

SYMPOSIUM: PREVAILING CONCEPTS IN ENERGY UTILIZATION BY RUMINANTS

Predicting Energy Values of Feeds¹

W. P. WEISS

Department of Dairy Science
Ohio Agricultural Research and Development Center
The Ohio State University
Wooster 44691

ABSTRACT

Accurate estimates of the available energy content of feeds are necessary to formulate diets and to evaluate the nutritional and economic value of different feedstuffs. Estimation methods must be rapid, inexpensive, and accurate before they are accepted widely by commercial feed testing laboratories. Currently, most laboratories use empirical equations based on ADF or NDF to estimate available energy content of feeds. Those equations are incorrect theoretically and lack adequate precision. Summative models that account for several sources of variation have been developed. These models are based on the composition of the fiber and nonfiber fractions. Adjustments are made to account for variations in digestibilities of fiber and protein and in the concentrations of fat and ash. Additional improvements are needed to adjust for associative effects, feed intake effects, and physical characteristics of the feed.

(**Key words:** feed energy, nutrient composition, statistical models)

Abbreviation key: DDM = digestible DM, DE = digestible energy, EE = ether extract, ME = metabolizable energy, NDS = neutral detergent solubles, NE = net energy, PDNDF = potentially digestible NDF, $s_{y \cdot new}$ = standard error of prediction, $s_{y \cdot x}$ = standard error of estimation.

Received June 8, 1992.

Accepted August 17, 1992.

¹Salaries and research support were provided by state and federal funds appropriated to the Ohio Agricultural Research and Development Center, The Ohio State University. Manuscript Number 108-92.

INTRODUCTION

The total amount of energy in a feed (gross energy) can be measured relatively simply using bomb calorimetry; however, the variability in digestibility and metabolism among feeds precludes the use of gross energy for formulation of diets or comparison of feeds. Sources of variation include animal, feed, and dietary factors. Different measures of available energy have been developed to account for some or all of the variation in energy utilization, but conversion among most measures of feed energy is possible.

Available energy of feeds must be known for diet formulation and for nutritional and economic comparisons among feedstuffs. The large demand for energy of high producing ruminants requires accurate determination of available energy of feeds. Unfortunately, available energy cannot be determined easily; therefore, estimation methods have been developed. Many commercial feed testing laboratories use equations in conjunction with data from chemical analyses to estimate available energy content of feeds. Because variability in chemical composition and available energy content usually is much greater for forages than for concentrates, the majority of equations have been derived from data of forages (36). The composition and energy content of concentrates also can vary significantly (7); therefore, equations are needed for concentrates. The objective of this paper is to outline methods to estimate available energy of feeds by integration of chemical analyses and mathematical models.

Conversions Among Energy Terms

Available energy can be expressed as digestible energy (DE), metabolizable energy (ME), net energy (NE), and TDN. Digestion

experiments are used to determine DE or TDN of diets. Metabolism trials are used to determine ME by measurement of urinary and methane energy, but those experiments require special equipment and are expensive. Whole body calorimetry is used to determine NE, but only a few laboratories in the world are equipped to conduct such experiments.

Each term accounts for different losses in energy that occur during digestion and metabolism. Energy lost in feces is the most variable of the losses among feeds. Fecal losses can range from near 0 to almost 100% of the gross energy (45). This large variation requires that fecal losses must be measured or estimated for each feed or diet fed. Two measures of feed energy, DE and TDN, account for digestibility losses. The TDN value also accounts for some urinary losses and is not equivalent to either DE or ME (32). For this paper, actual DE and TDN were determined by feeding cattle or sheep at maintenance and measuring digestibility. On average, 1 kg of TDN equals 4.409 Mcal of DE (49).

Metabolizable energy usually is calculated from DE or TDN using standard equations (38). Those equations are based on the proportionality of TDN or DE to ME and do not consider what compounds contribute to the total available energy. The ME values in most composition tables are calculated using Equation [1].

$$\text{ME(Mcal/kg)} = -0.45 + 1.01 \times \text{DE(Mcal/kg)}. \quad [1]$$

Equation [2] is approximately equivalent to Equation [1] when feeds contain between 2 and 4 Mcal/kg of DE.

$$\text{ME(Mcal/kg)} = .82 \times \text{DE(Mcal/kg)}. \quad [2]$$

Both equations will yield ME values for feeds when they are fed at maintenance. Those two equations do not account for variability in the conversion of DE to ME. Within each equation, feeds with the same DE have the same ME.

Both NE for gain and NE for maintenance are calculated from ME (determined using Equation [2]) using polynomial equations derived by Garrett (22). Most NE_L values in NRC feed composition tables (38) were calculated from TDN using Equation [3].

$$\text{NE}_L(\text{Mcal/kg}) = .0245 \times \text{TDN}(\%) - .12. \quad [3]$$

Van Es (53) proposed using ME to calculate NE_L . The equations used to calculate NE values of feeds adjust for intake effects so that NE values are for feeds when they are fed at productive intake levels.

