazing animals on the basis of chemical and physical characteristics of different plants and/or plant parts (see Section III), it is necessary to model degradation and passage before describing digestibility and consequent nutrient supply. This requires dynamic models.

2. Even the most recent requirements systems do not take into account explicit protein–energy interactions (Oldham, 1984; Preston

and Leng, 1987). Lack of rumen-degradable protein reduces microbial growth and depresses the rate of structural carbohydrate digestion (Ørskov, 1992). Therefore, the effect of some supplementation strategies on animal performance cannot be predicted adequately (Preston and Leng, 1987).

3. Most requirements systems do not take into account interactions between different feeds [except limited interactions modeled by Sniffen et al. (1992) and NRC (1996)]. For example, the reduction in cell wall digestibility is a well-known consequence of reduced rumen pH caused by feeding large quantities of concentrates (Istasse et al., 1986; Argyle and Baldwin, 1988), and this, and the subsequent forage/concentrate substitution rates, cannot be predicted adequately by some requirements systems.

4. Requirements systems require knowledge of the current level of production to calculate requirements and are therefore not *predictors* of animal performance. Since they were designed mainly from observations of stall-fed animals, they were implemented to calculate the quantities and types of feeds to give to an animal at a known level of production. In other words, animal performance was not predicted, it was usually an input to the calculation (even when using the intake prediction equations in these systems). The rationale behind prediction of animal performance in grazing systems should be exactly the opposite: What level of production can be attained, relative to the potential production of an animal of a given size and in a given physiological state, by following a particular grazing and overall nutritional strategy? Potential production is a function of the animal's genetic characteristics (Oldham and Emmans, 1988), while actual production is dependent on the resources available to the animal, the way it can utilize them, and the overall management of the grazing system.

We believe that the place of these systems in grazing systems models lies in the estimation of only the potential requirements, which are dependent mainly on body weight, physiological state, and level of production. However, the estimation of the supply of nutrients to meet those requirements needs a different approach, namely, dynamic models of digestion.

C. Dynamic Models of Digestion

A wide range of dynamic models of digestion can be found in the literature (e.g., Waldo et al., 1972; Mertens and Ely, 1979; Forbes, 1980; Black et al., 1980; Bywater, 1984; Fisher et al., 1987; Hyer et al., 1991;

Illius and Gordon, 1991, 1992; Sniffen et al., 1992; Fisher and Baumont, 1994). These types of models have been recently reviewed by Illius and Allen (1994), and Baldwin (1995) reviewed research models representing metabolism and the formation of end products of fermentation in ruminants* (e.g., Baldwin et al., 1970, 1977, 1987; Gill et al., 1984; Murphy et al., 1986; Danfaer, 1990; Dijkstra et al., 1992, 1993; Poppi et al., 1994). A range of approaches to model digestive processes can also be found in Forbes and France (1993).

The basic objectives of dynamic models of digestion are to predict potential intake, digestibility, and animal performance as a function of the nutritional quality of plants on offer and a range of animal characteristics. There is evidence that such models are better at predicting nutrient supply and animal performance than requirements systems (Fox et al., 1992, 1995; Ainslie et al., 1993). However, there are certain basic aspects that need to be considered that define the accuracy and flexibility of the model. A discussion of these follows.

Description of Feed Fractions The basic fractionation of feedstuffs is represented in Fig. 9. The separation of dry matter into its basic chemical entities is important because different feed fractions of different forages have different degradation and passage rates (Illius and Gordon, 1991; Russell et al., 1992) and therefore have different digestibilities. Consequently, they supply different amounts of nutrients to the animal (Murphy et al., 1982; Gill et al., 1990). These fractionations are also important into predicting effects of supplementation on the rate of cell wall digestion (Argyle and Baldwin, 1988), modeling protein–energy interactions, and using recent standards of protein requirements (e.g., Fox et al., 1992; O'Connor et al., 1993; AFRC, 1993). Nevertheless, other authors consider that the nutritional description of the potentially degradable fractions of feedstuffs requires yet further fractionations (Mertens and Ely, 1979; Sniffen et al., 1992), although it is questionable that they provide better predictions than simpler approaches (Illius and Allen, 1994). The fractionation presented here is robust, simple, and suitable for use in whole grazing system models.

Degradation Kinetics The concentration and potential degradation kinetics of the cell wall of forages are among the important determinants of intake and digestibility (Mertens, 1987; Illius and
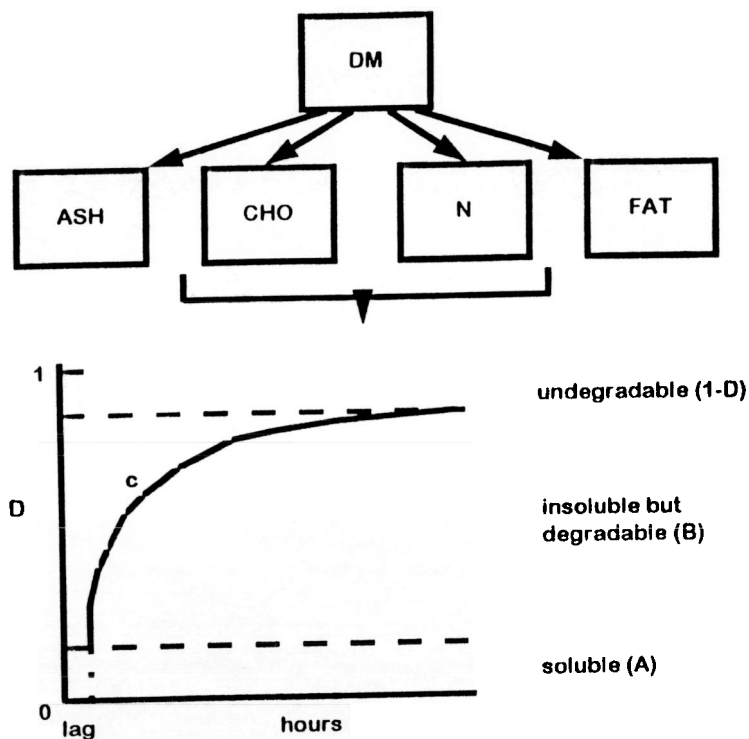
FIGURE 9   Basic nutritional characterization of forages.

Gordon, 1991). The degradation kinetics of the crude protein fraction reflect nitrogen supply to rumen microbes (Czerkawski, 1986; Ørskov, 1992; AFRC, 1993) and therefore have an effect on cell wall degradation rates. Potential degradation characteristics are a function of plant characteristics (Russell et al., 1992; Ørskov, 1994).

Parameters reflecting the potentially degradable fraction can be obtained from dacron bag studies (McDonald, 1981; Dhanoa, 1988) or in vitro gas production measurements (Herrero and Jessop, 1996, 1997; Herrero et al., 1996b; Jessop and Herrero, 1996; Jessop et al., 1996) by fitting the first-order model described by Waldo et al. (1972) and McDonald (1981), where the rate of degradation is proportional to the amount of substrate:

$$D = A + B(1 - \exp^{(c \cdot t)}) \tag{16}$$

where D = degradation, A = soluble fraction (usually determined as the washing loss in degradation studies), B = insoluble but potentially degradable fraction, degraded at a fractional rate c (h^{-1}), lag = lag phase before degradation begins (h), and t = time. See Jessop and Herrero (1996) and Herrero and Jessop (1996) for a description of the method when gas production measurements are used. Second-order models are also used to describe degradation kinetics, but the complexity of the analysis increases, since several microbial pools need to be represented to ensure proper biological behavior of the model (Illius and Allen, 1994). For alternative descriptions of degradation kinetics see Mertens (1993).

