



Feed quality and animal performance[☆]

Sam W. Coleman^{a,*}, John E. Moore^b

^aUSDA, ARS, SubTropical Agricultural Research Station, 22271 Chinsegut Hill Road, Brooksville, FL 34601, USA

^bUniversity of Florida, Gainesville, FL 32611, USA

Abstract

A sound theoretical definition for forage or feed quality is animal performance. This definition may be useful as a relative comparison among forages when given to growing or lactating animals. Voluntary intake and nutrient digestibility have been used to form indices of forage quality, and most feeding standards and models are based on the assumption that animal performance is related closely to intake of available nutrients. Due to variation in measurements of intake, digestibility, and animal performance, however, relationships used to develop prediction equations for animal performance from intake and digestibility are often less accurate than desired. Some of the causes for inaccurate predictions include nutrient imbalances, environmental constraints on the animals used for measurements, and individual animal differences. Variation in voluntary intake is greater than that for digestibility, and appears to be more important in assessment of forage quality. Yet intake is more difficult to determine in animal trials and to predict from forage characteristics. To be useful in livestock feeding, forage quality information must be available before feeding. Due to expense, labor, time, and amount of the feed required, animal trials are not suitable for screening large numbers of feeds or forages such as those from genetic improvement trials. Therefore, prediction of forage quality from feed attributes taken from small samples is necessary. Chemical composition, *in vitro* bioassays, and near-infrared reflectance spectroscopy have been used successfully to predict intake and digestibility of defined sample sets such as those from genetic improvement trials, but have been more difficult to implement on unknown or open populations such as producer samples. The challenge to progress in this area is obtaining accurate intake, digestibility and performance data on an adequate number of samples under standardized conditions so that a suitable database is available for development of either robust equations, or equations with sufficient specificity to discriminate among different forage and genetic types.

© 2003 Elsevier B.V. All rights reserved.

Keywords: Feed quality; Intake; Digestibility; Performance; Prediction

1. Introduction

Animals have a genetic potential to produce meat, milk and fiber, depending on the species and genetic selection within that species. The goal of most animal

farming systems is to allow the animal to express its genetic potential in an economical manner. In developing countries, animals are likely to have a lower genetic potential for production, and to partition proportionally more nutrients into maintenance and survival strategies than those found in industrialized countries. Also, dual and triple purpose animals may have different efficiencies for any one of the major uses of energy than animals that have been highly selected for a single production goal, such as high producing dairy cows.

[☆] Joint contribution of the USDA-ARS and the Florida Experimental Station Journal Series No. R-09255.

* Corresponding author. Tel.: +1-352-796-3385;

fax: +1-352-796-2930.

E-mail address: swcol@ifas.ufl.edu (S.W. Coleman).

Major nutrients required by ruminant animals include protein, vitamins, and minerals. Energy is also required, but is not a chemical entity. Energy is a unit of work and may be supplied by several different nutrient constituents, including starch, sugar, fiber, lipids, and protein. Energy substrates, largely fiber, make up a greater proportion of common forages, fodders and crop residues. For optimum utilization, all necessary nutrients must be available so that only the animal's genetic potential limits productivity. The nutrient that is first limiting governs the extent of expression of genetic potential by a given animal. A feed resource is usually chosen because of its availability or relative expense. If that resource does not supply all required nutrients, they must be supplied by a supplemental source for optimum production.

Current definitions for forage quality and feed value have been developed for conventional forages, plants grown and harvested primarily to feed ruminants. Non-conventional feeds, such as residues and stovers from plants primarily harvested as crops when mature, are often severely deficient in one or more primary nutrients, e.g., protein. Hence, when such feeds are fed as the sole feed source other aspects of quality may be masked. Furthermore, animals may not consume enough to support even maintenance. In such cases, the potential energy value of the resource as feed for ruminants can be assessed only if the minimum nutrient requirements for the rumen and the animal are met. The purpose of this paper is to provide an overview of the relationships between nutrient composition, feed intake, digestibility, and animal performance, and briefly discuss methods to assess attributes of feed quality.

