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Evaluation of the Energy Value of Feeds for Ruminants

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Evaluation of the Energy Value of Feeds for Ruminants

Proceedings from a Minisymposium at the XIX'th NJF Congress, Uppsala, Sweden, 17-20 June 1991

Editor Frik Sundstøl

Norwegian Agricultural Advisory Service
Ås, Norway

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1 Preface

FRIK SUNDSTØL
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Over the years, several attempts have been made to reach an agreement on one common feed evaluation system for the Nordic countries, but until now they have all been unsuccessful (see Nordisk Jordbruksforskning 1951 (4), 562-568).

Since A.J.H. van Es described the Dutch net energy lactation (NEL) system in 1975 and 1978, this system, or a similar one, has been introduced in many European countries including:

The Netherlands	(1977)
France	(1978)
Switzerland	(1979)
Federal Republic of Germany	(1982)
Austria	(1982)
Yugoslavia	(1984)
Italy	(1986)
Greece	(?)

In Finland NEL was included in the feed table from 1982, and in Norway a change from the FFU to the NEL system was discussed.

On 3 July 1987, at a board meeting of Section V of NJF (Nordic Association of Agricultural Scientists), a working group was appointed with the mandate (translated from the Danish): To assess the present systems in various countries, and to prepare a proposal and a project application for research needed to work out a common Nordic system.

Members of the working group were: Verner Friis Kristensen, Denmark, Frik Sundstøl, Norway, Erik Lindgren, Sweden, Mikko Tuori, Finland, Gunnar Gudmundsson, Iceland (contact person).

The working group found the task very demanding, and at its first meeting (Sweden 8 December 1987) it was decided: 1) to increase membership of the group by one representative from each country, and 2) to apply to the Nordisk Ministerråd for funds to continue the work.

These proposals were carried in agreement with the chairman of Section V, NJF. Financial support was granted by the Nordisk Ministerråd in late 1988 for continuation of the work. Gunnar Gudmundsson, the Icelandic contact person, was replaced by Olafur Gudmundsson, who became a full member of the group, and the actual work started in January 1989, with the following members:

Denmark: Verner Friis Kristensen

	Martin Riis Weisbjerg
Finland:	Mikko Tuori
	Pekka Huhtanen
Iceland:	Olafur Gudmundsson
Norway:	Frik Sundstøl (Chairman)
	Lars Bævre
Sweden:	Erik Lindgren
	Rolf Spørndly

Erling Thuen (Norway) was appointed secretary.

In addition, Jan Berg (Norway) has taken part in some of the work as a consultant, and other scientists have attended the meetings (7) in the various countries.

The working group found it appropriate to organize a mini-symposium highlighting some of the themes that are of greatest importance in a discussion of future feed evaluation systems.

Calculations have been carried out to find which energy evaluation system best explains variations in milk yields in dairy cow experiments and daily gain in growing animals (Paper 2). In the case of grazing animals (Paper 3) specific factors have to be taken into consideration. Associative effects have always puzzled animal nutritionists and deserve particular attention (Paper 4). Also of fundamental importance is the discussion of current and future feed analyses (Paper 5). The working group spent a considerable amount of time discussing a new approach to feed evaluation, i.e. a "substrate-based system" (Papers 6 and 7). Any change from a feed evaluation system that may have been used for generations also has some practical implications (Paper 8). For the conclusions and recommendations from the working group the reader is referred to Paper 9.

The chairman takes this opportunity to thank NJF for the initiative in establishing the working group. This work would not have been possible without the financial support of the Nordisk Ministerråd, and this is greatly appreciated. Thanks are also extended to all Nordic colleagues in the working group for their good cooperation and many valuable contributions and constructive discussions.

2 A comparison between some feed energy systems based on Nordic production experiments in cattle

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Berg J. & E.Thuen. 1991. Feed energy evaluation systems for ruminants. Norwegian Journal of Agricuktural Sciences, Supplement No. 5: 7-15. ISSN 0801-5341.

On the basis of results from 39 production experiments with dairy cows and 11 experiments with heifers and bulls conducted in the Nordic countries, four energy evaluation systems are compared; metabolizable energy used in Sweden (MES), fattening feed unit used in Finland, Iceland and Norway (FFU), Scandinavian feed unit used in Denmark (SFU) and the feed unit for milk production (VEM) and for growth and fattening (VEVI) used in the Netherlands. The dairy cow experiments included both individual observations and treatment means, while in the growth experiments only the SFU and Dutch systems were tested on the basis of individual observations. To compare the four systems the following parameters were calculated: (a) Predicted milk yield or daily gain and the standard error of prediction (SEP), (b) energy as a proportion of requirement (RAT) and the standard error and coefficient of variation of RAT. The results of the dairy cow experiments showed that the SFU and VEM systems gave a somewhat higher precision for all the parameters calculated than the MES and FFU systems. Between SFU and VEM, and MES and FFU there were only minor differences. The MES and FFU systems resulted in an overestimation of the production potential of the diet, which clearly shows that the energy content of feed should be corrected for feeding level as in the SFU and VEM systems. In the growth experiments only minor differences were observed between the SFU and VEM systems for all parameters calculated.

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The main objective of a feed energy system is to evaluate the relative energy value of feed correctly in different productions. This criterion is difficult to fulfil and has led to the development and employment of several energy systems throughout the world.

In the Nordic countries different systems are used to evaluate the energy value of feeds for ruminants; metabolizable energy in Sweden (MES), net energy fattening expressed as fattening feed unit (FFU) in Norway, Finland and Iceland and Scandinavian feed unit (SFU) in Denmark.

Numerous experiments with ruminants have shown that the content of both metabolizable and net energy in the feed varies with type of production and energy concentration.

The content of metabolizable energy (ME) in feeds does not account for the utilization of ME and results in an overestimation of roughage relative to concentrate in all productions. Net energy fattening, on the other hand, expresses the productive value of feeds for fattening and results in an underestimation of the energy value of roughage compared to that of concentrate when used for maintenance and milk production.

During the seventies in the Netherlands energy systems were developed to evaluate the net energy value of feeds for milk production and growth/fattening separately (Van Es 1975, 1978). The two systems were based on metabolizable energy and the utilization of metabolizable energy for milk production (VEM) and for growth/fattening (VEVI). Theoretically the systems should give a correct evaluation of the relative energy value between feeds in the two main productions by ruminants. Similar systems are now in common use in many European countries.

In order to judge their fitness, the different energy systems should be compared in production trials. The response of the feeds in terms of milk or growth should ideally be in accordance with their estimated energy values. An important precondition in such comparisons is that the experiments selected vary widely in ration composition, i.e. energy concentration, because most of the current energy evaluation systems for ruminants work quite well when the energy concentration (q) is about 60, which is normally found in rations for dairy cattle.

An important problem in the comparison of energy systems from production experiment data is live-weight changes both with respect to the composition and energy value of changes in live weight.

In the paper MES, FFU, SFU, VEM and VEVI are compared on the basis of results from several production trials with dairy cows and growing heifers and bulls conducted in the Nordic countries over recent decades.

MATERIALS AND METHODS

The experiments used in the comparisons are listed in Table 1. The milk production data include 127 treatment means from 39 dairy cow experiments with a total of 1397 cows, and 753 individual observations from 16 of the experiments.

Eight of the dairy experiments involved a comparison of hay and grass silage harvested at the same or at different stages of maturity (Presthegge 1959; Bertilsson 1983). The effects of cutting time of grass silage and feeding level on performance were studied in five experiments (Bergheim 1979; Kristensen 1989), and in another five the grass silages made from two grass species were compared (Mo 1975; Hole 1985). Two levels of concentrate during lactation were investigated in 12 experiments (Ekern 1972; Berg 1988; Svendsen et al. 1990). Aaes (1990) conducted four experiments where the ratio of roughage to concentrate varied from 18/82 to 66/34 in complete rations fed *ad libitum*. In the five experiments of Heikkilä et al. (1988) barley and oats were compared as the only concentrate in rations based on grass silage *ad libitum* and some hay.

The growth data comprise 375 individual observations from 11 experiments. In the two experiments of Strudsholm et al. (1985) heifers were given *ad libitum* or minimum quantities of barley straw supplied with concentrate. Daily energy intake was similar in all

Table 1. Nordic experiments included in the comparisons.

References	Country	No. of experiment	Data used Treatment means	Individual observations
A. <u>Milk production experiments</u>				
Presthegge 1959	Norway	5	16	-
Ekern 1972	"	3	6	-
Mo 1975	"	2	4	-
Bergheim 1979	"	2	8	-
Hole 1985	"	3	6	-
Berg 1988	"	3	12	72
Svendsen et al. 1990	"	6	12	353
Heikkilä et al. 1988	Finland	3	10	-
Aaes 1990	Denmark	4	19	169
Kristensen 1989	"	3	27	159
Bertilsson 1983	Sweden	3	7	
Total			127	753
B. <u>Growth experiments</u>				
Andersen & Andersen 1981	Denmark	2		97
Strudsholm et al. 1982	"	2		97
Andersen & Ingvartsen 1983	"	4		87
Strudsholm et al 1985	"	1		27
Foldager et al 1988	"	2		67
Total				375

treatments. Foldager et al. (1988) carried out two experiments where four rations with different proportions of roughage to concentrates on an SFU basis were fed *ad libitum* to heifers. Andersen & Andersen (1981), Strudsholm et al. (1982) and Andersen & Ingvartsen (1983) carried out altogether six experiments with bulls, where the concentrate fed varied from 25 to 100% *ad libitum* in rations of different amounts and quality of roughage.

The calculations from the milk production experiments are based on average daily feed intake, live weight (LW), live-weight change (LWC)) and milk production during the experimental period per treatment group or per cow. In the growth experiments only individual observations, where average daily gain at a given live weight or during the whole experimental period, were used.

The intake of energy in MES, FFU, SFU, VEM and VEVI and the requirements were all calculated according to the description of European energy systems given by van der Honing & Alderman (1988).

To compare the different energy systems the following parameters were calculated:

(a) Predicted milk yield or daily gain
(b) Standard error of prediction (SEP)
(c) Energy supply as a proportion of the requirements (RAT) and the standard deviation and coefficient of variation of RAT i.e., SD (RAT) and CV (RAT).

Predicted milk yield was calculated as the energy intake above maintenance corrected for daily live-weight change divided by the energy requirement of 1 kg energy-corrected milk (ECM) within each system.

In the growth experiments equations to predict daily gain at a given live weight at different feed intakes were only available in the SFU and Dutch systems. Predicted daily gain (PDG) of growing heifers was calculated in the SFU system according to Foldager et al. (1988):

$$PDG = 3079\ E^{0.28} - 258\ .\ E^{0.28}\ .\ Ln(LW) - 1738$$

where E = SFU per day
LW = live weight (kg)

PDG of bulls in the SFU system was found by using the following equation (Ingvartsen pers. comm.):

$$PDG = 2.17e^{(0,00256\ LW)}/E \cdot \left[1 - (1.62 - 0.579\ I + 6.13 \cdot 10^{-4}\ I^2 - 1.96 \cdot 10^{-6} \cdot I^3)\right]$$

where E = SFU per day
LW = live weight (kg)
I = feeding level

According to van Es (pers. comm.), the equations for growing cattle in the VEM (heifers) or VEVI (bulls) system are somewhat lacking in precision. Young cattle, and especially bulls, do not like being in respiration chambers and having to wear equipment for collecting excreta. However, the requirement tables for heifers and bulls (van Es 1978) have taken into account the results of several feeding trials. Therefore, to predict PDG of heifers and bulls in the Dutch system, calculated feed intake has been compared with these tables.

Standard deviation of predicted milk yield or daily gain was calculated according to the equation:

$$SEP = 1/n\text{-}1\sqrt{\Sigma\ (x_i - x_i)^2}$$

where n = number of observations
x_i = observed milk yield or gain
x_i = predicted milk yield or gain

RESULTS AND DISCUSSION

In all systems, both for treatment means and individual data, predicted milk yield and the actual energy supply were quite close to the observed milk yield and calculated requirement, respectively (Tables 2-3). In the SFU and VEM systems there was almost no difference between the predicted and the observed milk yields. On the other hand, the MES and FFU systems gave a somewhat higher predicted yield than observed milk yield, indicating an overestimation of the production potential of the diet, reflected in a high RAT value, above

100. The standard error of prediction (SEP) for milk is clearly higher for the MES and FFU systems than for both the SFU and the VEM systems. For standard deviation and coefficient of variation of RAT the variation was somewhat higher in the FFU system compared with the other systems.

Similar calculations came out in Finland (Huhtanen 1990) showed the best fit for net energy fat (NEF) according to the Rostock system (Schiemann et al. 1971). This comparison was based on 10 Finnish feeding trials where different concentrate supplements were given together with grass silage *ad libitum*.

Table 2. Individual data for cows. Observed and predicted milk yield. Standard error of prediction (SEP), energy supply as a proportion (%) of requirement (RAT) with standard deviation (SD (RAT)) and coefficient of variation (CV(RAT))

	Energy evaluation system			
	MES	SFU	FFU	VEM
No. of animals	753	753	753	753
Observed daily mean milk yield(ECM)	20.8	20.8	20.8	20.8
Predicted " " " " *	22.2	20.3	21.9	20.1
SEP	4.1	3.3	4.2	3.5
RAT	104	100	103	97
SD (RAT)	10.9	10.0	11.8	10.0
CV (RAT)	10.4	10.0	11.4	10.3

* Energy value of 1 kg live-weight change equal to 10 kg milk in the FFU, SFU and MES systems, or 6.7 kg milk in the VEM system.

Table 3. Treatment means data. Observed and predicted milk yield. Standard error of prediction (SEP), energy supply as a proportion (%) of requirement (RAT) with standard deviation (SD(RAT)) and coefficient of variation (CV(RAT))

	Energy evaluation system			
	MES	SFU	FFU	VEM
No. of treatments	127	127	127	127
Observed daily mean milk yield(ECM)	20.6	20.6	20.6	20.6
Predicted " " " " *	22.5	20.8	21.9	20.3
SEP	2.9	1.9	2.8	2.0
RAT	106	101	103	99
SD (RAT)	6.3	6.3	7.0	6.0
CV (RAT)	5.9	6.2	6.8	6.1

* Energy value of 1 kg live-weight change equal to 10 kg milk in the FFU, SFU, and MES systems, or 6.7 kg milk in the VEM system.

The relationships between observed milk yield (ECM) and predicted milk yield are shown in Figs. 1-4. Line a represents the perfect predicted milk yield (unbiased) and line b the regression of observed and predicted milk yield. If lines a and b differ, then the predicted milk yield is biased. Except for milk yield predicted in the SFU system (Fig. 3), prediction of milk yield in different systems is more (MES and FFU) or less (VEM) biased

(Figs. 1, 2 and 4). However, there was almost no difference between the SFU and VEM systems in the SEP for milk yield, which was clearly lower compared with the SEP in the FFU and MES systems (Tables 2-3).

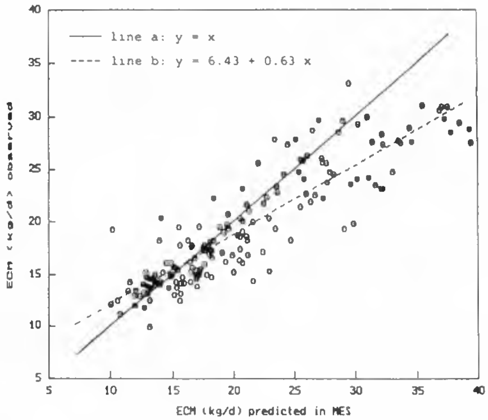

Fig. 1.

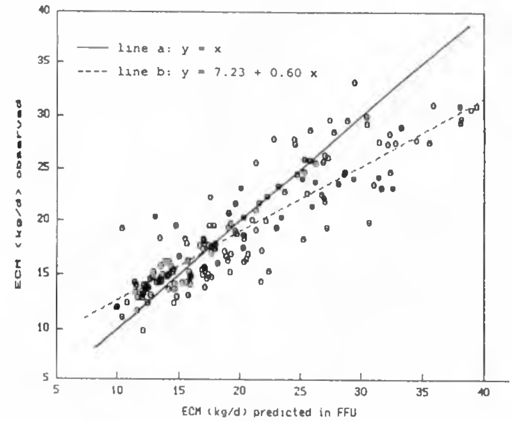

Fig. 2.

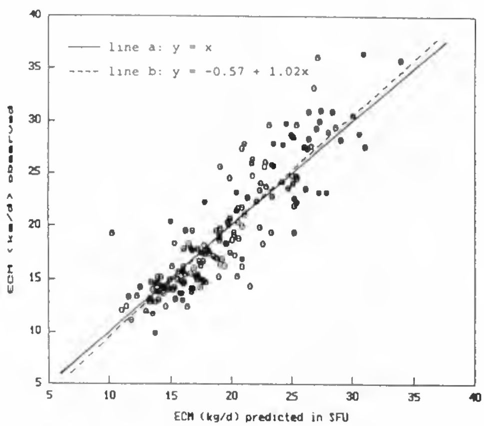

Fig. 3.

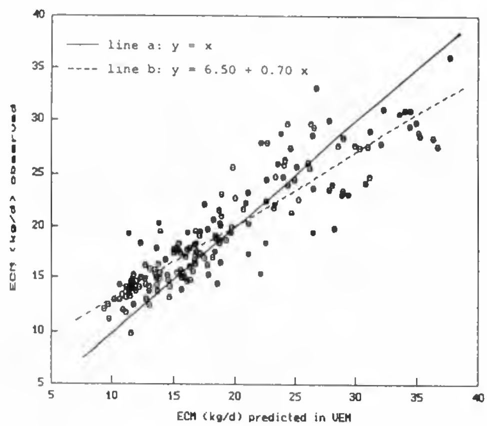

Fig. 4.

Fig. 1. Observed milk yield related to the predicted milk yield in the MES system. Individual observations (n = 753)

Fig. 2. Observed milk yield related to the predicted milk yield in the FFU system. Individual observations (n = 753)

Fig. 3. Observed milk yield related to the predicted milk yield in the SFU system. Individual observations (n = 753)

Fig. 4. Observed milk yield related to the predicted milk yield in the VEM system. Individual observations (n = 753)

On a theoretical basis the FFU and SFU systems tend to underestimate, while the MES system overestimates the energy value of forages in relation to concentrate when used for milk production (Thuen 1990). In this investigation only mixed rations are used in the comparison between energy systems. However, with practical rations covering a wide range of composition of the diet and with a wide range in mean milk yield, there is hardly any difference between the MES and FFU systems in any of the parameters. In both systems the milk production potential of diet is underestimated on low mean milk yield; milk yield less than 16-18 kg and overestimated on high milk yield; more than 20 kg (Figs. 1, 2).

Table 4. Individual data for heifers. Observed and predicted live-weight gain (kg/day), and standard error of prediction (SEP).

	Energy evaluation system SFU	VEM
No. of animals	94	94
Live weight 225 kg		
Observed gain	0.71	0.71
Predicted gain	0.51	0.49
SEP	0.35	0.41
Live weight 375 kg		
Observed gain	0.68	0.68
Predicted gain	0.66	0.44
SEP	0.41	0.40

Table 5. Individual data for bulls. Observed and predicted live-weight gain (kg/day) and standard error of prediction (SEP)

	Energy evaluation system SFU	VEVI
Live weight 225 kg		
No. of animals	281	281
Observed gain	1.295	1.295
Predicted gain	1.191	1.329
SEP	0.29	0.26
Live weight 425 kg		
No. of animals	184	184
Observed gain	1.197	1.197
Predicted gain	1.154	1.208
SEP	0.31	0.32
Live weight 525 kg		
No. of animals	93	93
Observed gain	1.047	1.047
Predicted gain	0.921	1.067
SEP	0.26	0.26

In the SFU and VEM systems the energy content of feed is corrected for feeding level, in Denmark by substracting 10% per multiple of maintenance feeding level above 2.9

(Andersen 1983), and in the Netherlands by decreasing the content of metabolizable energy by 1.8% per multiple of maintenance feeding level (van Es 1978). The correction for feeding level in the SFU and VEM systems may explain the lower variation between the observed and predicted milk yields compared with the MES and FFU systems. Even with some bias in the prediction of milk in the VEM system, the variation between observed and predicted milk yields was no greater than that in the SFU system.