Passage Rates   While there have been great efforts to describe degradation characteristics of forages, substantially less information is available on passage rates. This is surprising, since digestibility and intake are functions of the competition between these two processes, and therefore passage rates are equally important. Passage rates are closely related to the mechanics of breakdown, largely caused by rumination, from large to small particles in the rumen (Kennedy and Murphy, 1988; Wilson and Kennedy, 1996), and this is why several models (Mertens and Ely, 1979; Fisher et al., 1987; Illius and Gordon, 1991) use different compartments reflecting pools of large to small particles to describe the different carbohydrate fractions. However, the required number of compartments to describe adequately particle dynamics and whether fractionation is really necessary to improve intake predictions are not known (Illius and Allen, 1994). Obviously, with this approach the understanding of the processes controlling the flow of material through the gut is greater, and this (depending on modeling objectives) should be seen as an advantage. It is convenient to represent rates of breakdown and passage as a function of animal characteristics (Illius and Gordon, 1991) since this improves the accuracy of predictions of intake (Illius and Allen, 1994). Illius and Gordon (1991) found the following relations for breakdown of large to small particles (BR):

$$BR = 0.144 \, ICW^{0.144} \, BW^{0.27}, \qquad r^2 = 0.62 \tag{17}$$

where ICW = indigestible cell wall (g/kg) and BW = body weight (kg).

They also found the following relationships for passage through the whole gut (PWG, the inverse of mean retention time) and passage of small particles (SPR) from the rumen, respectively:

$$PWG = 0.071 \, BW^{0.27}, \qquad r^2 = 0.76 \tag{18}$$

$$SPR = 0.75 \text{ PWG}, \quad c.v. \ 15.5\% \tag{19}$$

We analyzed the data of Shem et al. (1995) on 17 forages and applied a scaling rule similar to that of Illius and Gordon (1991). We found that particle passage rate (PR) from the rumen could be described by

$$PR = (0.0256 - 0.00007B$$

$$+ 0.00127cB)(3.96 \ BW^{-0.27}), \quad r^2 = 0.82 \tag{20}$$

For nomenclature see Eqs. (16) and (17). These passage rates apply to the B fraction and the indigestible fraction of cell wall of forages and represent mostly small particles. Passage rates also depend on the feeding level of the animal (AFRC, 1993). To account for effects of feeding level (FL, in multiples of maintenance), these should be multiplied by 0.25 FL, and a scaling rule similar to that claimed by Sniffen et al. (1992) is obtained. Other relations can be found in Sauvant et al. (1995) but for total DM. Certainly more work is required on this subject to understand the factors affecting passage rates (e.g., buoyancy and its relation to particle fermentation and density). For concentrated feeds, Sniffen et al. (1992) describe the passage rate (PRC) as

$$PRC = -0.424 + (1.45 \ PR) \tag{21}$$

Rumen Size For intake predictions, most dynamic models require that a threshold value be set for the maximum capacity of the rumen or total gut. Accurate allometric relations for these parameters are found in the literature [see Peters (1983), Demment and van Soest (1985), Mertens (1987), Demment and Greenwood (1988), and Illius and Gordon (1991)], Illius and Gordon (1991) determined this allometric relation for 18 species and found that the relationship between the weight of dry matter in the rumen (DMR) and body weight could be described by

$$DMR = 0.021 \ BW, \quad r^2 = 0.98 \tag{22}$$

Mertens (1987) found a very similar relation when expressing rumen content on the basis of neutral detergent fiber.

Dynamic models of digestion and their descriptions of feed and animals are useful for the integration of other processes within the grazing system. Since models of this nature monitor the flow of feed components through the gastrointestinal tract, they predict their excretion patterns and the composition of excreta, which are integral to linking the animal with the soil fertility subsystems and their consequent effects on pasture growth in grazing models.

V. OTHER RELATIONS BETWEEN PLANTS AND ANIMALS

There are other relations that need to be taken into consideration when modeling the plant/animal interface that are particularly difficult to model. For example, treading, poaching, and fouling can reduce herbage availability and the subsequent regrowth of the sward (Brockington, 1972; Christian, 1981; Wilkins and Garwood, 1986).

Forage is damaged due to trampling and poaching, especially in wet soils (Wilkins and Garwood, 1986) and/or in very high swards (Herrero, unpublished), but, as Christian (1981) states, it would be difficult to account for these effects in a grazing model.

Dung pats and urine affect herbage availability and modify diet selection patterns of ruminants (Brockington, 1972), thus leading to the spatial effect of patchy swards in some cases. The effects of excreta are greater than those of urine and are mediated by the number of dung pats, the area they cover, and the stocking rate. The most common way to model these effects is by empirical relations that are usually dependent on stocking rate (Brockington, 1972; Hanson et al., 1994) to scale the amount of herbage available to the animal. Dung pats can also affect herbage growth by excluding light from the patches for several months (Wilkins and Garwood, 1986), but this effect can be reduced by management practices, at least in intensive systems. In rangelands it is difficult to control but stocking rates are also lower and therefore the effect of dung on animal consumption is, perhaps, less important.

Nevertheless, quantification of these aspects is important, because significant amounts of dung can be deposited in pastures. Its contribution to nutrient cycles cannot be neglected due to its key role in the sustainability of the grazing system and the overall dynamics of the biology of grazing cycles. However, better approaches are required to quantify the fate of minerals from ruminant excretions to the soil, water, and atmosphere (Scholefield et al., 1991; Humphreys, 1994).

VI. FUTURE RESEARCH AND DEVELOPMENT NEEDS

Future research needs can be divided into two groups: research on aspects dealing with the knowledge acquisition and representation of the main biological processes and definition of an integrated ap-

proach for the selection of management interventions leading to sustainable grazing systems.

A. Biological Processes

In terms of biological processes, there are aspects in both the plant and animal sciences that need to be addressed. For example, although mechanistic models of single pasture species are available and have proven robust in their predictions, there is a need for better understanding of the processes controlling growth in grass–legume associations and rangelands. Understanding competition for resources (light and nutrients) by different species and finding suitable mathematical definitions that reflect the biological processes is not a trivial task. This is closely linked with the representation of grazing processes and diet selection, even in single-species pastures. Most representations of diet selection have been empirical, and until the mechanisms that control diet selection have been elucidated, little progress is going to be made in modeling diet selection. A key issue in solving this problem is the need to link the behavioral aspects of grazing to digestion and metabolism models, since the release and balance of nutrients and pattern of supply play an important part in controlling rates of intake and what the animal chooses to eat (Gill and Romney, 1994). In terms of intake prediction, it appears that the weakest information is related to the flow of material through the gut. More efforts should be directed toward research into the factors controlling the passage of feed particles through the gastrointestinal tract.

B. Decision Support Systems: An Integrated Approach

Models can be built solely to increase our understanding about systems under study and the nature of the functional relations between parts of the system. For example, many authors have investigated the effect of certain variables on the stability and steady states of grazing systems (Noy-Meir, 1975, 1976, 1978; Johnson and Parsons, 1985; Thornley and Veberne, 1989), and other scientists have looked at more fundamental relationships between the animal and plant communities in terms of body weight effects (allometry) (Belovsky, 1987; Dement and van Soest, 1985; Illius and Gordon, 1987; Taylor et al., 1987), grazing behavior (Ungar and Noy-Meir, 1988, Ungar et al., 1991; Laca et al., 1992; Parsons et al., 1994), diet selection (Belovsky, 1987; Parsons et al., 1994; Newman et al., 1994b), or digestive processes (Illius and Allen, 1994; Baldwin, 1995). Increased understanding of these processes has led to improved methods for modeling grazing systems
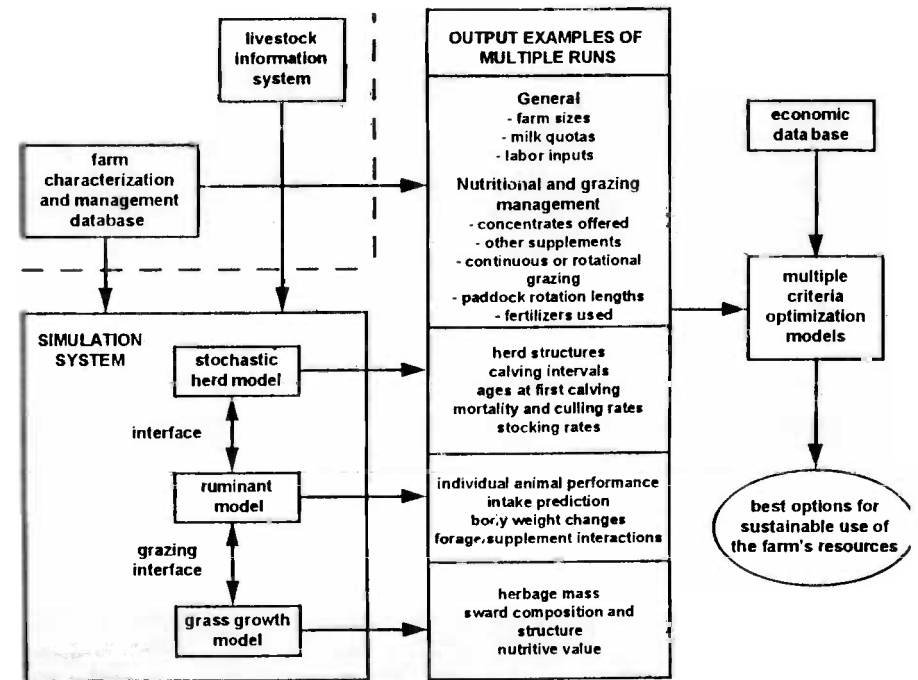

Figure 10 A decision support system for grazing systems. [From Herrero et al. (1996a).]

at various levels of detail. However, it is important to emphasize the trade-off between the objective of the model and its accuracy and level of detail if cost-effective models are to be built.