2. What is feed quality?

When feed is offered alone and of free choice to animals having production potential, feed quality may be defined in terms of animal performance (e.g., daily gain). Heaney (1970) combined digestibility and intake into a single index as a means of evaluating the feeding value of forages. Raymond (1969) proposed a similar concept, but added utilization of the digested nutrients to the equation, similar to the concept proposed by Mott and Moore (1970). Voluntary intake is the consumption of feed when there is no

limitation on the amount of feed available. Nutritive value includes nutrient composition (i.e., protein, carbohydrates, vitamins, and minerals) of the feed, availability (digestibility) of nutrients and energy, and efficiency of nutrient and energy utilization. Digestible dry matter (or organic matter) is used as a proxy of digestible energy (DE). Utilization refers to the relative efficiency of DE conversion to metabolizable energy (ME) and the efficiency of conversion of ME to energy available for tissue accretion, milk production, or fiber production.

The combination of digestibility with intake is a reasonable determinant of feed quality and is quite well accepted as an indicator of potential animal production. In fact, most feeding standards (i.e., ARC, 1980; AFRC, 1992; NRC, 1996) predict ME intake and energy available for production (net energy (NE) in the National Research Council (NRC) system) from DE intake. However, these systems were developed from feeding trials where high-quality forages or cereal grain comprised a significant portion of the diet. With other forages, however, good agreement has been observed between average daily gain (ADG) and intake of digestible dry matter (DDMI) for *Paspalum* spp./white clover (*Trifolium repens*) hay (Fig. 1; Holmes et al., 1966) and for bermudagrass (*Cynodon dactylon*) or sorghum-sudan hybrid (*Sorghum bicolor*) hays (Lippke, 1980).

2.1. Voluntary intake

Measured voluntary intake is a function of both the intake potential of the feed and the nutrient demand by the animal. The relative contributions of intake and digestibility to variability in forage quality are not equal. Digestible dry matter intake of tropical grasses (Milford and Minson, 1965) and animal gain (Lippke, 1980) were more correlated with intake of dry matter than with its digestibility. Crampton et al. (1960) reported that variations in intake accounted for 70% of the variability in the nutritive value index. Crampton (1957) and Ventura et al. (1975) agreed that intake is the more important factor in determining quality, but intake of a forage is more variable among animals fed alike than is digestibility (Blaxter et al., 1961; Minson et al., 1964).

While intake may be considered more important than digestibility for predicting performance, the

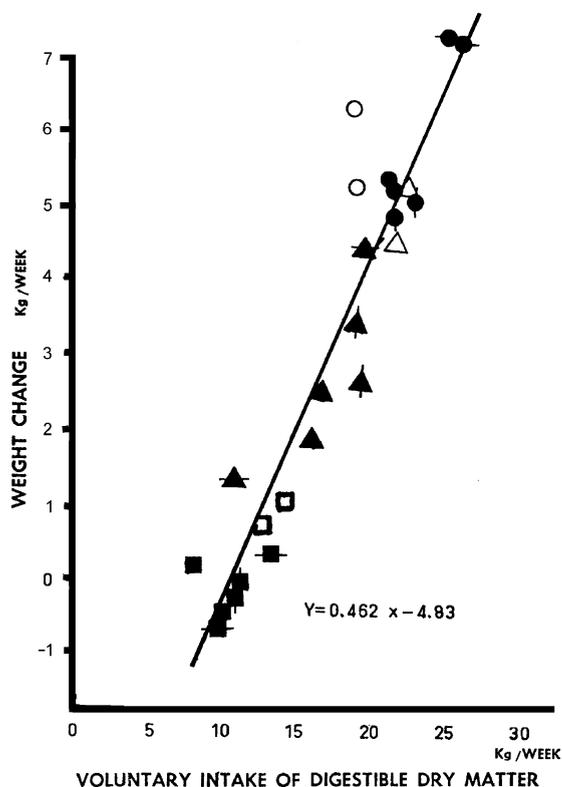


Fig. 1. Relationship of performance to intake of digestible dry matter of Paspalum or white clover hay (from Holmes et al., 1966).