The VEM system is the result of numerous balance experiments with dairy cows and SFU of similar trials with fattening steers. Despite the different ways of estimating the energy value of feed, the results of this investigation clearly show that the precision in estimating the energy value of practical feed rations in milk production is very much improved by correction for feeding level.

The results from the growing experiments with heifers and bulls are presented in table 4 and 5.

For growing heifers there was some difference between the predicted and observed gain, especially in the VEM system (Table 4). For both systems the SEP for growth was high, with hardly any difference between the two systems. In the growth experiments with bulls predicted gain was close to the observed gain in both systems, with a comparatively low value of SEP (Table 5).

Both the VEM and VEVI and the SFU systems are based on a large number of feeding trials with growing cattle, which may explain the small difference in practice between the two systems.

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3 Evaluation of feed energy in relation to grazing livestock

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Gudmundsson, O. 1991. Evaluation of feed energy in relation to grazing livestock. Norwegian Journal of Agricultural Sciences, Supplement No. 5: 17-35. ISSN 0801-5341.

Systems of feed evaluation and ration formulation need to be adapted to the biology of grazing systems. Attention is drawn to the use of such systems and to several biological factors including ingestive behaviour such as plant selection and intake, quantity and quality of available forage, supplementary feeds, utilization efficiency and energy cost of grazing and environment. It is concluded that increased research is needed on the subject and that the energy systems now in use should be replaced with more mechanistic system over a period of years as appropriate knowledge becomes available, including that on the biology of grazing, but the system should be kept simple enough for the practical farmer to understand and use.

Key words: Energy, environment, grazing, ingestive behaviour, intake, livestock, nutritive value, pastures, plant selection, supplementation.

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In general, systems for describing and evaluating feed according to its usefulness are essential as they allow rational approaches to be made to the feeding of livestock, whether by grazing or in confinement. They enable economic assessment of the merit of different animal grazing systems and the feed purchase policies such systems require. Increased use of computers for programming in grazing management, feed formulation, mathematical modelling and other techniques to meet the production targets adds to this importance. The feeding standards, for example, may be applied for assessment of pasture and animal condition, both intensively and extensively managed, in order to determine short-term changes in grazing policies, or as a long-term assessment of a complete grazing system with the aim of evaluating different management policies. Feed evaluation is also important to the plant breeder and farmers as a basis for selection of the right plants and for decisions on fertilizer application, harvest time, and so on. Further, it is important to the science of agriculture as a scientific knowledge and a means of communication.

The plant-animal interface is a complex system of interactions that exist during grazing, when the animals spend much of their time consuming food. It seems logical to assume that this has a major effect on the energy balance of grazing livestock, depending largely on the quantity and quality of the available forage and the efficiency of the animal to harvest and utilize it. Ingestive behaviour and animal performance are therefore just as important and useful parameters in evaluation and utilization of energy evaluation systems for livestock as the metabolic parameters of the animal itself. Ingestive behaviour is generally divided into plant selection and intake. These factors are highly interrelated, but are also greatly dependent on the sward conditions, both chemical and physical. Usually plant selection and total intake are also the main factors affecting animal response.

The digestion, absorption and utilization of nutrients is altered by the climatic environment, physiological status of the animal and gastric conditions. There are many unanswered questions about the relation of these factors to grazing animals and a great number of conflicting experimental results. Grazing animals were not considered during the development of the existing energy systems thus making their usefulness questionable under grazing conditions.

Grazing conditions vary, both within and between the Nordic countries as well as throughout the world. Under the northern conditions the season of vegetative growth is short and extensive grazing on native pastures is common, but declining. There are significant differences between these countries geologically, botanically and topographically. The climate is variable, ranging from oceanic, humid and rather cool in Iceland and the west of Norway to the inland climate in central Scandinavia. The pastures and ranges include a broad spectrum of sward conditions and plant species, both extensively and intensively managed. Because of these variations the present report will emphasize general grazing principles and theories as they relate to ingestive behaviour, metabolism and energy systems, but omitting principles and findings specific for individual countries or more local areas. The paper is empirical in nature, although comprehensive work has been done on mechanistic and/or dynamic modelling of ingestive behaviour, nutrition and performance of the grazing ruminant. These models, however, will not be discussed as they are best dealt with in a separate report.

INGESTIVE BEHAVIOUR

Plant selection

Grazing ruminants select diets from the plants available to them in the sward structure. They do not forage at random, but how often a plant is selected is more or less governed by its frequency, height, density and mass in the pasture (Penning 1986; Hodgson 1986). The common belief is that sheep and cattle prefer to graze vegetation that is relatively short (Van Soest 1982). It has been suggested that cattle may avoid taller patches of vegetation created and contaminated by urine and faeces (Bjarnason 1984). However, recent experiments indicate that sheep grazing ryegrass monoculture communities prefer tall patches created by sheep urination and defecation (Bazely 1990).

Diets selected by grazing livestock usually have higher nutritive value than the available herbage (Arnold 1981; Hodgson 1982, 1985). This does not necessarily mean that the animals can sense nutrients and select in accordance with higher nutritive value, but rather that the nutritive value is associated with factors selected by the animal, such as green plants rather than dead ones; immature rather than mature plants, and leaves rather than stems (Arnold & Dudzinski 1978). White and red clover are often more nutritious than grasses, especially in the latter half of the grazing season (Gudmundsson 1986), and in mixed grass clover swards the diets usually contain a higher proportion of clover than does the sward as a whole (Hodgson 1981).

However, work on natural pastures, for example those dominated by the rather unpalatable *Nardus stricta*, suggests that avoidance of unpreferred species may have as great an influence on selective behaviour as has selection for preferred species, and that under extreme conditions this avoidance can dominate selective behaviour (Grant & Hodgson 1986). Selection can also be affected by the chemical and morphological defence system of the plants; however, only a limited amount of work has been done on investigating how ruminants can directly sense nutrients or toxins in a diverse array of plants (Malechek et al. 1986; Provenza & Balph 1990).

Studies of individual plant selection of ruminants grazing multispecies plant communities under more northern conditions are scarce and have local but very limited general application to the energy metabolism of grazing herbivores in the Nordic countries. However, a general view of results from some sheep experiments in Iceland will be used as an example (Thorsteinsson 1981). Most of the experiments on individual plant selection have been carried our using fistulated ewes (Thorsteinsson & Olafsson 1965a; Bjarnason & Blafeld 1981), although other methods have also been used (Thorsteinsson 1964). During the plant growing season herbs, many grasses, different forbs and sedges tend to constitute the major part of the diet. In the winter the sheep consume mainly leaves and twigs of woody plants (Fig. 1).

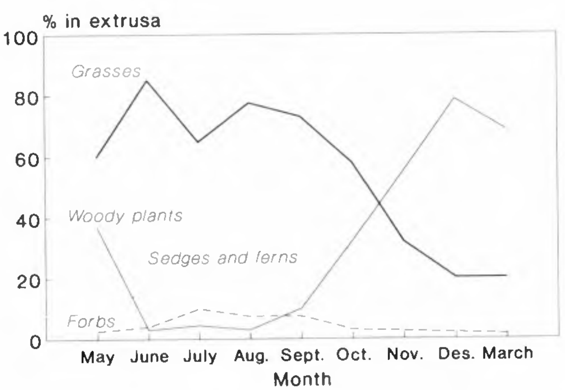


Figure 1. Percentage plant composition in extrusa from oesophageally fistulated ewes grazing at one location (Hestur in Borgarfjördur) in Iceland (Source: Thorsteinsson 1980).

Many plants are poorly utilized even though dominant in the sward, and the relationship between the amount of grass in the sward in the summer and the amount of grass selected is often poor. For example, when grass is limited the sheep completely remove it from the sward before they start grazing other species (Thorsteinsson 1981). Also a very high variability has been found in plant selection between individual sheep (A. G.

Thorhallsdottir, pers. comm.). Therefore, the results obtained do not necessarily reflect upon the general preference of the sheep for different plants as selection is greatly governed by the variability between individual animals and the availability of each particular vegetation species, which change with time but can also be changed by stocking rate. It is possible, for example, that under heavy grazing over a considerable period the more preferred species disappear from the pasture and less preferred plants become dominant in the diet, thus usually changing the nutrient composition and reducing the energy value of the available herbage and greatly affecting the animal's metabolizable energy (ME) utilization.

Intake

It is well established that the availability of nutrients and therefore the energy from feedstuffs depends on level of intake (ARC 1980). In the long term, intake is controlled by the animal's energy balance, but in the short term it is probably controlled by a combination of plant structural factors that influence rate of ingestion and the effect of the masticated forage on gut fill, and by social behavioural and environmental factors affecting the appetite-satiety complex (Forbes 1988). Many of these are independent of whether the animal is grazed or fed in confinement, and are largely outside the scope of this paper. However, two of the most important factors specific for grazing are the quantity and quality of the available herbage. These, therefore, are often the first limiting factors governing intake; they act before the animal's physiological feed intake regulators and explain much of the variation in palatability and intake between plant species and grazing seasons.

A linear relationship has been found between intake and digestibility within plant species in individual experiments (Hodgson 1977; Minson 1982), increasing progressively in organic matter (OM) digestibility to levels close to maximum for fresh herbage. However, this is more complex under grazing conditions in general because of variation with time in availability and physical structure of the forage, as well as the changes in the environment (Hodgson 1986). This variation is both inter- and intrarelated. Therefore, some factors that are easily measured, such as plant mass, height, density and digestibility, are often poor determinants of herbage intake and utilization when uded individually. Zero grazing is also questionable for this purpose as it eliminates factors such as the environment and sward condition.

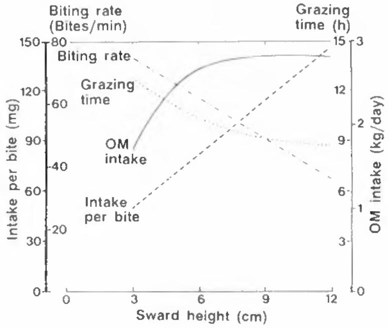
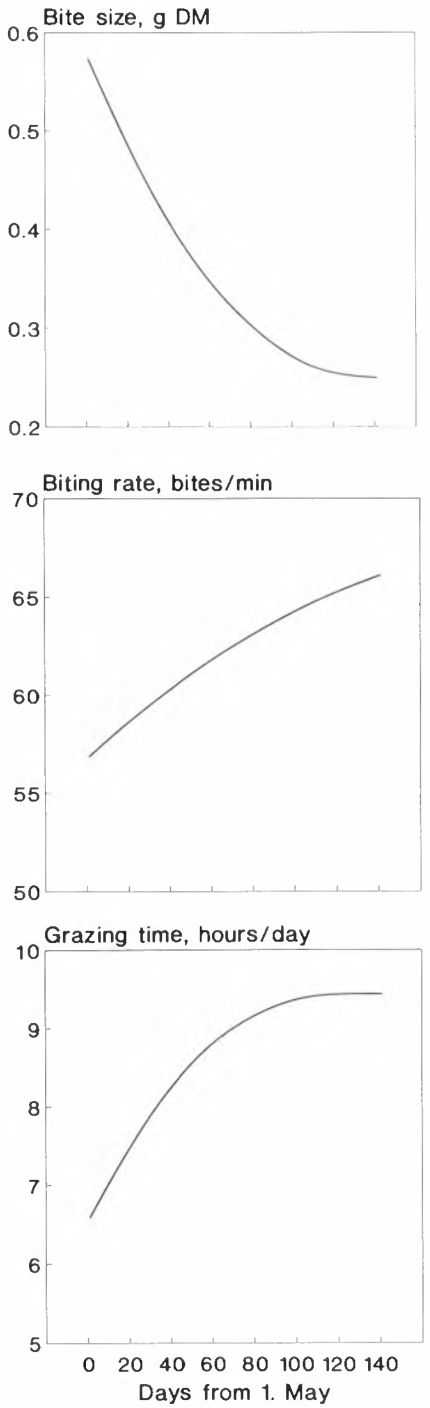


Figure 2. Influence of sward surface height on the components of ingestive behaviour (Source: Penning 1986; Hodgson 1986).

Intake is affected by how fast and how easily the animal can consume the vegetation (Arnold 1981; Hodgson 1982). This is to a great extent governed by the sward, which affects bite size, bite rate and grazing time (Penning 1986). With grazing on uniform grassland the sward surface height has a great effect on the OM intake (see Fig. 2), with biting rate and grazing time inversely related and bite size and OM intake positively related to grass height (Penning 1986). As the herbage becomes lower the effect of density on intake increases and vice versa (Arnold & Dudzinski 1967). It is also generally accepted that ruminants, when grazing mixed grass/clover pastures, consume more clovers than grasses (Thomson 1984). When grazing native vegetation under more extensive natural conditions these rules do not necessarily apply. These areas are often composed of mosaics of small, versatile plant communities of low herbage density. Under these conditions there is often very little or no relationship between the vegetation mass, density or height and the intake.



In experiments with dairy cows (Phillips & Leaver 1986) both grazing time and biting rate increased asymptotically over the grazing season (Fig. 3), but the bite size declined, with the rate of decline being most rapid early in the season. Ruminating time increased from spring until midsummer, but was depressed in the autumn when intake was reduced. These factors emphasize the importance of grazing behaviour limitations in energy metabolism of high producing ruminants.

When the sward factors are not limiting and the hunger of the animal is not satisfied, animal factors take over the regulating of the intake. Body size, biological type and related animal variables appear to have important consequences for grazing behaviour and energy intake (Ferrell & Jenkins 1987; Havstad & Doornbos 1987;

Figure 3.Seasonal variation in grazing time, biting rate and biting size (Source: Phillips & Leaver 1986).

Illius & Gordon 1990). It is also important to keep in mind that the effect of intake on ME is not constant across all feeds, although in most feed energy systems it is assumed to be so. However, increasing the intake has a more decreasing effect on digestible energy (DE) and related values than ME because of some decrease in urinary energy and methane as intake goes up (Van Es 1975).

Effects of plant selection and intake of ruminants have to be studied in relation to energy metabolism, with emphasis on the capabilities of ruminants to differentiate among dietary items and sense plant nutritional components.

NUTRITIVE VALUES OF PASTURES AND RANGES

The energy-yielding substances of forages are still in many instances stated in terms of the Weende method or proximate analysis method for chemical analysis of feeds, that has in principle been used world-wide since 1860. The energy systems used in the Scandinavian countries are to a great extent still based on this method. However, improved methods have been developed that have gained popularity during the last two decades, such as the one by Van Soest (1963a, b 1967). The development of a methodology for the study of digestibility has also been slow, with the first major breakthrough being the Tilley & Terry (1963) method of *in vitro* digestibility. More recently Near Infrared Reflectance Spectroscopy instrumentation has shown promise in both these aspects of feed evaluation.

The balance rather than amount of available nutrients or energy yielding substrates in the forage is perhaps the most important factor concerning energy utilization in the animal. However, this has only received limited attention in research on grazing ruminants. Still, the amounts of nutrients in the herbage are very important as they often become limiting factors in the growth of the grazing livestock, apparently independently of the nutrient balance.

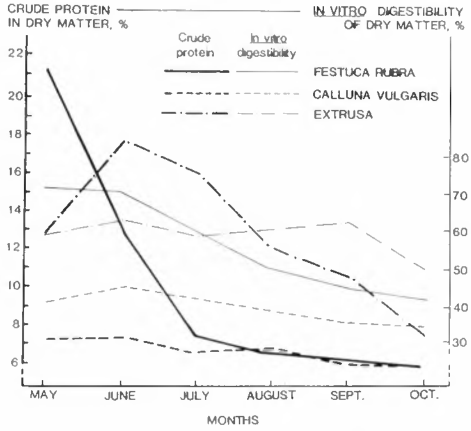


Figure 4. Changes in *in vitro* digestibility and protein content of two types of plants and extrusa during the grazing season under northern conditions (Source: Olafsson 1973b).

The nutritive value of vegetation grazed by livestock changes with time and amount and consequently the balance of nutrients is constantly changing. The nutritive value is highest in the spring and lowest in the autumn. There is a reduction in the digestibility of dry matter and the percentage of crude protein, with increasing cell wall as the plants mature. By late August the nutritive value of the range plants under the most northern conditions reaches quite low levels (Thorsteinsson & Olafsson 1965b, 1969) and is not able to support the animal's energy requirements. On cultivated pastures containing grass/clover mixtures, for example, those changes are not as profound, especially not in balanced grazing systems, although the trends are generally the same. Although legumes are not always more digestible than grasses the ME content is usually higher (Thomson 1977).

Figure 4 illustrates how the protein content and digestibility may change during the grazing season (Olafsson 1973b). For example, *Festuca rubra* has a digestibility value of approximately 70% in May but only 45% in October. Similar results can be found for most other forages. However, in some of the woody species, especially evergreens, such as *Calluna vulgaris*, both the protein content and digestibility appear to be much more constant during the grazing season. Animal grazing also affects the nutritive value of the plants, by keeping digestibility higher in the autumn, and at the same time the sheep try to keep the digestibility of their diet constant from spring to autumn by selection (Olafsson 1970, 1973a), as shown in the extrusa (Fig. 4), although there is a considerable drop in the protein content. However, this situation may change if the sheep are not allowed to select freely, especially when heavily stocked. It should also be pointed out that there is a steady fluctuation in the ratio between protein and digestibility.

It is important to realize that an increase in digestibility from, for instance, 50 to 55% entails an increase in the voluntary daily dry matter intake from 62 to 72 g $kg^{-.73}$, and an increase in the energy digested per day by 32% or from 152 to 200 kcal $kg^{-.73}$. A 10% increase in the digestion coefficient, in this range of digestibility, can therefore increase the amount of energy available above maintenance from 51 to 99 kcal $kg^{-.73}$ or approximately 100% (Blaxter et al. 1961). It is very important to keep the nutritive value, in this case the digestibility of the pasture, as high as possible throughout the grazing season.

SUPPLEMENTATION

When herbage fails to supply the energy requirements of grazing animals, supplementary feeds are often fed to maintain or increase the total daily intakes and performance. Generally energy supplements decrease forage intake, whereas protein supplements are known to do the opposite (Gill et al. 1989). The reduction in herbage intake resulting from energy supplementation is manifested mainly through a reduction in grazing time, with little effect on rate of biting or bite size (Leaver 1986). Still, both energy and protein supplements increase the total energy intake in general and it is possible that supplementation to ruminants grazing poor pastures can markedly improve the ME utilization (Leng 1990).

In the literature variable substitution rates have been reported and there are conflicting reports on the influence of amount of concentrate in these, probably depending on variations in experimental conditions (Leaver 1986; Horn & McCollum 1987). The desired level of substitution of concentrate depends on the amount and quality of available forage as well as the limits of feed intake and the constraints of the total feed eaten in meeting nutrient requirements. The type of energy and protein supplementation can therefore have a profound effect on total energy intake and utilization. It is not always the supplement with the highest energy/protein concentration that gives the best results, due to lower substitution rates (Jennings & Holmes 1984). The palatability of the concentrates and degradability of the protein supplements are also very important.

Most often supplementation is necessary where the amount of forage is limited, but also during periods of decreasing herbage quality or during peak production. Supplementation may also be necessitated by environmental conditions which increased maintenance energy requirements (Christopherson & Young 1986). Further, under grazing conditions where herbage available for grazing is limited it can be desirable to decrease forage consumption in order to stretch the forage supply during periods of poor vegetative growth (Horn & McCollum 1987).

It has to be borne in mind that strategies of supplementation depend mostly on the grazing location and vary according to climate, management and production targets.

EFFICIENCY OF UTILIZATION

It is important to keep in mind that the requirements of the microbes in the rumen have to be met to maximize the energy-supplying end products of the rumen fermentation and their utilization. At the same time it is important to supply enough critical nutrients that bypass or escape rumen fermentation. The major end products of rumen fermentation are the volatile fatty acids (VFA). They provide more than half of the ME gained from forages by the grazing ruminant (Corbett 1987). The ratio of the VFA in the rumen varies, but the amount of acetate is always highest, the rest being propionate and butyrate, with relatively small amounts of valerate and branch chain acids. With increased maturity of the forage the amount of acetate increases and propionate decreases. This reflects the reduction in soluble carbohydrates in the plants, which is primarily the substrate for propionate production and which also occurs with vegetative re-growths (Corbett et al. 1966).

