

Past and Present Definitions of the Energy and Protein Requirements of Ruminants

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ABSTRACT : The genesis of methods for defining the nutritional value of feeds and the nutrient requirements of animals, and their development in the late 19th and early 20th centuries in Europe and the USA are outlined. Current energy and protein feeding systems for ruminants are described. Particular reference is made to the Australian systems which are applicable to grazing animals as well as to those given prepared feeds, and enable the effective nutritional management of animals at pasture by means of the decision support tool GrazFeed. The scheme for predicting intakes by cattle and sheep from pastures allows for the effects of selective grazing on the composition of the feed eaten, and for reduction in herbage intake when a supplementary feed is consumed. For herbage of any given concentration of metabolizable energy (ME) in the feed dry matter the changes with season of year in the net efficiency of use of the ME for growth and fattening and in the yield of microbial crude protein, g/MJ ME, which both vary with latitude, are defined. An equation to predict the energy requirements for maintenance (ME_m) of both cattle and sheep includes predictions of the additional energy costs incurred by grazing compared with housed animals and the cost, if any, of cold stress. The equation allows for the change in ME_m with feed intake. A flexible procedure predicts the composition of liveweight gain made by any given breed or sex of cattle and sheep at any stage of growth, and the variation with rate of gain. Protein requirements for maintenance, production including wool growth, and reproduction, are related to the quantities of microbial true protein and undegraded dietary protein truly digested in the small intestine. (*Asian-Aust. J. Anim. Sci.* 2003, Vol 16, No. 4 : 609-624)

Key Words : Cattle, Sheep, Nutrient Requirements, Energy, Protein, Feed Value, Feeding System

INTRODUCTION

In 1573 in Tudor England the 'Five Hundreth Pointes of Good Husbandrie' written by Thomas Tusser included the couplet "From Christmas to May/Weak cattle decay". The problem of providing feed for animals during the winter period in northern latitudes that these words illustrate began to diminish with the introduction of new crops and improved farming techniques. In England, for example, the field cultivation of turnips (*Brassica rapa*) and sowings of legumes and grasses had their beginnings in the mid 17th century, following practices in the 'Low Countries' (now the Netherlands and adjacent lands), but it was another 100 years before these crops were becoming widely grown. Stimuli for those developments were the improvements in methods for the cultivation of arable land set out by Jethro Tull, the inventor of the seed drill, in his book 'Horse-Hoeing Husbandry' published in 1733, and their vigorous adoption by progressive landowners such as 'Turnip' Townshend and Coke of Norfolk.

Improvements in farming practices, including the rotation of crops, increased food supplies for the human population and reduced fears of famine. Continuity of feed supplies for animals became reasonably assured and so there could now be continuity in the selection and breeding

of improved livestock which, in turn, focused attention on methods of feeding that would enable expression of their production potential. Thus, whereas the average weights of cattle and sheep at the Smithfield Market for meat animals in London in 1710 were 170 and 13 kg respectively, in 1795 they had increased to 360 and 36 kg (Ernle, 1936). Economic feeding, that is a favourable input-output costs ratio, became increasingly important and, therefore, it became necessary to define the nutrient requirements of animals and of the ability of feeds to meet those needs.

This paper outlines the genesis of energy and protein feeding systems, their development in the late 19th and early 20th centuries, and describes current systems with particular reference to the Australian systems.

EARLY DEVELOPMENT OF ENERGY FEEDING SYSTEMS

The first attempts at establishing a systematic basis for the feeding of livestock, described by Tyler (1975), were made in England and Germany in the 18th and early 19th centuries when 'hay equivalents' were used, notably by Albrecht Thaer, to compare the nutritive values of feeds. According to one report, for example, 100 parts by weight of 'ordinary' hay was equal in value to 800 parts of turnips (roots only), but in other reports the values varied from 525 to 885. This variation reflects their derivation from simple, and rather few, observations on the performance of animals

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given the feed. It is also because comparisons were made on an 'as fed' and not dry matter (DM) basis. Other measurements that might be described as chemical were rudimentary, though perhaps they were beginnings for the development later in the 19th century by W. Henneberg and F. Stohmann of what, from their location at the Weende Experiment Station near Göttingen, became known as the Weende system of 'proximate' analysis. This isolated crude fibre (CF), fat (EE), protein (crude protein, CP=N×6.25, and true protein, TP), ash and, by difference, 'nitrogen free extract' (NFE) which is an approximation to carbohydrate.

The bases for understanding energy metabolism were established by A. L. Lavoisier (France, b. 1743, guillotined 1794), J. Priestley (England, 1733-1804) and C. W. Scheele (Sweden, 1742-1786) who discredited the phlogiston theory of combustion by identifying oxygen and its role in life processes. Animal calorimetry was initiated by Lavoisier, P. S. de Laplace (France, 1749-1827), and A. Crawford (Ireland, 1748-1795) who estimated heat production directly, and indirectly from gaseous exchanges. Calorimetric techniques were established by J. von Liebig (Germany, 1803-1873, body composition and metabolism), M. von Pettenkofer and C. Voit (Germany, 1818-1901 and 1831-1908, the open circuit chamber), J. B. Boussingault (France, 1802-1887, carbon, nitrogen, hydrogen and oxygen balances), V. Regnault and J. Reiset also of France (1849, closed circuit chamber, and respiratory quotient), M. Rubner of Germany who in 1894 demonstrated agreement between direct and indirect determinations of heat production, and W. O. Atwater and E. B. Rosa of the USA (1899, direct and indirect calorimetry).

Starch equivalent

The Starch Equivalent (SE) system was established by Oscar Kellner whose career after graduation from the Universities of Breslau and Leipzig, as described in a biography by Breirem (1952), began with two years as an assistant in animal chemistry at an agricultural academy in Silesia. In 1876 he moved to Hohenheim at Stuttgart as an assistant to Emil Wolff who had been the first Director of the agricultural experiment station at Möckern, near Leipzig, where Kellner himself later became Director. Wolff had made a considerable advance by expressing the nutrient requirements of dairy cows in terms of digestible protein, carbohydrate and fat and had published information on the composition of feeds. Kellner became acquainted with the problems of feed evaluation and, as joint and as sole author, published significant papers on both animal and plant chemistry.

In 1880, aged 29, Kellner was appointed Professor of Agricultural Chemistry at the Imperial University, Tokyo. During his 12 years in that position he played a leading role in the organization of agricultural experiment agencies and,

in addition to his burden of teaching, worked on a wide range of problems that included soil chemistry and fertility in relation to rice production, nutrition of the silkworm, ensilage, and the nutritional value of roughages.

In 1892 the Director of Möckern since 1867, Gustav Kühn, died when only 53 years old. He had recognized and stressed the importance of distinguishing between the maintenance and production portions of a ration, and its DM content. Kellner returned to Germany to succeed him. In his first year he prepared for publication (on no less than 580 pages) the work that had been done by Kühn, and brought into full use the recently built respiration chambers for determinations of energy balances from measurements of respiratory gaseous exchanges and of carbon and nitrogen balances. By the time of Kellner's death in 1911 at age 60 his SE system (Kellner, 1905) was becoming used throughout Europe and Britain.

The SE of a feed is its net energy (NE) value expressed as an equivalent quantity of pure starch (w/w) on the basis that 1 kg of wholly digested starch was found to promote the retention of 2.360 kcal (9.87 MJ) as fat in the body of cattle; other values for the NE value of the starch unit were used for sheep, rabbits, pigs and hens.

Determination of SE requires the measurement of energy balance at a feed intake that is not below the maintenance level, and at a higher level. The difference between the two balance measurements is the energy gain by the animal in response to the increase in the feed energy intake. The rate at which such information could be gained in those times was very slow. Blaxter (1956) noted that over a period of 50 years at Möckern, with Kellner and his successor Gustav Fingerling as Directors, the total number of difference experiments with cattle, including all duplicates, was 110. Consequently the SE of many feeds was calculated from a relationship that was established with digestible (D) proximate constituents. The version used in the UK was:

$$SE=0.95[(DCP+DTP)/2]+bDDE+1.0DNFE$$

where b=1.91 for fodders and root crops

2.12 for grains and their by-products

2.41 for oilseeds, oilseed by-products, and feeds of animal origin

There were discrepancies between SE calculated by that means and measured values which Kellner ascribed to an energy cost of the 'work of digestion' (verdaungsarbeit). Feeds other than green fodder's, hays and straws were each assigned a 'value (V) number' which was a multiplier to adjust its calculated SE. For some feeds such as maize (corn) grain, potatoes, and fish and meat meals, the multiplier V as a decimal was 1.0 and, at the other extreme,

was as low as 0.76-0.82 for a range of silages (i.e. the calculated SE were reduced by, respectively, 24 and 18%); for oats, rye and wheat grains V was 0.95 and for barley 0.98.