effect may be overestimated due to variability in determinations (Heaney et al., 1968). Heaney et al. (1969) determined that the use of 11 sheep per feed would not reliably detect real differences of 10 intake units ($\text{g}/\text{BW}^{0.75}$) whereas real differences of 30 g kg^{-1} digestibility units could be determined with as few as four sheep. Waldo (1970) noted that complex interactions of feed, animal, and the animal's environment cause great variation in the measurement of intake, and the variation caused difficulty in developing a unifying concept of forage intake by ruminants. To reduce the effects of animal variation among trials on estimates of mean voluntary intake, Abrams et al. (1987) proposed the use of a standard forage in each trial, but the practice has not been adopted widely.

Regulation of intake is an interaction of forage characteristics, the rumen, and the host animal. The French 'fill unit' system (Jarrige et al., 1986) describes the fiber-bulk limitations imposed by the forage. Weston (1996) described the interplay between the

animal's ability to use and dissipate energy (demand), and the characteristics of the feed that limit the animal's capacity to consume sufficient amounts to meet that demand. Regulation is based on the assumption that roughage feeds rarely supply sufficient energy to meet the animal's energy demand. In such cases, intake may be constrained due to resistance to removal of feed from the rumen, low diet palatability, nutrient imbalances, and environmental stress. The interplay may be modified by non-chemical effects such as physical form. For instance, grinding and pelleting increases intake (Coleman et al., 1978; Minson, 1990), whereas steminess and other physical characteristics may impede rate, and eventually level of intake (Kenney and Black, 1984).

The constraint to intake (Weston, 1996) is calculated as the difference in quantity of forage that is eaten and the amount expected to be eaten when constraints are absent. The concept largely fits the Conrad et al. (1964) model in which they stated that intake increases with digestibility to a point (about 650 g/kg) and then declines as the energy balance of the animal assumes control in regulation of satiety. However, the Conrad model was developed with totally mixed, pelleted diets suitable for dairy cows, and likely will not be applicable where forages or residues are fed as the sole source of energy.

2.2. Nutrient content

Of the nutrients required for animal production, protein and energy occur in the greatest amount, are the most costly, and usually are the first limiting for fibrous feeds. Vitamins and minerals may limit production, often at chronic levels, but response is often slow. Furthermore, they can usually be supplied as supplements in low levels when deficient in the available feedstuffs, and while the supplements have a cost, they are normally economically feasible. Minson (1990) and McDowell (1985) have published reviews on vitamins and minerals for ruminants so they will not be considered further in this review.

Crude protein (CP; $\text{N} \times 6.25$) in feeds serves two functions in ruminant animals. The first is to supply N for the rumen microorganisms, and the second is to supply amino acids to the small intestine for absorption and use by the host ruminant animal. Amino acid supply comes from two sources, feed protein escaping

microbial degradation and microbial protein (MP), derived from assimilating ruminal NH_3 (Broderick, 1994). Both amino sources are subsequently hydrolyzed and absorbed from the small intestine. It is the quantity of amino nitrogen, as well as the relative ratio of amino acids reaching the small intestine, that is important for optimum utilization. Amino acids in short supply are considered limiting, and often are those containing sulfur, especially for milk and wool production.

Dietary true protein not degraded in the rumen is referred to as ruminally undegraded intake protein (UIP), also referred to as escape, bypass, or protected proteins (NRC, 1996). Ruminally degraded intake protein (DIP) is available for microbial growth and fermentative activity. The UIP and synthesized microbial protein flow into the abomasum and small intestine where they are subject to digestion by enzymes produced by the host animal, and absorbed. Methods for assessment of forage protein should describe the degree to which the forage contributes to MP and UIP to meet the animals absorbed protein requirement.