Efficiency of utilization of ME (k) in feedstuff is similar, whether it is fed indoors or consumed during grazing. It is also similar for maintenance (k_m) and milk production (k_l), but the ME energy is utilized less efficiently for growth and fattening (k_f). The efficiency is positively related to the metabolizability of the gross energy (q) of the diet.

As early as 1785 Lavoisier, working with a human subject, discovered that ingestion of food increased heat production. In late 1800 Natan Zuntz, mainly working with horses, discovered that this heat loss increased when the animals were fed highly fibrous feeds (Blaxter 1980). Since then it has been recognized that the heat produced from similar amounts of ME in grazing ruminants or ruminants fed roughage-based diets is greater than that produced when the animals are fed more concentrate-based diets. This low efficiency of utilization of ME, and associated heat increment particularly on poor quality forages, was in earlier work (Armstrong & Blaxter 1957a, b) explained by the indication that ruminants do not utilize acetic acid as efficiently as propionic or butyric acid. This has been summarized by Blaxter (1980) who shows further that heat increment is lower below compared with above maintenance and considerably higher than of glucose. The reason for this has yet to be fully explained and the mediation of the effects may be more complex than was originally envisaged (Blaxter 1980; Thomas & Chamberlain 1990). Recently Ørskov & MacLeod (1990) have indicated, based on high utilization of acetic acid in many published experiments, that the work of digestion as described by Kellner around the turn of the 19th century is the main reason for this difference rather than variation in the supply of acetogenic substrate. Others have indicated that differences in heat increment will depend on the pattern of fermentation in the rumen as well as the balance of protein available and VFA produced for absorption, and have pointed out several situations that could improve efficiency of acetic acid utilization (MacRae 1986; Leng 1990).

A hypothesis has been suggested (MacRae & Lobley 1982; MacRae 1986) proposing that many of the seemingly contradictory experimental observations can probably be rationalized by the dependence of acetate utilization on its conversion to fatty acids and then into triglycerides. The precursors of co-factors needed for this to happen are adequate when the ruminants are fed some type of concentrate with the grazing or roughage fed, but can be very limited when no concentrate is fed, especially when they are grazing low quality forage or being fed poor roughage, resulting in lower efficiency of utilization of ME. Indications that the availability of precursors, in the form of propionate or glucogenic amino acids, can influence the efficiency of utilization of ME may have major implications for both the present energy and protein requirement schemes (MacRae 1986) because if glucogenic amino acids are used to aid the conversion of acetate into fatty acids, they will not be available for protein synthesis and protein deposition, and could change the requirements considerably (Lobley & MacRae 1987; Girdler & et al. 1986).

It is also possible that the low and variable efficiency of ME utilization indicates some imbalance of protein and energy substrates reaching the intestine for absorption because of lack of precursors of co-factors needed for adequate fermentation and utilization of the substrates entering the rumen. These questions will not be resolved until there is more comprehensive knowledge available about the utilization and interaction of individual substrates for particular functions in the animal.

ENERGETIC COST OF GRAZING AND ENVIRONMENT

Grazing activity

Maintenance requirements are greater for grazing than for confined livestock, largely due to the increased movement of the grazing animal when obtaining feed or water and environmental factors such as temperature. Maintenance requirements are variable as they are affected by many factors, the main one being the location and type and condition of grazing area used. Different experiments have also yielded different results. There is a great difference in maintenance requirements, depending on whether the animal is grazing cultivated or native pastures, wet or dry areas, level or mountainous pastures, or warm or cold environments.

The energy cost of grazing includes muscular work due to locomotion, prehension, mastication and ingestion of forage. This energy expenditure increases when the speed of muscular work exceeds the optimal rate. It can be assumed that grazing animals only exceed the optimal speed for short periods of time when grazing (Morris & Sanchez 1987). The daily travelling distance by the grazing livestock depends on the species, breed, grazing conditions and proximity to water. Under favourable conditions dairy cattle walk up to 2.7 km day^{-1}, but under extensive conditions this increases up to 9 km day^{-1}. Similarly beef cattle walk about 3 km day^{-1}, which increases up to 5 km day^{-1} under more extensive conditions and may go up to 12 km day^{-1}. Sheep, however, travel approximately 1.5 to 3.0 km day^{-1} under favourable grazing conditions, but up to 14 km day^{-1} under extensive conditions (Arnold & Dudzinski 1978).

From the literature, British standards (ARC 1980) deduce the increase in maintenance requirements for cattle as 2.0 J m^{-1}kg^{-1} and for sheep as 2.6 J m^{-1}kg^{-1} for horizonal movement, which increases over ten times for vertical movement to 28 J m^{-1}kg^{-1} for both cattle and sheep. Therefore the increase in the maintenance requirement can reach 15-16%. American standards (NRC 1978) reckon that the maintenance requirement of dairy cows increases by approximately 3% for each km they walk on level ground or approximately 10% on good grazing, which can increase to 20% as the grazing becomes poorer. On native or rangeland grazing with sheep the requirement is assumed to increase by 60-70% (NRC 1985). In the Netherlands grazing cows on good pasture is estimated to increase the maintenance energy need by about 30% (Van Es 1974), but in their feeding standards the difference is considered negligible (Van Es 1978).

In Australia, Corbett et al. (1985) have proposed a generalized equation to predict the varying maintenance metabolisms of sheep and cattle and the additional energy expenditures of grazing animals. The first term in the equation predicts the additional net energy (NE) cost of eating, with different rates of eating for sheep and cattle. The second predicts the walking NE cost, varying with topography and herbage availability, and the last term converts to ME per animal (Corbett 1987):

$$ME_mG\text{-}ME_mH = [2.5DMI.a(0.9\text{-}D) + 50F/(Y+3)]/k_m(W/1000)$$

where ME_mG and ME_mH are the energy costs (MJ day^{-1}) required by grazing and housed animals respectively; DMI (kg day^{-1}) is the dry matter intake of digestibility D; the multiplier (a) is 32 for sheep and 4 for cattle; F is the terrain (level = 1.0, undulating = 1.5, hilly = 2.0); Y is herbage availability (tones DM ha^{-1}); km is the efficiency of use of ME for maintenance in relation to metabolizability (q_m) according to ARC (1980) ($0.35q_m$ + 0.503) and W is the liveweight (kg).

It is difficult to separate the energy costs of eating from those associated with locomotion. Osuji (1974) and Osuji et al. (1975) suggested that energy expenditure of sheep is proportional to the time spent grazing. This is supported by the earlier findings of Graham (1962), where no significant difference was detected in energy expenditure of sheep per unit time, whether fed chopped grass or grass on pasture turf. However, the grazing from the turf took twice as long as eating the chopped grass for the same feed intake. Time spent grazing is a function of pasture quantity and quality, but is usually in the range of 4 to 13 hours (Arnold & Dudzinski 1978).

A limited number of experiments have been carried out on energy expenditure of indigenous ungulates of the northern latitudes (White & Fancy 1986), and the same is true for grazing livestock. However, in most of the Nordic countries requirement schemes do

not allow for an increase due to grazing. In general there is a dearth of information on this increase in energy expenditure, but some information applicable to Nordic conditions can be gathered from review articles (Osuji 1974; Webster 1979; Corbett 1980, 1981, 1987), articles on energy utilization (Logan & Pigden 1969; Baker 1982) and individual experiments (Wallace 1956; Lambourne & Reardon 1963; Clapperton 1964; Graham 1964; Young & Corbett 1972). Based on their results the following suggestions have been made for Icelandic conditions (Gudmundsson 1987):
(1) 10% increase in maintenance requirement due to grazing on good cultivated land in good weather, where the grazing time is under 6 hours/day;(2) 25% increase on average cultivated grazing or on good native grassland, where grazing time is 6-8 hours/day; (3) 50% increase on very heavily grazed cultivated land or average native pastures, where grazing time is over 8 hours/day; (4) 75% increase on mountainous rangeland, where the grazing time is 10-13 hours/day and (5) over 100% increase on poor mountainous rangeland, especially in wet and cold weather, for example for sheep shortly after shearing. In general it would therefore be advisable in Iceland, for example, to increase the maintenance energy requirement for sheep by 50% during summer grazing on common native grasslands, when estimating the carrying capacity of the land. Similarly, on cultivated land close to the farm, this increase could on the average be estimated to be 10-20%. An example of the effect of increase in maintenance requirement due to grazing on the carrying capacity of rangeland and total daily requirement of a ewe suckling 1.3 lambs is shown in Fig. 5.

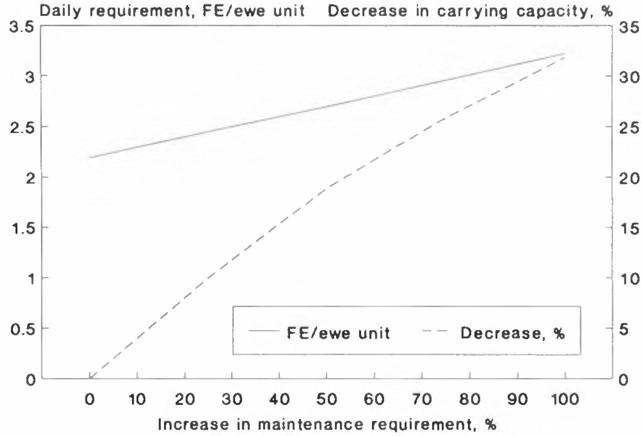


Figure 5. An example of changes in daily requirement of ewe suckling 1.3 lambs (ewe unit) and percentage decrease in carrying capacity due to increase in maintenance requirement because of grazing.

Climatic environment

The climatic conditions in the Nordic countries are very variable, differing both between and within locations. This variability can have a considerable effect on the animal's energy utilization. However, physiological and nutritional consequences attributable to changes in the environmental temperature are very complicated (Slee 1979). A heat increment is used to keep the body warm, independent of whether it is really due to fermentation in the rumen, the work of digestion or general metabolism in the body. The nutritional condition and hair coat of the animal are also important in this respect. However, there have to be considerable changes in the temperature before it starts to affect the energy requirement.

There is a range of environmental temperatures in which an animal maintains a constant body temperature in the short term with little or no energy expenditure. This is known as the thermoneutral zone (NRC 1981). Its lower limit is called the lower critical temperature, i. e. the temperature below which an animal must increase its heat production to maintain deep body temperature (White & Fancy 1986), and the upper limit, the upper critical temperature (NRC 1981), i. e. the temperature above which an animal must increase its rate of evaporative heat loss to prevent a rise in body temperature (Young 1987). These critical temperatures change with the level of energy intake. Within the thermoneutral zone there is another narrower zone, close to its upper limit, known as the zone of thermal comfort, the preferred environmental temperature of an animal which is given a choice of various thermal environments (Robertshaw 1987). However, this narrow zone does not have any bearing on the energy expenditure of the animal.

Table 1. Estimates of resting heat production (RHP), lower critical temperatures (LCT) and increase in heat production per degree by which the effective temperature falls below LCT (ΔHp) (Source: Christopherson & Young 1986).

	RHP ($KJkg^{.75}d^{-1}$)	LCT (°C)	ΔHp ($KJkg^{.75}d^{-1}$)
Sheep:			
Newborn lamb	491	27	33.7
Adult sheep, shorn	345	25	16.1
Adult sheep, fleece	345	-3	5.7
Adult sheep, fleece	532	-26	6.1
Pregnant ewe, shorn	644	2	16.2
Lactating ewe, shorn	808	-8	18.2
Cattle:			
Newborn calf	583	9	17.2
Month old calf	682	0	15.8
Growing calves	600	2	14.0
Growing calves	629	-6	13.2
Holstein calves	723	-18	12.2
Hereford calves	723	-21	11.6
Beef cows:			
Not pregnant	458	-14	8.3
Late pregnancy	572	-21	8.4
Lactating dairy cow	998	-45	11.7

Examples are given in Table 1. of the estimated lower critical temperatures and increases in heat production per degree by which the effective temperature falls below the lower critical temperature in relation to resting heat production for sheep and cattle. It is apparent that under normal summer grazing in the Nordic countries it is unlikely that healthy adult ruminants would reach the lower critical temperature. However, newborn, newly shorn sheep and underfed livestock can easily encounter a cold stress. It is not only the ambient temperature that is important, but rather the combination of temperature, moisture and wind. For example wet and/or windy weather usually causes much more stress to the animal than the environmental temperature alone (NRC 1981). These conditions are rather common in the grazing season under northern conditions, especially during early spring and late autumn.

In the more southern and inland areas, for example in mid-Scandinavia, warm spells that inflict heat stress on the grazing livestock are also possible. Then the animals reach the upper critical temperature and may be forced to increase their rate of evaporative heat loss to prevent a rise in body temperature. This results in inappetence, which causes a reduces metabolic rate, reduces the heat load and at the same time markedly reduced protein synthesis, milk production and overall performance. This, however, only occurs when the capability of evaporative heat loss has been exceeded (Robertshaw 1987). Heat stress like this has supposedly very little impact on the maintenance energy of grazing livestock in the Nordic countries, but could possibly impair the productive process by suppressing food intake.

The environment can also impair the voluntary feed intake and affect the efficiencies of feed utilization by changing the rumen turnover rate and altering the partitioning of nutrients into productive functions (Leng 1990). Oxidation of individual nutrients, especially fat, depends on the animal's thermal balance (Graham et al. 1959). Ruminants appear to oxidize fat for heat production when cold stressed. Therefore availability of the oxidative substances, discussed previously, to meet energy requirements for maintenance and production can be influenced by the requirements for heat production to maintain body temperature and possibly increase the ratio of amino acids available for production. When surplus oxidative substrates have been totally utilized, mobilized fat can serve as a source for maintaining body heat (Leng 1990).

These and other responses to environmental stress tend to disrupt the energy balance of the animal, both by increasing the energy requirements and by reducing the available ME. These responses will further be elevated by changes in the behaviour of animals under stress, to avoid uncomfortable conditions (Young 1987).

CONCLUSIONS

The vast majority of the ruminant livestock of the world depend on grazing rather than confined feeding. Nevertheless, current information on grazing ruminant energy intake and utilization is extremely limited. This is especially true in the Nordic countries where very limited or virtually no experiments on the subject have been carried out. In spite of the relatively short grazing season in these countries research on this subject has to be increased.

The efficiency of production of the grazing ruminant is based on voluntary intake, digestion and metabolism of various nutrients in the digestive tract and their interactive processes and the efficiency with which the absorbed nutrients are utilized to meet precisely the requirement for each individual nutrient, either for maintenance, reproduction, milk or gain. The utilization of ME is only a part of this much more complicated system. Therefore, although necessary as a part of the whole scheme, the energy systems that are now in use should be replaced over a period of years, as the appropriate knowledge becomes available, by a more sophisticated system based in general on the approach suggested by Kristensen & Weisbjerg (1990). It is necessary to include in this system voluntary intake, utilization and metabolism under grazing, which must be considered if the needs of grazing ruminants are to be accurately applied in practice. It is important, however, to keep the system simple enough for the practical farmer to understand and use, while still fulfilling its purpose. This is the task of future working groups, and it is hoped not just within the Nordic countries but rather in a cooperation between the Nordic countries and other countries working in this direction, thus paving the way for one internationally recognized system.

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4 Associative effects of feeds in ruminants

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Negative associative effects of feeds on digestibility exist mainly in animals fed at high levels of intake, while experiments conducted at maintenance level have failed to show such effects. Non-additivity is most commonly observed when the digestion of the forage component of a diet is depressed by the addition of rapidly fermentable carbohydrate or fat supplements. Positive associative effects have been observed mainly with protein and digestible fibre supplements. The utilization of dietary energy depends not only on the profile of nutrients made available from a particular feed but also from nutrients made available from other feeds. The nutrient profile is a major factor determining the partition of energy between milk and body tissue synthesis or between fat and lean growth.

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In the majority of the feed evaluation systems the energy values of feeds are used as if they were additive, irrespective of feeding level or other components of the diet. The effect of feeding level is taken into account in most current feed evaluation systems (e.g. NEL, Van Es 1975; ARC 1980). These systems recognize that the digestibility of the diet is depressed at high intake. However, the effect of feeding level on metabolizability of the diet is smaller than on digestibility. The ratio metabolizable energy (ME) to digestible energy (DE) increased with the level of feeding from 0.81-0.82 at maintenance (M) to 0.87 at 3-4 M (Van Es & Van der Honig 1977). This is mainly due to smaller relative energy losses in urine and methane.

In the formulation of rations it is assumed that the energy values of the components of the diet are additive. This approach assumes that there are no interactions in the digestibility or in the efficiency of the utilization of dietary energy caused by mixing the components of the diet. There is, however, much evidence showing that these assumptions are not always valid. The interactions of feeds can affect the nutritive value, ie. the nutrient content of a feed per unit of mass. In many circumstances two feeds may be of similar nutritive value but of differing feeding value, because of their effects on forage intake or their synergistic or antagonistic interactions with other feeds in the diet (Thomas 1990).

In this paper the associative effects of feeds on the digestion of nutrients and the possible causes of these effects are discussed. In the following sections some aspects of the associative effects of feeds on the efficiency of energy utilization and on animal production will be given attention. Finally, practical aspects of associative effects are discussed.

ASSOCIATIVE EFFECTS IN DIGESTIBILITY

Associative effects occur when the apparent digestibility of a mixture of feedstuffs does not equal the sum of the separately determined digestibilities of its components (Mould 1988). These effects can be positive; the digestibility of the mixed diet is higher than the mean of its components. Campling et al. (1962) provided an example of the manner in which the variation in dietary urea supply can affect digestibility of straw by cattle with associated changes in voluntary intake. In this situation improved forage digestibility is usually due to alleviation of a nutrient deficiency rather than a real associative effect (Mould 1988). Most commonly the associative effects are negative; the apparent digestibility of the diet is lower than the value calculated from the digestibilities of the ingredients of the diet. Negative associative effects occur most often when the level of concentrate supplementation is high, leading to reduced digestibility of forages.

Protein supplements

Although the responses to protein supplementation in digestibility of low quality roughage diets can be considered an alleviation nitrogen deficiency of rumen microbes, increasing crude protein content of the supplement has also improved OM digestibility in dairy cows given high quality forages (see Oldham 1984). With grass silage-based diets the mean increase in total DM digestibility was 0.007 units per 10 g/kg increase in dietary crude protein content. Gordon et al. (1981) reported the corresponding response of 0.0025 units per 10 g/kg increase in crude protein content of the supplement. Assuming a proportion of 400 g/kg of the supplement in the diet, the value would be 0.0063 units per unit increase in crude protein content of the total diet, similar to that reported by Oldham (1984).

In Finnish dairy cow experiments (Tuori & Syrjälä-Qvist 1988, Tuori 1989, unpublished) a replacement of barley-oats mixture with rapeseed meal (RSM) improved OM digestibility of the diet by 0.01 - 0.02 units. Although the response was quite small, it was very consistent ranging from 0.017 to 0.021 units with 3 levels of RSM in the first trial and from 0.008 to 0.011 units in the second trial with 4 RSM treatments. The positive responses to protein supplementation with high quality forages are more likely to occur in dairy cows fed at the high level of feeding than in sheep fed at M or in growing cattle fed approximately at 2M. In growing cattle, responses in OM digestibility to protein supplements have been small (Steen 1985; Steen 1989; Jaakkola et al. 1990). When silage has been fed as the only feed to young cattle, fish meal has sometimes improved OM digestibility significantly (Thomas et al. 1980; England & Gill 1985).

The explanation for these responses probably lies in the manner in which the rumen microbial population responsible for carbohydrate fermentation varies according to form of food eaten and the balance of nutrients available. Of particular importance is the amount and form of dietary crude protein (Oldham 1984). Increasing the supply of amino acids and peptides may stimulate the growth of cellulolytic bacteria in the rumen. In dairy cows, large responses in milk yield to protein supplementation have been associated with increases in digestibility and feed intake. In this respect, the additional ME supply can account for the major proportion of the response (Oldham 1984; Thomas & Rae 1988). These responses are good examples of positive associative effects in feeding value, ie. the capacity of a feed to contribute directly or indirectly to the utilization of another feed by the animal.