The adjustment used for fodders was based on their crude fibre content. For long hay and straw their calculated SE were reduced by 0.58 for each 1% CF, but if these feeds were chaffed the rate of reduction was 0.29. The reduction for every percent CF in green fodders was 0.29 when these contained 4% CF and increased with increasing CF to a maximum value of 0.58 for CF contents of 16% or more.

When these adjustments were devised, neither the information on the chemical composition of feeds obtainable by the analytical techniques then available nor the knowledge of metabolic processes in the animal could yield understanding of the discrepancies between calculated and measured SE. Changes were made in subsequent decades to the SE system, but none was truly a positive development. Wood (1921), for example, increased the SE values for hay and straws by 20% because he accepted the NE values for roughages of Armsby which were higher than those of Kellner, not appreciating that this was because Armsby had measured net energy for maintenance (NE_m) while Kellner had measured net energy for gain (NE_g). Woodman (1948) subsequently removed the 20% increment for straws but retained it for hays. This lack of realization of the difference between NE_m and NE_g had other consequences. Phillipson (1959) showed that UK estimates of the maintenance requirements of sheep then current were too high because they were calculated using the energy values of feeds for fattening.

Elsewhere, continuing to avoid expressing the energy values of feeds in energy units - calories and now, preferably, joules - the values used were in units that it was thought farmers would better understand. The Scandinavian Feed Unit, a modification of the Kellner system, was 1 kg barley with a NE value that varied with feed DCP and was about 1,650 kcal (0.7 of a starch unit). The feed unit used in the Soviet Union was 1 kg oats with 1414 kcal NE (0.6 of a starch unit). In Denmark, H. Møllgaard introduced the term NK_F , net kilocalories for fattening. By this convention 1000 NK_F produces 1,000 kcal in the form of fat in the animal but only 840 NK_F are required to produce 1000 kcal milk. Leitch (1959) noted that this suggests that the value of a calorie, a physical constant, varies with the use to which it is put, and that when the scheme is applied to the maintenance requirement of a 1,000 lb (454 kg) cow, taken as 7,700 kcal (32.2 MJ), the 5,835 NK_F requirement "looks as if the cow had suddenly become less expensive".

All these changes and modifications of SE were principally arithmetic and were not based on, nor did they advance, the science of the system.

Net energy (USA)

In the USA, over nearly the same period that saw the development of the SE system, H. P. Armsby was developing his net energy system from determinations at Pennsylvania State College of the energy balances of cattle given various feeds (Armsby, 1909, 1917). Energy losses as heat were measured directly in a calorimeter built in collaboration with J. A. Fries; their balance data, like those of Kellner, of course yielded information on the energy requirements of the animals for maintenance and production. Their method of direct calorimetry was considerably more laborious than the indirect determination of heat loss, and though work continued through several subsequent decades (e.g., Forbes et al., 1927) the number of measurements that could be made fell far short of the number that was required to establish the NE values of a wide range of individual feeds. Values for feeds representing rather broad categories were bolstered by inclusion of SE from Kellner expressed as therms per 100 lb (1 therm=1 Mcal=4.184 MJ). A problem not then realized, and only properly identified by K. L. Blaxter many years later (e.g., Blaxter, 1956), is that Armsby obtained net energy values by measuring the increase in energy retention by an animal in response to an increase in feed intake from a low level (or fast) to a near-maintenance intake, whereas both levels of feeding used by Kellner were above maintenance. Consequently, for any given type of feed, the Armsby NE overestimates its value for production and underestimates the quantity needed to promote a required liveweight gain or yield of milk. Conversely, the NE measured by Kellner is less than that obtained by Armsby and colleagues because it is the value for growth and fattening.

Total digestible nutrients

There was little practical use in the USA of Armsby's NE, and the Total Digestible Nutrient (TDN) system came into universal use in that country. Stemming from the work of Wolff in Germany, it was introduced by T. L. Haecker in Minnesota in the early 1900s, though perhaps it is more generally associated with F. B. Morrison of Cornell University who described and elaborated the system as 'Morrison Feeding Standards' in a succession of new editions over many years of the text 'Feeds and Feeding'. TDN in the feed DM is calculated as:

$$TDN = DCP + DNFE + DCF + 2.25(DEE)$$

The value obtained represents the digestible energy (DE) content of the feed, as may readily be confirmed by converting a feed TDN tabulated by the National Research Council, USA (e.g. NRC, 1996) on the basis that TDN has a caloric value of 2,000 kcal/lb (Swift, 1957). The corresponding metabolizable energy (ME) tabulated is consistently about 0.8 of the TDN as kcal, which is similar

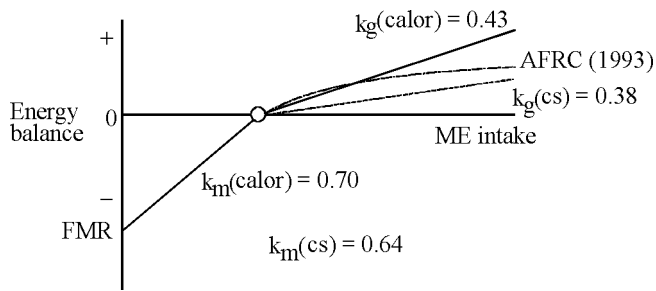


Figure 1. Efficiencies of use of metabolizable energy (ME) for maintenance (k_m) and for growth and fattening (k_g) as determined by calorimetry (calor) and by comparative slaughter (CS) for a feed with 10 MJ ME per kg dry matter. The AFRC (1993) adjusts k_g (calor), from ARC (1980), for level of feeding (L). The k_g by CS, from NRC (1996), is not adjusted for L. FMR is fasting metabolic rate (measured heat production plus energy of urine excreted during fast).

to the generally observed relationship between ME and DE.

TDN describes what the feed contains and not what production by the animal it will promote. This can be a problem in practical application as illustrated by reports (e.g., Huffman and Duncan, 1950) that replacement of grain in a dairy cow diet by an amount of alfalfa hay providing an equal quantity of TDN resulted in a reduction in milk production. It was supposed that this was because alfalfa hay is deficient in some factor(s) necessary for milk production. Nowadays it is recognized that though two diets provide equal quantities of DE (and ME), there is lower production from the diet with the lower energy density (MJ/kg DM).

DEVELOPMENT OF ENERGY FEEDING SYSTEMS AFTER 1950

There was a renaissance in calorimetry in the 1950s, and the equipment and techniques used in several countries were described at the first EAAP (1958) Symposium on Energy Metabolism at Copenhagen. Contributions to subsequent Symposia, held every three years, described the resolution of problems in calorimetry and in the interpretation of results, a number of which had been discussed in 1935 at a Conference on Energy Metabolism held at the State College, Pennsylvania (NRC, 1935). The EAAP also extended the scope of its Symposia to (e.g.) energy transactions at the molecular level and to a wide range of species, including man.

The Oscar Kellner Institute was established in 1953 at Rostock, East Germany, to continue the work of Kellner and Fingerling and develop a generally applicable system of feed energy evaluation (Nehring and Haenlein, 1973). The work employed four respiration chambers for steers and lactating cows, two for sheep, four for pigs, and several closed circuit chambers for rats, rabbits and chickens

(Schiemann, 1958). It resulted in the publication of 'The Evaluation of Feedingstuffs in Terms of Energy Standards' (Schiemann et al., 1971; title translated) which contains an immense amount of valuable information. Feed values are derived from their contents of digestible nutrients measured under standard conditions. The Weende analytical methods are used and this is one reason why the system has not been widely adopted. In addition the complications are many (Leitch, 1972). These include retention from the SE system of correction factors, though V numbers are applied to the calculated energy values of rations as a whole and not to individual feeds as in SE; the factors vary with DE% and the CF% correction formerly applied to fodders is not used (Nehring and Haenlein, 1973; Schiemann, 1977).

In the USA, tables on the composition and nutritional value of feeds (e.g. NRC, 1996) continue to list TDN but this system has been superseded by definitions of the energy requirements of animals and the value of feeds in NE terms. Feeds have to be given three energy values: for maintenance (NE_m), lactation (NE_l), and gain (NE_g). Two different techniques were used to establish these values and the corresponding energy requirements of the animals. The requirements of dairy cows for maintenance and milk production (NRC, 2001) were determined calorimetrically, but for beef cattle (NRC, 1996) and sheep (NRC, 1985) the requirements for maintenance and gain were both determined by comparative slaughter.