Non-protein N (NPN) and DIP are equally effective as N sources for the ruminal microorganisms, and microbial enzymes are largely indiscriminate concerning which N source is used. Ruminally fermentable N substances are largely converted to ammonia that, in turn, is used by the microorganisms. If the ruminal NH_3 concentration becomes excessive, then NH_3 may be absorbed into the blood and converted to urea by the liver. This urea may be excreted as a loss or recycled back into the rumen as NPN. However, regardless of pathway, NH_3 absorbed into the blood represents an energy cost for the conversion to urea, and therefore is undesirable.

Until the minimum requirement for N is met in the rumen to satisfy microbial needs, ruminal fiber digestion is depressed, undigested residues accumulate in the rumen, and intake is depressed. For this reason, when dietary CP is below about 8% of the diet, CP content has a strong relationship with intake (Fig. 2). However, when that requirement has been met there is little or no relationship with intake. Many tropical forages (especially mature) and crop stovers are severely deficient in CP. Often an NPN source, such as biuret or urea, can improve intake by supplying N for ruminal microorganisms (Fig. 3; Coleman and Barth, 1977). An adaptation period may be required

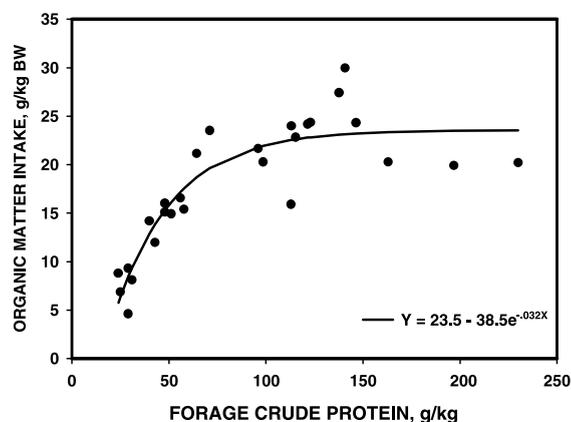


Fig. 2. Relationship of voluntary intake with crude protein content of the forage. Adapted from data of Moore et al. (1999).

to achieve synchrony between the carbon supply derived from fermented energy sources and the available N. The adaptation is normally a ruminal effect, as rumen microbes increase their effectiveness for digesting fiber, which in turn increases the capacity of the animal to consume more forage. Note from Fig. 3 that intake of the Pangola digitgrass (*Digitaria decumbens* Stent.) hay control diet also improved over the 7-week trial, probably due to increased efficiency of N recycling.

Efficiency of microbial protein production is one of the more important factors in the evaluation of feeds.

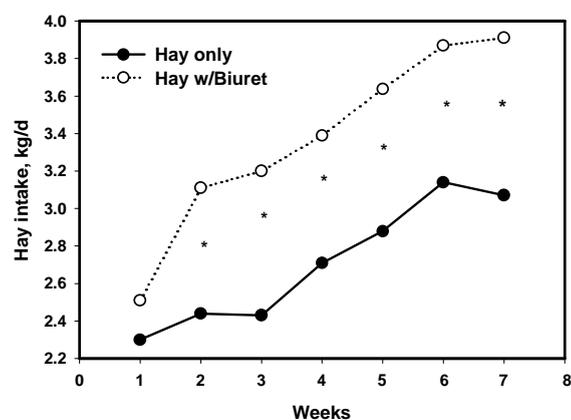


Fig. 3. Intake of Pangola digitgrass hay (3.7% CP) fed alone or when supplemented with 120 g per day biuret (40% N). Asterisk denotes significant differences ($P < 0.05$) between hay only and hay supplemented with biuret (adapted from Coleman and Barth, 1977).