Concentrate supplements

Level of supplementation

Negative associative effects occur principally where the energy value of the diet has been reduced by inhibition or depression of cell wall or starch digestion (Mould 1988). The main cereal grains used for ruminants in Nordic countries are barley, oats and wheat, and depressions in starch digestion are unlikely to occur, providing that the grain is properly processed. Even at high levels of inclusion or high levels of feeding the total digestibility of barley starch is almost complete, while considerable amounts of corn starch are excreted in the faeces (Sutton 1985).

Therefore, with our typical diets the negative associative effects are most likely to occur when the intake of high producing animals is limited by physical factors, and concentrate supplements are needed to meet the energy requirements. Increasing the level of concentrates in the diet results in a reduced rate of cell wall digestion, and calculated increases in digestibility and metabolizability of the total diet are not achieved. The extent of the depression in fibre (cell wall) digestion with increasing levels of concentrate in the diet depends on many factors: level of supplementation, carbohydrate composition of the supplement, level of feeding, quality of forage used, animal species, use of buffers, etc. There may also be interactions between many of these factors.

The main reason for inhibition of fibre digestion with easily fermentable carbohydrates is low rumen pH. Rapid fermentation of soluble carbohydrates in the rumen produces volatile fatty acids, and sometimes also lactic acid, at higher rates than can be absorbed through the rumen wall. Cellulolytic bacteria are more sensitive to low pH than those utilizing starch or sugars. Fibre digestion in the rumen has been reported to be totally inhibited when pH is reduced below 6.0 - 6.1 (Stewart 1977; Mould & Ørskov 1983). Increasing rumen pH by bicarbonate buffers can partly alleviate the adverse effect of easily fermentable carbohydrates (Mould et al. 1983), although in many cases not completely. The adverse effects of concentrates on rumen cellulolysis can be differentiated into a "pH effect" and a "carbohydrate effect". The depression in fibre digestion which could not be attributed to increased rumen pH was designated as the "carbohydrate effect" and the part which is due to low pH was designated the "pH effect" (Mould et al. 1983). The results of Rooke et al. (1987) and Huhtanen (1987a) support the concept that continuous availability of soluble carbohydrates can depress fibre digestion without affecting rumen pH (Table 1).

In young cattle given grass silage *ad libitum* sucrose supplementation (150 g/kg DM) decreased cellulose digestibility from 0.748 to 0.694 (England & Gill 1985). The extent of the reduction in fibre digestion was similar irrespective of the method of feeding sucrose, i.e. twice daily or a continuous intraruminal infusion, (Khalili & Huhtanen 1991b). In the studies of England & Gill (1985), Huhtanen (1987a) and Khalili & Huhtanen (1991a), the expected increase in total OM digestibility with sugar supplements (50-200 g/kg total DM) was 0.0326 units (n = 11) while the observed increase was only 0.0013 units. The difference can partly be attributed to decreased cell wall digestion and partly to increased faecal output of metabolic organic matter.

Table 1. The effects of intraruminal infusions of soluble carbohydrates on digestibility in cattle fed on grass silage-based diets.

Ref.	Infusion	Rumen pH	ADF digestibility Rumen	Total
Rooke et al. 1987	Control	6.8	0.85	
	Glucose	6.8	0.81	
	Glucose + Casein	6.7	0.77	
Huhtanen 1987	Control	6.63	0.650	0.676
	450 g/d*	6.64	0.566	0.604
	900 g/d*	6.57	0.543	0.584

* Means of sucrose and xylose infusions

Increasing the level of barley supplementation in the diets of sheep (Bøe 1989a) and of cattle (Jaakkola & Huhtanen 1990, unpublished) markedly depressed silage digestibility. Silage digestibility calculated as a difference decreased from 0.665 to 0.615 in sheep when the barley proportion of the diet increased from 0 to 550 g/kg DM. In cattle, the corresponding decrease was from 0.712 to 0.615 when the barley was increased from 250 to 750 g/kg DM. In cattle the depression in silage digestibility was curvilinear; when barley provided 500 g/kg of the diet, silage digestibility was only slightly lower than when it formed 250 g/kg of the diet. The results for the degradation of forage DM in the rumen also demonstrate the curvilinear effect of concentrate level on forage DM degradation (Fig. 1). In our study the adverse effect of increasing concentrate supplementation was similar for dried grass and silage, both cut at the same stage of growth. On the other hand, Udèn (1984) found in one study a greater depression in OM digestibility with increasing levels of concentrate for hay than for silage diets.

Effect of feeding level on associative effects

Most feed evaluation systems use digestibility coefficients determined at the maintenance level of feeding. According to van der Honing (1975) digestibility of organic matter depresses 0.03 units for each incremental increase in intake over maintenance. NRC (1988) adopted a corresponding value of 0.04 units. Even depressions of 0.06-0.09 units for each multiple of maintenance have been reported (Anderson et al. 1959, Rust & Owens 1982, Staples et al. 1984). The highest values have mainly been reported for corn-containing diets. In a digestion study with cows fed various proportions of corn-based concentrate at two levels of intake starch was also responsible for the depression of OM digestibility (Colucci et al. 1989). In cattle fed a hay-barley diet at 40 and 80 g/kg $LW^{0.75}$ the depression in OM digestibility was most closely linked to NDF fraction, and cell solubles (OM-NDF) accounted proportionally only for 0.17 of the depression in OM digestibility (Huhtanen & Kukkonen 1990, unpublished).

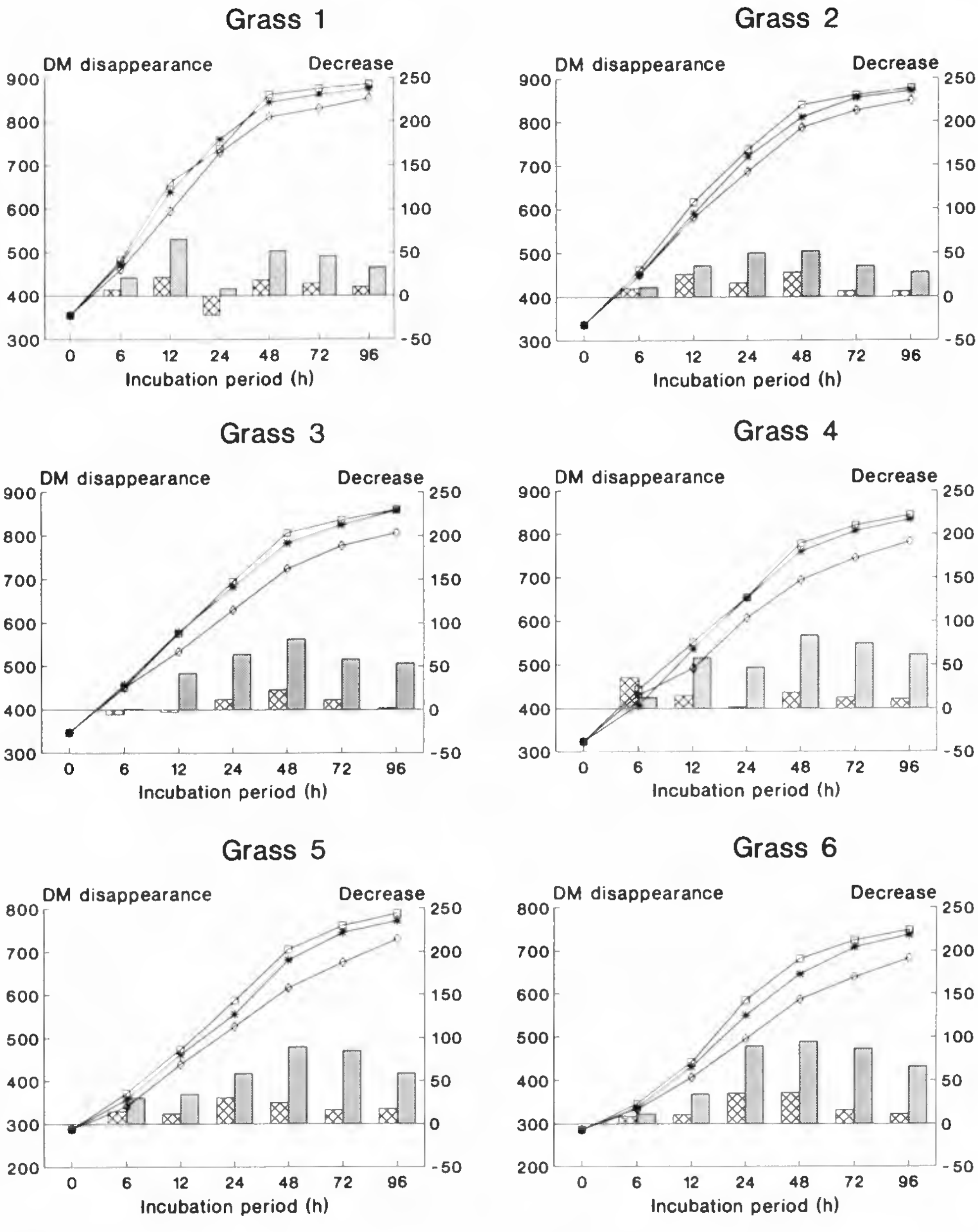

Fig. 1. The effect of concentrate level (□ 250, * 500 and ◇ 750 g/kg total DM) on DM disappearance (mg/g) of grasses at 7- day inteval (1 = early-cut,...6 = late cut) and the decrease in DM disappearance (mg/g) due to increased concentrate levels (▒ from 250 to 500 g/kg DM and ▩ from 250 to 750 g/kg DM).

Negative associative effects are not always observed, especially when the diets are offered at or below maintenance requirements (Fig. 2). The data in Fig. 2 demonstrate that there are no interactions between the quality of forage and the proportion of grain in the diet. Using the work conducted by Feedingstuff Evaluation Unit, Blaxter (1979) reported that there is no evidence for associative effects between the components of the diet, and that a unique ME value can be assigned to a feed irrespective of the other feeds which are given. Similarly, no interactions between the level of concentrate (250, 500 and 750 g/kg) and the type of forage were observed in ME value (see Thomas 1990).

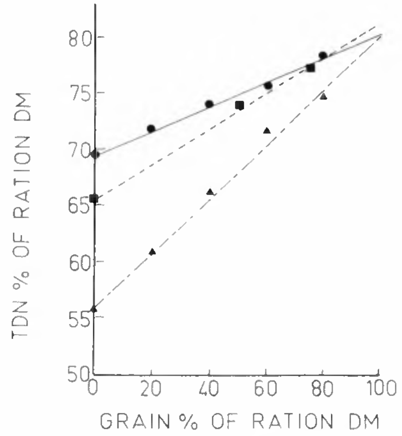

Fig. 2. Linear relationship between the proportion of grain in total DM and total digestible nutrients (TDN) in DM in steers fed at maintenance (● early-cut hay, ■ medium-cut hay and ▲ late-cut hay; taken from Tyrrel & Moe 1975).

The level of feeding appears to have a great influence upon whether associative effects occur; they have only been observed in those studies where the diets were offered above maintenance (Mould 1988). The negative associative effects can be very large at high levels of feeding (Fig. 4). The digestibility of all ratios, irrespective of proportion of grain, can become equal at an intake between four and five times maintenance (Wagner 1965; ref. Tyrrel & Moe 1975). The data from the study of Wagner (Fig. 3) imply that the digestive efficiency reached maximum at approximately 3.2 times maintenance with cows consuming 375 g/kg of grain. The additional benefit of increasing the proportion of grain in the diet was an increase in DM intake. Colucci et al. (1989) reported a greater depression in OM digestibility with increasing intake on high concentrate diet. The depression of OM digestibility for each multiple of maintenance was 0.020, 0.026 and 0.041 units for diets containing 200, 550 and 700 g/kg of concentrates in the total diet.

The negative associative effects are likely to be smaller with barley-based concentrates, because the digestibility of barley starch is not markedly decreased with the level of intake like maize starch (Sutton 1985). However, in dairy cows increasing concentrate supplementation has increased OM digestibility much less than would be estimated from digestibility coefficients determined at maintenance level. Despite a higher digestibility of concentrates than of forages, the digestibility of OM did not change when the amount of concentrate was increased (Krohn et al. 1984, Udèn 1984). Although the effects of feeding level and the level of concentrates were confounded in these studies, the results demonstrate the negative associative effects of feeds. The recent results of Murphy (1989) also showed that increasing the proportion of concentrate from 350 to 650 g/kg in dairy cows fed approximately 17 kg DM/d had no effect on OM digestibility; the intermediate level (500 g/kg) had slightly higher digestibility. Consistent with this, increasing the proportion of concentrate above 500 g/kg showed a very small effect on the digestibility of the total diet (Jaakkola & Huhtanen 1990).

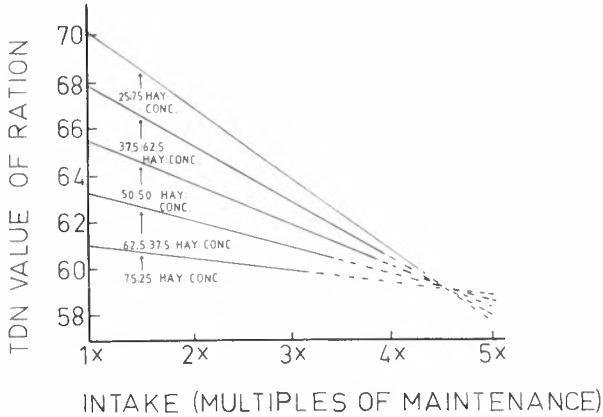

Fig. 3. Generalized figure of the interaction between proportion of hay to grain in the total ration and the rate of depression in digestibility (taken from Tyrrel & Moe 1975).

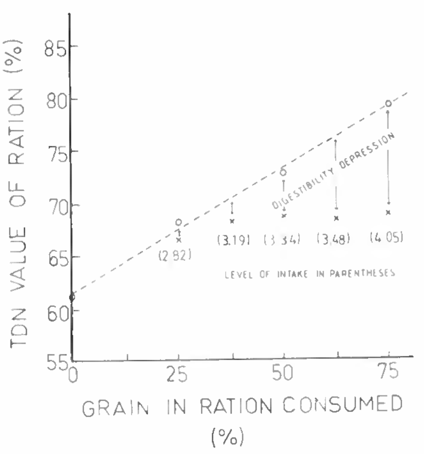

Fig 4. TDN value of the ration when fed to dry cows fed at maintenance (o) and when forage is fed ad libitum and concentrate to meet energy requirements of lactation (x). The number in parentheses is the average intake in multiples on maintenance (taken from Tyrrel & Moe 1975).

The more profound negative associative effects at high levels of intake may be related to changes in rumen environment, digesta retention time in the rumen or interactions between these two. With increasing intake of diets of a constant forage to concentrate ratio rumen pH decreases (Staples et al. 1984; Nørgaard 1987), and as a consequence critical pH for rumen cellulolysis is therefore more likely to occur at a high level of feeding. This also implies that more concentrate can be used at a low level of feeding while still maintaining optimal rumen pH for cellulolytic bacteria. At a high level of intake digesta retention time also is shorter, which reinforces the effect of lower pH on fibre digestion. With practical mixed dairy cow diets (300-650 g/kg concentrates of total DM) the changes in the two most important constraints of fibre digestion, rate of digestion and rate of passage, may lead to severe overestimation of energy intake when digestibility coefficients determined in sheep fed at maintenance are used.

Reduced ruminal fibre digestion at high levels of intake is compensated to some extent by increased postruminal digestion. However, this compensation is never large enough to account totally for the reduced rumen digestion. Potential digestibility of fibre entering the hind-gut is much lower than that of the original feed, and digesta retention time in the hind-gut is relatively short in animals fed at a high level. Administering the markers (CoEDTA, Cr-mordanted and Yb-labelled duodenal digesta particles) in the duodenum, the retention times of Co, Cr and Yb in the hind-gut were 7.4, 7.6 and 7.2 h in cattle fed at 1M and only 4.3, 4.4 and 3.9 h in those fed at 2M, respectively (Kukkonen & Huhtanen 1991). Similar retention time for liquid and particles indicates that there was no selective retention of digesta in the hind-gut. Further, if fibre digestion in the hind-gut is characterized by a similar lag phase as in the rumen, marked compensation for the reduced rumen digestion cannot be expected. The supply of both energy and protein to the host animal will be lower if the fermentation occurs in the hind-gut instead of the rumen, since microbial OM synthesized therein is not absorbed.

At a low level of intake the adverse effects of suboptimal rumen environment on fibre digestion can be compensated for by a longer digesta retention time in the rumen. For example, because of slower rate of passage the depression in NDF digestibility with the proportion of concentrate was less than could be expected from reduced rate of digestion in cattle fed approximately at 2M (Huhtanen & Jaakkola 1990). In cattle fed at 40 g DM/kg $W^{0.75}$ NDF retention time in the rumen was 98 h, and the total digestibility of the potentially digestible NDF was almost complete (Huhtanen & Kukkonen 1990, unpublished). Doubling the feeding level decreased retention time to 67 h, and as a consequence NDF digestibility decreased from 0.758 to 0.707 despite the unchanged rate of digestion. In other studies (Staples et al. 1984; Bøe 1989a) the rate of digestion of NDF or silage DM was also depressed with the level of feed intake, probably because of lower rumen pH.

Type of carbohydrate supplements

Soluble carbohydrates (sugars) affect fibre digestion even at reasonably low levels as discussed above. In cattle, barley can provide up to 400 - 500 g/kg of the diet without markedly depressing fibre digestion. At higher levels of concentrate a replacement of starchy concentrate (barley) with fibrous concentrate (sugar beet pulp (SBP)) in sheep has maintained rumen pH at a higher level and depressed cellulolysis less (Fahmy et al. 1984). However, in cattle fed on a grass silage-based diet (500 g/kg) a replacement of barley with unmolassed SBP or barley fibre had only minor effects on rumen pH and virtually no effect on DM degradation of forages (Huhtanen 1988, 1991a). These observations are not very surprising considering the very small effect of increasing the proportion of barley from 200 to 400-500 g/kg in cattle. At a high level of concentrate inclusion the depression in rumen pH and cellulolysis may be smaller with fibrous than with starchy supplements as indicated by greater forage intakes (Sutton et al. 1987; Phipps et al. 1987).

With a diet based on untreated straw, sugar beet pulp (SBP), dried grass or citrus pulp supplements have increased the rate of degradation of NH_3-treated straw *in situ* (Silva & Ørskov 1988). SBP also increased *in vivo* digestibility and intake of untreated straw but not of NH_3-treated straw (Silva et al. 1989). A concentrate based on SBP had no effect on the digestibility of ammonia-treated straw, whereas barley depressed the digestibility of straw from 0.559 to 0.393 (Istasse et al. 1986). Supplements of digestible cellulose and/or hemicellulose can be used to raise ME content of the diet without affecting or even stimulating the utilization of straw. Whether these effects can be obtained with high quality forages is uncertain, since they also contain highly digestible cellulose and hemicellulose.

Effect of forage quality

The depression in fibre digestibility may be greater with high quality than with low quality forages. Vadiveloo & Holmes (1979) proposed that the effect may be due to a higher content of soluble carbohydrates in high quality forages. Further supplementation would be more likely to depress rumen pH and consequently cellulolysis with early-cut than with late-cut forages. In practical feeding regimes this problem is probably of minor importance, since with high quality forages less concentrate is needed to meet the energy requirements of the animals than with low quality forages.

On the other hand, the decrease in forage digestibility with increasing feeding level was greater with late-cut than with early-cut ryegrass (Blaxter 1969). The reason for greater depression in digestibility with lower quality feeds is that the quantity containing nutrients for maintenance is greater with poor quality feeds and so an increase from 1M to 2M will involve a proportionally greater increase in total feed intake (Garnsworthy & Cole 1990). Also the higher cell wall content of mature grasses may be involved in the greater depression in digestibility, since the cell wall fraction accounted for nearly all the depression in DM digestibility of forages (Osbourn et al. 1974).