For some purposes, the use of grazing systems models is not complete if mechanisms to select between alternative grazing strategies are not available (Herrero et al., 1996a, 1997). This is specially valid if the models are to be used in farm management or in a regional planning context.

The classical approach to selection of management strategies has been to use linear programming (LP) models with the objective of optimizing economic performance (Dent et al., 1986; Conway and Killen, 1987; Kleyn and Gous, 1988; Olney and Kirk, 1989), but these have not used whole system simulation models to provide the inputs for the LP models. Two important things need to be considered. First,

it is well recognized that economic optimization is only one and not necessarily the main objective of farmers (Gasson and Errington, 1993; Perkin and Rehman, 1994; Dent et al., 1994; Dent, 1996). Therefore, the selection mechanism needs to consider several simultaneous objectives and trade-offs between them. Herrero et al. (1996a, 1997) consider that the use of multiple-criteria decision-making models (MCDM), which are extensions of linear programming models, can be linked to a simulation system to create a DSS and provide options for the management of the grazing system (Fig. 10).

A similar approach was used by Veloso et al. (1992) with crop models. Since a range of multiple objectives can be represented, they have the flexibility of dealing with different types of farmers and their managing capacities. The simulation system provides the dynamics of the system under a variety of management scenarios, and the MCDM selects the best alternatives according to the farmer's objectives. Improved selection of strategies can be gained if the objectives of the farmers are better represented, and this requires a further substantial input from the social and behavioral sciences (Dent, 1996).

REFERENCES

AFRC. 1993. *Energy and Protein Requirements of Ruminants*. An advisory manual prepared by the AFRC Technical Committee on Responses to Nutrients. Wallingford, UK: CAB International.

Ainslie, S. J., D. G. Fox, T. C. Perrey, D. J. Ketchen, and M. C. Barry. 1993. Predicting amino acid adequacy of diets fed to Holstein steers. *J. Anim. Sci.* 71:1312–1319.

Allden, W. G. 1962. Rate of herbage intake and grazing time in relation to herbage availability. *Proc. Aust. Soc. Anim. Prod.* 4:163–166.

Allden, W. G. 1981. Energy and protein supplements for grazing livestock. In: *Grazing Animals*. F. H. W. Morley (Ed.). World Animal Science. B1. Amsterdam: Elsevier, pp. 289–307.

Allden, W. G., and I. A. M. Whittaker. 1970. The determinants of herbage intake by grazing sheep: The interrelationship of factors influencing herbage intake and availability. *Aust. J. Agric. Res.* 21:755–766.

Argyle, J. L., and R. L. Baldwin. 1988. Modeling of rumen water kinetics and effects of rumen pH changes. *J. Dairy Sci.* 71:1178–1188.

Arnold, G. W. 1975. Herbage intake and grazing behaviour in ewes of four breeds at different physiological states. *Aust. J. Agric. Res.* 26:1017–1024.

Arnold, G. W. 1981. Grazing behaviour. In: *Grazing Animals*. F. H. W. Morley (Ed.). World Animal Science, B1. Amsterdam: Elsevier, pp. 79–104.

Arnold, G. W., and M. L. Dudzinski. 1967a. Studies on the diet selected of the grazing animal. II. The effect of physiological status in ewes and pasture availability on herbage intake. *Aust. J. Agric. Res.* 18:349–359.

Arnold, G. W., and M. L. Dudzinski. 1967b. Studies on the diet selected of the grazing animal. III. The effect of pasture species and pasture structure on the herbage intake of sheep. *Aust. J. Agric. Res.* 18:657–666.

Arnold, G. W., N. A. Campbell, and K. A. Galbraith. 1977. Mathematical relationships and computer routines for a model of food intake, liveweight change and wool production in grazing sheep. *Agric. Syst.* 2:209–225.

Baker, B. B., R. M. Bourdon, and J. D. Hanson. 1992. FORAGE: A model of forage intake in beef cattle. *Ecol. Modelling* 60:257–279.

Baldwin, R. L. 1995. *Modelling Ruminant Digestion and Metabolism*. London: Chapman & Hall.

Baldwin, R. L., H. L. Lucas, and R. Cabrera. 1970. Energetic relationships in the formation and utilization of fermentation end-products. In: *Physiology of Digestion and Metabolism in the Ruminant*. A. T. Phillipson (Ed.). Newcastle Upon Tyne, UK: Oriel Press, pp. 319–334.

Baldwin, R. L., L. J. Koong, and J. Ulyatt. 1977. A dynamic model of ruminant digestion for evaluation of factors affecting nutritive value. *Agric. Syst.* 2:255–288.

Baldwin, R. L., J. H. M. Thornley, and D. E. Beever. 1987. Metabolism of the lactating cow. II. Digestive elements of a mechanistic model. *J. Dairy Res.* 54:107–131.

Barthram, G. T., and S. A. Grant. 1984. Defoliation of ryegrass-dominated swards by sheep. *Grass Forage Sci.* 39:211–219.

Belovsky, G. E. 1987. Foraging and optimal body size: An overview, new data and a test of alternative models. *J. Theor. Biol.* 129:275–287.

Black, J. L., and P. A. Kenney. 1984. Factors affecting diet selection by sheep. II. Height and density of pasture. *Aust. J. Agric. Res.* 35:565–578.

Black, J. L., D. E. Beever, G. J. Faichney, B. R. Howarth, and N. M. Graham. 1980. Simulation of the effects of rumen function on the flow of nutrients from the stomach of sheep: Part 1. Description of a computer program. *Agric. Syst.* 6:195–219.

Blackburn, H. D., and M. M. Kothmann. 1989. Forage dynamics model for use in range or pasture environments. *Grass Forage Sci.* 44:283–294.

Blackburn, H. D., and M. M. Kothmann. 1991. Modelling diet selection and intake for grazing herbivores. *Ecol. Modelling* 57:145–163.

Blaxter, K. L. 1989. *Energy Metabolism in Animals and Man*. Cambridge, UK: Cambridge Univ. Press.

Bowman, P. J., D. A. Wysel, D. G. Fowler, and D. H. White. 1989. Evaluation of a new technology when applied to sheep production systems. *Agric. Syst.* 29:35–47.

Bransby, D. I. 1984. A model for predicting livemass gain from stocking rate and annual rainfall. *J. Grassland Soc. Southern Africa* 1:22–26.

Brockington, N. R. 1972. A mathematical model of pasture contamination by grazing cattle and the effects on herbage intake. *J. Agric. Sci. Camb.* 79: 249–257.

Brody, S. 1945. *Bioenergetics and Growth.* New York: Reinhold.

Brougham, R. W. 1956. The rate of growth of short-rotation ryegrass pastures in the late autumn, winter and early spring. *N. Z. J. Sci. Technol.* A38:78–87.

Brumby, P. J. 1959. The grazing behaviour of dairy cattle in relation to milk production, liveweight and pasture intake. *N. Z. J. Agric. Res.* 4:798–807.