Once TDN or DE is known, all other expressions of energy can be calculated by using appropriate equations. Actual DE or TDN values can be determined only by digestion trials, which are too laborious and expensive to be conducted on all possible feeds and diets. Estimation of DE or TDN by using a combination of chemical and mathematical techniques is the principal subject of this paper.

Statistical Evaluation of Models

Many chemical components are related to the available energy concentration of a feed. The relationship can be simply a statistical correlation or a direct cause and effect relationship. A strong statistical relationship does not necessarily imply a direct causal relationship. A direct causal relationship between a feed constituent and its available energy concentration should be population-independent; i.e., the same relationship exists for a group of corn samples as exists for a group of alfalfa samples. Statistical relationships are population-dependent.

Extrapolation beyond the limits of the population that was used to derive statistical relationships usually is ill-advised. To avoid extrapolation, the population used to derive a statistical equation must be well defined. The type of feedstuff, growing conditions, and postharvest processing and storage can influence available energy concentration. When an individual observation deviates from those used to derive the equation, the accuracy and precision of the estimate are questionable. The population of data used to derive the statistics must be considered in comparison of different equations or statistical measures of relationships.

The most commonly used measures of the strength of the relationship between a dependent variable and an independent variable are the coefficient of correlation (r) and coefficient of determination (r^2 for a simple regression

and R^2 for multiple regression). The r^2 is the proportion of variability in the dependent variable that is accounted for by the independent variable, but it does not imply a causal relationship (39). The r is an index of the strength of the relationship but has no direct meaning; therefore, r^2 will be used as the measure of correlation. The r^2 statistic is population-dependent. The r^2 usually is higher when the range of independent variables is wide instead of narrow (39). Additionally, when dependent variables are spaced widely apart, r^2 is usually higher than when the values are equally distributed (39). This means that, when used for comparison of different models that were derived from different populations, r^2 should not be the sole statistic used to evaluate the models. Finally, r^2 measures how well a population of observations fits a particular model; it does not indicate how well a single observation fits the model. In estimation of energy values, the accuracy of the individual prediction is most important.

For determining how well a model will predict a dependent variable from the independent variable or variables, two measures of variability are used: standard error of estimation ($s_{y \cdot x}$) and standard error of prediction ($s_{y \cdot \text{new}}$). The equations for these measures are in the text by Neter and Wasserman (39). Basically, $s_{y \cdot x}$ considers errors only in the regression parameters. The $s_{y \cdot x}$ is valid for estimation of the mean dependent variable for a given independent variable. For prediction of energy values of feeds, individual observations are most useful; therefore, $s_{y \cdot \text{new}}$ should be used. The $s_{y \cdot \text{new}}$ includes both regression error and the variation in the dependent variable. The $s_{y \cdot \text{new}}$ is always larger than the $s_{y \cdot x}$. A confidence interval for prediction is constructed using the appropriate t value and $s_{y \cdot \text{new}}$. Confidence intervals increase as the independent variable deviates from its mean. All regression equations are more precise predictors when the value of the independent variable is near the mean than when they deviate greatly from the mean.

Single Component Models to Estimate Feed Energy

Feed constituents or fractions can be classified as uniform or nonuniform based on the Lucas test (50). Uniform fractions have con-

stant digestibility or availability across all feeds. With respect to available energy, ash, lignin, neutral detergent solubles (NDS), and fatty acids are considered to be uniform fractions. The concentrations of these components in feeds have a direct impact on available energy concentration. These compounds contain no DE (ash and lignin), have constant digestibilities (NDS and fatty acids), or contain more energy per unit than other chemical fractions (fatty acids). Often, concentrations of these compounds in feeds are poorly correlated with available energy concentration, probably because their concentrations are relatively low and do not vary greatly among or within most feedstuffs. Ash concentrations of most feedstuffs are between 1 and 10% of the DM (45). The relatively low ash in feeds makes ash inadequate for estimation of available energy content of most feeds. For example, both corn grain and cottonseed hulls have about 2% ash; yet on average, corn has about 40 percentage units more TDN than cottonseed hulls. The value of ash in estimation of available energy within a feedstuff class depends on the amount of ash and its variability. Fisher and Fowler (20) reported that ash content of cereal grain forages varied enough to be correlated ($r^2 = .6$) with digestible DM (DDM). Alfalfa samples compiled by Mertens (34) averaged 9.1% ash; the 95% confidence interval was 6.2 to 12.0%. Use of the average ash concentration instead of actual ash may increase error by up to 3 TDN units. For corn gluten feed (7), ash content averaged 6.5%; the 95% confidence interval was 6.0 to 7.0%. In that case, use of the average ash content could increase error in TDN by about .5 unit. In either case, ash is not sufficient to account for large variation in available energy content.