Estimates of the ME requirement for maintenance (ME_m) obtained by the two techniques are similar. With calorimetry its value is the quantity of ME used with an efficiency (k_m) that will meet the basal NE needs of the animal; the efficiency varies directly with the ME concentration in the diet (MJ/kg DM=M/D). The basal needs are determined by measuring the energy loss by the animal during fast under standardized conditions (fasting metabolic rate, FMR=fasting heat production, FHP, plus urine energy), and $ME_m = FMR / k_m$.

With the comparative slaughter technique animals are not fasted and are not given significantly less than a maintenance intake. A calculated, not determined, value of the basal energy need (Garrett, 1980) was used to establish the relationship between NE and ME for intakes below maintenance. The relationship is curvilinear, not rectilinear as obtained with calorimetry, and this is reflected in the predicted k_m . For M/D of 9 and 12 those of the NRC (1996) are 0.60 and 0.68 respectively; the corresponding k_m obtained by calorimetry (e.g., ARC, 1980) are 0.69 and 0.74 (Figure 1, and see 'Requirement for maintenance' on page 616). Clearly, a determination by calorimetry of the NE requirement for maintenance (i.e., the FMR) must not be converted to ME with a relationship established by comparative slaughter; the result would be gross overestimation of ME_m .

In continental Europe generally, as in the USA, the NE requirements for lactation have been established by calorimetry, and for growth and fattening by comparative slaughter and feeding trials (van der Honing and Alderman, 1988). The NE value of feeds are mostly expressed as feed units (e.g., 1 kg 'standard barley'=1.650 kcal NE₁) and not directly in MJ per kg feed DM.

However, the European systems for growing cattle and sheep do not convert the NE requirements for gain to a feed ME requirement by applying values for conversion efficiency (NE/ME= k_g) that have been obtained by comparative slaughter (e.g., those of Garrett, 1980, adopted by the NRC, 1996); these k_g do not require adjustment for level of feeding (L). Instead, they adopted the ARC (1965) values, similar to those of ARC (1980), which were obtained calorimetrically and do require adjustment for L. In practice, for any given diet a single k_g adjusted to L=1.5 (i.e., 1.5 ME_m) is used for all levels of feeding but, as discussed later, it is probable that the consequent estimate of the ME required for gain is too low.

In the UK the Agricultural Research Council adopted the energy feeding system developed by K.L. Blaxter (ARC, 1965 and 1980). Like other current systems it is an NE system, but the energy value of a feed is defined by a single value, namely its ME content (M/D) measured at L=1. 'Rules', which can be refined as new knowledge accrues, define the net efficiency with which the ME is used for maintenance, the production of milk, and energy gain in body tissues (k_m , k_l , k_g , respectively). The amounts of various feeds that will provide the ME required for the desired production are then calculated.

Complexities in the ARC (1965) system that made practical application somewhat difficult were reduced by modifications and simplifications (MAFF, 1975) devised by a committee under the leadership of G. Alderman, who further refined and extended that practical manual (AFRC, 1993) following revision of the system by the ARC (1980) and the AFRC (1990).

The Australian system

Use in Australia of both the TDN and SE systems continued into the 1970s and though these began to be superseded by use of MAFF (1975), none was really satisfactory for Australian conditions where the majority of sheep and cattle obtain most of their feed by grazing. In addition there were obvious benefits of having one system used throughout the nation, and a Working Party for the Introduction of Nationally Uniform Feeding Standards for Livestock was established. The Report for Ruminants (SCA, 1990) includes detailed information on requirements for minerals, vitamins and water, and discusses a number of matters for consideration in nutritional management including gastrointestinal parasitism, frequency of feeding

for survival or production, feeding behaviour, physical form of diet, and feed additives. Its recommendations on the prediction of intakes of energy and protein and estimates of the requirements for maintenance and production are incorporated in the GrazFeed decision support tool (Freer et al., 1997; Horizon Agriculture, Roseville, NSW 2069) which predicts the performance of grazing animals without and with supplementary feed. With continuing development of that computer program to incorporate new knowledge and from experience in its wide practical application there has been continuing refinement of the SCA (1990) recommendations. Current specifications in GrazFeed are available at www.pi.csiro.au/grazplan.

A prime task of the approach adopted was to extend to grazing animals procedures for quantitative nutritional management that elsewhere were developed essentially for the informed and profitable rationing of prepared feeds.

Feed energy : The energy of a feed is described by a single value, M/D, and not by multiple entries (NE_m etc.). Clearly it would neither be practicable, nor useful, to attempt to tabulate the various NE values for the immense range in Australia of types and qualities of material available for grazing and of what might actually be grazed. The M/D of a forage is calculated from the digestibility of its dry matter (DMD, as a decimal; equation 1) and 'energy feeds' and protein supplements from DMD and EE (g/g DM; equation 2).

$$M/D = 17.2DMD - 1.47 \quad (1)$$

$$M/D = 13.3DMD + 23.4EE + 1.32 \quad (2)$$

Standard reference weight : Voluntary feed intake per unit of liveweight (W) changes with age, and the intake by a fully grown animal of small mature size will be different from that of an animal of similar W that has a larger mature size and is not fully grown. To facilitate the prediction of intake, and of the composition of liveweight gain as described later, the concept of a Standard Reference Weight (SRW) was devised. This is analogous to a mature W, but has a purpose-specific definition: it is the liveweight attained by an animal of any given type when its skeletal development is complete and it has a condition score in the middle of the range of values for that measure.

Prediction of intake : Formulation of rations for housed animals requires knowledge of the amounts of feed that they can eat. With grazing animals, in contrast, it is necessary to know what quantities of feed they are eating from their pastures. Many schemes adopt a retrospective approach to the prediction of intake, using milk yield and other measures of current animal performance as predicting variables (eg., Ingvarsten, 1994), but this severely constrains nutritional management. For animals at pasture,

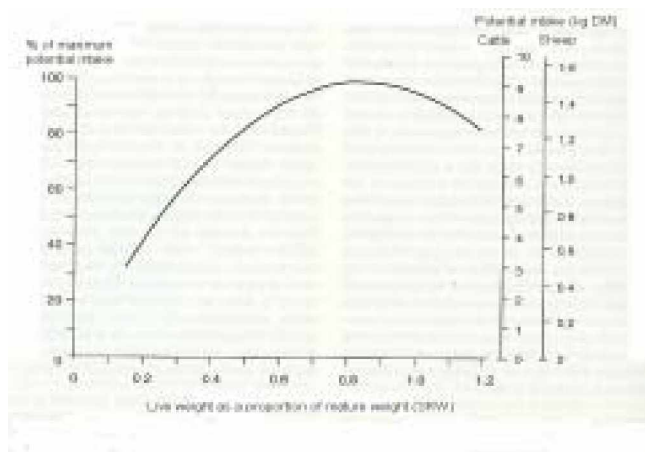


Figure 2. General relationship between the live weight of the animal, expressed as a percentage of the mature weight (SRW), and the potential intake, expressed as a percentage of the maximum possible for the animal: with, in the case of cattle a SRW of 500 kg and in the case of sheep, a SRW of 50 kg. Values of <1.0 on the X-axis indicate the degree of maturity of the growing animal; values of 1.0 or more indicate relative body condition of the mature animal.

especially, the reverse procedure is necessary: predict the quantity of pasture eaten and the yields of energy and protein and then, after allowing for maintenance requirements, determine the resulting production.

The scheme for predicting intake, applicable to housed animals eating long or chopped forages with some other feeds as well as to animals at pasture, relates the 'potential intake' (I_{max}) of an animal to its current liveweight expressed as a decimal fraction (Z) of its SRW (Figure 2). The potential intake of sheep and cattle of any given age and physiological state is defined as the quantity that would be eaten if there was abundant pasture herbage with a DM digestibility of at least 80% (≥ 11 MJ ME/kg DM). The right-hand scales in Figure 2 show the I_{max} values (kg DM/d) relative to Z for non-lactating cattle (C) and sheep (S) with SRW of 500 and 50 kg respectively.

It will be seen that intakes per unit W are predicted to be greatest when the animal is young and that with mature animals the potential intake declines with increasing body condition. For lactating animals I_{max} is multiplied by a factor that increases to a maximum value 4-5 weeks after parturition and then decreases. Allowance is also made for relatively low intake in unweaned young owing to incomplete development of rumen function; growing animals of less than normal weight for age recovering from a period of undernutrition; the effects on intake of ambient temperature which are adverse when it is persistently high but positive when it falls below an animal's lower critical temperature; and for an insufficient intake of rumen degraded protein (see page 620).