Burlison, A. J. 1987. Sward canopy structure and ingestive behaviour in grazing animals. Ph.D. Thesis. University of Edinburgh, Scotland.

Burlison, A. J., J. Hodgson, and A. W. Illius. 1991. Sward canopy structure and the bite dimensions and bite weight of grazing sheep. *Grass Forage Sci.* 46:29–38.

Bywater, A. C. 1984. A generalised model of feed intake and digestion in lactating cow. *Agric. Syst.* 13:167–186.

Chacon, E., and T. H. Stobbs. 1976. Influence of progressive defoliation of a grass sward on the eating behaviour of cattle. *Aust. J. Agric. Res.* 27:709–727.

Chambers, A. R. M., J. Hodgson, and J. A. Milne. 1981. The development and use of equipment for automatic recording of ingestive behaviour in sheep and cattle. *Grass Forage Sci.* 36:97–105.

Charles-Edwards, D. A., P. Tow, and T. R. Evans. 1987. An analysis of the growth rates of pastures and animal production. *Agric. Syst.* 25:245–259.

Christian, K. R. 1981. Simulation of grazing systems. In: *Grazing Animals.* F. H. W. Morley (Ed.). World Animal Science, B1. Amsterdam: Elsevier, pp. 361–377.

Christian, K. R., M. Freer, J. R. Donnelly, J. L. Davidson, and J. S. Armstrong. 1978. *Simulation of Grazing Systems.* Wagenigen, The Netherlands: Pudoc.

Conrad, H. R., A. D. Pratt, and J. W. Hibbs. 1964. Regulation of feed intake in dairy cows. 1. Change in importance of physical and physiological factors with increasing digestibility. *J. Dairy Sci.* 47:54–62.

Conway, A. G., and L. Killen. 1987. A linear programming model of grassland management. *Agric. Syst.* 25:51–71.

Coughenour, M. B. 1984. A mechanistic simulation analysis of water use, leaf angles, and grazing in East African graminoids. *Ecol. Modelling* 26:203–230.

Coughenour, M. B., S. J. McMaughton, and L. L. Wallace. 1984. Modelling primary production of perennial graminoids—uniting physiological processes and morphometric traits. *Ecol. Modelling* 23:101–134.

Cowan, R. T., T. M. Davison, and R. K. Shephard. 1986. Observations on the diet selected by Friesian cows grazing tropical grass and grass-legume pastures. *Trop. Grasslands* 20:183–192.

Czerkawski, J. W. 1986. *An introduction to Rumen Studies.* Oxford, UK: Pergamon.

Danfaer, A. 1990. *A Dynamic Model of Nutrient Digestion and Metabolism in Lactating Dairy Cows.* No. 671. Beretning. Foulum, Denmark.

Demment, M. W., and G. B. Greenwood. 1988. Forage ingestion: Effects of sward characteristics and body size. *J. Anim. Sci.* 66:2380–2392.

Demment, M. W., and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125: 641–671.

Demment, M. W., J. L. Peyraud, and E. A. Laca. 1995. Herbage intake at grazing: A modelling approach. In: *Recent Developments in the Nutrition of Herbivores.* M. Journet et al. (Eds.). Paris, France: INRA Editions, pp.121–141.

Dent, J. B. 1996. Theory and practice in FSR/E: Consideration of the role of modelling. In: *Systems-Oriented Research in Agriculture and Rural Development.* M. Sebillotte (Ed.). Montpellier, France: CIRAD-SAR, pp. 100–110.

Dent, J. B., S. R. Harrison, and K. B. Woodford. 1986. *Farm Planning with Linear Programming: Concept and Practice.* London, UK: Butterworths.

Dent, J. B., M. J. McGregor, and G. Edwards-Jones. 1994. Integrating livestock and socio-economic systems into complex models. In: *The Study of Livestock Farming Systems in a Research and Development Framework.* A. Gibbon and J. C. Flamant (Eds.). EAAP Publication No. 63. Wageningen, The Netherlands: Wageningen Pers, pp. 25–36.

Detling, J. K., W. J. Parton, and H. W. Hunt. 1979. A simulation model of *Bouteloua gracilis* biomass dynamics on the North American shortgrass prairie. *Oecologia* 38:167–191.

Dhanoa, M. S. 1988. On the analysis of dacron bag data for low degradability feeds. *Grass Forage Sci.* 43:441–444.

Dijkstra, J., H. D. St. C. Neal, J. France, and D. E. Beever. 1992. Simulation of nutrient digestion, absorption and outflow in the rumen. Model description. *J. Nutri.* 122:2239–2256.

Dijkstra, J., H. Boer, J. van Bruchem, M. Bruining, and S. Tamminga. 1993. Absorption of volatile fatty acids from the rumen of lactating dairy cows as influenced by volatile fatty acid concentration, pH and rumen liquid volume. *Br. J. Nutri.* 69:385–396.

Dougherty, C. T., T. D. A. Forbes, P. L. Cornelius, L. M. Lauriault, N. W. Bradley, and E. M. Smith. 1988. Effects of supplementation on the ingestive behaviour of grazing steers. *Grass Forage Sci.* 43:353–361.

Doyle, C. J., J. A. Baars, and A. C. Bywater. 1989. A simulation model of bull beef production under rotational grazing in the Waikato region of New Zealand. *Agric. Syst.* 31:247–278.

Edelsten, P. R., and J. E. Newton. 1975. A simulation model of intensive lamb production from grass. Technical Report No. 17. Grassland Research Institute. Hurley, UK.

Edelsten, P. R., and J. E. Newton. 1977. A simulation model of a lowland sheep system. *Agric. Syst.* 2:17–32.

Edye, L. A., W. T. Williams, and W. H. Winter. 1978. Seasonal relations between animal gain, pasture production and stocking rate on two tropical grass-legume pastures. *Aust. J. Agric. Res.* 29:103–113.

Finlayson, J. D., O. J. Cacho, and A. C. Bywater. 1995. A simulation model of grazing sheep. 1. Animal growth and intake. *Agric. Syst.* 48:1–25.

Fisher, D. S., and R. Baumont. 1994. Modeling the rate and quantity of forage intake by ruminants during meals. *Agric. Syst.* 45:43–54.

Fisher, D. S., J. C. Burns, and K. R. Pond. 1987. Modeling ad libitum dry matter intake by ruminants as regulated by distension and chemostatic feedbacks. *J. Theor. Biol.* 126:407–418.

Flores, E. R., E. A. Laca, T. C. Griggs, and M. W. Demment. 1993. Sward height and vertical morphological differentiation determine cattle bite dimensions. *Agron. J.* 85:527–532.

Forbes, J. M. 1977. Interrelationships between physical and metabolic control of voluntary feed intake in fattening, pregnant and lactating sheep: A model. *Anim. Prod.* 24:90–101.

Forbes, J. M. 1980. A model of the short term control of feeding in the ruminant: Effect of changing animal or feed characteristics. *Appetite* 1:21–41.

Forbes, J. M. 1993. Voluntary feed intake. In: *Quantitative Aspects of Ruminant Digestion and Metabolism.* J. M. Forbes and J. France (Eds.). Wallingford, UK: CAB International, pp. 479–494.

Forbes, J. M., and J. France. 1993. Quantitative aspects of ruminant digestion and metabolism. Wallingford, UK: CAB International.

Forbes, T. D. A. 1982. Ingestive behaviour and diet selection in grazing cattle and sheep. Ph.D. Thesis. University of Edinburgh, Scotland.

Forbes, T. D. A. 1988. Researching the plant-animal interface: The investigation of ingestive behavior in grazing animals. *J. Anim. Sci.* 66:2369–2379.

Forbes, T. D. A., and J. Hodgson. 1985. Comparative studies of the influence of sward conditions on the ingestive behaviour of cows and sheep. *Grass Forage Sci.* 40:69–77.

Fox, D. G., C. J. Sniffen, J. D. O'Connor, J. B. Russell, and P. J. van Soest. 1992. A net carbohydrate and protein system for evaluating cattle diets. III. Cattle requirements and diet adequacy. *J. Anim. Sci.* 70:3578–3596.