Most feeds contain between 0 and 5% ether extract (EE) on a DM basis (45). Fatty acids behave as a uniform feed fraction (43), but digestibility of EE (the most common measure of feed fat) varies among feeds, especially when forages are compared with concentrates. Equations based solely on EE are not accurate for estimation of available energy values for a diverse population of feeds. A relatively strong statistical relationship ($r^2 = .7$) between TDN and EE has been observed when only data from concentrate feeds were used in the regression analysis (21). The r^2 was relatively strong,

but the error ($s_{y.new} = 9.7$ TDN units) was too large for acceptable predictions of energy. Fat content can vary considerable within a feed. Belyea et al. (7) reported that 10 samples of corn gluten feed had a mean concentration of 6.6% EE; the 95% confidence interval was 5.2 to 8.0%. In this case, the maximum error introduced by using the mean instead of an extreme value is about 3 TDN units. The data collected by Belyea et al. (7) were from a single source and represented only variation caused by production of the feed. Variations in composition of feeds would be much greater if more sources of variation were included.

Even though lignin constitutes only a small proportion of feeds [about 1 to 12% of the DM; (38)], lignin has a relatively high correlation with digestibility (47, 54). Theoretically, lignin is indigestible and should account for some of the variation in fiber digestibility (56). Minson (36) compiled 34 different equations that estimate DDM of forages from lignin content. Most of the equations had $r^2 > .8$ and $s_{y.new} < 4\%$ DDM. The error increased as the population used to derive the equation became more diverse. For an equation based on legume samples, $r^2 = .81$, and $s_{y.new} = 2.3\%$ DDM (48), but, when grasses were included, $r^2 = .49$, and $s_{y.new} = 5.8\%$ DDM. The regression coefficients varied greatly, depending on the type of forage and method of lignin analysis. Based on the summary by Minson (36), different lignin-based equations should be used for cool season grasses, warm season grasses (including corn silage), and legumes. Furthermore, an equation derived using a particular method of lignin analysis is not valid for lignin data measured using a different method. No data were available on the use of lignin for prediction of available energy in concentrate feeds. Because of the extremely low lignin content of most concentrate feeds (ca. 1 to 2%), lignin as the sole independent variable is unlikely to have much value for prediction of available energy of concentrates.

Crude protein functions as a uniform fraction for most feeds (28). Concentrations of CP are correlated positively ($r^2 = .15$ to $.90$) to available energy concentrations of forages (36). Crude protein content also is correlated positively ($r^2 = .40$ to $.65$) to the concentration of NDS and negatively to the fiber content in feeds (34). Several equations have been used

to estimate DDM from CP concentrations in forages (36), but $s_{y.new}$ are relatively high (6 to 7 percentage units of DDM). Type of forage (grass or legume), cutting, and stage of growth influence the regression parameters to such an extent that several different equations are needed (37, 48). Even though CP is a uniform feed fraction, it is not an accurate predictor of available energy in forages because it constitutes a relatively small fraction (5 to 25%) of the total forage, and the variability in the digestibility of the nonprotein fraction can be high. Foncesbeck et al. (21) reported that CP was not a good predictor of available energy in concentrates.

Fiber is the most common variable used to predict energy content of feeds (40). Forages contain relatively large amounts of fiber, it is easy to measure, and a large database is available. Fiber can be measured several different ways, but ADF and NDF are used most frequently by ruminant nutritionists. The negative relationship between fiber content and available energy occurs because fiber is, in general, less digestible than nonfiber. Theoretically, NDS (the converse of NDF) is more correct to use in regression models because it is a uniform fraction with true digestibility near 100% (56). Fiber, however, is not a uniform feed fraction, and its digestibility varies both among and within feedstuffs (9, 56). The most comprehensive compilation of equations for prediction of available energy from ADF or NDF was published by Minson (36), but several newer equations are available (16, 27). Correlations between ADF or NDF content and DDM are relatively high ($r^2 > .6$), but $s_{y.new}$ also are relatively high [2 to 8 percentage units (33, 55)]. Prediction error is less when one equation is used for grasses and another for legumes. Generally, equations based on ADF have lower $s_{y.new}$ than equations based on NDF, but the difference is not large (27, 36). The precise prediction of available energy from a single component (e.g., ADF) is questionable. Lack of fit (regression error) accounted for 55% of the total error in prediction of energy using ADF (1).

Single-component equations have several limitations: they are empirical and, therefore, population-dependent. Feeds not represented in the data set used to derive the equation may not be predicted with sufficient degree of ac-

curacy or precision. Because of the effects of growing conditions and postharvest factors, feedstuffs continuously change. No individual feed that is currently fed has been truly represented in a population collected in the past. Different equations are needed for each feedstuff class (e.g., concentrates and forages, grasses and legumes, and high and low fiber concentrates), and classification often is difficult, especially for forage mixtures. In an attempt to alleviate some of these problems, different types of multicomponent models have been developed.

Multicomponent Equations

Multicomponent models can be empirically or theoretically based. Multicomponent empirical models are derived similarly to single-component models. The concentrations of several feed fractions are regressed on available energy, usually stepwise. Variables with a significant effect are included in the final model. Multiple regression models for prediction of available energy using proximate analysis components [CP, EE, crude fiber, and N-free extract (17, 21)] and NDF and CP (41, 51) have been derived. Typically, R^2 for most multiple regression models are between .5 and .7, which are only slightly higher than for single-component models. The improvement in R^2 probably is only a statistical artifact, because R^2 almost always increases as the number of independent variables increase (39). The $s_{y \cdot x}$ of most multiple regression models is similar to the $s_{y \cdot x}$ for single-component models based on fiber.