The digestibility of low quality forages may be depressed more than that of high quality forages when the rumen environment is changed by feeding more concentrates. Increasing the proportion of grass silage from 200 to 600 g/kg decreased the degradation of NH_3-treated straw but only minor effects were found in the degradation of grass silage (Fahmy & Sundstøl 1985; Bøe 1989b). In our study (Jaakkola & Huhtanen 1990, unpublished) the adverse effect of concentrate on forage DM degradation increased with the maturity of forage (Fig. 1). This may be due to the higher cell wall content in late-cut than in early-cut forages. Differences in rumen environment affect the digestion of cell wall carbohydrates more than that of cell solubles (OM-NDF). Sucrose supplements depressed NDF degradation markedly but had virtually no effect on the degradation of cell solubles (Khalili & Huhtanen 1991b).

Effect of animal species
Although a number of trials have been conducted to compare digestive efficiency of cattle and sheep, comparisons including diets consisting of different proportions of forage to concentrate, each diet fed at both maintenance and *ad libitum* intake are few. Data from Colucci et al. (1989) showed that the depression in digestibility of different feed fractions with increasing intake was greater for cows than for sheep. An increase in intake depressed the digestion of cell wall fractions and cell solubles including starch in cattle, whereas in sheep, an increase in intake reduced cell wall digestion and to a lesser extent cell solubles, without affecting starch digestion (Table 2). They concluded that the digestive physiology of these species is sufficiently different to preclude the use of sheep data in formulating nutrient requirements for cows.

On the other hand, when concentrate forms more than 400-500 g/kg of the diet, the rate of forage degradation in the rumen seems to be more depressed in sheep than in cattle. In sheep, large depressions have been observed with increasing levels of barley in the diet (Chimwano et al. 1976; Mould et al. 1983; Fahmy et al. 1985; Bøe 1989a), while in cattle the effect has been much smaller (Fahmy & Sundstøl 1985; Bøe 1989b; Jaakkola & Huhtanen 1990, unpublished). Although direct comparisons cannot be made, the results indicate that when the concentrates provide up to 500 g/kg the depression in forage degradation is fairly small in cattle but quite large in sheep. These differences may be related to the animals' ability to buffer increases in rumen acidity as indicated by large differences found among sheep in bromegrass degradation at high levels of concentrate (Franklin et al. 1981). In addition to possible differences between animal species, there are also many other sources of error in estimating the associative effects of the components of diets by nylon bag technique. For example, the results may be biased because the microbial population (Meyer & Mackie 1986) and particle-associated enzyme activities (Huhtanen & Khalili 1989) within the bags are different from those in the surrounding digesta.

Fat supplements
Non-additivity has also been observed when fat supplements are included in ruminant diets. The higher energy content of fat compared to carbohydrates and the possibility of manipulating milk fatty acid composition have made them attractive supplements. However, added fats in excess of 20-30 g/kg are inhibitory to rumen microbial activity, especially to cellulolytic organisms (Palmquist 1988). The effects of fats on fibre digestibility have been variable (for reviews see: Palmquist & Jenkins 1980; Børsting & Weisbjerg 1989)). The extent of the depression in fibre digestion depends on the amount, degree of saturation and form (free oil, free fatty acids, oilseeds; unprotected vs. protected) of fat supplements, type of the basal diet, method of feeding, and animal (sheep, dairy cow). Removing starch from the diet by lipid supplementation has sometimes even improved fibre digestibility (Palmquist & Conrad 1978).

Although it has been suggested the depressive effect of fat supplements on fibre digestion is smaller in dairy cows when rumen retention time is shorter and overall fibre digestibility lower than in sheep, large decreases in NDF (Murphy et al. 1987) or DM (Mohammed et al. 1988) digestibility were observed in dairy cows in response to feeding crushed rapeseed (2 kg/d) or soybean oil (40 g/kg). As a consequence of depressed fibre digestion fat supplements have decreased voluntary intake (Clapperton & Steele 1983;

Steele 1985; Mohammed et al. 1988) and the increases in ME intake have been smaller than expected from the higher energy density of the diet. On the other hand, theoretical calculations (Kronfeld 1976) suggest that the addition of fat in the diet could improve the efficiency of ME utilization for milk fat synthesis.

Table 2. The effects of feeding level and proportion of concentrate (LC = 200, IC = 450 and HC = 700 g/kg total DM) on digestibility of nutrients in sheep and cows (Colucci et al. 1989).

	Sheep					
	Low intake			High intake		
	LC	IC	HC	LC	IC	HC
Organic matter (g/kg BW)	14.3	13.2	12.2	27.2	29.7	27.6
Digestibility						
DM	0.665	0.747	0.823	0.641	0.702	0.772
Energy	0.652	0.732	0.814	0.623	0.684	0.760
NDF	0.532	0.564	0.618	0.496	0.482	0.479
ND solubles	0.778	0.853	0.897	0.766	0.826	0.870
Starch	0.995	0.998	0.994	0.981	0.982	0.995
	Cattle					
	Low intake			High intake		
	LC	IC	HC	LC	IC	HC
Organic matter (g/kg BW)	12.9	12.0	11.1	30.6	33.4	32.9
Digestibility						
DM	0.657	0.717	0.799	0.610	0.643	0.685
Energy	0.648	0.714	0.800	0.584	0.619	0.669
NDF	0.527	0.534	0.662	0.468	0.420	0.402
ND solubles	0.770	0.825	0.853	0.736	0.759	0.774
Starch	0.995	0.982	0.986	0.929	0.904	0.902

ASSOCIATIVE EFFECTS IN ME/DE RATIO

Although the digestibility of energy accounts for most of the variation in the ME content of a feed, changes in methane production can also affect ME value. Within the range of inclusion of dietary components, the changes in rumen fermentation pattern are not always linear and depend on feeding level (Broster et al. 1978). As a consequence of these non-linear changes in rumen fermentation pattern there can be associative effects between dietary components in methane production. For example, including small amounts of polyunsaturated fats in the diet markedly depresses methane production (Czerkawski 1969). The use of feed additives (eg. monensin, salinomycin, avoparsin) can increase the ME content of a feed by decreasing rumen acetate to propionate ratio, thereby decreasing methane production and increasing metabolizability of DE. Monesin addition to concentrate-based diets (500-700 g/kg) has decreased methane production from 15 to 31% (Garret & Johnson 1983). However, with forage diets the effect of monensin on methanogenesis is smaller or absent.

INTERACTIONS IN THE UTILIZATION OF ME

In simple-stomached animals it is still uncertain if the composition of absorbed nutrients affects utilization of ME. In ruminants, however, it is generally recognized that heat production from similar amounts of ME is greater from a diet based on roughage than from one based on concentrates (Ørskov & MacLeod 1990). Especially the utilization of energy of acetate for fattening has varied largely (see Thomas 1988). It has been suggested that the low values occur only when the supply of glucose or glucose precursors from the basal diet is restricted (see MacRae & Lobley 1982). Consistent with this, Tyrrel et al. (1979) found inefficient use of acetate (0.27) when the diet consisted solely of hay, but more efficient use (0.69) in animals given a hay-concentrate (30:70) diet.

More efficient utilization of acetate when given as a supplement to concentrate feeds suggested the presence of a factor in concentrate diets which potentiates acetate utilization (see MacRae & Lobley 1982). Reduced NADP, derived mainly from glucose metabolism, is essential for biosynthesis of fatty acids. Propionate is considered to be the most important precursor of glucose. Consequently, on roughage diets rumen fermentation creates an excess of acetate relative to propionate. If the latter is insufficient to provide adequate $NADPH_2$, then acetate may be converted to heat to prevent metabolic excess. Also an adequate supply of amino acids could spare propionate for production of $NADPH_2$ to permit more efficient utilization of acetate (MacRae & Lobley 1982).

Consistent with this, MacRae et al. (1985) observed a greater utilization of ME above maintenance when spring-harvested grass (SHG) was given (k_f 0.54) than when autumn-harvested grass (AHG) was given (k_f 0.43). They suggested that greater incremental absorption of amino acids in sheep given SHG was associated with improved energy utilization. Abomasal infusion of casein improved the utilization of AHG from 0.45 to 0.57 suggesting that the supply of amino acids can influence the efficiency of ME utilization in sheep given a forage diet where the rumen acetate:propionate ratio is high (MacRae et al. 1985).

Large responses to protein supplementation in the energy retention of cattle given straw diets (with or without barley) were observed by Ortiques et al. (1989). The greater energy retention in response to both barley or fish meal supplementation was related to increased absorption of amino acids. Also with a silage diet, fish meal supplementation improved the efficiency of energy utilization (Gill et al. 1987), suggesting an improved balance of absorbed nutrients as compared with silage alone. Fish meal increased the rates of protein accretion without any effect on fat accretion. The mean increase in energy retention was 0.88 MJ/MJ increase in DE intake, a value considerably higher than the theoretical maximum of the use of DE for growth. Also calculations of the efficiency of energy utilization of grass silage-based diets for dairy cows showed consistent increases in k_{l0} (efficiency of ME utilization at zero energy balance) in response to protein supplementation (Chamberlain et al. 1989).

The efficiency of utilization of silage ME has been lower than predicted from ARC (1980) equations (see Thomas & Thomas 1985, Thomas et al. 1988). Substitution of late-cut silage with rolled barley increased energy retention and the efficiency of ME utilization for growth (Table 3). The values for late-cut silage with a high level of barley were higher than those for early-cut silage alone despite the higher intake of ME with early-cut silage. The increase in energy retention was 0.85 MJ/MJ increase ME supply in response to 560 g barley in the diet DM, suggesting a positive associative effect between the components of the diet. However, the supply of absorbed non-ammonia N/MJ ME was greater with silage diets (Beever et al. 1988). This implies that a limited supply of amino acids was not the reason for the low efficiency of ME utilization with unsupplemented silage diets. The low k_f for silage diets may be related to the proportion of ME derived from digestible cell walls (Thomas et al. 1988) or to the extent or type of silage fermentation (Thomas & Thomas 1985). Accordingly, high liveweight gains, approximately 1 kg/d, were achieved with high quality silage as the only feed (Lampila et al. 1988). The carcass classification data showed no trend towards higher protein to fat ratio, rather the reverse was true. The silage used by Lampila et al. (1988) had much lower concentrations of fermentation products than that used by Thomas et al. (1988). Similar liveweight gains with SBP (Jaakkola & Huhtanen 1990b) or with barley fibre (Huhtanen et al. 1989) as compared with barley supplements in cattle given grass silage-based diets do not support the concept that there is an inverse relationship between the efficiency of ME utilization and the proportion of ME derived from digestible cell walls. The lower utilization of digestible cell walls from forage may be related to greater work of digestion (Ørskov & MacLeod 1990). The review and summary by ARC (1980) showed that there were no differences in the utilization of ME between roughages and concentrates when roughages were ground and pelleted.

Table 3. Energy utilization by cattle given early-cut silage (H) or late-cut silage alone (L) or with 260 g barley DM/kg total DM (LC1) or 560 g barley DM/kg total DM (LC2) (Thomas et al. 1988; Beever et al. 1988).

Diet	H	L	LC1	LC2
Digestibility				
Gross energy	0.735	0.619	0.668	0.705
NDF	0.798	0.653	0.610	0.562
Intake				
DM (kg/d)	6.21	5.96	6.13	6.31
ME (MJ/d)	73.5	58.9	65.3	69.6
Absorbed NAN g/MJ	1.47	1.33	1.17	1.23
Gain (g/d)				
Live-weight	661	369	582	798
Empty-body-weight	696	292	552	800
Carcass	504	243	443	587
Fat	260	121	189	302
Protein	86.9	31.1	76.0	116.1
Energy (MJ/d)	12.24	5.48	9.23	14.58
Energy utilization				
Observed k_f	0.33	0.26	0.33	0.46
Predicted k_f	0.49	0.41	0.45	0.47
Proportion of ME from digestible cell walls	0.42	0.55	0.39	0.26

Small positive associative effects in milk yield were observed when the concentrates were comprised of different types of carbohydrates than when the corresponding ingredients were fed alone. The mean response in three trials (Huhtanen 1987b; 1991b; Huhtanen et al. 1988) to more complex mixtures of concentrates was 0.65 kg milk/d. In a later study the cows given a concen-trate comprised (g/kg) of barley (200), oats (200), SBP (240) wheat bran (120), barley fibre (120), potato pulp (60) and dried grass pellets (60) produced more milk than those given barley alone despite approximately 15% higher energy value of barley (Table 4). There was also a trend towards an interaction between the type of concentrate and protein supplementation. The results demonstrate quite clearly that the balance between absorbed nutrients can markedly affect production response or nutrient partitioning.

Energy balance experiments also have shown that the productive value of a mixed diet is often greater than the mean of the ingredient feedingstuffs (Moe et al. 1972). Although the full explanation of this associative effect is not clear, it is likely that at least a portion of the effect is due to nutritional imbalances in one or both ration components. When the diets are comprised of carbohydrates fermented at different rates in the rumen, better synchrony in the supply of absorbed nutrients may enhance energy utilization.

The net energy (NE) values of some feeds can vary with the level of inclusion in the diet. For example, the NE value of molasses decreased approximately 50% when the proportion in the diet was increased from 100 to 250 or 400 g/kg in steers and from 100 to 300 g/kg in dairy cows (Lofgreen & Otagaki 1960a, b). Soluble carbohydrates are rapidly fermented in the rumen possibly leading to temporal imbalances in nutrient supply. The importance of a constant supply of energy was provided by Robb & Reid (1972) who found a greater efficiency of the utilization of energy of acetate and glycerol with continuous infusion than when they were infused over a 1-h period after feeding.

Table 4. The effects of carbohydrate composition of the supplement (B = barley, F = fibrous supplement; see text) and protein supplementation (N = no protein supplement, P = 1 kg of concentrate replaced with fish meal/d) in dairy cows given grass silage ad libitum (Huhtanen 1990, unpublished).

	Diet			
	BN	BP	FN	FP
Intake				
Silage (kg DM/d)	10.76	10.36	11.00	10.96
Total DM (kg/d)	18.97	18.89	19.27	19.46
ME (MJ/d)	218	218	211	215
FU/d	15.82	16.00	15.12	15.52
Production				
Milk (kg/d)	24.1	26.6	26.1	27.6
Fat (kg/d)	1.00	1.09	1.06	1.08
Protein (kg/d)	0.75	0.85	0.79	0.87
Lactose (kg/d)	1.15	1.26	1.25	1.32
Energy (MJ/d)	78.2	86.0	83.1	87.3
Live weight change (kg/d)	-0.05	0.39	-0.03	0.37

Taken together, these results demonstrate that to sustain predictable rates of carcass gain and milk production a more integrated approach to the description of nutrient allowances is needed. The results also show that in addition to digestibility, there are interactions between the components of the diet in the utilization of ME. These interactions can not be predicted by any of the current feed evaluation systems

PRACTICAL ASPECTS OF ASSOCIATIVE EFFECTS ON FEED EVALUATION

There is evidence of both positive (protein supplements, digestible cellulose and/or hemicellulose) and negative (easily fermentable carbohydrates, fat supplements) associative effects of feeds. Both of these are more likely to occur at high than at low levels of feeding. Depressions in the rate of digestion will affect ruminal cell wall digestion more when the feed intake and passage rate are high. Together with the effect of feeding level, negative associative effects of the components of the diet can result in a much lower digestibility in dairy cows at high level of feeding than that predicted from coefficients determined in sheep fed at maintenance. As a consequence of negative associative effects, much of the potential increase in DE intake from concentrate addition is lost when the intake of concentrate is increased; the major factor causing greater energy intake is intake per se. For example, it can be calculated from the results of Jaakkola & Huhtanen (1990) that the increase in DE intake was only about 0.25 the expected increase when the proportion of concentrate was increased from 500 to 750 g/kg diet. The corresponding value was 0.85 when the concentrate formed 250-500 g/kg diet. Similar effects may be observed with fat supplements; the increase in observed energy content of the diet is smaller than expected because of depression in fibre digestion.

It may be difficult to take these effects in feed evaluation or ration formulation into account because the extent of depression in the digestibility under different feeding regimes may be variable and unpredictable. However, the magnitude of negative associative effects may be of considerable importance (e.g. in a recent study of Tesfa (unpublished) supplementation of grass silage-based diet with rapeseed oil depressed NDF digestibility from 0.768 to 0.667 in cattle). Although there are many sources of error in predicting associative effects of the components of the diet, omitting them totally may lead to an even greater error in feed evaluation and ration formulation.

The changes in balance between protein and energy-yielding nutrients can cause marked deviations from predicted rates of carcass gain or milk production. A more integrated approach to description of nutrient allowances than is currently used will be needed. Protein and energy allowances should be considered together, not separately. Partitioning of energy (e.g. body tissues vs. milk, protein vs. fat accretion), which is crucial in determining animal performance, cannot be predicted from current systems. Partitioning of nutrients can be changed by manipulating the proportions of absorbed nutrients or by a number of growth and production-promoting substances.

Because of interactions between the components of the diet in both digestion and metabolism, the current feed evaluation systems cannot always predict the production level, in particular with rations which do not guarantee optimal rumen function. At present, feed evaluation systems should provide evidence of the potential nutritive value of feed. The ration fed and feeding level will determine whether the animal is able to make full use of it. The effects of feeding level and associative effects between the components of the diet on digestibility may be integrated into current feed evaluation systems. Other aspects, i.e. interactions in metabolism of absorbed nutrients and nutrient partitioning are difficult to include in current feed evaluation systems, and possible effects may be taken into account only in ration formulation. In the future, models of digestion and metabolism should result in new systems which can predict the feeding value of a feedstuff under variable conditions and which can also predict animal performance more accurately than the current systems.

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5 Analytical methods for energy evaluation

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Any determination of the energy value of a feed is based on a number of chemical or biological analytical methods. These methods must be biologically relevant as well as have a certain predictive reliability, and they must be standardized to allow comparisons within and between countries. In the present paper some of the many possible analytical methods involved in energy evaluation are discussed and common Nordic standard methods are suggested for the determination of *in vivo* digestible energy; dry matter, ash, crude protein, crude fat, long chain fatty acids, and NDF contents; enzymatic, *in vitro* and *in sacco* degradation of the feed.

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All energy evaluation systems are reliant on a number of analytical methods to describe the feed. The aim of this paper is to overview the analytical methods used for energy evaluation and also to suggest common methods for future energy evaluation within the Nordic countries.

Virtually all energy evaluation systems used in Europe are based on the Weende analytical system of Henneberg & Stohmann (1860). The analyses required are dry matter (DM), ash, crude fibre, crude fat and crude protein. The Weende system is essentially based on the solubility of chemical fractions in different solvents. During the considerable time that has elapsed since the introduction of the system, many modifications of the analytical procedures have been applied. For example, there is the use of different solvents for crude fat analysis and even the general inclusion of hydrolysis prior to extraction (e.g. the EC method). Another example is that of crude fibre analysis, where a change from inverse to direct filtration through sintered glass filters (Tecator AN 01/78) gives slightly altered values. Even the simple determination of ash content is done differently. Ashing temperatures from 500 to 700°C have been reported which will certainly lead to differences in the analytical results. Finally, the chemical definition of NFE, if at all meaningful, is completely dependent on the other analytical procedures used. Thus, in addition to the need for relevant analytical methods, there is an obvious need for improvement and standardization of the methods chosen.

The Weende method has been criticized for many years, but has survived because of the great experience gained with it. It may also be argued that the system works reasonably well, at least when feeding within the normal practical range. Furthermore, known errors have been eliminated by means of special corrections or rules which vary among countries.

ENERGY VALUE DETERMINED *IN VIVO*

The energy value of a feed is not a property directly dependent on its chemical composition, but is rather a product of its chemical structure and the digestion of the animal. The relationship between chemical composition and energy value must therefore be determined by means of animal experiments. Techniques for digestibility experiments have been extensively reviewed by Schneider & Flatt (1975). In the Nordic countries digestibility experiments on ruminants are mostly and routinely carried out on sheep. Animals are fed the near maintenance requirement of energy and total collection of faeces is made for 10 days after an adaptation period of 10-11 days. The proposed standardized method for the determination of digestible energy (DE), the suggested common energy evaluation base in the Nordic countries, is as follows:

Animals: 3-4 castrated male sheep (wethers) of at least 1.5 years of age.