Fox, D. G., M. C. Barry, R. E. Pitt, D. K. Roseler, and W. C. Stone. 1995. Application of the Cornell net carbohydrate and protein model for cattle consuming forages. *J. Anim. Sci.* 73:267–277.

Freer, M. 1981. The control of food intake by grazing animals. In: *Grazing Animals.* F. H. W. Morley (Ed.). World Animal Science, B1, Amsterdam: Elsevier, pp. 105–124.

Freer, M., J. L. Davidson, J. S. Armstrong, and J. R. Donnelly. 1970. Simulation of summer grazing. Proc. 11th. Int. Grassland Congress. Queensland: Surfer's Paradise.

Freer, M., A. D. Moore, and J. R. Donnelly. 1997. GRAZPLAN: Decision support systems for Australian grazing enterprises. II. The animal biology model for feed intake, production and reproduction and the GrazFeed DSS. *Agric. Syst.* (in press).

Gartner, J. A., and D. Hallam. 1984. A quantitative framework for livestock development planning. Part 3. Feed demand and supply. *Agric. Syst.* 14:123–142.

Gasson, R., and A. J. Errington. 1993. *The Farm Family Business.* Wallingford, UK: CAB International.

Gilbert, B. J. 1975. RANGES: Grassland simulation model. Fort Collins, CO: Colorado State University.

Gill, M., and D. Romney. 1994. The relationship between the control of meal size and the control of daily intake in ruminants. *Livest. Prod. Sci.* 39:13–18.

Gill, M., J. H. M. Thornley, J. L. Black, J. D. Oldham, and D. E. Beever. 1984. Simulation of the metabolism of absorbed energy-yielding nutrients in young sheep. *Br. J. Nutr.* 20:13–23.

Gill, M., D. E. Beever, and J. France. 1990. Biochemical basis needed for the mathematical representation of whole animal metabolism. *Nutr. Res. Rev.* 2:181–200.

Gordon, I. J. 1995. Animal-based techniques for grazing ecology research. *Small Ruminant Res.* 16:203–214.

Greenwood, G. B., and M. W. Demment. 1988. The effect of fasting on short-term cattle grazing behaviour. *Grass Forage Sci.* 43:377–386.

Guerrero, J. N., H. Wu, E. C. Holt, and L. M. Schake. 1984. Kleingrass growth and utilization by growing steers. *Agric. Syst.* 13:227–243.

Hacker, R. B., and G. S. Richmond. 1994. Simulated evaluation of grazing management systems for arid chenopod rangelands in Western Australia. *Agric. Syst.* 44:397–418.

Hacker, R. B., K. M. Wang, G. S. Richmond, and R. K. Lindner. 1991. IMAGES: An integrated model of an arid grazing ecological system. *Agric. Syst.* 37:119–163.

Hanson, J. D., J. W. Skiles, and W. J. Parton. 1988. A multi-species model for rangeland plant communities. *Ecol. Modelling* 44:89–123.

Hanson, J. D., B. B. Baker, and R. M. Bourdon. 1994. SPUR2 Documentation and User Guide. GPSR Tech. Report No. 1. Fort Collins, CO: USDA-ARS, Great Plains Systems Research Unit.

Hendricksen, R., and D. J. Minson. 1980. The feed intake and grazing behaviour of cattle grazing a crop of *Lablab purpureus. J. Agric. Sci., Camb.* 95:547–554.

Herrero, M. 1995. Grassland modelling: A decision-support tool. In: *Central America: Conservation and Sustainable Development.* Proceedings of a workshop on Sustainability of Livestock Production Systems, Aug. 8–11, 1995, San José, Costa Rica. *Cienc. Vet.* 17:72–79.

Herrero, M., and N. S. Jessop. 1996. Relationship between in vitro gas production and neutral detergent fibre disappearance in three tropical grasses. *Anim. Sci.* 62:682.

Herrero, M., and N. S. Jessop. 1997. In vitro gas production of tropical pasture legumes. Proceedings of the XVIII International Grassland Congress, Saskatchewan, Canada. (In press).

Herrero, M., R. H. Fawcett, and J. B. Dent. 1996a. Integrating simulation models to optimise nutrition and management for dairy farms: A methodology. In: *Livestock Farming Systems: Research, Socio-Economics and The Land Manager.* J. B. Dent et al. (Eds.). EAAP Publication No. 79. Wageningen, The Netherlands: Wageningen Pers, pp. 322–326.

Herrero, M., I. Murray, R. H. Fawcett, and J. B. Dent. 1996b. Prediction of the chemical composition and in vitro gas production of kikuyu grass by near-infrared reflectance spectroscopy. *Anim. Feed Sci. Technol. 60:*51–67.

Herrero, M., R. H. Fawcett, E. Perez, and J. B. Dent. 1997. The role of systems research in grazing management: applications to sustainable cattle production in Latin America. In: *Applications of Systems Approaches of the Farm and Regional Levels.* D. P. Teng et al. (Eds.). London, UK: Kluwer Academic, pp. 129–136.

Hodgson, J. 1981. Variations in the surface characteristics of the sward and the short-term rate of herbage intake by calves and lambs. *Grass Forage Sci. 36:*49–57.

Hodgson, J. 1982. Influence of sward characteristics on diet selection and herbage intake by the grazing animal. In: *Nutritional Limits to Animal Production from Pastures.* J. B. Hacker (Ed.). Wallingford, UK: CAB International, pp. 153–166.

Hodgson, J. 1985. The control of herbage intake in the grazing ruminant. *Proc. Nutr. Soc. 44:*339–346.

Hodgson, J. 1986. Grazing behaviour and herbage intake. In: *Grazing.* J. Frame (Ed.). British Grassland Society Occasional Symposium No. 19. pp. 51–64.

Hodgson, J., D. A. Clark, and R. J. Mitchell. 1994. Foraging behaviour in grazing animals and its impact on plant communities. In: *Forage Quality, Evaluation and Utilization.* G. C. Fahey et al. (Eds.). Madison, WI: American Society of Agronomy, pp. 796–827.

Holder, J. M. 1962. Supplementary feeding of grazing sheep—Its effects on pasture intake. *Proc. Aust. Soc. Anim. Prod. 4:*154–159.

Humphreys, L. R. 1991. *Tropical Pasture Utilisation.* Cambridge, UK: Cambridge Univ. Press.

Humphreys, L. R. 1994. *Tropical Forages: Their Role in Sustainable Agriculture.* Essex, UK: Longman Scientific and Technical.

Hunt, H. W., M. J. Trlica, E. F. Redente, J. C. Moore, J. K. Detling, T. G. F. Kittel, D. E. Walter, M. C. Fowler, D. A. Klein, and E. T. Elliott. 1991. Simulation model for the effects of climate change on temperature grassland ecosystems. *Ecol. Modelling 53:*205–246.

Hyer, J. C., J. W. Oltjen, and M. L. Galyean. 1991. Development of a model to predict forage intake by grazing cattle. *J. Anim. Sci. 69:*827–835.

Illius, A. W. 1986. Foraging behaviour and diet selection. In: *Grazing Research at Northern Latitudes.* O. Gudmundsson (Ed.). Proceedings of NATO Workshop, Reykjavik, Iceland: Nato Publishers, pp. 227–236.

Illius, A. W., and M. S. Allen. 1994. Assessing forage quality using integrated models of intake and digestion in ruminants. In: *Forage Quality, Evaluation*

and Utilization. G. Fahey et al. (Eds.). Madison, WI: American Society of Agronomy, pp. 869–890.

Illius, A. W., and I. J. Gordon. 1987. The allometry of food intake in grazing ruminants. *J. Anim. Ecol. 56:*989–999.

Illius, A. W., and I. J. Gordon. 1991. Prediction of intake and digestion in ruminants by a model of rumen kinetics integrating animal size and plant characteristics. *J. Agric. Sci., Camb. 116:*145–157.

Illius, A. W., and I. J. Gordon. 1992. Modelling the nutritional ecology of ungulate herbivores: Evolution of body size and competitive interactions. *Oecologia 89:*428–434.

Innis, G. S. 1978. *Grassland Simulation Model.* Ecol. Stud. No. 26. New York: Springer-Verlag.