A more robust method of prediction of available energy from feed constituents uses theoretical rather than empirical relationships. Theoretically based models should be population-independent. Goering and Van Soest (25) developed a simple, theoretically sound, summative equation that can be used to estimate DDM.

$$\text{DDM} = .98 \times \text{NDS} + \text{dNDF} - \text{M} \quad [4]$$

where dNDF = digestible NDF, M = metabolic fecal losses (approximately 12.9), and all values are expressed as a percentage of DM. The .98 is the true digestibility of the NDS fraction. Equation [4] could be expanded to

include terms for ash and fat content, which would make the estimation of available energy appropriate for most feeds. The limitation of Equation [4] is that digestibility of NDF must be known. Because NDF digestibility is not constant across or within feeds, several different constants are needed. To overcome this problem, Goering and Van Soest (25) estimated NDF digestibility using an empirical equation based on the logarithm of the lignin: ADF ratio. Equation [4] produced accurate values for forages and roughages (12, 44, 46), but not for concentrate feeds (12, 23). Many concentrate feeds have relatively low ADF compared with forages but have high NDF concentrations; for those feeds, ADF represents a small proportion of the total fiber (estimated as NDF).

Conrad et al. (12) derived a summative equation based on the same principles outlined by Goering and Van Soest (25). The model included terms for CP, EE, nonstructural carbohydrate, and potentially digestible NDF (PDNDF). The digestibility of the CP fraction was calculated using ADIN. Nonstructural carbohydrate was considered to be essentially 100% digestible. Ether extract was used as the measure of fat and given a constant digestibility (85%). The novel aspect of the model of Conrad et al. (12) was the use of surface area relationships to estimate the proportion of NDF unavailable for digestion. Two corrections for lignin were made by Conrad et al. (12). First, because lignin is indigestible, it was subtracted from NDF, thus yielding lignin-free NDF. Second, to correct for the inhibition by lignin of cellulose and hemicellulose digestion, the proportion of NDF surface area covered by lignin surface area was calculated. Surface area was calculated by raising mass to the .67 power. The equation (12) for estimation of PDNDF was

$$\text{PDNDF} = (\text{NDF} - \text{lignin})(1 - [\text{lignin}/\text{NDF}]^{.67}) \quad [5]$$

where all variables are expressed as a percentage of the DM, and lignin was measured using the ADF-sulfuric acid method. Then, PDNDF was multiplied by its digestibility coefficient. The digestibility coefficients for PDNDF and EE were the only empirical coefficients in the model. Estimated NE_L values were correlated

strongly with actual NE_L ($r^2 = .96$) for a highly diverse population of feeds, including forages and concentrates. The s_{y-new} was .022 Mcal of NE_L .

Girard and Dupuis (24) evaluated the model of Conrad et al. (12) and reported that PDNDF as calculated using the model functioned as a uniform fraction. Harlan et al. (27) reported that the lignin:NDF surface area term was highly correlated with digestibility for a range of forages and that the term accounted for many differences between grasses and legumes. However, Girard and Dupuis (24) pointed out that the total model contained a theoretical flaw. Conrad et al. (12) used mostly theoretical true digestibilities for each feed fraction to estimate TDN of feeds, but TDN is based on apparent digestibilities, not on true digestibilities. When true digestibility coefficients are used, metabolic fecal excretion must be considered. Girard and Dupuis (24) added a term to the model of Conrad et al. (12) to account for metabolic fecal losses. Additional modifications to the model were made to improve the accuracy for estimation of available energy of high fiber concentrate feeds (e.g., distillers grains) and high fat feeds (61, 62). Those improvements included replacement of EE with fatty acids, correction for N contamination of the NDF fraction, and addition of a term for metabolic fecal TDN. Girard and Dupuis (24) corrected for metabolic fecal DM. The abridged modified model (61, 62) is

$$TDN = .98 \times (100 - NDF_N - CP - ash - FA - 1) + .93 \times CP + 2.25 \times FA + .75 \times (NDF_N - lignin) \times [1 - (lignin/NDF_N)^{.667}] - 7 \quad [6]$$

where FA = fatty acids, NDF_N = N-free NDF, and all values are expressed as a percentage of DM. The full model (61, 62) includes terms for ADIN to adjust for depressed CP digestibility. Equation [6] was tested on a database of 247 feeds, which included forages, roughages, grains, protein feeds, and high fiber concentrates (62). The estimated values were unbiased and highly correlated ($r^2 = .78$) with actual values and had a low error ($s_{y-new} = 2.5$ TDN units). Correlations and s_{y-new} varied among feedstuff classes (r^2 ranged from .54 for forages to .74 for grains, and s_{y-new} ranged from 1.5 TDN units for grains to 2.8 TDN units for protein feeds). The TDN values obtained using Equation [6] were then converted to NE_L using Equation [3].

The NE_L values obtained using Equations [6] and [3] were compared with values obtained using equations based on ADF (Table 1). Both methods produced accurate results, but a single multicomponent model was used for all forages; whereas three separate equations based on ADF were used. The same equation was used to estimate NE_L for concentrates and compared with values in NRC (38)

TABLE 1. Chemical composition and actual and estimated NE_L for forages.