In practice, pasture conditions will generally not allow

achievement of I_{0max} . The predicted actual intake is the calculated I_{max} discounted according to (i) the extent that the herbage supply is less than abundant, abundance taken to be >1,500 kg DM/ha for sheep and >2,200 kg DM/ha for cattle, and (ii) the extent that digestibility (D) is <80%. It should be noted that the intake of pasture herbage varies directly with its digestibility over its whole range, though the relationship between these variables differs between tropical pasture species with their C_4 photosynthetic pathway (Hatch and Slack, 1970) and temperate (C_3) species. The C_4 grasses are commonly about 15 percentage units lower in D than C_3 at the same stage of maturity, but at the same D there is a greater voluntary intake of the C_4 . Allowance is also made for (i) the positive effect on pasture intake of the presence of legume, (ii) the spatial distribution of the herbage, indicated by mean pasture height, because an animal will have greater difficulty obtaining feed from a pasture providing, say, 500 kg DM/ha that is evenly distributed than if that feed is present as tall clumps among some bare ground and (iii) the consequences of strip or rapid rotational grazing on intake pattern owing to progressive reductions in herbage mass during a day's grazing.

To apply this scheme, as well as assigning an appropriate SRW to the animal, estimates are made of the amounts of green and dead herbage present on the pasture being grazed (kg DM/ha), the mean digestibility of both categories, the mean pasture height, and the proportion of legume. The computer program has default values for DMD and CP that can be over-ridden. It has been found that the skill of assessing herbage quantities and legume proportion can readily be acquired by farmers and their advisers (Bell and Allan, 2000).

To accommodate selective grazing the total herbage DM available is perceived as being present in six digestibility classes, with corresponding CP, the animal grazing first from the class of highest DMD and then the others in succession in an attempt to satisfy its potential intake. The reduction in intake that will occur when a supplement is given is allowed for by assuming that the animal will eat that feed before selecting herbage in a class of the same or lower digestibility. This substitution effect decreases as the quantity of herbage available decreases and animals have increasing difficulty in satisfying the appetite from pasture alone. The reduction in DM intake from a highly digestible pasture will nearly equal the DM in a similarly digestible supplement, but with the same supplement there will be a lesser reduction in the intake of a herbage of lower digestibility. If there is a nutrient inadequacy in a forage (e.g., N) the amount eaten will of course be increased by provision of an appropriate supplement.

As shown in Table 1, digestibility of the total intake is

Table 1. Predicted intake of feed (kg DM/d) by a Hereford steer 15 months old, 350 kg liveweight, from a pasture (25% legume) providing 1.4 tonnes DM/ha of green herbage with mean digestibility 71%, and 0.8 tonnes DM/ha of dead herbage with mean digestibility 45%; potential intake (I_{max} , see text) 10.2 kg DM/d

(a) Feed selected: quantities grazed from each of six digestibility classes comprising the total herbage available (see text) without and with the provision of 4 kg (air dry) of a supplement (75% digestibility)							
Digestibility class:	80	75	70	60	50	40	30
Pasture weight (t DM/ha)	0.48	-	0.63	0.37	0.30	0.29	0.12
Supplement (kg DM/d)		3.59					
Crude protein (%)	27	14	19	13	8	3	2
Intake (kg DM) Without supplement	5.38		2.71	0.55	0.20	0.09	0.00
With supplement	5.38	3.59	1.06	0.07	0.03	0.01	0.00
(b) Predicted quantities and qualities of pasture intake							
Supplement:	0 kg	4 kg					
Pasture intake (kg DM)*	8.93	6.55 (Total intake 10.14)					
Mean digestibility	75	78					
M/D (MJ ME/kg DM)	10.8	11.3					
Mean crude protein (%)	23	26					

* The intake of 4 kg supplement has resulted in a 2.38 kg reduction in pasture DM intake, a substitution rate of (2.38:3.59) = 66%.

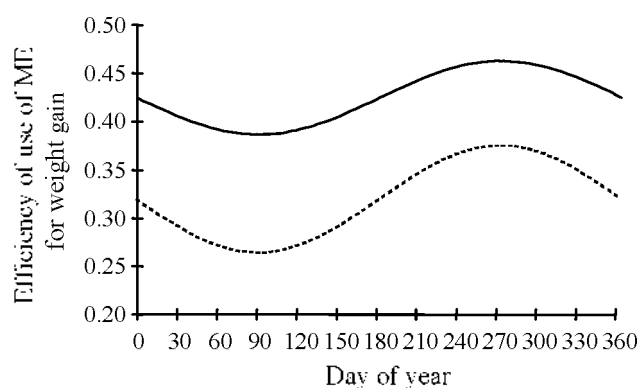


Figure 3. Predicted values, for pasture diets, for the efficiency of use of metabolizable energy (ME) for weight gain (k_g). The variation with time of year is for latitude 35° with day 1=January 1 (southern hemisphere) or =July 1 (northern hemisphere), its extent decreasing towards zero at the equator. Values for k_g are for a pasture diet containing 30% legume at ME concentrations (MJ/kg DM) of 11.0 (solid line) and 9.0 (broken line).

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the weighted mean of the amounts of the several digestibility classes eaten, and thence total ME intake is calculated as are total CP intake and its rumen degradability.

Efficiency of ME use: The efficiency values k_m and k_l are calculated with equations modified from ARC (1980):

$$k_m = 0.02M/D + 0.5 \quad (3)$$

$$k_l = 0.02M/D + 0.4 \quad (4)$$

Efficiency of ME use for pregnancy is taken to be 0.13 for all M/D. This low value reflects the fact that because of the method of estimation it is a gross and not a net

efficiency. All energy costs of gestation, including the growth and maintenance of uterine, mammary, and other tissues, the maintenance of the foetus, and any augmentation of maternal metabolism, are expressed as a function of gain by the conceptus only. Estimates of the net energy and protein needs for development of the conceptus are made by means similar to those of the ARC (1980).

Corbett et al. (1966) showed that the net energy value (NE_g) of an early season (spring) growth of temperate pasture herbage was significantly greater than that of a late (autumn) growth even though the two feeds were similar in digestibility. While the AFRC (1993) predicts that k_g for the early growth with ME/GE (q_m)=0.51 would be 0.40 and for the late growth (q_m =0.49) would be 0.39, the values actually measured were 0.435 and 0.325 respectively. This significant difference was ascribed to the substantially greater concentration of water-soluble carbohydrates (SCHO) in the early growth, 161 vs 90 g SCHO/kg DM, resulting in a higher proportion of propionate in the ruminal VFA, a reduced methane production and, as indicated by later work (Corbett and Pickering, 1983; Dove and Milne, 1994) a greater yield of microbial CP per MJ of fermentable energy. Herbage with an SCHO content that promotes these desirable outcomes might best be identified by an acetate:propionate ratio in the ruminal VFA of animals grazing the feed that is 3:1 or narrower (Corbett, 1987). This appears to be sustained for a longer time with leguminous than grass pastures (Freer and Jones, 1984). Seasonal variation in k_g has not been reported for tropical pastures, which reflects the differences in their chemical composition from temperate pastures. Relative to the temperate C_3 grasses the tropical C_4 species generally have lower SCHO and higher structural CHO contents which result in wider acetate:propionate ratios.

The equation used to predict k_g for fresh forages yields values that vary with the proportion of legume present, and

vary cyclically through the year but with an amplitude that decreases with latitude towards zero at the equator (Figure 3).

$$k_g = (0.3Le + 0.9) [0.053M/D - 0.154 + (\lambda/40)(0.154 - 0.01M/D \sin(0.0172 T))] \quad (5)$$

where: Le = The fractional contribution of legume to total forage DM.

λ = Latitude: positive if N, negative if S.

T = Day of year from January 1.

For all feeds other than fresh forages and milk diets (modified from MAFF, 1975):

$$k_g = 0.043M/D \quad (6)$$

For calves and lambs fed milk or milk replacer diets.

$$k_g = 0.7 \text{ (ARC, 1980).}$$

Requirement for maintenance: The nature of the energy expenditures in the maintenance 'support' metabolism and the variation in this overhead cost of production have been discussed by Corbett and Ball (2002) in a review primarily concerned with sheep nutrition but the information given is equally applicable to cattle. A major cause of variation is level of feed intake, an increase resulting in higher energy costs associated with increases in blood flow rate and oxygen consumption by organs, in ion pumping by the active transport system Na^+K^+ -ATPase, in protein synthesis and degradation, in substrate cycling, and in urea synthesis.