Feeding: 900 g total feed/day fed twice daily. (Maintenance requirements for sheep in metabolic crates can be estimated calorimetrically to be approximately 0.12 live weight(kg) + 1.2 MJ digestible energy per day (calculated from Lindgren & Lindberg 1988). Wethers weighing 70-80 kg require 9.6-10.8 MJ/ day, which is provided by 900 g if it contains 11-12 MJ DE. This corresponds to a normal to low quality forage. Feeding 900 g/day of a wide range of rations will provide energy for 0.9 to 1.2 times the maintenance requirement).

Feeds: Individual meals are weighed (within 1 g accuracy) for the entire experiment before commencing. Samples should be taken throughout weighing; they should be immediately prepared and then analysed for DM content. Temperature during pre-drying should not exceed 60-70°C. Animals are fed twice daily.

Preperiod: 11 days

Collection: 10 days collection of total faeces, once daily.

Live weight: Animals are weighed before and after the collection period.

Analysis: Gross energy in feeds and dried faeces is determined by direct calorimetry in a bomb calorimeter. Gross energy in silage may be determined on fresh samples with plastic foil as a primer or on dried samples. Dry samples must be corrected for losses of volatile energy sources during drying.

Digestible energy can also be calculated from digested nutrients, as made in for example Denmark (Möller et al. 1989):

$DE = 24.23\ D_{cp} + 34.11\ D_{cfat} + 16{,}99\ D_{NFE} + 18.50\ D_{cfibre}$ (minus 0.77 sugar if the sugar content exceeds 200 g kg^{-1} DM, where D_{cp} is digestible crude protein, D_{cfat} digestible crude fat, D_{NFE} digestible nitrogen free extractives and D_{cfibre} digestible crude fibre.

ENERGY VALUE PREDICTED USING LABORATORY METHODS

Principally two methods have been used for predicting the energy value of a feed. In the first, and most widely used method, it is calculated from table values for digestibility of nutrients and standard energy constants for each nutrient. The constants used in different European countries are given in detail by de Boer & Bickel (1988). There are no large differences between the constants. In general, the energy values for NFE, crude fibre, crude fat and crude protein are related 1 : 0.8-1 : 1.9-2.6 : 0.9-1.4 , respectively. The values have been obtained by regression against results from *in vivo* experiments although the constituents used are not independent variables.

The second method employs direct regression of only one constituent against the energy value measured *in vivo*. This has not been very successful for chemical constituents like crude fibre, but is superior when using more biologically related analyses. There exist several useful relationships between *in vivo* and *in vitro* digestibility (e.g. Tilley & Terry 1963; Möller et al. 1989; Lindgren 1979), enzymatic degradation (Jones & Hayward 1973; Dowman & Collins 1982), and even *in sacco* degradation (Aerts et al. 1977; Karlsson 1986) .

The precision of any estimated energy value is mainly determined by the biological relevance of the analysis made. Biological methods, like the *in vitro* methods, are more closely related to ruminant digestion than the Weende analysis system and therefore give a better prediction of the energy value of roughages. Other problems occur with *in vitro* methods, notably interactions between method and feed caused by the more complex biological analysis. In all cases standardized methods are required for obtaining reliable results. The analytical methods used within the Nordic countries are similar even although certain differences do occur. One example of this is the use of a one-stage *in vitro* method (den Braver & Eriksson 1969) in Sweden.

Most of the variation in true digestibility is due to the fibre fractions of the feed, and analytical methods exist for determining the fibre content/quality for the purpose of energy evaluation. Crude fibre is not chemically definable. During acid and alkaline extractions, the hemicellulose, some of the cellulose and a variable part of the lignin are dissolved. There are more accurate methods for the determination of various polysaccharides but these are often very expensive and time-consuming. Very few methods are simple enough to serve as routine methods. The most common are NDF and ADF (Van Soest 1963; Van Soest & Wine 1967,1968).

NDF contains most of the hemicellulose, all of the cellulose and, provided no sodium sulphite is used in the analysis, lignin. Starch containing feeds must be pretreated with amylase, since starch is only partly soluble in the detergent solution (Robertson & Van Soest 1977). Determination of NDF gives a reasonable estimate of the cell-wall content in most feeds.

ADF gives an estimate of lignocellulose and may, after oxidation and removal of lignin, or alternatively, removal of cellulose after treatment with 72% sulphuric acid, be divided into these two fractions. The ratio of lignin to ADF is related to fibre quality and thus also to digestibility. The predictive strength is limited, however.

The inherent precision of the predicted energy values will vary with the analytical methods used and with the type of feed. Therefore no single analytical method can be devised for the evaluation of all types of feed. Relevant information on feeding value is given by the contents of DM, ash, crude protein, crude fat or fatty acid composition and NDF. It could be argued that analysis of highly digestible nutrients such as starch and sugars could also provide useful information. The analytical methods used, reviewed by NJF (Åman et al. 1987) are comparatively complicated and generally show lower analytical reproducibility when compared with the methods mentioned above. It is therefore suggested that highly digestible nutrients should in future be calculated as a residue. Biological methods are recommended for fibre-rich material and feeds where the nutritional quality of fibre varies.

SUGGESTED STANDARD METHODS

Chemical methods

Dry matter (ISO 6496). The determination is made gravimetrically as loss of moisture during drying at 103 ± 1°C for 4 h. Further drying for 2 h should not yield a difference exceeding 0.2% of DM. Fatty samples should be dried at 130°C for 30 min. The sample size should not be larger than an 0.3 g/cm^2 crucible and the sample is dried in a well-ventilated oven with a maximum of one sample per litre of volume. This general method cannot be used for all feeds. For example molasses, which is mixed with sand and vacuum-dried at 65°C for 20 h (Norway) or at 80°C (Denmark). Also silages and other fermented products need other methods since drying inevitably will result in loss of DM. Dry matter can be accurately determined by distillation with toluene (Dewar & McDonald 1961) provided the water content of the distillate is determined. More common is drying at 80°C for 20 h or a correction of losses of DM from analysis of volatile fatty acids. In Sweden 1.4 percentage units is added to the results of normal drying, which gives a reasonable estimate reflecting higher relative loss in wet and thus generally more fermented silages.

Ash content (ISO 5984). Ashing is done after charring by ashing at 550 ± 5°C for 3 h in a preheated oven. If the resulting ash contains visible carbon, the ashing is continued for another hour. If it then still contains carbon, the ash is moistened with water, dried and finally ashed for one hour.

Crude protein (NMKL No 6, 1976). The determination of nitrogen according to the Nordic Committee on Food Analysis agrees with the international standard (ISO 5509) as well as with the EC standard (Official J. of the EC, No. 123, 1972, 9-11). The Nordic standard is based on the use of Cu as a catalyst, whereas the others also allow Hg, which cannot be recommended for environmental reasons. The Nordic standard allows a range of different types of equipment to be used.

Crude fat (Official J. of the EC, No. 15, 1984, 29-30, Method B). The sample is hydrolysed in diluted HCl, washed and dried before extraction with petroleum ether.

Long chain fatty acids (Preparation of methyl esters of fatty acids, ISO 5509, 1978). In this method the methyl esters of fatty acids with six or more carbon atoms are prepared. It is applied to all kinds of feeds. An internal standard is included to enable quantitative determination by gas chromatography.

NDF (Goering & Van Soest 1970). The sample is extracted with a buffer - detergent solution at pH 7. The residue is determined gravimetrically.

Biological methods

ENZYMATIC DEGRADATION. Proposed standard method used in EC, modified from Jones & Hayward (1973): A test sample (0.5 g) is incubated together with 50 ml pepsin/HCl (pepsin diluted 1:10 000; 2 g of this is made up to 1 l with 0.1 M HCl) for 24 h at 39°C, transferred to a waterbath (80°C for 0.5 h) and filtered. This is followed by incubation with amylase/cellulase (2 ml amylase + 10 g BDH-cellulase is made up to 1 l with 0.2 M acetate buffer, pH 5) for 24 h at 39°C. All incubations are done in the same filtration tube (porosity 1). Concentrates are extracted in the cold with petroleum ether 40/60 for 15 min in the same tubes before incubation with pepsin (van der Meer 1985).

IN VITRO DEGRADATION. Standard procedure of Tilley & Terry (1963). A test sample (0.5 g) is incubated with 10 ml of strained rumen fluid and 40 ml of a buffer (McDougall 1948) for 48 h at 38-39°C. Centrifugation or filtration is followed by a second incubation with pepsin-HCl (2.0 g pepsin 1:10 000 is made up to 1 l with 0.1 M HCl) for 48 h at 38-39°C. After centrifugation (or filtration) and drying the residue is weighed.

IN SACCO DEGRADATION. Standard procedure for protein degradation used within the Nordic countries in accordance with the EC regulations. The standard method has not yet been published but was presented by Dr John Oldham at a CEC-EAAP seminar in Brussels in 1986. The method can be summarized as follows:

Bag specification: Bags are made from polyester with a mean pore size of 35-40 μm. Sample size should be 10-15 mg per square centimetre of bag. Bag dimension should be 1:1.5.

Sample preparation: Samples should be dried only when containing more than 15% water. They should be milled to pass through a 1.5 mm screen.

Animals, replication: Three mature cattle fed near maintenance requirement for energy. The animals are fed two parts grass hay to one part concentrate. The concentrate should contain a minimum of 13% crude protein and should contain as many different feedstuffs as possible. Duplicate bags are placed in the rumen for each of the following incubation periods: 0, 2, 4, 8, 16, 48 h (72 and 96 h may be used for roughages). Bags are inserted at feeding time.

Washing: Bags are washed in cold water for 10-15 min. A washing machine is preferred.

Rate of passage correction: In the calculation of effective protein degradation, dilution rates from 2 to 8 %/h are used. For energy evaluation this matter needs further discussion, since the dilution rate of organic matter will vary even more than for protein depending on the level of feeding.

The results of the methods described are all calculated as digestion coefficients. Dry matter, organic matter or even gross energy can be used as the basis for the calculations. Organic matter is preferred over DM because of the variation in energy-free ash in feeds. Degradable NDF is also a constituent that could be used for the evaluation of fibre quality. All methods have to be calibrated against results from *in vivo* experiments as described above.

NIR analysis

NIR analysis is a method that usually accurately predicts analytical results or *in vivo* performance from spectral data (e.g. Helläkäki & Moisio 1983; Lindgren 1988; Kjos 1989). The technique has no accuracy in itself. The result is totally dependent on the quality of the reference analysis or animal experiment and the sample matrix used for calibration. This fact leads to the conclusion that standardization is difficult. There are, however, two alternatives, namely universal calibrations and regular interlaboratory ring tests on defined materials. Both approaches are feasible, although universal calibrations tend to be more static and resistant to development.

The NIR technique enables us simultaneously to predict many constituents or characters of the feed that would be impossible to predict in practice with conventional methods. This is a desirable characteristic and the method provides a challenge in the future search for new and more dynamic systems for feed evaluation.

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6 A new approach to feed evaluation for ruminants

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Existing feed evaluation systems are based on empirical relationships and static models. However, digestion and metabolism are dynamic processes. Feed efficiency and product composition varies in relation to changes in feeding level and composition of the diet. Therefore, future feed formulation systems should be based on mechanistic and dynamic models that are descriptive of ruminant nutritional physiology. A model for calculating "truly" digested energy is proposed. This is a simplified model based on the assumptions of first-order kinetics (fractional rate constants and steady state conditions) of digestion and passage. The model calculates "truly" absorbed energy from predicted amounts of absorbed volatile fatty acids (VFAs), amino acids and long chain fatty acids (LCFAs). Production is calculated by means of values for efficiency of utilization of metabolizable energy. Effects of feed level and ration composition on absorbed amounts of nutrients are included in the model. The proposed model is not yet ready for use and has not been validated against experimental results. The need for further research is discussed.

Keywords: Digestion, feed evaluation, ruminants.

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Feed evaluation systems have until now been based mainly on empirical relationships rather than on mechanistic and descriptive models of ruminant physiology. Also most existing energy evaluation systems are built on a chemical fractionation (the proximate analysis) which is not satisfactorily related to the different ways of digestion and utilization of the various fractions of the feeds. The purpose of feed evaluation is to describe relationships between intake of feedstuffs on one hand and maintenance, growth and production on the other. In traditional feed evaluation systems fixed energy values are ascribed to feedstuffs and fixed requirements to given productions. However, input-output relationships in animal production are often subject to the law of diminishing returns, and feed utilization and product composition vary in relation to changes in feed composition. Therefore, it is necessary to change from systems with fixed requirements to systems for prediction of responses. Simple empirical equations have been developed to describe the relations between intake of concentrate and milk production, feed units and milk production, protein and milk production, and fat and milk production (Østergaard & Neimann-Sørensen 1983). Such simple equations have a limited validity.

PRINCIPLES OF A FUTURE FEED FORMULATION SYSTEM

A future system for feed planning should be capable of predicting voluntary feed intake, absorption of nutrients (volatile fatty acids (VFAs), longer chain fatty acids (LCFAs), amino acids and glucose) from the digestive tract, partitioning of absorbed nutrients between milk and various body tissues, and growth and production of milk components.

The term, "System of feed evaluation" is not an appropriate one for such a system. We would prefer to call it a "feed formulation system". In such a system more emphasis will be placed on the characteristics and reactions of the animals instead of just on the value of feedstuffs.

The digestion and metabolism of various nutrients in the digestive tract are so interdependent that the digestion should be regarded as one coherent process. It means that the system cannot be separated into energy evaluation and protein evaluation, as is the case in existing systems. This is especially so for ruminants, where the greater part of the feed is metabolized through microbial fermentation in the forestomachs.

Digestion and metabolism are dynamic processes and therefore time dependent (amount per time unit). For instance, rate of fermentation and rate of passage are important determinants for the amounts of nutrients absorbed from the digestive tract. These rates may be strongly affected by the feeding level, by the composition of the total diet, and by the principles of feeding.

Similarly, the internal metabolic processes in the body of the animals are dynamic and subject to great variation in relation to the amount and composition of absorbed nutrients. This variation determines the distribution of absorbed nutrients between milk production and growth of various tissues.

The systems of feed evaluation used until now have been based on static models. Such models cannot take the variation in digestion and metabolism into consideration. In order to obtain a satisfactory prediction of animal performance it is necessary to use models which are more descriptive of animal physiology.

Comprehensive work has been carried out on developing models that simulate ruminant digestion and absorption (e.g. Waldo et al. 1972; Baldwin et al. 1977; Mertens & Ely 1979; Beever et al. 1980-81; Black et al. 1980-81; France et al. 1982; Mertens & Ely 1982; Murphy et al. 1986; Baldwin et al. 1987b; Mertens 1987; Allen & Mertens 1988; Dijkstra & Neal 1990). Some of these are simple models describing only a few important mechanisms involved in the process of digestion of fibres, while others are much more complicated models with many physical and biochemical details. Similar simulation models are created for metabolism in body tissues and organs and for the digestive and metabolic functions of the whole animal (e.g. Koong et al. 1982; Baldwin & Bauman 1984; Baldwin et al. 1987a; Danfær 1990).

This ruminant modelling has not been made primarily for providing new systems for practical feed formulation, but it may be used as a means for development of such systems (Danfær 1990). A beginning has been made with new protein evaluation systems, which include mechanistic statements (INRA 1978; Madsen 1985).

The following objectives or criteria are proposed for a system for practical use:

- The system should be based on mechanistic or dynamic rather than empirical models and make systematic use of as much of the existing knowledge about the dynamic processes of digestion and metabolism as possible.

- The system should be based on measurements or estimates (chemical composition, digestibility, degradability, structure, etc.) that are robust and can be obtained as a routine and for an acceptable price by farmers and feed compounders.

- The model should be the simplest possible presentation that can fulfil the desired function.

- Only those variables and descriptions of mechanisms that increase precision of predictions should be included in the model.

- When tested on results from production trials the new system should prove to be better than existing systems.

- The system should be primed for easy inclusion of new knowledge.

- The description of the system should provide information about what can be satisfactorily predicted by the system.

The first goal would be to derive a system for prediction of the true absorption of nutrients (or maybe energy) from the digestive tract. The absorption of LCFAs (Børsting & Weisbjerg 1989) and of amino acids (Hvelplund & Madsen 1990) may be predicted in a usable manner by existing systems, although the prediction of amino acid absorption could be further improved by a mechanistic model which predicts the digestion and metabolism of carbohydrates in the digestive tract.

Unfortunately, data on rates and patterns of absorption of individual VFAs, which are prerequisites to the development of descriptive quantitative models, are severely limited and inconsistent (Sutton 1985). There are still many technical difficulties to be solved concerning methods for measuring VFA production or absorption (Sutton 1985; Oldham & Emmans 1989). Furthermore, models aimed at prediction of VFA proportions must be rather complicated. For instance, at least feeding patterns and diurnal fluctuations should be included if the distribution of VFAs is to be predicted. It must be expected that some considerable time will elapse before models for a satisfactory prediction of the absorption of individual VFAs are available.

It is therefore suggested that a first approach to a new feed evaluation system should probably not include models on internal metabolism in the organs and tissues of the body, as this would require a rather precise estimation of absorbed amounts and probably diurnal distribution of absorption of single nutrients (Sutton 1985).

The first version of a new system could be based on a mechanistic model for prediction of "truly" absorbed energy. The utilization of absorbed energy could then be calculated by means of the coefficients of utilization of ME for maintenance and various kinds of production, which is well documented and uniformly described in the literature (ARC 1980). "Truly" absorbed energy should be calculated from estimated amounts of absorbed VFAs, amino acids, LCFAs and glucose from the digestive tract.

The absorption of VFA could initially be calculated from estimated amounts of digested carbohydrates and protein using stoichiometric equations. In this way predictions of the total amount of VFAs can be made satisfactorily (Sutton 1985; Dijkstra & Neal 1990), but the predicted distribution of absorbed VFAs will probably be rather erroneous.

The digestibility of diets is very much affected by feeding level and diet composition and the interaction between these two parameters (Tyrrell & Moe 1975; Kristensen & Aaes 1989). If a new, rather simple practical system could predict these effects with some accuracy it would certainly be a considerable improvement compared with existing systems.

Dewhurst et al. (1986) and Webster et al. (1988) have proposed a simple model for estimating the true absorbable energy in feedstuffs. In the following a similar model is described and proposed as a first step toward a new system for feed evaluation and feed planning. It is based on a mechanistic description of the digestion processes aiming at a more correct prediction of absorbed energy under various conditions of feeding and composition of the diets.

DESCRIPTION OF A SYSTEM FOR PREDICTION OF "TRULY" ABSORBED ENERGY

The aim of the model is to predict the "truly" absorbed amounts of VFAs, amino acids and LCFAs, and from these values the "truly" absorbed energy is calculated. The model is shown in Figure 1 and explained in the following subsections.

An attempt has been made to include only the most important parameters, and to use well-documented facts. This is a simplified model based on assumptions of first-order kinetics (fractional rate constants and steady state conditions) of digestion and passage.

FEED ANALYSIS

A good prediction of absorbed energy and nutrients is dependent upon an appropriate separation of the feeds into fractions with important differences in digestion characteristics. It is assumed that the feeds principally should be separated into four fractions:

(1) Fractions which are quickly and completely or almost completely fermented or degraded in the rumen (mono-, di-, and oligosaccharides, starch (from rolled or ground oats, barley and wheat) fructosans, pectin, organic acids, glycerol).

(2) Fractions which are slowly and incompletely degraded or fermented in the rumen, part of which may be digested or fermented in the lower digestive tract (protein, cell wall substances (cellulose, hemicellulose)).

(3) Fractions which are not fermented or degraded in the rumen but are digested in the lower tract (LCFAs).

(4) An undigestible fraction (lignin). The latter does not necessarily need to be determined.