Forage	NDF	ADF	Lignin	Actual	Est.	Est.	Ref. ⁴
				NE_L^1	NE_L^2	NE_L^3	
			(%)	(Mcal/kg)			
Alfalfa	38	29	7.4	1.47	1.42	1.54	(63)
Alfalfa	49	37	7.7	1.37	1.30	1.33	(6)
Alfalfa	58	42	8.4	1.20	1.18	1.20	(6)
Bromegrass	56	34	3.3	1.40	1.40	1.46	(30)
Bromegrass	70	39	4.5	1.30	1.25	1.32	(35)
Grass-legume mix	49	41	9.1	1.15	1.28	1.24	(29)
Grass-legume mix	65	41	6.3	1.30	1.35	1.24	(34)
Corn silage	51	28	4.0	1.60	1.56	1.48	(38)
Corn silage	57	29	3.8	1.40	1.33	1.46	(50)

¹Actual NE_L determined by converting TDN (measured by digestion trials) to NE_L using Equation [3].

²Estimated NE_L calculated using Equation [6] and chemical composition data.

³Estimated NE_L calculated using ADF and equations from Adams (2): legume, $NE_L = 2.297 - .0262 \times ADF$, grass, $NE_L = 2.387 - .0273 \times ADF$, and corn silage, $NE_L = 2.297 - .0290 \times ADF$. Grass legume mix estimated by averaging results obtained from the legume and grass equations.

⁴Reference source for the composition and TDN data.

tables (Table 2). The equation yielded accurate values for grains and by-products. Using table values for energy, especially for by-product feeds, can be extremely inaccurate.

Other Factors Affecting Energy Values

All of the equations discussed address only the chemical composition of the feed without consideration of physical characteristics of the feed, animal factors, and associative effects. Processing of grains and forages affects digestibility and metabolizability of their energy (8, 42). Grinding forages and grains increases the surface area of particles (relative to mass) and reduces rumen retention time. Increased surface area probably is the reason that digestibility of grains increases when they are ground (8). Grinding forages, especially high quality forage, generally reduces their digestibility (42). Grinding increases passage rate, which decreases the amount of fiber (the major source of energy in forages) that is digested. Grinding forages also decreases methane loss and other metabolic costs (42). Use of particle size of feeds in energy prediction models has not been investigated extensively. Additional terms to account for depressed digestibility of fiber by reduced particle size could be added to the summative models when an appropriate mathematical function is identified.

The major animal factor that affects energy availability is feed intake; as ruminants consume more DM, digestive efficiency decreases (52). Most tabular values for DE and TDN are for maintenance feeding; NE values have been

adjusted to reflect the feed intake appropriate for production. The adjustment for depressed digestibility made by the NRC (38) is constant for most feeds. Relative to digestibility at maintenance, the NRC reduces TDN by 8 percentage units for feeds when they are fed at amounts appropriate for production. This adjustment is incorporated in Equation [3]. However, the effect feed intake has on digestibility is not constant (11, 18, 57, 59). Variation in fiber digestibility can be explained partially by differences in rates of digestion and passage among feeds and diets (3, 60). The interaction between digestion and passage rates is shown clearly in Equation [7], which was derived by Waldo and Smith (60).

$$D = k_d / (k_d + k_p) \quad [7]$$

where D = fiber digestibility, and k_d and k_p = rates of digestion and passage, respectively. Accurate rates of passage and digestion are needed to make use of Equation [7], but they are difficult to obtain and are variable. Factors that affect rate of passage include type of feedstuff (10), forage to concentrate ratio (10), and particle size (31). Rate of digestion is affected by type of feedstuff (58), particle size (19), and rumen pH (26). Those effects and interactions must be quantified before Equation [7] can be incorporated into Equation [6] to be used to estimate accurately the digestibility coefficient for PDNDF.

Because many of the components of NDS can be digested readily in the intestines, Equation [7] should not be used for that fraction.

TABLE 2. Chemical composition and actual and estimated NE_L for concentrate feeds.

Feedstuff	NDF	ADF	ADL	Actual	Est.	Est.	Ref. ⁴
				NE_L ¹	NE_L ²	NE_L ³	
			(%)	(Mcal/kg)			
Corn grain	11	3	.3	2.06	2.10	1.96	(5)
Barley grain	17	7	.8	1.90	1.95	1.94	(5)
Soybean meal	10	5	.6	2.10	1.97	2.01	(5)
Soyhulls	60	43	1.9	1.64	1.60	1.77	(29)
Corn gluten feed	38	10	.6	1.78	1.74	1.91	(5)
Cottonseed hulls	65	49	17.5	1.02	1.15	.98	(29)

¹Actual NE_L determined by converting TDN (measured by digestion trials) to NE_L using Equation [3].

²Estimated NE_L calculated using Equation [6] and chemical composition data.

³Estimated NE_L from NRC Feed Composition Table (38).

⁴Reference source for the composition and TDN data.