With calorimetry, NE_m is measured as the energy loss by the animal during a fast that follows a period of not less than three weeks during which it has been fed at the maintenance level ($L=1$). There is much evidence (Corbett and Ball, 2002) that if the pre-fast L has been >1 or <1 , then the FHP and determined NE_m are respectively increased and decreased. With the comparative slaughter (CS) technique, NE_m similarly is determined by measurements of the performance of the animals fed at $L=1$ and its value is similar to that obtained by calorimetry. However, the two techniques yield different k_g , those obtained by comparative slaughter being substantially lower (Figure 1). Graham (1982) suggested that because the response in the maintenance metabolism to change in feed intake is rather slow, an increase in L is not allowed time for full expression in calorimetric studies in which the amount of feed given to animals is usually changed at intervals of about three weeks. Consequently, when animals in those studies are fed at production levels they will tend to use a smaller fraction of their ME intake for maintenance and will have a greater amount of ME available for production, resulting in higher k_g , than when the same L is sustained over longer periods, as with CS. Values of calorimetric k_g are decreased with increasing L to avoid progressive overestimation of

predicted gain from a given ME intake (Figure 1: AFRC, 1993). There is evidence that this adjustment is not fully effective in eliminating this bias, and the consequent underestimation of the ME needed for a desired gain (e.g., AFRC, 1990). It does not reduce the k_g to the values from CS, which are not varied with L and have been obtained with animals kept in essentially practical conditions of management.

None of the feeding systems established in the UK, Europe, and North America vary the efficiency of use of ME for milk production (k_l) with L . All use fixed values for the maintenance requirement per unit W (NE_m , and ME_m for a given M/D).

The Australian system accepts that the maintenance metabolism increases with L expressed as total ME intake (MEI , MJ/d) or as the intake available for production (ME_p , MJ) above ME_m at $L=1$ and, as a corollary, neither k_g nor k_l is varied with level of feeding. An alternative view of these procedures is that their effect is equivalent to varying both k_g and k_l with L in association with a fixed NE_m .

To predict ME_m , SCA (1990) adopted the generalized equation of Corbett et al. (1987) derived from Graham et al. (1974) which is applicable to both sheep and cattle. When MEI is known, or predicted:

$$\text{ME}_m = [K S M (0.26W^{0.75} \exp(-0.03A))] / k_m + 0.09 \text{ MEI} + E_{\text{cold}} + E_{\text{graze}} / k_m \quad (7)$$

When used for ration formulation, with ME_p in place of MEI , the coefficient for $W^{0.75}$ changes:

$$\text{ME}_m = [K S M (0.28W^{0.75} \exp(-0.03A))] / k_m + 0.1 \text{ ME}_p + E_{\text{cold}} + E_{\text{graze}} / k_m \quad (8)$$

In these equations:

$K=1.0$ (sheep), or 1.2 (*Bos indicus*), or 1.4 (*B. taurus*), or 1.3 ($F1 B. indicus \times taurus$)

$S=1.0$ (females and castrates), or 1.15 (entire males)

M =Proportion of dietary energy from milk. Estimated as $[1+(0.26-Ba)]$. At pasture, $B=0.015$ for suckled lambs, or $B=0.01$ for suckled calves, assuming that age at weaning (a , weeks) is 17 or 26 respectively, when M takes its minimum value of 1.0.

W =Liveweight, kg.

A =Age, years, with a maximum value of 6.0, when the value of $[\exp(-0.03A)]$ is 0.84.

k_m =Net efficiency of use of ME for maintenance

MEI =Total ME intake, MJ/d

ME_p =ME MJ/d required for production

E_{cold} =Additional ME used in response to cold-stress. Full details for its calculation are given by SCA (1990) and by Freer et al. (1997)

E_{graze} = Additional energy expenditure incurred by animals at pasture compared with similar housed animals, as defined below.

The term $[K S M (0.28W^{0.75} \exp(-0.03A))]$ in equation 8 defines the net energy requirement for the maintenance of zero energy balance (NE_m). Its validity is demonstrated in SCA (1990) by the similarity between values predicted with this term and the "preferred values" of the ARC (1980); the effect of the adjustment for age (A) is consistent with the limited information available on the decrease in NE_m for cattle and sheep as they grow older. The term has an additional attribute: it allows the effective biomasses of widely varying types of animals to be compared on the objective, common, basis of their NE_m instead of by uncertainly based livestock units. For example, 10 female or castrate sheep six months old, each 36 kg W with $NE_m=4.83$ MJ, are nearly equivalent to one four-year old bull of 600 kg W ($NE_m=48.8$ MJ).

Estimates of the quantities of ME required by growing animals made with the use of equation 7 (SCA, 1990) are greater than those of the AFRC (1993) but are similar to those obtained from feeding experiments with animals in practical conditions. There is evidence that allowing for variation in the maintenance metabolism (equations 7 and 8) also results in more realistic values for the energy requirements of lactating cows than do the estimates made with the systems currently used in the UK, Europe, and North America. Agnew and Yan (2000) show that the ME_m defined by those systems are lower than those recently reported; the mean value from four studies with large numbers of cows was $0.63 \text{ MJ/kg}^{0.75}$. They discuss possible reasons for this difference. It might reflect improvements in genetic merit, a higher metabolic rate possibly being a consequence of an increased potential for milk production. When cows are grazing a failure to account properly for their energy expenditures at pasture, as discussed below, would result in underestimation of ME_m but virtually all the recent studies on maintenance were made with cows given rations of forages (hay, silage) plus concentrate feeds. An increase in the fibre content of diets may increase the work of rumination and digestion and the metabolic rate but it is improbable that the maximum fibre intake feasible in the feeding of high yielding dairy cows could account for the higher than expected maintenance requirements that have been observed. Agnew and Yan (2000) do not refer to the effect of level of feeding on the maintenance metabolism.

Kebreab et al. (2003) have made detailed analyses of energy balance data for 652 dairy cows. The ME_m yielded by the two mathematical models that gave best fit to the data were 0.62 and $0.64 \text{ MJ/kg}^{0.75}$. These values are similar to those discussed by Agnew and Yan (2000) and are substantially higher than that of the AFRC (1993) which,

including the recommended activity allowance, may be taken as $0.35 \text{ MJ NE/kg}^{0.75}$. With $k_m=0.73$, a value appropriate for diets of the quality (M/D) given to the cows in the recent studies, the AFRC value for ME_m is $0.48 \text{ MJ/kg}^{0.75}$. Agnew and Yan (2000) and Kebreab et al. (2003) do not specify the ME_m of non-lactating dairy cows. If, say, $0.63 \text{ MJ/kg}^{0.75}$ were adopted during lactation, perhaps the lower ME_m of the AFRC (1993) would be applied up to the time of parturition and then stepped up to the higher value which would be used throughout lactation until its end when ME_m would be stepped back down to $(0.35/k_m) \text{ MJ/kg}^{0.75}$.

In the Australian system the ME_m is variable with feed intake and, therefore, with production (milk yield, liveweight gain). It changes progressively with parturition, the development of lactation, and its decline. For a non-lactating dairy cow four years old the NE_m is 0.36 (equation 8), and ME_m is 0.49 at $k_m=0.73$. For 600 and 800 kg cows of the same age yielding respectively 80 and 160 MJ in milk their ME_m are respectively 0.59 and $0.66 \text{ MJ/kg}^{0.75}$ (yields equivalent to 25.8 and 51.6 kg 4% fat corrected milk; these and the W are similar to the mean and maximum values in the balance data of Kebreab et al., 2003). In the calculation of those ME_m no account was taken of contributions of body tissue energy to milk production. The GrazFeed program properly takes account of those contributions. The ME_m of a lactating 600 kg cow, for example, increases from $0.50 \text{ MJ/kg}^{0.75}$ when milk yield is 80 MJ/d to $0.61 \text{ MJ/kg}^{0.75}$ when the yield is 130 MJ.

Energy costs of grazing: Calorimetric measurements of the energy expenditures of freely grazing animals (e.g., Young and Corbett, 1972; Corbett et al., 1980, 1982) confirmed a number of estimates of E_{graze} that had been made by less direct means, including factorial estimates made by summation of the energy costs of the various activities at pasture. The measurements showed that, in the absence of cold stress, the value of ME_m at pasture would not be more than 40 to 50% greater than the ME_m for a similar housed animal, even in the most severe grazing conditions. In best conditions, with abundant and highly digestible pasturage, the difference might be as little as 10%.