Istasse, L., R. I. Smart, and E. R. Ørskov. 1986. Comparison between two methods of feeding concentrate to sheep given a diet high or low in concentrate with or without buffering substances. *Anim. Feed Sci. Technol. 16:*37–49.

Jamieson, W. S., and J. Hodgson. 1979. The effects of variation in sward characteristics upon the ingestive behavior and herbage intake of calves and lambs under a continuous stocking management. *Grass Forage Sci. 34:*273–282.

Jarrige, R. (Ed.). 1989. *Ruminant Nutrition. Recommended Allowances and Feed Tables.* Paris, France: INRA Editions.

Jessop, N. S., and M. Herrero. 1996. Influence of soluble components on parameter estimation using the in vitro gas production technique. *Anim. Sci. 62:*626–627.

Jessop, N. S., S. Nagadi, and M. Herrero. 1996. Use of in vitro gas production method to study ruminal protein–energy interactions. *J. Dairy Sci. 79*(Suppl. 1):182.

Johnson, I. R., and A. J. Parsons. 1985. A theoretical analysis of grass growth under grazing. *J. Theor. Biol. 112:*346–368.

Johnson, I. R., and J. H. M. Thornley. 1983. Vegetative crop growth model incorporating leaf area expansion and senescence, and applied to grass. *Plant, Cell and Environ. 6:*721–729.

Johnson, I. R., and J. H. M. Thornley. 1985. Dynamic model of the response of a vegetative grass crop to light, temperature and nitrogen. *Plant, Cell Environ. 8:*485–499.

Jones, R. J., and R. L. Sandland. 1974. The relation between animal gain and stocking rate. Derivation of the relation from the results of grazing trials. *J. Agric. Sci. 83:*335–342.

Journet, M., and C. Demarquilly. 1979. Grazing. In: *Feeding Strategies for the High Yield Dairy Cow.* W. H. Broster and H. Swan (Eds.). London, UK: Granada Publishers, pp. 295–321.

Journet, M., E. Grenet, M.-H. Farce, M. Theriez, and C. Demarquilly. 1995. *Recent Developments in the Nutrition of Herbivores.* Paris, France: INRA Editions.

Kahn, H. E., and C. R. W. Spedding. 1984. A dynamic model for the simulation of cattle herd production systems. 2. An investigation of various factors influencing the voluntary intake of dry matter and the use of the model in their validation. *Agric. Syst.* 13:63–82.

Karnezos, T. P., N. M. Tainton, and D. I. Bransby. 1988. A mathematical model used to describe animal performance on kikuyu and coastcross II pastures. *J. Grassland Soc. S. Africa* 5:38–41.

Kennedy, P. M., and M. R. Murphy. 1988. The nutritional implications of differential passage of particles through the ruminant alimentary tract. *Nutr. Res. Rev.* 1:189–208.

Kibon, A., and E. R. Ørskov. 1993. The use of degradation characteristics of browse plants to predict intake and digestibility by goats. *Anim. Prod.* 57: 247–251.

Kleyn, F. J., and R. M. Gous. 1988. Mathematical programming model for the optimisation of nutritional strategies for a dairy cow. *S. African J. Anim. Sci.* 18:156–160.

Konandreas, P. A., and F. M. Anderson. 1982. Cattle herd dynamics: An integer and stochastic model for evaluating production alternatives. ILCA Res. Rep. No. 2. Addis Ababa, Ethiopia: International Livestock Centre for Africa.

Laca, E., and M. W. Demment. 1996. Foraging strategies of grazing animals. In: *The Ecology and Management of Grazing Systems.* J. Hodgson and A. W. Illius (Eds.). Wallingford, UK: CHB International, pp. 137–158.

Laca, E. A., E. D. Ungar, N. Seligman, and M. W. Demment. 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. *Grass Forage Sci.* 47:91–102.

Laca, E. A., E. D. Ungar, and M. W. Demment. 1994. Mechanisms of handling time and intake rate of a large mammalian herbivore. *Appl. Anim. Behav. Sci.* 39:3–19.

Laredo, M. A., and D. J. Minson. 1973. The voluntary intake, digestibility, and retention time by sheep of leaf and stem fractions of five grasses. *Aust. J. Agric. Res.* 24:875–888.

Lauenroth, W. K., D. L. Urban, D. P. Coffin, W. J. Parton, H. H. Shugart, T. B. Kirchner, and T. M. Smith. 1993. Modeling vegetation structure–ecosystem process interactions across sites and ecosystems. *Ecol. Modelling* 67:49–80.

Leaver, J. D. 1986. Effects of supplements on herbage intake and performance. In: *Grazing.* J. Frame (Ed.). British Grassland Soc. Occasional Symp. No. 19, pp. 79–88.

Loewer, O. J., K. L. Taul, L. W. Turner, N. Gay, and R. Muntifering. 1987. GRAZE: A model of selective grazing by beef animals. *Agric. Syst.* 25: 297–309.

Lopez-Tirado, Q., and J. G. W. Jones. 1991a. A simulation model to assess primary production and use of *Bouteloua gracilis* grasslands. Part I. Model structure and validation. *Agric. Syst.* 35:189–208.

Lopez-Tirado, Q., and J. G. W. Jones. 1991b. A simulation model to assess primary production and use of *Bouteloua gracilis* grasslands. Part II. Experimentation. *Agric. Syst.* 35:209–227.

McCall, D. G. 1984. A systems approach to research planning for North Island hill country. Ph.D. Thesis. Massey University, New Zealand.

McCaskill, M. R., and J. G. McIvor. 1993. Herbage and animal production from native pastures and pastures oversown with *Stylosanthes hamata*. 2. Modelling studies. *Aust. J. Exp. Agric.* 33:571–579.

McDonald, I. 1981. A revised model for the estimation of protein degradability in the rumen. *J. Agric. Sci. Camb.* 96:251–252.

McDonald, P., R. A. Edwards, J. F. D. Greenhalgh, and C. Morgan. 1995. *Animal Nutrition.* 5th ed. London, UK: Longman.

McIvor, J. G., and R. Monypenny. 1995. Evaluation of pasture management systems for beef production in the semi-arid tropics: Model development. *Agric. Syst.* 49:45–67.

McLeod, M. N., P. M. Kennedy, and D. J. Minson. 1990. Resistance of leaf and stem fractions of tropical forage to chewing and passage in cattle. *Br. J. Nutr.* 63:105–119.

Marsh, R., R. C. Campling, and W. Holmes. 1971. A further study of a rigid grazing management system for dairy cows. *Anim. Prod.* 13:441–448.

Mayne, C. S., and I. A. Wright. 1988. Herbage intake and utilization by the dairy cow. In: *Nutrition and Lactation in the Dairy Cow.* P. C. Garnsworthy (Ed.). London: Butterworths, pp. 280–293.

Mayne, C. S., R. D. Newberry, S. C. F. Woodcock, and R. J. Wilkins. 1987. Effect of grazing severity on grass utilization and milk production of rotationally grazed dairy cows. *Grass Forage Sci.* 42:59–72.

Mertens, D. R. 1987. Predicting intake and digestibility using mathematical models for ruminal function. *J. Anim. Sci.* 64:1548–1558.

Mertens, D. R. 1993. Rate and extent of digestion. In: *Quantitative Aspects of Ruminant Digestion and Metabolism.* J. M. Forbes and J. France (Eds.). Wallingford, UK: CAB International, pp. 13–52.

Mertens, D. R., and L. O. Ely. 1979. A dynamic model of fiber digestion and passage in the ruminant for evaluating forage quality. *J. Anim. Sci.* 49: 1085–1095.

Milne, J. A., J. Hodgson, R. Thompson, W. G. Souter, and G. T. Barthram. 1982. The diet ingested by sheep grazing swards differing in white clover and perennial ryegrass content. *Grass Forage Sci.* 37:209–218.

Monsi, M., and T. Saeki. 1953. Uberden Lichtfaktor in den Pflanzengesellschaften und seine Bedentung für die Stoff produktion. *Jap. J. Botany* 14: 22–52.

Monteith, J. L. 1972. Solar radiation and productivity in tropical ecosystems. *J. Appl. Ecol.* 9:747–766.