The digestibility of NDS decreases about 2 percentage units for every increment of energy intake above maintenance and is not affected greatly by forage to concentrate ratio (11). This discount could be added to the digestibility coefficient of the NDS fraction in Equation [6].

Adjustment for Variable Metabolic Efficiencies

Digestibility has been the only variable discussed relative to available energy concentration. Fecal losses of energy account for the greatest variation in available energy content among feeds. Conversion of DE to ME and NE is much less variable, and reasonable accuracy can be obtained using standard equations. However, the efficiencies of conversion of DE to ME or NE vary among feeds. Some variation can be accounted for by chemical composition and mathematical modeling. The ME content of feeds can be determined from the composition of feeds using an equation based on proximate analysis or on the detergent system, but digestibility of the individual fractions must be known (41). Summative models that can be used to predict digestibility of individual components (12, 62) could be modified to predict ME or NE by use of appropriate coefficients for each fraction. More complex models using more specific composition data (ash, CP, EE, starch, cellulose, and fermentation acids in silages) have been derived and appear to be accurate (15). Models for prediction of ME or NE based on nutrient composition account for additional variation, so two feeds with the same DE may have different ME, depending on their nutrient composition. Fat is used more efficiently for production than carbohydrate (4). Therefore, ME and NE for feeds with high concentrations of fat are underestimated when standard conversion equations are used. The amount of carbohydrate fermented to propionate (inversely proportional to methane production) in the rumen (14) affects conversion efficiency. This effect can introduce relatively large error when individual feeds are used (13), but much less error when total diets are evaluated. The main limitation to improved accuracy of conversion of DE or TDN to ME or NE is the limited number of actual ME and NE values.

CONCLUSIONS

Because of the variability within and among feedstuffs (including concentrates), accurate determination of available energy for feeds and diets are economically and nutritionally important. Actual ME and NE values are difficult to obtain because of the cost and equipment needed. Measurement of DE or TDN is easier but still not practical for commercial application. Accurate equations based on theoretically sound principles are needed to estimate energy of feeds. Estimation of available energy using empirical equations is population-specific and imprecise. Complex equations require more composition data but are more robust (less population-specific) and usually more accurate and precise. Additional factors, such as interactions among feeds, rate of passage, and diet composition, must be further researched so that mathematical models can be derived to account for additional variation. Variation among feeds in the efficiency of conversion of DE or TDN to other energy measures also must be explored further.

REFERENCES

- 1 Abrams, S. M. 1988. Sources of error in predicting digestible dry matter from the acid-detergent fiber content of forages. *Anim. Feed. Sci. Technol.* 21:205.
- 2 Adams, R. S. 1980. Penn State forage testing service revised regression equations. *Dairy Sci. Ext. Memo DSE-90-56*, Pennsylvania State Univ., University Park.
- 3 Allen, M. S., and D. R. Mertens. 1988. Evaluating constraints on fiber digestion by rumen microbes. *J. Nutr.* 118:261.
- 4 Andrews, S. M., H. F. Tyrrell, C. K. Reynolds, and R. A. Erdman. 1991. Net energy for lactation of calcium soaps of long-chain fatty acids for cows fed silage-based diets. *J. Dairy Sci.* 74:2588.
- 5 Aufrere, J., and B. Michalet-Doreau. 1988. Comparison of methods for predicting digestibility of feeds. *Anim. Feed. Sci. Technol.* 20:203.
- 6 Atwal, A. S. 1983. Effects of preserving alfalfa forage as formic acid-treated silage, wilted silage, and as hay in large round bales on chemical composition, recovery of nutrients, and digestibility and heifer growth. *Can. J. Anim. Sci.* 63:925.
- 7 Belyea, R. L., B. J. Steevens, R. J. Restrepo, and A. P. Clubb. 1989. Variation in composition of by-product feeds. *J. Dairy Sci.* 72:2339.
- 8 Campling, R. C. 1991. Processing cereal grains for cattle—a review. *Livest. Prod. Sci.* 28:223.
- 9 Colburn, M. W., J. L. Evans, and C. H. Ramage. 1968. Apparent and true digestibility of forage nutrients by ruminant animals. *J. Dairy Sci.* 51:1450.
- 10 Colucci, P. E., L. E. Chase, and P. J. Van Soest. 1982. Feed intake, apparent diet digestibility, and rate of