Whether ME_m values for penned animals are derived from feeding trials or are determined as FMR/k_m , they allow for the energy costs of the various physical activities associated with the consumption of a maintenance feed intake. Consequently, in an assessment of E_{graze} the unit costs of various activities, such as eating (kJ/h per kg W) and walking (kJ/kg W per horizontal and vertical km) should not be applied to the total time spent on eating by the grazing animal nor to the total distance walked, etc.; account should be taken only of the extent to which the activities of grazing animals are greater than of those housed. No account need be taken of rumination because it

can be assumed that for any given amount and quality of feed the time and energy spent on this activity will be the same whether the feed is eaten from a trough or is grazed from pasture.

$$E_{\text{graze}} = \text{MJ net energy/d per kg } W = C[\text{DMI}(0.9-D)] + [0.05T/(\text{GF}+3)] \quad (9)$$

where: $C=0.02$ for sheep, or 0.0025 for cattle.

DMI = Dry matter intake, kg/d

D = Digestibility of the dry matter

T = A value varying with terrain from 1.0 for level ground to 2.0 for steep, hilly

GF = The quantity of green forage available, tonnes DM/ha

The first term predicts the additional cost of grazing the DMI rather than eating it from a trough: the values of the coefficient C , reduced from those in SCA (1990) on grounds that the variation in k_m allows for increasing costs of prehension and chewing as M/D decreases, implies that the relative rates of intake by sheep and cattle, kg DM/h, are 1:8 respectively. The second term predicts the additional costs, variable with terrain (T), of walking and other physical activities associated with grazing over distances up to about 7 km/d. These costs decrease as GF increases because with a decreasing need to search for feed the animals will walk correspondingly shorter distances. When there is very little GF in a larger mass of dry forage, animals are likely to abandon attempts at selection of the green material: in these circumstances, GF is replaced by the value for the total forage DM tonnes/ha.

Equation 9 has been adopted by the NRC (1996). The AFRC (1993) applies a range of fixed values for "activity allowances" which vary with type of animal and their management. They are based on assumed distances walked, time spent standing and number of position changes and their energy costs. For example the allowances for ewes grazing lowland and hill pastures are respectively 0.0107 and 0.024 MJ NE/kgW; these are not varied for other pasture conditions, such as the amount of herbage available. The AFRC (1993) makes no recommendation on an activity allowance for grazing dairy and beef cattle.

Composition of liveweight gain : The relative proportions of fat and protein in unit gain or loss of body tissue mass by an animal vary with its breed, sex, and current liveweight, and with the rate of gain or loss. Some schemes to predict the composition of gain, for example those of the ARC (1980) for sheep, take account only of W without reference to genotype, and can yield improbable values. For cattle the ARC (1980), as well as allowing for effects of sex and rate of gain, also recognize that the composition of gain at given W varies with genotype,

differing between 'small' (or 'early maturing'), 'medium', and 'large' (or 'late maturing') breeds. Difficulties in associating particular breeds with these discrete subdivisions of a variable are described by the AFRC (1990) as a major weakness of this approach. These difficulties are illustrated by their uncertainty on which of the three maturity classes applies to Friesian cattle; 'late' was assumed, but that would underestimate the energy requirement for gain by 30% if, as the AFRC (1990, 1993) suggest, a more appropriate classification is 'early'. Animals within a breed could so differ in genotype as to be classified variously as early, medium, and late maturity types. Aberdeen Angus, for example, are classified by the AFRC (1990) as 'early', but selective breeding in the USA has resulted in animals that would be better classed as 'medium', or even as 'large/late maturing'.

The equations of the SCA (1990) to predict the composition of gain are applicable to both sheep and cattle; they allow for variation in genotype between and within breed, and for sex type, liveweight (i.e., stage of growth), and rate of gain. This versatility is achieved by relating composition to Z , the current W as a decimal fraction of a Standard Reference Liveweight (SRW) appropriate for each type of animal: the value of Z , as noted earlier, indicates its stage of growth. As with I_{max} used in the prediction of intake, provision is made for a less than normal weight for age caused by a period of undernutrition. Within a breed the value of an assigned SRW is less for a female than for a castrate and greatest for an entire male; between breeds it is, for example, less for a Jersey cow than a Holstein, for a Hereford steer than a Charolais, and for a Southdown than a Border Leicester sheep. Consequently, at a given liveweight, the predicted fat and energy contents of unit gain will be greater and the protein content less for the female than for, in order, the castrate and the entire male. Also at a given liveweight, predicted fat and energy will be greater and protein less for the Hereford than the Charolais and for sheep with lower compared with higher SRW. The validity of assigned SRW can be confirmed by experiment. If, for example, fat and energy values determined directly were less than predicted, and protein greater, then the SRW for the particular type of animal would be increased to a value where prediction agreed with observation.

The equations are applicable to both cattle and sheep. It was concluded by Searle et al. (1972), and confirmed by Blaxter et al. (1982), that for any particular type of animal at a given W the composition of a loss in bodyweight is similar to the composition of a gain. The equations may therefore be used to predict losses of protein, fat and energy from the body during inanition. It is known that there is generally a greater proportion of protein in gain by a number of European breeds of cattle (*Eur.* e.g., Charolais, Simmental, Limousin, Chianina, Saler, Maine Anjou,

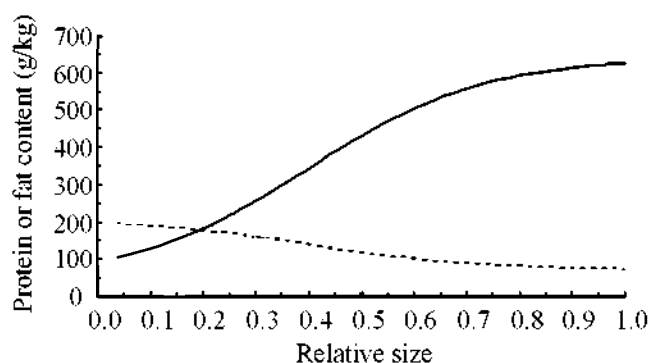


Figure 4. Protein and fat content of empty weight gain in sheep and 'standard' cattle types, at a feeding level of twice maintenance, in relation to the weight of the immature animal as a fraction of its mature weight (SRW); fat, solid line; protein, broken line. At any given relative size the predicted protein and fat in gains by some European cattle (*Eur*; see text) are respectively higher and lower than those shown here

Blonde d'Aquitane) than in gain by most British and other breeds of cattle, including *B. indicus*, though *Eur* probably includes the South Devon breed. It was found that this difference was best allowed for by an adjustment of one coefficient in each equation.

$$\text{Protein g/kg EBG} = (212 - 4R) - (A - 4R) / [1 + \exp(-6(Z - 0.4))] \quad (10)$$

$$\text{Fat g/kg EBG} = (43 + 28R) + (B - 28R) / [1 + \exp(-6(Z - 0.4))] \quad (11)$$

where: EBG=Empty body gain (or loss), taken to be 0.92 of change in liveweight

Z=Current W/SRW

A=120 if *Eur* (see above), or 140 for other cattle and all breeds of sheep

B=490 (*Eur*), otherwise 601

R=Adjustment for rate of gain or loss

When EBG is known, then: $R = [(EBG \text{ g/d}) / (4 \text{ SRW}^{0.75})] - 1$

When MEI is known and gain or loss is to be predicted,

then: $R = 2[(NE_g / NE_m) - 1]$

where: NE_m =net energy requirement for maintenance (equation 7)

NE_g =net energy available for gain, which is $[k_g(\text{MEI} - \text{ME}_m)]$; or for intakes less than maintenance, and with 0.8 efficiency of use of energy from body tissue, it is the NE loss which is $[1.25(k_m(\text{ME}_m - \text{MEI}))]$

The equations to predict the gross energy of protein and fat deposited (or catabolised) and total gross energy gain or

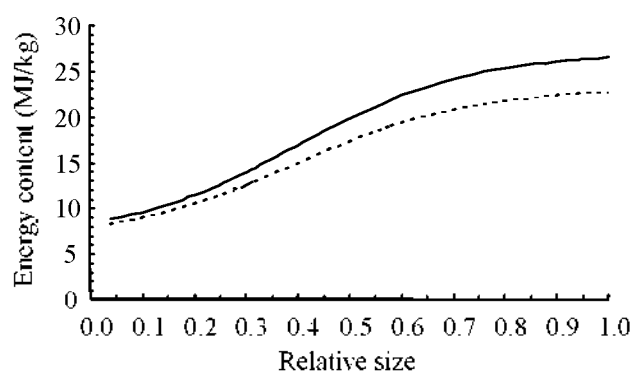


Figure 5. Energy content of empty weight gain at a feeding level of twice maintenance, in relation to the weight of the immature animal as a fraction of its mature weight (SRW); upper line for sheep and standard cattle; lower line for *Eur* cattle.

loss are:

$$\text{Protein (MJ/kg EBG)} = (5.0 - 0.1R) - (C - 0.1R) / [1 + \exp(-6(Z - 0.4))] \quad (12)$$

$$\text{Fat (MJ/kg EBG)} = (1.7 + 1.1R) + (D - 1.1R) / [1 + \exp(-6(Z - 0.4))] \quad (13)$$

$$\text{Total energy (MJ/kg EBG)} = (6.7 + R) + (E - R) / [1 + \exp(-6(Z - 0.4))] \quad (14)$$

where: C = 2.8 if *Eur*, otherwise 3.3.