Energy supply to the microorganisms appears to be a major driver in the incorporation of N into microbial biomass and the synchrony of N and energy release is crucial for efficient incorporation. Therefore, solubility and degradability of both N and energy substrates are important for optimal efficiency. When animals are fed young, vegetative forage, either grazed from pasture (e.g., grazing spring growth of improved pasture species) or by cutting and manger feeding, protein content is unlikely to limit production (Dove, 1996). Under these circumstances when the animals diet is high in CP, the CP is often rather inefficiently used (Nolan, 1993).

However, deficiency of protein can be a major limitation to the intake and utilization of most tropical forages due to rapid growth and maturity during the wet season (see Minson, 1990). When animals consume low-quality roughages such as mature stovers, crop residues, and dead pasture, the CP content may be so low (~4%) that requirements of both the host animal and rumen microbes may not be met. Nolan (1993) points out that marginal protein deficiency in ruminants may be quite common and unconsidered by nutritionists. This is particularly true of high producing animals, whether for growth, lactation or wool production. The deficiency may manifest itself when one or more critical amino acids are missing, or available to the small intestine in deficient quantities. This type deficiency then causes wastage and elimination of other non-essential amino acids that cannot be used to fabricate needed proteins by the host animal.

While the CP content of feeds is rather easily ascertained, determination of DIP and UIP are quite difficult and the results often variable. Various *in vivo* (see Tamminga and Chen, 2000) and *in situ* (see Hvelplund and Weisbjerg, 2000) techniques have been developed to evaluate feeds for their protein value. Sniffen et al. (1992) incorporated the dynamic aspects of ruminal degradation in their model. A simplified method that does not require animals or rumen microorganisms, but is based on solubility characteristics, was proposed by Chalupa et al. (1991) to categorize N fractions. In some tropical grasses, especially bahia-grass (*Paspalum notatum* Flugge.), much of the N is slowly degradable true-protein (Fig. 4; Johnson et al., 2001). This could be detrimental if passage rate is sufficiently rapid so that release of the N never occurs.

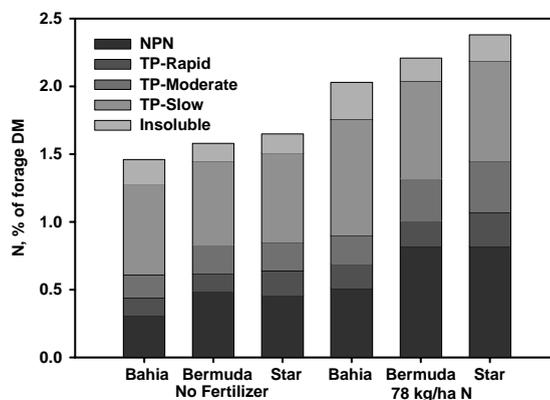


Fig. 4. Nitrogen fractionation of three C_4 grasses without N fertilizer and with 78 kg/ha N applied after each cutting date. NPN: non-protein nitrogen; TP-Rapid: rapidly degradable true protein; TP-Moderate: moderately degradable true protein; TP-Slow: slowly degradable true protein; and Insoluble: true protein insoluble in acid-detergent solution (adapted from Johnson et al., 2001).

However, it is more likely a benefit as the N is more slowly released in synchrony with fiber hydrolysis and energy release. Unfortunately the fractionation scheme may not be as good a predictor of protein degradability with forages, particularly tropical grasses, as with conventional protein sources, because of the amount of slowly degradable N.

2.3. Digestibility

The largest loss of the ingested feed dry matter, particularly from forages and other fibrous feeds, occurs in the feces. Digestibility is often used as a proxy for nutritive value, and deterministically, is the difference between the amount of a nutrient eaten and the amount voided in the feces. While digestibility is perhaps the oldest form of nutritive evaluation other than chemical composition, the relationship of forage digestibility to animal performance is often low ($r^2 = 0.41$; J.E. Moore, unpublished data). However, it is an important part of the primary determinant of performance, the intake of digestible energy (see Fig. 1).