- particulate passage in dairy cattle. *J. Dairy Sci.* 65: 1445.
- 11 Colucci, P. E., G. K. Macleod, W. L. Grovum, L. W. Cahill, and I. McMillan. 1989. Comparative digestion in sheep and cattle fed different forage to concentrate ratios at high and low intakes. *J. Dairy Sci.* 72:1774.
 - 12 Conrad, H. R., W. P. Weiss, W. O. Odwongo, and W. L. Shockey. 1984. Estimating net energy lactation from components of cell solubles and cell walls. *J. Dairy Sci.* 67:427.
 - 13 Cooke, B. C. 1988. Evaluation of feeds for ration formulation. *Proc. Nutr. Soc.* 47:135.
 - 14 Demeyer, D. I., and C. J. Van Nevel. 1975. Methanogenesis, an integrated part of carbohydrate fermentation, and its control. Page 366 in *Proc. 4th Int. Symp. Ruminant Physiol.* I. W. McDonald and A. C. Warner, ed. Sydney, Aust. Univ. New England Publ. Unit, Armidale, New South Wales, Aust.
 - 15 Dewhurst, R. J., A. J. Webster, F. W. Wainman, and P. J. Dewey. 1986. Prediction of the true metabolizable energy concentration in forages for ruminants. *Livest. Prod. Sci.* 43:183.
 - 16 Donker, J. D. 1989. Improved energy prediction equations for dairy cattle rations. *J. Dairy Sci.* 72:2942.
 - 17 Donker, J. D., and D. G. Naik. 1979. Predicting total digestible nutrients and estimated net energy of dairy cow rations from chemical components. *J. Dairy Sci.* 62:424.
 - 18 Edionwe, A. O., and F. G. Owens. 1989. Relation of intake to digestibility of diets containing soyhulls and distillers dried grains. *J. Dairy Sci.* 72:1786.
 - 19 Fadlalla, B., R. N. Kay, and E. D. Goodall. 1987. Effects of particle size on digestion of hay by sheep. *J. Agric. Sci. (Camb.)* 109:551.
 - 20 Fisher, L. J., and D. B. Fowler. 1975. Predicted forage value of whole plant cereals. *Can. J. Anim. Sci.* 55: 975.
 - 21 Fonnesbeck, P. V., M. F. Wardeh, and L. E. Harris. 1984. Mathematical models for estimating energy and protein utilization of feedstuffs. *Utah Agric. Exp. Stn. Bull.* 508, Logan.
 - 22 Garrett, W. N. 1980. Energy utilization of growing cattle as determined in seventy-two comparative slaughter experiments. Page 3 in *Energy Metabolism*. L. E. Mount, ed. Eur. Assoc. Anim. Prod. Publ. No. 26, Butterworths, London, Engl.
 - 23 Gasa, J., C. Castrillo, M. D. Baucells, and J. A. Guada. 1989. By-products from the canning industry as feedstuffs for ruminants: digestibility and its prediction from chemical composition and laboratory bioassays. *Anim. Feed Sci. Technol.* 25:67.
 - 24 Girard, V., and G. Dupuis. 1988. Effect of structural and chemical factors of forages on potentially digestible fiber, intake, and true digestibility by ruminants. *Can. J. Anim. Sci.* 68:787.
 - 25 Goering, H. K., and P. J. Van Soest. 1970. *Forage Fiber Analyses (Apparatus, Reagents, Procedures, and Some Applications)*. Agric. Handbook No. 379. ARS-USDA, Washington, DC.
 - 26 Grant, R. J., and S. J. Weidner. 1992. Digestion kinetics of fiber: influence of in vitro buffer pH varied within observed physiological range. *J. Dairy Sci.* 75: 1060.
 - 27 Harlan, D. W., J. B. Holter, and H. H. Hayes. 1991. Detergent fiber traits to predict productive energy of forages fed free choice to nonlactating dairy cattle. *J. Dairy Sci.* 74:1337.
 - 28 Holter, J. A., and J. T. Reid. 1959. Relationship between the concentration of crude protein and apparently digestible protein in forages. *J. Anim. Sci.* 18: 1339.
 - 29 Hsu, J. T., D. B. Faulkner, K. A. Garleb, R. A. Barclay, G. C. Fahey, Jr., and L. L. Berger. 1987. Evaluation of corn fiber, cottonseed hulls, oat hulls and soybean hulls as roughage sources for ruminants. *J. Anim. Sci.* 65:244.
 - 30 Laforest, J. P., J. R. Seoane, G. Dupuis, L. Phillip, and P. M. Flipot. 1986. Estimation of the nutritive value of silages. *Can. J. Anim. Sci.* 66:117.
 - 31 Martz, F. A., and R. L. Belyea. 1986. Role of particle size and forage quality in digestion and passage by cattle and sheep. *J. Dairy Sci.* 69:1996.
 - 32 Maynard, L. A. 1953. Total digestible nutrients as a measure of feed energy. *J. Nutr.* 51:15.
 - 33 McLeod, M. N., and D. J. Minson. 1972. The effect of method of determination of acid-detergent fibre on its relationship with digestibility of grasses. *J. Br. Grassl. Soc.* 27:23.
 - 34 Mertens, D. R. 1973. Application of theoretical mathematical models to cell wall digestion and forage intake in ruminants. Ph.D. Diss., Cornell Univ., Ithaca, NY.
 - 35 Messman, M. A., W. P. Weiss, and D. O. Erickson. 1991. Effects of nitrogen fertilization and maturity of bromegrass on in situ ruminal digestion kinetics of fiber. *J. Anim. Sci.* 69:1151.
 - 36 Minson, D. J. 1982. Effect of chemical composition on feed digestibility and metabolizable energy. *Nutr. Abstr. Rev. Ser. B* 52:591.
 - 37 Minson, D. J., and C. D. Kemp. 1961. Studies on the digestibility of herbage. 9. Herbage and faecal nitrogen as indicators of herbage organic matter digestibility. *J. Br. Grassl. Soc.* 16:76.
 - 38 National Research Council. 1982. *United States-Canadian Tables of Feed Composition*. Natl. Acad. Press, Washington, DC.
 - 39 Neter, J., and W. Wasserman. 1974. *Applied Linear Statistical Models*. Richard D. Irving, Inc., Homewood, IL.
 - 40 Nichols, E. L., and R. C. Dixon. 1984. Forage energy prediction equations used by private laboratories. Page 32 in *Proc. Am. Feed Manuf. Assoc. Nutr. Coun., Am. Feed Manuf. Assoc.*, Arlington, VA.
 - 41 Osbourn, D. F. 1978. Principles governing the use of chemical methods for assessing the nutritive value of forages: a review. *Anim. Feed Sci. Technol.* 3:265.
 - 42 Osbourn, D. F., D. E. Beever, and D. J. Thomson. 1976. The influence of physical processing on the intake, digestion and utilization of dried herbage. *Proc. Nutr. Soc.* 35:191.
 - 43 Palmquist, D. L. 1991. Influence of source and amount of dietary fat on digestibility in lactating cows. *J. Dairy Sci.* 74:1354.
 - 44 Rebole, A., P. Alvira, and G. Gonzalez. 1990. Relationship among compositional data of fibrous by-products as determined by two different extractions in the detergent system of analysis. Influence on the prediction of the digestibility. *J. Sci. Food Agric.* 53: 15.