Moore, A. D., J. R. Donnelly, and M. Freer. 1997. GRAZPLAN: Decision support for Australian grazing enterprises. III. Pasture growth and soil moisture submodels and the GrassGro DSS. *Agric. Syst.* (In press).

Morley, F. H. W. 1968. Pasture growth curves and grazing management. *Aust. J. Exp. Agric. Anim. Husbandry* 8:40–45.

Mott, G. O. 1961. Grazing pressure and the measurement of pasture production. Proceedings of the VIII International Grassland Congress, Hurley, UK, pp. 606–611.

Murphy, M. R., R. L. Baldwin, and L. J. Koong. 1982. Estimation of stoichiometric parameters for rumen fermentation of roughage and concentrate diets. *J. Anim. Sci.* 55:411–421.

Murphy, M. R., R. L. Baldwin, and M. J. Ulyatt. 1986. An update of a dynamic model of ruminant digestion. *J. Anim. Sci.* 62:1412–1422.

Murtagh, G. J. 1988. Factors affecting the growth of kikuyu. II. Water supply. *Aust. J. Agric. Res.* 39:43–51.

Newman, J. A., A. J. Parsons, and P. D. Penning. 1994a. A note on the behavioral strategies used by grazing animals to alter their intake rates. *Grass Forage Sci.* 49:502–505.

Newman, J. A., A. J. Parsons, J. H. M. Thornley, P. D. Penning, and J. R. Krebs. 1994b. Optimal diet selection by a generalist grazing herbivore. *Funct. Ecol.* 9:255–268.

Noy-Meir, I. 1975. Stability of grazing systems: An application of predator–prey graphs. *J. Ecol.* 63:459–481.

Noy-Meir, I. 1976. Rotational grazing in a continuously growing pasture: A simple model. *Agric. Syst.* 1:87–112.

Noy-Meir, I. 1978. Grazing and production in seasonal pastures: Analysis of a simple model. *J. Appl. Ecol.* 15:809–835.

NRC. 1989. *Nutrient Requirements of Dairy Cattle.* 6th rev. ed. Washington, DC: National Research Council. National Academy Press.

NRC. 1996. *Nutrient Requirements of Beef Cattle.* 7th rev. ed. Washington, DC: National Research Council. National Academy Press.

O'Connor, J. D., C. J. Sniffen, D. G. Fox, and W. Chalupa. 1993. A net carbohydrate and protein system for evaluating cattle diets. IV. Predicting amino acid adequacy. *J. Anim. Sci.* 71:1298–1311.

Oldham, J. D. 1984. Protein–energy interrelationships in dairy cows. *J. Dairy Sci.* 67:1090–1114.

Oldham, J. D., and G. C. Emmans. 1988. Prediction of responses to protein and energy yielding nutrients. In: *Nutrition and Lactation in the Dairy Cow.* P. C. Garnsworthy (Ed.). London, UK: Butterworths, pp. 76–96.

Olney, G. R., and G. J. Kirk. 1989. A management model that helps increase profit on Western Australian dairy farms. *Agric. Syst.* 31:367–380.

O'Reagain, P. J., and J. Schwartz. 1995. Dietary selection and foraging strategies of animals on rangeland. Coping with spatial and temporal variability. In: *Recent Developments in the Nutrition of Herbivores.* M. Journet et al. (Eds.). Paris, France: INRA Editions, pp. 407–423.

Ørskov, E. R. 1992. *Protein Nutrition in Ruminants.* 2nd ed. London: Academic Press.

Ørskov, E. R. 1994. Plant factors limiting roughage intake in ruminants. In: *Livestock Production in the 21st Century—Priorities and Research Needs.* P. A.

Thacker (Ed.). Saskatoon, Saskatchewan, Canada: University of Saskatchewan, pp. 1–10.

Parsons, A. J., I. A. Johnson, and A. Harvey. 1988. Use of a model to optimize the interaction between frequency and severity of intermittent defoliation and to provide a fundamental comparison of the continuous and intermittent defoliation of grass. *Grass Forage Sci.* 43:49–59.

Parsons, A. J., A. Harvey, and I. R. Johnson. 1991. Plant–animal interactions in a continuously grazed mixture. II. The role of differences in the physiology of plant growth and of selective grazing on the performance and stability of species in a mixture. *J. Appl. Ecol.* 28:635–658.

Parsons, A., J. H. M. Thornley, J. Newman, and P. D. Penning. 1994. A mechanistic model of some physical determinants of intake rate and diet selection in a two-species temperate grassland sward. *Funct. Ecol.* 8:187–204.

Penning, P. D. 1986. Some effects of sward conditions on grazing behaviour and intake by sheep. In: *Grazing Research at Northern Latitudes.* O. Gudmundsson (Ed.). Proceedings of NATO Workshop. Reykjavik, Iceland: Nato Publishers, pp. 219–226.

Penning, P. D., A. J. Parsons, R. J. Orr, and T. T. Treacher. 1991. Intake and behaviour responses by sheep to changes in sward characteristics under continuous stocking. *Grass Forage Sci.* 46:15–28.

Penning, P. D., A. J. Parsons, R. J. Orr, and G. E. Hooper. 1994. Intake and behaviour responses by sheep to changes in sward characteristics under rotational grazing. *Grass Forage Sci.* 49:476–486.

Perkin, P., and T. Rehman. 1994. Farmers objectives and their interactions with business and life styles: Evidence from Berkshire, England. In: *Rural and Farming Systems Analysis. European Perspectives.* J. B. Dent and M. J. McGregor (Eds.). Wallingford, UK: CAB International, pp. 193–212.

Peters, A. 1983. *The Ecological Implications of Body Size.* Cambridge, UK: Cambridge Univ. Press.

Petersen, R. G., H. L. Lucas, and G. O. Mott. 1965. Relationship between rate of stocking and per animal and per acre performance on pasture. *Agron. J.* 57:27–30.

Poppi, D. P., D. J. Minson, and J. H. Ternouth. 1981. Studies of cattle and sheep eating leaf and stem fractions of grasses. 1. The voluntary intake, digestibility and retention time in the reticulo-rumen. *Aust. J. Agric. Res.* 32:99–108.

Poppi, D. P., M. Gill, and J. France. 1994. Integration of theories of intake regulation in growing ruminants. *J. Theor. Biol.* 167:129–145.

Preston, T. R., and R. A. Leng. 1987. *Matching Ruminant Production Systems with Available Resources in the Tropics and Sub-tropics.* Armidale, Australia: Penambul Books.

Richardson, F. D., B. D. Hahn, and P. I. Wilke. 1991. A model for the evaluation of different production strategies for animal production from rangeland in developing areas: An overview. *J. Grassland Soc. S. Africa* 8:153–159.

Rodriguez, A., J. N. Trapp, O. L. Walker, and D. J. Bernardo. 1990. A wheat grazing systems model for the US southern plains: Part I. Model description and performance. *Agric. Syst.* 33:41–59.

Rook, A. J., C. A. Huckle, and P. D. Penning. 1994. Effects of sward height and concentrate supplementation on the ingestive behaviour of spring-calving dairy cows grazing grass-clover swards. *Appl. Anim. Behav. Sci.* 40: 101–112.

Russell, J. B., J. D. O'Connor, D. G. Fox, P. J. van Soest, and C. J. Sniffen. 1992. A net carbohydrate and protein system for evaluating cattle diets. I. Ruminal fermentation. *J. Anim. Sci.* 70:3551–3561.

Sanders, J. O., T. C. Cartwright. 1979. A general cattle production systems model. Part 2. Procedures used for simulating animal performance. *Agric. Syst.* 4:289–309.

Sauvant, D., J. Dijkstra, and D. Mertens. 1995. Optimisation of ruminal digestion: A modelling approach. In: *Recent Developments in the Nutrition of Herbivores*. M. Journet et al. (Eds.). Paris, France: INRA Editions, pp. 143–165.

SCA. 1990. Feeding systems for Australian livestock: Ruminants. Standing Subcommittee on Agriculture, Commonwealth Scientific and Industrial Research Organisation (CSIRO). Melbourne, Australia: CSIRO Publications.

Scholefield, D., D. R. Lockyer, D. C. Whitehead, and K. C. Tyson. 1991. A model to predict transformations and losses of nitrogen in UK pastures grazed by beef cattle. *Plant Soil* 132:165–177.