The controlling factors for *in vivo* digestibility include an interplay involving competition between rates of passage and digestion. The potentially digestible portion of the consumed diet leaves the rumen through hydrolysis by microbial enzymes and absorption across

the rumen wall (e.g., volatile fatty acids), or by passage to the lower tract. [Waldo et al. \(1972\)](#) modeled the interplay and suggested that extent of digestion is a function of the rate of digestion and the amount of time available for the enzymes to act. Rate of passage then becomes an antagonist to the extent of digestion since faster passage rate would reduce the amount of time available for digestion. On the other hand, the more rapid the removal of undigested residue, whether potentially digestible or indigestible, the more space available for new feed, and intake may be increased. To further complicate the matter, increased intake could increase rate of passage, and thus reduce extent of digestion. This interplay could explain why the relationship between intake and in vivo digestibility is so variable ([Moore and Coleman, 2001](#)). Practically, however, the depression in digestibility by increased intake and rate of passage appears to be rather small and is variable among forages. [Varga et al. \(1990\)](#) observed a 2% depression in digestibility when intake of orchardgrass (*Dactylis glomerata*) was increased from 16 to 19 g/kg BW (16% change). There was no effect with alfalfa (*Medicago sativa*). [Mertens \(1973\)](#) found the depression ranged from –192 to 249 g/kg DM of the diet with an average of 14.9 g/kg DM. He suggested variability in fecal microbial mass and endogenous matter could contribute to the large variation.

2.4. Utilization of digested energy

While most feeding standards assume a constant conversion ratio for DE to ME (about 0.8), it can vary considerably ([NRC, 1996](#)). [Varga et al. \(1990\)](#) found that efficiency of DE conversion to ME was similar for alfalfa and orchardgrass, but was greater (83.9 vs. 82.9) when intake was increased by 15%.

Another issue is the conversion of ME to meat, milk or wool. [Tudor and Minson \(1982\)](#) found differences in utilization of ME for fattening when Pangola and setaria (*Setaria sphacelata*) were fed to growing beef cattle. [Minson \(1990\)](#) compiled results from many trials and found a loose relationship between ME content and utilization for fattening. [Varga et al. \(1990\)](#) and [Waldo et al. \(1990\)](#) in companion studies observed lower efficiency of ME conversion for orchardgrass than for alfalfa. These differences in efficiency of utilization appear to be intake independent,

Table 1

Data statistics for digestibility, intake and gain by steers eating various kinds of hay (from Coleman, S. W., unpublished results)^a

Item	Mean	Range	S.E. ^b	CV ^c
DMD (g kg ⁻¹)	625	464–750	37.2	5.95
NDFD (g kg ⁻¹)	609	383–754	56.7	9.32
Intake (g kg ⁻¹ BW per day)	21.6	12.5–29.4	2.05	9.55
Daily gain (kg per day)	0.25	–0.29–0.79	0.19	73.3

^a $N = 3$ animals/hay for digestibility; 4 animals/hay for intake and gain (56 days).

^b Standard error among animals fed the same hay.

^c Residual coefficient of variation among animals fed the same hay.

yet the difference in efficiency at different levels of intake were three to six times greater than the difference between forages. [Dhiman et al. \(1995\)](#) observed that differences in actual energy output and calculated energy output ([NRC, 1989](#)) differed dramatically among diets and between multiparous and primiparous cows. These data illustrate the difficulty of determinations of efficiency, and are likely to be exacerbated when forages are fed at maintenance or near maintenance. Variation among animals given the same feed is large for performance in terms of gain (e.g., see [Table 1](#)) when compared to intake and digestibility, and this variation contributes to variation in efficiency. The variability among animals fed alike, and the error of a given determination make it difficult indeed to predict production from more easily determined measurements such as digestibility estimates. However, given the expense, time and feed resources needed to conduct animal production trials, the only solution is to develop a database under standardized conditions to provide the relationships necessary to predict the desired production trait.