- 45 Schneider, B. H. 1947. Feeds of the World; Their Digestibility and Composition. West Virginia Agric. Exp. Stn., Morgantown.
- 46 Smith, L. W., H. K. Goering, D. R. Waldo, and C. H. Gordon. 1971. In vitro digestion rate of forage cell wall components. *J. Dairy Sci.* 54:71.
- 47 Sullivan, J. T. 1959. A rapid method for the determination of acid-insoluble lignin in forages and its relationship to digestibility. *J. Anim. Sci.* 18:1292.
- 48 Sullivan, J. R. 1964. The chemical composition of forages in relation to digestibility by ruminants. Publ. 34-62, USDA-ARS, Washington, DC.
- 49 Swift, R. W. 1957. The caloric value of TDN. *J. Anim. Sci.* 16:753.
- 50 St-Pierre, N. R., R. Bouchard, G. J. St-Laurent, C. Vinet, and G. L. Roy. 1983. Effects of stage of maturity and frost on nutritive value of corn silage for lactating dairy cows. *J. Dairy Sci.* 66:1466.
- 51 Terry, R. A., D. F. Osbourn, S. B. Cammell, and J. S. Fenlon. 1974. In vitro digestibility and estimation of energy in herbage. Page 19 in Proc. 5th Gen. Mtg. Eur. Grassl. Fed., Uppsala, Sweden.
- 52 Tyrrell, H. F., and P. W. Moe. 1981. Effect of intake on digestive efficiency. *J. Dairy Sci.* 58:1151.
- 53 Van Es, A. J. 1975. Feed evaluation for dairy cows. *Livest. Prod. Sci.* 2:95.
- 54 Van Soest, P. J. 1964. Symposium on nutrition and forage and pastures: new chemical procedures for evaluating forages. *J. Anim. Sci.* 23:838.
- 55 Van Soest, P. J. 1965. Comparison of two different equations for prediction of digestibility from cell contents, cell-wall constituents and lignin content of acid detergent fiber. *J. Dairy Sci.* 48:815.
- 56 Van Soest, P. J. 1967. Development of a comprehensive system of feed analysis and its application to forages. *J. Anim. Sci.* 26:119.
- 57 Van Soest, P. J., D. G. Fox, D. R. Mertens, and C. J. Sniffen. 1984. Discounts for net energy and protein—4th revision. Page 121 in Proc. Cornell Nutr. Conf. Feed Manuf., Syracuse, NY. Cornell Univ., Ithaca, NY.
- 58 Varga, G. A., and W. H. Hoover. 1983. Rate and extent of neutral detergent fiber degradation in situ. *J. Dairy Sci.* 66:2109.
- 59 Wagner, D. G., and J. K. Loosli. 1967. Studies on the energy requirement of high-producing dairy cows. Cornell Agric. Exp. Stn., Memoir 400, Ithaca, NY.
- 60 Waldo, D. R., and L. W. Smith. 1972. Model of cellulose disappearance from the rumen. *J. Dairy Sci.* 55:125.
- 61 Weiss, W. P. 1991. Predicting available energy in ruminant feedstuffs. Page 67 in Proc. Maryland Nutr. Conf., Baltimore. Univ. Maryland, College Park.
- 62 Weiss, W. P., H. R. Conrad, and N. R. St. Pierre. 1992. A theoretically-based model for predicting TDN values of forages and concentrates. *Anim. Feed Sci. Technol.* 39:95.
- 63 Yu, Y. 1974. Comparisons of chemical, in vitro and in vivo methods for estimating nutritive values of normal and chemically treated haylages. Ph.D. Diss., Michigan State Univ., East Lansing.