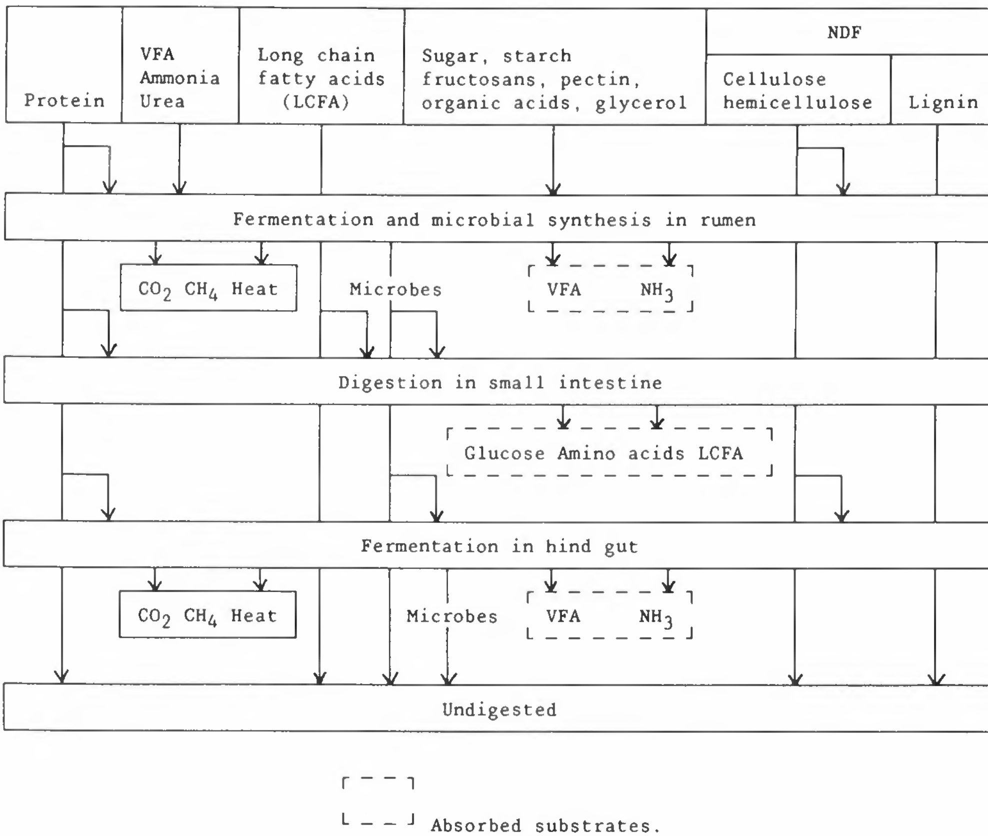

Fig. 1. Model of digestion and nutrient absorption.

A satisfactory fractionation can be obtained by the following chemical analyses: Dry matter, ash, crude protein, ammonia and urea (in silages and compound feeds), LCFAs and NDF, the latter according to the method developed by Van Soest. The quickly and almost completely fermentable fraction is then determined as the difference between organic matter and protein, LCFAs plus NDF. Glycerol may be calculated as 0.1 times the LCFA.

It may be necessary to separate the quickly fermentable fraction into high molecular weight carbohydrates (starch, pectin, fructosans) and low molecular weight substances (mono-, di- and oligosaccharides and organic acids) because of the difference in energy concentration. An approximation may be obtained for some feedstuffs by determination of either the sugar or the starch content.

The content of alcohol, lactic acid, VFAs and the pH must be known for silage. When this information is available the dry matter content can be predicted satisfactorily by oven drying and by using a correction equation (Pedersen & Møller 1965). This is not only important for a correct determination of the intake and absorption of energy-yielding nutrients but even more so for a correct evaluation of the protein value in silages.

In addition to chemical composition, degradation equations and information on passage rate for protein and slowly fermentable carbohydrates (cellulose plus hemicellulose) should also be available. Also, a degradation equation and passage rate for starch would be necessary if a relatively slowly fermented source of starch (i.e. maize, chemically or otherwise treated grain) is fed. Not all the information mentioned earlier is available in Nordic feedstuff tables at the moment. Therefore, some approximations have been made in the following attempts to describe a new feed evaluation system and its function. Values from the Danish feedstuff table (Landsudvalget for kvæg 1990) or similar information on feedstuff composition are used. In this table the content of NDF is missing. An approximation for the content of cell wall substances is therefore calculated as the difference between the total organic matter and crude protein, crude fat, sugar plus starch (Thomsen 1983). This can give a rather erroneous fractionation in some feedstuffs because the cell wall fraction as calculated this way will include considerable amounts of quickly fermentable substances such as pectin, oligosaccharides and organic acids.

VFA PRODUCTION AND ABSORPTION

The produced VFAs are assumed to be totally absorbed. The stoichiometric parameters for the fermentable substrates are shown in Table 1 (Murphy 1984). Stoichiometric parameters for substrate fermentation are given both for concentrate-rich and for roughage-rich rations. Sugar, glycerol and starch are assumed to be totally digested in the rumen. All sugars are assumed to be disaccharides. For amino acids and NDF the extent of degradation in the rumen is calculated from protein and NDF degradation curves, respectively, and the outflow rate from the rumen as:

(I) $$\text{Proportion degraded} = a + (b \cdot c / (c + k))$$

where a = water soluble proportion (of protein, zero for NDF)
b = potentially degradable proportion
c = rate constant for degradation (h^{-1})
k = outflow rate from the rumen (h^{-1})

Protein degradation curves have not yet been calculated, and until degradation curves are available protein degradation at 8% outflow rate is used for amino acid degradation (Hvelplund & Madsen 1990). Amino acids degraded in the rumen will only give rise to a VFA production if the amount is larger than the amount of amino acids incorporated in the microbes. In roughage and in concentrate, 65% and 85% of the protein, respectively, is assumed to be amino acids (Hvelplund & Madsen 1990). The calculated mean mole weight of amino acids (unhydrated) in feedstuffs is 116. This is a mean of both concentrate-rich and roughage-rich rations used by Hvelplund & Madsen (1989).

Only a few degradation curves have so far been determined for the NDF fraction. As degradation curves are determined, they will be included in the feed table. Until then, a b-value is estimated from the table value for the digestion coefficient for cell wall carbohydrates (DCCW) as:

(II) $$b = 0.38 + 0.63\ (DCCW/100)$$

estimated from values of Weisbjerg et al. (1990).

If the c value is lacking, the value 0.041 is used. This is the mean rate constant for NDF degradation of nine roughages examined by Weisbjerg et al. (1990).

Table 1 Stoichiometric parameters used for rumen and hind gut fermentation for roughage (R) and concentrate (C) rations (Murphy 1984).

Substrate	Proportion fermented	Moles substrate/kg fermented substrate*	Moles produced / mole substrate fermented							
			C2 R	C2 C	C3 R	C3 C	C4 R	C4 C	C5 R	C5 C
Sugar	1	5.85	1.38	0.90	0.41	0.42	0.10	0.30	0.00	0.04
Glycerol	1	5.56								
Starch	1	6.17	1.19	0.80	0.28	0.60	0.20	0.20	0.06	0.10
Amino acids	Feed table values	8.62	0.40	0.36	0.13	0.16	0.08	0.08	0.33	0.33
Cell wall carbohydrates										
Rumen	NDF degradation	6.17								
Hind gut	0.09 · (1 - NDF deg.)	6.17	1.23	1.35	0.27	0.32	0.22	0.09	0.04	0.08
Residual fraction	0.85	6.17								

* Carbohydrates in moles hexose equivalent, amino acids in moles amino acids.

If an NDF analysis is available the NDF degradation curve is used on this fraction. The residual fraction (difference between calculated cell wall substances and NDF), which includes pectin and organic acids, is assumed to have a rumen fermentability of 0.85. To this residual fraction the difference between crude fat and the sum of LCFAs plus glycerol is also added. For the residual fraction the same stoichiometric parameters are used as for NDF fermentation. The rate of degradation of NDF is negatively affected by an increased proportion of easily degradable carbohydrates in the diet. Furthermore, this negative effect is dependent on the feeding level. A correction of the degradation rate constant dependent on the sugar and starch proportion of total carbohydrates is implemented in the model, but has not been validated yet. The correction used at present is a modification of the reduction used by Danfær (1990):

(III) C corrected = C(1-((1-f2)f1))

where f1 = feed level (kg DM) / 25
f2 = kg cell wall carbohydrates / ((kg sugar+starch) 1.5) if the proportion is less than 1, else f2 = 1.

This will only give a full reduction at high feeding levels and will only give a reduction if cell wall carbohydrates are less than 40% of the total carbohydrates. The rumen undigested cell wall carbohydrates are assumed to be 9% digested in the hind gut (Zinn & Owens 1982; cf. Dewhurst et al. 1986).

The degraded NDF and residue fraction are assumed to produce VFAs in the proportions given in Table 1. This is a mean of the stoichiometric parameters for cellulose and hemicellulose given by Murphy (1984). Use of the stoichiometric parameters for both cellulose and hemicellulose fractions would demand an extension of the feed table with values for ADF and ADL. However, the distinction between cellulose and hemicellulose in fermentation products is not obvious (Chesson 1990). The stoichiometric relations for hind gut fermentation are assumed to be similar to rumen fermentation of cell wall carbohydrates.

Murphy et al. (1982) found that the roughage:concentrate ratio is important for the fermentation products of the individual substrates. However, the distinction between roughage and concentrate rations is imprecise and does not account for the smooth change from purely roughage- to concentrate-rich rations. In the present model the ratio between sugar + starch and total carbohydrates is used to determine whether a ration is mostly concentrate or roughage.

Fermentation products are calculated from both the concentrate and roughage stoichiometric parameter in Table 1 as:

(IV) R (fermentation products calculated for concentrate stoichiometric) + (1-R) (fermentation products calculated from roughage stoichiometric)

where R = (((R1 - 0.45) 3) + 0.45) / 0.9
$0 < R < 1$ and R1 = (sugar + starch + glycerol)/total carbohydrates

R is calculated from R1 to increase the variation in the range from 0 to 1, first by multiplying around 0.45, which is assumed to be the point where the ration changes from roughage to concentrate, and, thereafter, by dividing by 0.9, which will move the breakpoint 0.45 to 0.5. R is never allowed to go outside the range between 0 and1. These calculations give smooth changes, but the variation in fermentation pattern is too small because rations need to be extremely rich in roughage or concentrate in order to be calculated only from one of the stoichiometric relationships. This was not the case with the material used by Murphy et al. (1982). This problem could be overcome by for example, using a larger multiplication factor than 3, and thereby extending the range for R from -0.5 to 1.5, but this has not been tried out yet.

OUTFLOW RATE FROM THE RUMEN

Rumen outflow rate is needed in order to calculate the NDF degradation described above. In the present model a simple relation between feed level (g DM/kg liveweight per day) and particle outflow rate is based on the following relation estimated from values in a review given by Lindberg (1985):

(V) Outflow rate (h^{-1}) = k + 0.000864 · feed level

The regression coefficient is the mean coefficient found within experiments, and the value 0.008 is used for the constant k. The regression coefficient is higher than the value 0.00037 found by Evans (1981).

AMINO ACID ABSORPTION

For amino acid absorption the new Nordic protein evaluation system has been used (Hvelplund & Madsen 1990). The only modification is that, instead of calculating microbial protein synthesis from totally digested carbohydrates from the feed table, the predicted amount of digested carbohydrates in the rumen is used. This amount is less than totally digested carbohydrates measured in sheep at maintenance (table values). Hvelplund & Madsen (1985) found that microbial synthesis calculated per unit of digested carbohydrates in the rumen was 1.2 times the microbial synthesis calculated per unit of totally digested carbohydrates, and therefore the factor for microbial synthesis per unit of digested carbohydrates has to be multiplied by the factor 1.20. Furthermore, the value of sugar is reduced to 0.95 and the value of glycerol is reduced to 0.90 of the value of polysaccharides for microbial synthesis.

MICROBIAL SYNTHESIS

For calculation of microbial organic matter synthesis, the values for synthesized microbial amino acid protein as calculated above are used, using a content of 0.33 g amino acid protein/g DM and 0.90 g organic matter/ g DM in bacteria (Børsting & Weisbjerg 1989). This production of microbial organic matter will reduce the amount of VFA produced. However, as mentioned earlier, the amino acids incorporated are assumed to stem directly from the feed when degradation is extensive enough, and give no VFA production. Therefore, in most cases only the amount of amino-acid-free microbial organic matter will reduce the VFA production. In the present model this reduction in VFAs is calculated as acetic acid equivalents in the amino-acid-free organic microbial matter, calculated as if all microbial amino-acid-free organic matter consisted of polysaccharides.

(VI) Acetic acid equivalents = kg microbial amino-acid-free organic matter · 6.17 moles hexose/kg · 2 moles acetic acid/mole hexose.

This reduction in VFA production is subtracted proportionally from the individual VFAs.

For amino-acid-free microbial organic matter a true digestibility of 70% is assumed (Storm et al. 1983).

LONG CHAIN FATTY ACIDS

The following equation for "truly" digested fatty acids is based on available results in the literature (Hagemeister & Kaufmann 1979; Møller & Børsting 1987; Murphy et al. 1987; Jenkins & Jenny 1989; Børsting & Weisbjerg 1989; Weisbjerg et al. 1991).

(VII) "Truly" digested fatty acids (kg) = 0.91 (kg fatty acid intake) - 0.16 (kg fatty acid intake)^2

This equation is calculated from 18 treatment means covering rations with no added fat and rations with added tallow and tallowlike fats. For the full model the intercept was -0.03, indicating an amount of 30 g undigested endogenous fatty acids per day (R^2 was 0.99 and root MSE was 0.024). When the intercept is omitted the equation describes the "truly" digested fatty acids.

CALCULATION OF "TRULY" ABSORBED ENERGY

The absorbed nutrients have been multiplied by the following energy values and added in order to calculate the true absorbed energy (Mølgård 1922; Blaxter 1962):

Acetic acid	0.875 MJ/mole
Propionic acid	1.534 MJ/mole
Butyric acid	2.192 MJ/mole
Valeric acid	2.836 MJ/mole
Amino acids	23.65 MJ/kg
Long chain fatty acids	40.0 MJ/kg
Microbial organic matter free of amino acid protein	17.4 MJ/kg (as carbohydrates)

Utilization of absorbed energy In the proposed model calculated utilization of "truly" absorbed energy is based on the large amount of published information on the utilization of metabolizable energy (ME). The values for utilization are taken from the review and conclusions given by ARC (1980). Before the calculations are made it is necessary to consider the differences between the two concepts: ME and "truly" absorbed energy. Fermentation heat is wrongly incorporated in ME. Furthermore, urinary energy losses are also wrongly subtracted from ME, although this is energy in the end products of the metabolism. Also, endogenous energy excreted in the faeces is not included in ME. The opposite occurs in "truly" absorbed energy, in which fermentation heat is not included but urinary energy and endogenous faecal energy are.

Although these losses are subject to variation, constant proportions for fermentation heat and urinary energy losses are used in the model. They are both assumed to amount to 0.07 of the amount of absorbed energy (Webster et al. 1975; Webster 1979; ARC 1980). Thus, when comparing the size of ME and "truly" absorbed energy, urinary energy and fermentation heat cancel one another out. Measurements of the heat of combustion of net excretion of endogenous substrates to the digestive tract are not found in the literature. These are probably of a rather small size. In the proposed model no correction is made for excreted endogenous energy.

Thus, since calculated ME and "truly" absorbed energy are assumed to be of the same size, the coefficients of utilization of ME may be used uncorrected to express the utilization of "truly" absorbed energy also.

As a first example of the model a system for dairy cows only is demonstrated. Based on the proposals of ARC (1980) the coefficients of utilization of absorbed energy for maintenance (k_m) and lactation (k_l) may be calculated as follows:

$$k_m = 0.35q + 0.503$$
$$k_l = 0.35q + 0.420$$

where $q = ME/GE$

$$GE\ (kJ\ kg\ DM^{-1}) = 24.14z_1 + 36.57z_2 + 20.92z_3 + 16.99z_4$$
(Schiemann et al. 1972)

Z_1, z_2, z_3 and z_4 are crude protein, crude fat, crude fibre and NFE, respectively, g kg DM^{-1}.

$$ME\ (kJ\ kg\ DM^{-1}) = 17.45x_1 + 31.21x_2 + 13.64x_3 + 14.77x_4$$
(Schiemann et al. 1972)

X_1, x_2, x_3 and x_4 are digestible nutrients (crude protein, crude fat, crude fibre and NFE, respectively), g kg DM^{-1}.

Net energy excreted in milk is 3140 kJ kg^{-1} energy-corrected milk (ECM) as defined by Sjaunja et al. (1990). Net energy for maintenance is calculated as (MJ day^{-1}):

$$0.53\ (W/1.08)^{0.67} + 0.0043W$$

where W = liveweight, kg

NE_l is reduced by 27.4 MJ kg^{-1} liveweight gain or increased by 21.8 MJ kg^{-1} liveweight loss.

CONCLUSION

There is still a severe lack of knowledge on the patterns of absorption of VFAs. It will therefore not be possible within the near future to obtain a useful prediction of the distribution of absorbed VFAs. This would be a necessary precondition for prediction of the partitioning of absorbed nutrients for different purposes in the body. Thus, for practical feed planning it would not be possible at the moment to make use of a model which describes the digestive and metabolic functions of the whole animal. It is suggested therefore that, as a first step, a mechanistic and static model for prediction of absorbed energy should be included in existing feed evaluation systems.

The suggested model, which includes only simple mathematics expressing the dynamics of the digestion parameters, is expected to improve the prediction of absorbed energy compared with existing empirical systems. As new knowledge is obtained it should gradually be included in the model. This can be done at any time without changing the essential structure of the system. Another important advantage of such a model is that it would promote more sound and precise formulation of nutritional problems and experiments. The basic principle of making a new system must be that it is based on experimental determinations of digestive and metabolic processes, and that no corrections are made retrospectively in order to increase the fitness of the model.

The proposed model is not ready for use. First, the model should be tested against digestibility determinations and results of production experiments. As discussed in the description, a new chemical fractionation of the feedstuffs is required. The optimal fractionation is broadly known but some details need to be studied further. Values on the NDF content do not exist in all Nordic feed tables, and in various countries analysis on the content of starch/sugar and of alcohol and acids in silage must be introduced. More studies have to be carried out on rates of fermentation and how they are affected by the ration composition. Knowledge on intestinal flow is also limited. It is discussed whether it is necessary to separate the slowly fermentable cell walls into several fractions because of different patterns of degradation (Mertens & Ely 1982; Robinson et al. 1986), or because of selective retention of particles from various parts of a plant as a result of differences in specific gravity (Bittante et al. 1990). The rate of passage is determined by particle size, rate of particle breakdown and differences in specific gravity (Welch 1986). Determinations of such properties may probably be used for prediction of passage rate. In the model described above values for utilization of metabolic energy used in existing energy evaluation systems have been used to predict the production. However, the proposed model will make it possible to obtain a better prediction of the loss of energy in urea, and probably also of the fermentation heat. Therefore the values from ARC (1980) used are only a temporary solution.

Although some developmental work has still to be done before the proposed model is ready for use, it is expected that a useful model which includes prediction of "truly" absorbed energy could be developed within relatively few years if enough effort is put into this work. It is believed that models of the proposed kind will be developed and used widely in the future. The Nordic countries should initiate a cooperative work on the development of a system. With a model of this kind the very important partitioning of absorbed nutrients between the synthesis of milk constituents and body tissue in lactating animals cannot be predicted. In the long term the goal must be to use more complete animal models which can predict directly the partitioning of nutrients and growth and production also.

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7 Aspects on ration formulation based on a substrate system

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The need for and the practical possibility of creating a ration formulation system based on a number of substrates rather than on the energy concept are discussed. A brief examination of the prevalence of relevant data is also made. It is concluded that in practical ration formulation the energy concept could be replaced by a number of substrates. This could be handled by ordinary computer program already available on the market if a requirement range is defined for each substrate and if the interaction between substrates could be dealt with additively. Ration formulation for *ad libitum* feeding practices is more easily adapted to a substrate system than when restricted feeding practices are used. There seems to be a theoretical background for basing a system on: rumen degradable protein, rumen degradable carbohydrates, microbial production in the rumen, fatty acids and the digestion in the abomasum and duodenum. The intake of dry matter could be the last and most critical factor still not under control.

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Until the present time the ration for ruminants has been formulated from the calculated need of total energy and protein. Both energy and protein have been expressed in a rough way with only one quality grade.

Development in protein evaluation has taken place during the 1980s, resulting in a system that also allows qualitative aspects. The AAT/PBV-system, developed by an internordic research team, is a system based on amino acid resorption from the duodenum. Feeds are evaluated accordingly to their capacity to provide the duodenum with amino acids. This can be achieved either by rumen undegradable proteins or by microbial protein synthesis in the rumen. In order to quantify this the system operates with rumen degradability of the protein fraction as well as with the content of carbohydrates that can serve as substrate for bacterial growth in the rumen.