Seligman, N. G., J. B. Cavagnaro, and M. E. Horno. 1992. Simulation of defoliation effects on primary production of a warm-season, semiarid perennial-species grassland. *Ecol. Modelling* 60:45–61.

Seman, D. H., M. H. Frere, J. A. Stuedemann, and S. R. Wilkinson. 1991. Simulating the influence of stocking rate, sward height and density on steer productivity and grazing behaviour. *Agric. Syst.* 37:165–181.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *Bioscience* 37:789–795.

Sheehy, J. E., F. Gastal, P. L. Mitchell, J. L. Durand, G. Lemaire, and F. I. Woodward. 1996. A nitrogen-led model of grass growth. *Ann. Bot.* 77: 165–177.

Shem, M. N., E. R. Ørskov, and A. E. Kimambo. 1995. Prediction of voluntary dry matter intake, digestible dry matter intake and growth rate of cattle from the degradation characteristics of tropical foods. *Anim. Sci.* 60:65–74.

Shiyomi, M., T. Akiyama, and S. Takahashi. 1986. Modelling of energy flows and conversion efficiencies in a grassland ecosystem. *Ecol. Modelling* 32: 119–135.

Sibbald, A. R., T. J. Maxwell, and J. Eadie. 1979. A conceptual approach to the modelling of herbage intake by hill sheep. *Agric. Syst.* 4:119–134.

Simpson, J. R., and T. H. Stobbs. 1981. Nitrogen supply and animal production from pastures. In: *Grazing Animals*. F. H. W. Morely (Ed.). World Animal Science, B1. Amsterdam: Elsevier, pp. 261–287.

Smith, E. M., L. M. Tharel, M. A. Brown, C. T. Dougherty, and K. Limbach. 1985. A simulation model for managing perennial grass pastures. Part I. Structure of the model. *Agric. Syst.* 17:155–180.

Sniffen, C. J., J. D. O'Connor, P. J. van Soest, D. G. Fox, and J. B. Russel. 1992. A net carbohydrate and protein system for evaluating cattle diets. II. Carbohydrate and protein availability. *J. Anim. Sci.* 70:3562–3577.

Stephens, D. W., and J. R. Krebs. 1986. *Foraging Theory*. Monographs in Behavior and Ecology. Princeton, NJ: Princeton Univ. Press.

Stobbs, T. H. 1970. Automatic measurement of grazing time by dairy cows on tropical grass and legume pasture. *Trop. Grasslands* 4:237–244.

Stobbs, T. H. 1973. The effect of plant structure on the intake of tropical pastures 1. Variation in the bite size of grazing cattle. *Aust. J. Agric. Res.* 24:809–819.

Stobbs, T. H. 1974. Components of grazing behaviour of dairy cows on some tropical and temperate pastures. *Proc. Aust. Soc. Anim. Prod.* 10:299–302.

Stobbs, T. H. 1975. Factors limiting the nutritional value of grazed tropical pastures for beef and milk production. *Trop. Grasslands* 9:141–150.

Stuth, J. W., and M. Stafford-Smith. 1993. Decision support for grazing lands: An overview. In: *Decision Support for the Management of Grazing Lands. Emerging Issues*. J. W. Stuth and B. G. Lyons (Eds.). Man Biosphere Ser. No. 11. Paris, France: UNESCO, pp. 1–35.

Taylor. St. C. S., J. I. Murray, and A. W. Illius. 1987. Relative growth of incisor arcade and eating rate in cattle and sheep. *Anim. Prod.* 45:453–458.

Thornley, J. H. M., and I. R. Johnson. 1990. *Plant and Crop Modelling. A Mathematical Approach to Plant and Crop Physiology*. Oxford, UK: Oxford Univ. Press.

Thornley, J. H. M., and E. L. J. Veberne. 1989. A model of nitrogen flows in grassland. *Plant, Cell Environ.* 12:863–886.

Thornley, J. H. M., A. J. Parsons, J. Newman, and P. D. Penning. 1994. A cost-benefit model of grazing intake and diet selection in a two-species temperate grassland sward. *Funct. Ecol.* 8:5–16.

Ungar, E. D., and I. Noy-Meir. 1988. Herbage intake in relation to availability and sward structure: Grazing processes and optimal foraging. *J. Appl. Ecol.* 25:1054–1062.

Ungar, E. D., N. G. Seligman, and M. W. Demment. 1992. Graphical analysis of sward depletion by grazing. *J. Appl. Ecol.* 29:427–435.

van Keulen, H., and J. Wolf. 1986. *Modelling of Agricultural Production, Weather, Soils and Crops*. Wageningen, The Netherlands: Pudoc.

van Keulen, H., N. G. Seligman, R. W. Benjamin. 1981. Simulation of water use and herbage growth in arid regions. A re-evaluation and further development of the model "Arid Crop." *Agric. Syst.* 6:159–193.

van Soest, P. J. 1994. *Nutritional Ecology of the Ruminant*. 2nd ed. Cornell, NY: Cornell Univ. Press.

Veloso, R. F., M. J. McGregor, J. B. Dent, and P. K. Thornton. 1992. Farm planning for the Brazilian "Cerrado" region: Application of crop simula-

tion models for yield forecasting. In: *Computers in Agricultural Extension Programs*. Proceedings of the 4th International Conference, Florida, pp. 13–18.

Vera, R. R., J. G. Morris, and L. J. Koong. 1977. A quantitative model of energy intake and partition in grazing sheep in various physiological states. *Anim. Prod.* 25:133–153.

Verberne, E. L. J. 1992. Simulation of the nitrogen and water balance in a system of grassland and soil. Nota 258. DLO-Institut voor Bodemurucht baaried. Haaren, The Netherlands, p. 56.

Vickery, P. J. 1981. Pasture growth under grazing. In: *Grazing Animals*. F. H. W. Morley (Ed.). World Animal Science, B1. Amsterdam: Elsevier, pp. 55–77.

Wade, M. H., J. L. Peyraud, G. Lemaire, and E. A. Comeron. 1989. The dynamics of daily area and depth of grazing and herbage intake of cows in a five day paddock system. Proceedings of the XVI Grassland Congress, Nice, France, pp. 1111–1112.

Waldo, D. R., L. W. Smith, and E. L. Cox. 1972. Model of cellulose disappearance from the rumen. *J. Dairy Sci.* 55:125–129.

Walker, J. W., J. W. Stuth, and R. K. Heitschmidt. 1989. A simulation approach for evaluating field data from grazing trials. *Agric. Syst.* 30:301–316.

Whelan, M. B., E. J. A. Spath, and F. W. H. Morley. 1984. A critique of the Texas A&M model when used to simulate beef cattle grazing pasture. *Agric. Syst.* 14:81–84.

White, D. H., P. J. Bowman, F. H. W. Morley, W. R. McManus, and S. J. Filan. 1983. A simulation model of a breeding ewe flock. *Agric. Syst.* 10:149–189.

Wilkins, R. J., and E. A. Garwood. 1986. Effects of treading, poaching and fouling on grassland production and utilisation. In: *Grazing*. J. Frame (Ed.). British Grassland Society Occasional Symposium No. 19, pp. 19–31.

Wilson, J. R. 1994. Cell wall characteristics in relation to forage digestion by ruminants. *J. Agric. Sci. Camb.* 122:173–182.

Wilson, J. R., and P. M. Kennedy. 1996. Plant and animal constraints to voluntary feed intake associated with fibre characteristics and particle breakdown and passage in ruminants. *Aust. J. Agric. Res.* 47:199–225.

Woodward, S. J. R., G. C. Wake, A. B. Pleasants, and D. G. McCall. 1993. A simple model for optimizing rotational grazing. *Agric. Syst.* 41:123–155.

Woodward, S. J. R., G. C. Wake, and D. G. McCall. 1995. Optimal grazing of a multipaddock system using discrete time model. *Agric. Syst.* 48:119–139.

Zemmelink, G. 1980. Effect of selective consumption on voluntary intake and digestibility of tropical forages. Agric. Res. Rep. No. 896. Wageningen, The Netherlands: Pudoc.