D = 19.3 if *Eur*, otherwise 23.6

E = 16.5 if *Eur*, otherwise 20.3

It will be seen that the equation for total energy (14) is the sum of those for protein and fat (12 and 13).

Changes with Z in the predicted proportions of protein and fat in gain are shown in Figure 4 and in energy content in Figure 5. It will be seen that the proportion of protein in gain is greatest in young animals; it decreases with age while the proportion of fat and the gross energy content both increase. Fat proportion and energy content also increase with increasing rate of gain.

The above equations apply to growing animals; in mature animals the composition of empty body weight change varies with the animal's body condition and is calculated from equations (15) and (16), derived from Wright and Russel (1984).

$$\text{Total energy (MJ/kg EBG)} = C + 13.8 Z \quad (15)$$

$$\text{Protein (g/kg EBG)} = D - 115 Z \quad (16)$$

where: C=9.4 if *Eur*, otherwise 13.2

D=207 if *Eur*, otherwise 187

EARLY PROTEIN FEEDING SYSTEMS

Kellner and Arnsby were mainly concerned with the energy of feeds and its use, but recognized the animal's need for protein. As Wolff had done, they expressed requirements in terms of digestible true protein (DTP). In the USA, as discussed by Morrison in 'Feeds and Feeding', non-protein nitrogen (NPN) was regarded as having the same nutritional value for ruminants as protein and digestible crude protein (DCP) was used; the UK used the compromise $(DTP + DCP)/2$ which was termed the 'protein equivalent' (PE). In both countries, attention was paid to the 'nutritive ratio', a comparison of the energy value of a feed with its protein content, calculated as $(2.3DEE + DNFE + DCF)$ divided by DCP (or by PE).

With increasing understanding of digestion in the ruminant developing from the mid 1800s, it was increasingly realized that the protein value of feeds and animal requirements could not be defined adequately simply by reference to the quantities of protein and NPN in the diet. By the mid-20th century, the work of Virtanen (1966), for example, had highlighted the role of the rumen microbiota in the protein nutrition of ruminants. He showed that cows could yield more than 4000 kg milk over a lactation although they were given a diet throughout that time which contained no protein, and only urea and ammonium salts as N sources.

PRESENT PROTEIN FEEDING SYSTEMS

McDonald (1950) wrote "The activities of the microbes in the rumen may lead, depending on the dietary conditions, to either a net gain or loss of nitrogen to the host animal", and that:

"Some of the chief aspects for further study of the digestion of protein by ruminants are:

- (i) The extent of degradation of proteins in the rumen to nitrogenous substances which are not available to the host, and the extent to which these, and similar substances in the food, can be used by the microbes for their growth.
- (ii) The influence of non-nitrogenous substances, e.g. carbohydrates, on the growth of microbes in the rumen.
- (iii) The relative proportions of protein N and non-protein N, especially nucleic acid, in the bodies of the microbes.
- (iv) The distribution of amino acids in the microbial proteins.
- (v) The digestibility of the proteins of the microbes.
- (vi) The relative proportions of unchanged food protein- and microbial protein in the digesta received by the true stomach (the abomasum)."

McDonald (1954, and pers. comm.) developed a method

for the determination of purines expressly for the estimation of microbial protein synthesis in the rumen.

The six "aspects" set out most of the considerations involved in modern systems for defining the protein value of feeds and requirements of ruminants. All those systems differ mainly in matters of detail which have been reviewed by the AFRC (1992); some will be referred to in the description of the Australian system.

The Australian system

The protein supply to the animal is termed the truly digestible protein leaving the stomach (DPLS: similar to the 'metabolizable protein', MP, of the AFRC, 1993) and which passes through the pylorus to the small intestine. The amino acids absorbed there are from (i) digestible undegraded dietary protein (DUDP), and (ii) the digestible true protein (DTP) in the microbial crude protein (MCP). The MCP has been synthesized by the microorganisms during their growth in the rumen where the N has been provided by rumen degraded protein (RDP); it may be augmented by N recycled to the rumen when the supply of RDP from the diet is insufficient to support the microbial growth that would be supported by the available energy. That potential MCP yield is the RDP requirement. If that requirement (RDPR) is not met by the intake (RDPI) then in the prediction of feed intake the value of I_{max} , the potential intake, is reduced by the factor $RDPI/RDPR$.

Rumen degradable protein : With stored and prepared feeds, including silage but excluding fresh forages and hays, the methods for estimating the degradability (dg) at various L of their crude protein (CP), and the yields of RDP and undegraded dietary protein (UDP), are as described by the AFRC (1992).

With young and highly digestible growths of pasture herbage, measured dg are often 0.8 or greater and the principal cause of lower values is plant maturation, manifest as increasing structural carbohydrate.

Microbial Crude Protein (MCP) : Capture of the N from RDP in MCP is assumed to be complete. The yield of MCP is related to the energy supply; the AFRC (1992) noted that some dietary components which contribute to ME for the animal do not contribute to energy supplies for rumen microbes and defined Fermentable ME (FME) as $[ME_{fat} - ME_{ferm}]$, where ME_{ferm} is the energy in the organic acids present in ensiled feeds. This approach has been adopted, but with the important modification that the energy content of undegraded dietary protein is also deducted from ME.

As with the prediction of k_g , the equation to predict MCP, g/MJ ME, from forage allows for variation with season, with modification for latitude (Figure 6). The adjustment for variation in L is from the AFRC (1992) but modified to allow for the effect of the seasonal adjustment.

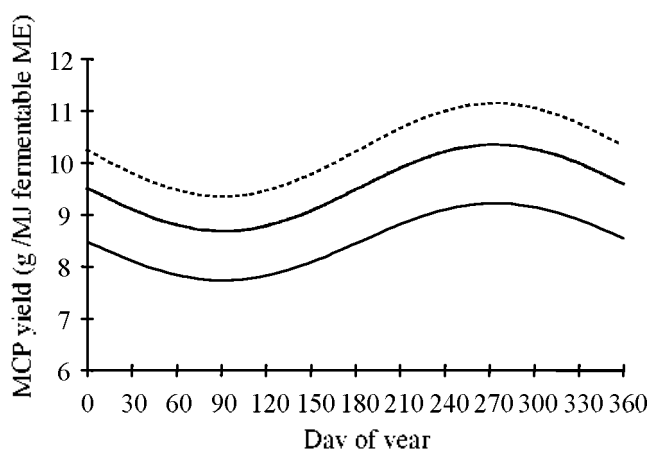


Figure 6. Predicted values, for pasture diets, for the efficiency of use of metabolizable energy (ME) for rumen microbial protein production (MCP, g/MJ fermentable ME). The variation with time of year is for latitude 35° with day 1=January 1 (southern hemisphere) or =July 1 (northern hemisphere), its extent decreasing towards zero at the equator. Values show the effect of feeding level relative to maintenance ($L=1$). Bottom line, $L=1$; middle, $L=2$; top, $L=3$. 'Elsevier' acknowledgment, as with fig 3. * Reprinted from Freer et al. (1997) with permission from Elsevier Science.

The MCP yield from the FME of supplementary feed is varied only with L .

$$\text{MCP g/MJME} = \text{VL}[\text{FME}_f(1+0.1\lambda/40\sin(2\pi T/365))+\text{FME}_s] \quad (17)$$

where: VL=Effect of variation in feeding level

$$= [0.7+0.5(1-\exp(-0.35L))]$$

FME_f =Fermentable ME from forage.

FME_s =Fermentable ME from supplementary feed.

λ =Latitude: positive if N, negative if S.

T=Day of year from January 1.

Digestible protein leaving the stomach (DPLS) :

Because the estimates of protein requirements allow for an endogenous faecal loss, the proportion of the protein entering the small intestine that is absorbed is properly described by its true digestibility.