It is also possible to apply a similar "substrate-based system" to other nutrients than the proteins. What normally goes under the energy term is the absorption of carbohydrates, volatile fatty acids (VFAs) and fatty acids. Such an overall approach was recently made by the Danish research workers Riis et al. (1990). In their work the following model was used:

I) A given diet was analysed and calculated for VFA absorption, carbohydrate absorption, amiono acid absorption and fatty acid absorption.

II) There were then taken into account the resulting supply of nutrients and the concentration of hormones that these gave rise to in the extracellular fluid, such as glucose, amino acids, acetate, keton bodies, FFA, total lipids, insulin, glucagon thyroxine, somatomedin and growth hormone.

III) Nutrient metabolism in the liver was calculated.

IV) Metabolism and consumption of nutrients by the adipose tissues and muscles was calculated.

V) Nutrient metabolism and synthesis in the mammary gland.

Finally, the expected milk production level and change in live weight resulting from the diet were calculated.

Observed and predicted production and live-weight change were compared and were shown to be in good agreement. It was therefore suggested that the reverse could also work, i.e. to calculate the predicted amount of nutrients needed to be absorbed in order to reach a certain production level. The same hypothesis is also presented by Oldham & Emmans (1989).

However, it is probably still not possible to produce a fully developed dynamic model covering all steps from nutrient consumption, nutrient decomposition, microbial growth, nutrient absorption and hormonal regulation in order to produce a fully reliable prediction of the response (Oldham & Emmans 1989; Riis et al 1990). A more realistic first step could be to develop a mechanistic calculation, with the aim of predicting the response on nutrient supply. If such a system is developed it is likely that it would result in a "requirement range" for a number of substrates of which the ration could consist in order to meet a certain production level. The present paper is an attempt to study whether it is possible to work with such an approach in the practical calculation of rations for dairy cows.

MATERIALS AND METHODS

A commercial program for ration calculation (Holvid 1990) was used to make rations for cows with a milk production of 10, 20, 30 and 40 kg per day. First, the ration was calculated using the standard requirement of metabolizable energy and digestible crude protein used in Sweden (Standard Calculation, SC). Thereafter, the ration was calculated without using the energy concept. Instead, the requirement for AAT and "requirement ranges" for PBV, fibre (NDF), starch, sugars and crude fat were used. The substrate-based calculation was made using either these parameters only (SBC I) also including a "requirement range" for total carbohydrates (SBC II). In all three calculations the program made up the feeds in such a way that the requirements were met in a ration at the lowest cost.

The analyses of the feeds were taken from the Swedish "Fodertabeller för idisslare" (Spörndly 1991".

The Standard Calculation (SC) was made with the Swedish standard requirement figures for metabolizable energy (0.507 MJ ME per kg metabolic live weight for maintenance and 5 MJ ME per kg of 4 % milk) and digestible protein (6.2 g dig.cp per MJ ME for maintenance and 60 g dig. cp per kg of 4 % milk). Other restrictions used in this calculation were the upper limits of roughages and other feeds, based on practical experience.

The requirements in the substrate-based calculations are at present only elaborated for amino acids. The requirements for AAT and PBV were therefore set in accordance with the current suggestions from Sweden (3.25 g rp AAT per kg metabolic live weight for maintenance and 40 g per kg 4% milk, 0-300 g rp PBV per day). Further "requirement ranges" for crude fat, sugar, starch, NDF and, in the case of SCB II, also total digestible carbohydrates were set up more or less by guess-work. Other restrictions used in these calculations were the minimum and maximum of NDF per DM and the same upper limits of individual feeds, e.g. rapeseed products due to glucosinolate contents, as were used in the SC. However, no upper level of roughages was used.

RESULTS

A summary of the resulting calculations is presented in Table 1. The ration composed by SBC I proved to be very low in energy allowance compared to the traditional ration. When a minimum level of total carbohydrates was introduced in the SBC II, the formulation resulted in rations surprisingly close to conventional ones when compared on an ME basis.

As pointed out before, the calculations were only made in order to test whether there were computor programs available which could cope with the task of formulating a ration by a number of factors. The actual values used are merely chosen as examples. NDF/kg DM derives from the 1989 NRC recommendation for minimum structural feed and estimated maximum consumption level (1.5% of live weight). The crude fat limits come from the recommended minimum and maximum fat allowance in Swedish extension work (15 and 25 g crude fat per kg of milk produced). The starch limits originate from what are common and by practice realistic cereal allowances in Sweden. The sugar limits originate from common sugar allowences in Sweden from hay and molasses. The limit used for total CHO was chosen from observed CHO allowances in a number of typical rations.

DISCUSSION

Formulating a ration based on number of substrates instead of the traditional single energy term seems to be within the capability of the computing facilities existing today.

In a substrate-based model a knowledge of how the carbohydrates are used is essential. The degree and the pattern of degradation of the carbohydrates in the rumen have to be included in the model.

The grouping of the carbohydrates in sugars, starch and NDF reflects the degradation rate to a certain extent. Fully developed degredation functions for the carbohydrate fraction would of course be the ultimate solution. There could, however, be problems in incorporating such functions into the ration calculations.

Table 1. Requirement ranges used in the substrate-based calculations (SBC) and resulting traditional parameters when rations are formulated according to SBC I and SBC II

	Requirement range used, per cow per day			
	production level, kg milk			
	10	20	30	40
AAT, g	794	1194	1594	1994
PBV, g	0-300	0-300	0-300	0-300
crude fat, g	150-250	300-500	450-750	600-1000
sugar, g	0-800	200-800	200-1500	1000-2000
starch, g	0-1000	1500-2500	2000-3500	2500-5000
NDF, g	5000-9000	5500-9000	5500-9000	5500-9000
NDF g/kg DM	400-1000	400-1000	400-1000	350-1000
dig. CHO, g	6200-99999	8000-99999	10100-99999	12200-99999
price	min	min	min	min

	Resulting traditional parameters, per cow per day			
	Production level, kg milk			
	10	20	30	40
SBC I				
ME, MJ	80	140	188	230
dig. CP, g	963	1690	2171	2622
DM, kg	8,7	12,2	16,4	19,7
roughage, kg DM	6,4	7,3	9,9	9,0
SBC II				
ME, MJ	118	160	207	253
dig. CP, g	922	1631	2196	2691
DM, kg	12,5	14,2	18,1	21,3
roughage, kg DM	12,5	10,7	12,8	11,5
Standard requirement				
ME, MJ	112	162	212	262
dig. CP, g	980	1580	2180	2780

An estimation of the rate of carbohydrate degradation could be made in different ways. One simple and rapid way is the method proposed by Menke, Raab et al. (1979), where the gas production from samples was measured after incubation in syringes.

Independently of the method used, it is possible to deal with the degradation rates by classifying the carbohydrates according to the time of degradation. Fermentation classes could, for example, comprise carbohydrates fermented within 2 h (class I), 2-6 h (class II), 6-24 h (class III) and >24 h (class IV).

The time and order of feeding the carbohydrates is also a highly relevant factor when considering the effect of carbohydrate utilization. If the feed is not given as a total mixed ration, then the feeding sequence must be incorporated in the calculation.

The type of carbohydrates fed influences to a certain extent the type of nutrients available for resorption. But a substantial portion of the carbohydrates is interchangeable. It could therefore be motivated to operate with the sum of carbohydrates. This is particularly the situation when restricted feeding with a concentrated feed is practised.

When *ad libitum* feeding is practised, a situation under which an increasing amount of milk is produced, the necessity of limiting the sum of the nutrients is of less interest. Instead, there is the feed intake as the regulating factor. This means that the system of ration formulation with a substrate-based system also needs a factor that describes the voluntary dry matter intake for different feeds under different conditions. This seems, so far, to be the area which suffers most from lack of research data.

The first steps towards a new thinking, including qualitative aspects and interaction between feedstuffs, was taken when the Nordic AAT/PBV-system was introduced for balancing the protein in dairy rations. The system is based on an estimation of the amount of amino acids being absorbed in the duodenum. The feed is described according to its capability to provide amino acids both via microbial growth in the rumen and directly from the feed.

Introducing similar systems for the other nutrients ought to be the next step. By setting up the same goals, the protein system could be expanded to include all nutrients, of which the protein is just one. This means:

1) A "requirement" of absorbed nutrients must be defined, e.g. amino acids, fatty acids, VFAs, carbohydrates.

2) The substrate needed for providing the nutrients to be absorbed must be qualitatively and quantitatively defined.

3) It must be possible for the interaction between the substrates to be handled additively (as with PBV).

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8 Practical implications of changing the energy evaluation system

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In Norway it has been decided that there will be a change in the energy evaluation system from FFU (fattening feed units), based on net energy for fattening, to FEm (feed unit for milk production), based on net energy for lactation, starting at the turn of the year 1992/93. One FEm will be defined as 6 900 KJ net energy for lactation. Before this change of energy system can take place, however, new figures for energy requirements and a feed table with new figures for the energy content of different feeds, will have to be established and published. Several computer systems, big mainframe systems and PC systems, will have to be reprogrammed. Some forms, textbooks, handbooks and booklets will also need amendment. Those who are responsible for teaching, concentrate production, data systems, advising on ruminant feeding and agricultural administration will have to be informed of the change taking place and what its consequences are likely to be. The total costs of changing feed evalution systems have not been estimated, but the cost of changing data programs is estimated to be about NOK 2 million. Expenses in connection with information activities and renewal of information aids will most probably be in the order av NOK 1-2 million.

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There are currently three different energy evaluation systems in use for ruminants in the Nordic countries. In Finland, Iceland and Norway the fattening feed unit (FFU) is used, while the Scandinavian feed unit (SFU) is used in Denmark and metabolizable energy expressed in MJ is used in Sweden.

The practical consequences of changing to a new energy evaluation system will differ somewhat from country to country. Changing from one net energy system to another will have less influence than changing from metabolizable energy to net energy, or vice versa.

The practical consequences will, of course, be greater if there is also to be a change in the unit for energy measurement than if we keep the old units such as FU or MJ. Despite some minor differences between countries, the main problems and consequences will be the same in all countries.

In Norway the decision has already been made to change to a new feed unit, FEm (feed unit for milk production) based on net energy for lactation, at the turn of the year 1992/93. At the same time, there will also be a change in the protein evaluation system from digestible crude protein to the AAT/PBV system.

Net energy for lactation will be calculated in the same way as in The Netherlands (Van Es 1975, 1978; Van der Honig & Alderman 1988). One FEm will be defined as 6900 KJ net energy for lactation; this is equivalent to the content of net energy for lactation in 1 kg of barley with 87% dry matter. FEm will be used for energy evaluation for both milk production and growth/fattening for cattle, sheep and goats. Some of the practical consequences of a change from FFU to FEm are listed as follows:

ENERGY REQUIREMENT

New figures for energy requirements and new feeding standards for cattle, goats and sheep will have to be established and published. This work will be done by researchers at the Department of Animal Science at the Agricultural University of Norway.

FEED TABLES

New feed tables with new figures for energy values must be established and published. "National Agricultural Inspection Service" (STIL) has already appointed a working group for this job. According to the plans, the work with the new feed table will be finished by August 1991.

DECLARATION OF ENERGY VALUE FOR CONCENTRATE MIXTURES

In Norway we have a system with standardized concentrate mixtures for different types of production. For these standarized concentrate mixtures, limits for variation in energy content as well as for other nutrients are defined.

STIL will have to give new directives for energy content expressed in FEm for standarized concentrate mixtures for ruminants. This must include instructions for calculation and presentation of the energy values.

PRACTICAL DETERMINATION OF ENERGY VALUE

There will be a need for new equations for practical calculations of energy values of different feeds based on different types of simplified analyses such as:

In Vitro digestibility, NDF, ADF, crude fibre etc.

New calibration equations for determination of FEm by near infrared spectroscopy (NIRS) have to be worked out for different feeds.

EFFECT ON COMPUTER SYSTEMS

Several computer systems have programs where energy value or energy requirement, expressed in FFU are included in some calculations. All these systems will have to be reprogrammed, with calculations in FEm. In Norway this will affect both the big mainframe systems and the smaller commonly used PC systems. The affected systems are listed in the following:

Mainframe systems

- Program for feed accounting in the production recording systems for dairy cows and goats.
- Program for calculation of concentrate allowance for dairy cows.
- Program for calculation of economical efficiency on dairy farms.
- Program for predicting milk production.
- The Central Bureau of Statistics collects information about yields of different crops and publishes statistics for average yield in different regions, expressed in FFU/daa. These programs will have to be changed to present the yields in FEm/daa. For roughage, this will result in an increased energy yield, compared with grain.

PC systems

- Program for calculation of feeding plans for dairy herds.
- Program for calculation of daily feed rations for dairy cows.
- Program for calculation of economical effect of different short-time dispositions of the herd on dairy farms.
- Program for calculation of optimal management of dairy herds. This program imports and exports data from and to a central data base.
- Program for calculation of fertilizer plans.

ADJUSTMENT OF FORMS

In Norwegian terminology, it has been decided that the abbreviation FEm ("fôrenheter mjølk") be used for the new feed unit and the abbreviation FFE ("fetningsfôrenhet") for the old fattening feed unit. The general abbreviation for feed unit will be FE ("fôrenhet"). Earlier, the most usual abbreviation for feed unit was f.e. In spite of this change in abbreviation for feed unit, we could have continued to use some of the old forms with the old abbreviation. Most of the forms both for data registration and for presenting the results of the calculations, will have to be changed anyway because of the change in protein evaluation to the AAT/PBV system.

Some forms for manual calculations of standard plans, where the energy requirements are printed on the form, must be renewed. This includes forms for manual feeding plans and feeding lists for cattle, sheep and goats, and gross-margin calculations for different types of animal production. In all, 15-20 different forms will have to be changed as a result of the change in energy and protein evaluation systems.

INFLUENCE ON GENERAL STATISTICS

The change to FEm will have some effect on statistical figures that have earlier been calculated in FFU. This will influence:

- Feeding accounts from the production recording systems for dairy cows and goats. The proportion of roughage in the feed rations will increase when the calculations are done in FEm compared to FFE.
- Feed efficiency in different animal productions (milk or meat/unit of feed energy). The output/input relationship will be lower when calculated in FEm than in FFE.
- Average energy yield of roughage will increase in relation to grain and other concentrated feeds.

INFLUENCES ON EXISTING INFORMATION AIDS

In connection with the change in the energy evaluation system, it will be necessary to revise a great many information aids pertaining to feed evaluation and ruminant feeding.

- Textbooks about feed evaluation, ruminant feeding, forage production and agricultural economics will need to be updated.
- Several handbooks, for example "K.K. Heje, Håndbok for jordbruket" and "Håndbok for driftsplanlegging" and all handbooks for the different production recording systems (dairy cows, goats, sheep) as well as for many of the PC programs, will have to be changed.
- Many booklets and other information aids concerning feed evaluation and ruminant feeding will also need to be revised. All types of handbooks must be available in corrected versions before the official change of energy system.

INFORMATION

Before we can start to use a new feed evaluation system, many people must be informed that a change will take place and what the consequences of this change are likely to be. The people who are responsible for teaching, concentrate production, data systems, advice in ruminant feeding and agricultural administration, must receive the information early so that they have time to make plans and get money for the changes they have to make before the new system is put into practice.

The list on the next page shows the different target groups, the type of information needed and which institutions are responsible for providing the information.

Last winter we already started to arrange courses in feed evaluation for some people from the feed industry, county agricultural administration, teachers and advisers. The main activity in this field, however, will take place in the winter of 1991/92 and in the autumn of 1992.

TARGET GROUP FOR INFORMATION:	TYPE OF INFORMATION:	RESPONSIBLE FOR INFORMATION:
Feed industry	Instructions for practising the new system. Letters	Min. Agr. (STIL)
Agricultural administration	General information	Min. Agr. (SFFL)
County	Letters, meetings	
Municipality	Leaflets	
Teachers	Particular information about energy evaluation in the new system. Meetings	Min. Agr. (SFFL)
Investigators and advisers in plant prod. economic, etc.	General information Articles and leaflets	Min. Agr. (SFFL/NLH)
Advisers in ruminant feeding and registrars in the recording systems	Instructions for practising the new system and conseque-nces for different types of data systems. Letters, new handbooks, meetings.	Norwegian Dairies Ass. Local dairies
Farmers	General information. Particular information about changes in copies from different data systems. Articles, letters, local meetings.	SFFL Norwegian Dairies Ass. Local adviser

Min.Agr. - Ministry of Agriculture
SFFL - Norwegian Agricultural Advisory Service
NLH - Agricultral University of Norway
STIL - National Agricultural Inspection Service

CONCLUSIONS

In Norway it was decided that the energy evaluation system should be changed from the first of January in an appointed year, as this would cause the fewest problems with data systems and statistics. The decision was made more than two years before the change is due to take place, because we will need this time to make the necessary adaptations in all affected systems.

The work with updating data systems and handbooks will have to start at least one year before the new system is ready for use. It will also take som time for plans and budgets for this work to be made, as well as for the work concerning information about the system itself.

Thus far, we do not have any exact estimation of the total costs of changing feed evaluation systems. The cost of changing data programs and forms is estimated to be about NOK 2 million. The expenses in relation to information activites and renewal of information aids are more difficult to estimate, but they will most probably be in the order of NOK 1-2 million.

The total expenses may well appear to be high. We must, however, remember that in addition to getting a better feed evaluation system, the increased information activity in connection with the change of systems will provide more knowledge about feed evaluation and feeding, both to advisers and to farmers. It is also obvious that work as well as money will be saved by changing both the energy and the protein evaluation systems at the same time.

The coordination of the work prior to the change should be led by a national working group with members from the organizations involved.

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9 Conclusions and recommendations

THE NORDIC WORKING GROUP ON ENERGY EVALUATION

Calculations carried out (Paper 2) indicated that the Dutch net energy lactation system (NEL) was better than metabolizable energy (ME) and the fattening feed unit (FFU) system when predicting milk yield from energy intake, but not better than the Scandinavian feed unit system (SFU).

It is important to note that many factors influence the feeding value of feedstuffs (see Papers 3 and 4). The group concluded, therefore, that there was little to gain by changing from the present energy evaluation systems, especially if these are to be replaced by a system based on absorbed nutrients in the near future. There was some disagreement within in the group as to how long it would take before a new "substrate-based system" would be available for practical use.

As a follow-up to the conclusions, the working group put forward the following recommendations:

* There should be cooperation between the Nordic countries with the aim of developing a "substrate-based" feed evaluation system.

* Digestible energy should be used as a common reference for energy evaluation in the Nordic countries.

* If a country wants to change its existing energy system, the Dutch NEL system is to be preferred.

With reference to the mandate given initially, the working group is in the process of writing an application to the Nordisk Kontaktorgan for Jordbruksforskning (NKJ) for a joint Nordic research programme with the following aim:

<u>To develop a mechanistic model for digestion and absorption of nutrients (VFA, LCFA, AA and glucose) from the digestive tract, and to use this model for improving ration formulation systems for ruminants</u>.

In order to develop a substrate-based system, research is needed within the following areas:

- Feedstuff analysis, especially for the carbohydrate fraction.
- Diurnal variation in the feed intake.
- The rates of ruminal degradation and passage of carbohydrate fractions from the forestomachs.

- The absorption of VFA (total and individual ?) from the forestomachs and hind gut.
- Microbial synthesis and passage from the rumen to the intestines.
- The development and use of mechanistic models for optimization of rations.

It is assumed that all five Nordic countries will participate in the research programme in accordance with their interests, competence and resources.

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The pages shall be numbered consecutively beginning with the title page.

Articles will usually be organized as follows: (1) introduction, (2) materials and methods, (3) results, (4) discussion and (5) summary. Up to three grades of headings can be used to divide up the text. Articles must not exceed 20 manuscript pages, and two copies should be submitted to the managing editor.

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Høeg, O.A. 1971. Vitenskapelig forfatterskap. 2. utg. Universitetsforlaget, Oslo. 131s.

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Aase, K.F., F. Sundstøl & K. Myhr 1977. Forsøk med strandrøyr og nokre andre grasartar. Forskning og forsøk i landbruket 27: 575-604.

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