The true digestibility of UDP in forages is estimated with a modification of an equation of Webster et al. (1982) and has a maximum value of 0.85 which is reached when forage CP is 187 g/kg DM or greater:

$$\text{DUDP}_f/\text{UDP}_f = (0.55 \text{ CP} - 17.8)/100 \quad (18)$$

For concentrate supplements, DUDP_s is calculated from its acid detergent insoluble protein (ADIP_s , g/g DM) with an equation based on Waters et al. (1992):

$$\text{DUDP}_s/\text{UDP}_s = 0.9[1 - (\text{ADIP}_s/\text{UDP}_s)] \quad (19)$$

There have been a number of estimates of the proportion of MCP that is microbial true protein (MTP) in the range of 0.7-0.8 with MTP true digestibilities of 0.8-0.9 (AFRC, 1992). An alternative approach from Russell et al. (1992) has been adopted: it is assumed that digestible true protein is 0.6 of MCP, and of the remainder 0.25 is microbial cell wall excreted in the faeces and 0.15 is nucleic acids, the N of those being excreted mainly in urine.

Efficiency of use of DPLS : In the absence of a well-founded basis for differentiating between the main productive functions, SCA (1990) adopted 0.7 as the efficiency of use of DPLS for growth, gestation and milk production and 0.6 as the efficiency of use for wool production. These factors contrast with the values of 0.59, 0.85, 0.68 and 0.26, respectively, adopted by AFRC (1993). The low value of 0.26 for the net efficiency of wool synthesis tallies with the mean estimate of 0.116 for the gross efficiency of conversion in Merino sheep (Hogan et al., 1979), the appropriate value for estimating wool synthesis (see below). However, it is not appropriate for the factorial estimation of total DPLS requirements because the circulating DPLS that remains after wool synthesis (and the selective removal of sulphur-rich amino acids at the follicle) is still of relatively high value for other productive purposes.

Animal requirement for maintenance: The AFRC (1993) adopted from ARC (1984) a single value for the endogenous N in faeces and urine termed the 'basal endogenous nitrogen' (BEN) loss; its value is 0.35 g $\text{kgW}^{0.75}$. This was derived from animals maintained wholly by intragastric infusion of nutrients (Ørskov et al., 1979); their N loss was wholly in urine, there being no voiding of faeces. It was stated by the ARC (1984) that BEN is applicable "at a maintenance level of metabolizable energy intake" but it is applied by the AFRC (1993) at all L and is taken to encompass any endogenous N loss in faeces by normally fed animals. By implication, any increase in a faecal loss with increasing L is matched by a corresponding reduction in the urinary endogenous loss. This method for assessing endogenous N losses was not adopted by the SCA (1990); reasons included uncertainty that BEN was applicable to normally fed animals because it was measured with animals that did not have a normally functioning rumen.

In the approach of Russell et al. (1992), endogenous faecal protein (EFP) includes enzymes and sloughed cell residues but not the indigestible fraction of MCP, which is included in the normal calculation of faecal protein. In this system, which has been adopted here, EFP is estimated as:

$$\text{EFP (g)} = 0.0387 \text{ CPI}_s(1 - \phi_{\text{milk}}) + \text{D MEI}_{\text{milk}} \phi_{\text{milk}} \quad (20)$$

where: CPI_s =intake of crude protein (g)

$$\begin{aligned} \text{MEI}_{\text{milk}} &= \text{ME intake from milk (MJ)} \\ \phi_{\text{milk}} &= \text{MEI}_{\text{milk}} \text{ as a fraction of total dietary ME} \\ D &= 0.46 \text{ for sheep and } 0.526 \text{ for cattle} \end{aligned}$$

Animals on N-free diets continue to lose N in urine mostly as urea resulting from catabolism of amino acids during protein turnover. This loss, expressed as endogenous urinary protein (EUP), is estimated by means developed from ARC (1980):

$$\text{EUP (g)} = 0.147 W + 3.375 \quad \text{for sheep} \quad (21)$$

$$\text{EUP (g)} = C \ln(W) - D \quad \text{for cattle} \quad (22)$$

where: $C = 16.1$ for *B.taurus* and 12.9 for *B.indicus*
 $D = 42.2$ for *B.taurus* and 33.8 for *B.indicus*

The dermal loss of protein (DP) from cattle in shed hair and scurf (from ARC, 1980) is estimated as $0.11 \text{ g/kg } W^{0.75}$. For sheep, the protein requirement for wool growth encompasses DP.

Requirements for reproduction, milk, and growth: The net protein requirement for pregnancy is the rate of protein accretion in the products of conception which is estimated by means similar to those of the ARC (1980). The net requirement for milk is its protein ($N \times 6.38$) content. Equation (10), above, predicts the protein requirements for growth.

Requirement for wool: It is appropriate to discuss the production of wool in the section on protein, though of course the synthesis of wool protein does have an energy cost.

Daily growth of clean wool (which is entirely protein) is predicted (equation 21) either from the DPLS available for wool production (i.e., after deduction of the needs for gestation and milk production) or from the ME similarly available for wool production, whichever is limiting. For an average Merino sheep (one in which the average greasy fleece weight, SFW, is about 0.1 of the SRW), Hogan et al. (1979) estimated a mean gross efficiency of 0.116 for the conversion of DPLS to wool. This sets a limit to wool synthesis until the ratio $\text{DPLS}_w : \text{ME}_w$ (g/MJ) reaches 12.0 (Kempton, 1979), at which point the limit is set by $0.116 \times 12 \text{ ME}_w$, i.e. 1.4 ME_w . The ratio SFW:SRW is used to scale the function for all other types of sheep.

$$\text{Wool growth (g)} = \text{MIN}(1.16 \text{ DPLS}_w, 1.4 \text{ ME}_w) \text{ FW/SRW} \quad (21)$$

where: DPLS_w and ME_w are the DPLS and ME, respectively, available for wool growth.

Adjustments are made to this estimate for young sheep in which the secondary follicles have not matured and for

genotypic differences in the effect of photoperiod on wool growth.

CONCLUSION

There is rather little variation in the amino acid composition of the microbial and dietary protein that enters the small intestine of ruminants unless the supply of a particular amino acid, such as methionine, has been increased because it, or a protein with a high content, have been protected from degradation in the rumen by chemical or physical processing. The characterization of a feed by its ME content or NE value, however, is a representation of a wide and varying array of nutrients, including protein. The variation in the energy value of feeds for the animal with that variation in nutrient supplies is allowed for in feeding systems by relating efficiencies of energy use to feed digestibility or metabolizability (M/D), and with fresh pasture herbage (in the Australian system) to season of growth. Detailed knowledge of the amounts and chemical nature of the products of digestion would allow definition of the utilization of energy and protein of animals, and their requirements, in terms more directly related to the biology of the processes involved in growth and reproduction. There is progress towards the practical use of such an approach for non-ruminants, for example in the feeding of pigs (Black et al., 1986; Whittemore et al., 2001). A similar approach for ruminants (e.g., Gill et al., 1984) might be adopted if detailed definitions of the outcomes of digestion in the rumen could be assured. Dijkstra et al. (1992) and Nagorcka et al. (2000) have developed models of fermentation in the rumen that predict the amounts of the various products that result and (Dijkstra et al., 1992) predict the rates of digestion of feed components. Rate of feed breakdown determines rate of digesta flow from the reticulorumen and so is importantly related to voluntary feed intake, but in current systems for predicting intake it is represented by the digestibility. The models of fermentation, however, require much more information on the chemical composition of feeds than is generally available or readily obtained, especially for grazed herbage.

More accurate and rapid feed analysis was one of the requirements for improvement in feeding systems identified by Blaxter (1989). This remains an important objective, particularly for defining herbage qualities and to facilitate better predictions of intakes of different plant species. Another requirement (Blaxter, 1989) was better estimation of the composition of body gains. With the use of the method illustrated in Figures 4 and 5 the estimation is less of a problem with steadily growing animals than it is with those losing and regaining weight, a common occurrence particularly in pastoral production. This problem is especially acute with lactating animals. In this connection,

much more knowledge is required on the partition of nutrients between competing needs, particularly in conditions of sub-optimal nutrition.

Feeding systems should not be seen as dictating inflexibly what an animal ought to be fed. They should be seen as a means of defining, in quantitative and therefore monetary terms, the responses of animals to their feed supplies and how changes in the supplies will affect their performance. Responses as presently defined are for what can be called the 'average' animal. With increasing knowledge of the nature and control of the responses it can be expected that there will increasingly be specificity in their definition for animals differing in genotype both within and between species.

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