3. Feed quality assessment with animal trials

[Murray \(1996\)](#) suggested three steps to feed assessment that are often confused. The first step is to ensure that a feed material is what it is stated to be (qualitative analysis). The second step is to quantify its ranking among like feeds (quantitative analysis). The third step is to determine (or predict) the likely animal performance that may be expected from feeding the material to a target animal (nutritional analysis).

All three steps are important and may apply to individual feed ingredients or to mixed feeds. Traditional feed chemistry analysis is usually used to evaluate step three but can only be used if the analyst knows the identification of the feed material. For instance, certain analyses (such as fiber and lipid) are different for different kinds of feed materials, and certainly the relationships differ among feed types.

Reviews on *in vivo* assessment of forage quality have been published previously by Minson (1990), Cochran and Galyean (1994), Coleman et al. (1999), and Rymer (2000). While the most accurate method of feed evaluation consists of measuring the production output from target animals consuming the feed or feeds (Leng, 1996), they are not practical for screening samples from plant breeders. These methods contribute to steps two and three of feed assessment; they can be used to rank feeds, and can help determine the likely animal performance to be expected. Due to the time and expense of performance trials, intake of digestible dry matter (DDMI), the product of forage intake and its digestibility, has been used to assess the nutritive potential of forages.

Voluntary intake is measured as the *ad libitum* intake of a single feed where choice and selection are eliminated as much as possible (Marten, 1970). The techniques and requirements for assessment have been discussed in reviews by Marten (1970), Heaney (1970), Greenhalgh (1982), Coleman and Windham (1989), Burns et al. (1994) and Van Soest (1994). The review by Heaney (1970) provides a comprehensive methodology for measuring intake, including the number of animals required and the length of time for a determination. Abrams et al. (1987) proposed the use of a standard forage to reduce effects of animal variation on estimates of voluntary intake. Daily variation in intake by a single animal can be substantial, and intake and gain should be measured over an extended period in which animals are free from as many constraints as possible (such as extreme confinement or temperature). Burns et al. (1994) advised that intake determinations should be over a 2-week period after intake has stabilized, but stabilization may take 10–15 days. If gain is to be measured, then longer periods, perhaps up to 60 days, may be necessary.

In vivo determination of digestibility is the *de facto* standard, but results can vary depending on whether animals are fed at maintenance or at some level above

maintenance. This variation occurs because of the relationship of intake to rate of passage and the resulting influence of residence time on ruminal fermentation.

Animal trials are laborious, time consuming, costly, require a substantial amount of the test feed, and are totally impractical in screening of genetic resources (Castler, 1997). Indirect methods are necessary, and techniques to assist plant breeders must be developed if progress in developing countries is to move toward that observed in the developed world. Since the labor and costs are so extensive, a single laboratory seldom has the resources to conduct sufficient animal trials on which to build an extensive database. Collaboration is necessary, which in itself contributes to variation in both absolute determinations and the relationships among feed characteristics and feed quality. Standardization, as much as possible, in the conduct of the trials is necessary.

Other bioassays are available for estimating digestibility such as *in vitro* (Tilley and Terry, 1963) and *in situ* (Orskov et al., 1988) methods. The two-stage *in vitro* method developed by Tilley and Terry (1963) along with many modifications, has probably aided selection for improved quality in forages than any other technique (Castler, 1997). Other reviews in this volume (Blummel et al., Mould) discuss the merits of more dynamic *in vitro* techniques that include rates of fermentation and gas production. The *in vitro* and *in situ* methods require fistulation of animals and in the long term animal welfare considerations may preclude this practice simply for feed characterization. Thus, alternative methods using cell-free enzymes to replicate the activity of the microbes have also been developed (Jones and Hayward, 1973; Goto and Minson, 1977). While these bioassays have enhanced our ability to estimate digestibility on large numbers of samples, a similar assay to estimate intake has been more elusive.

4. Forage quality prediction and monitoring

Since assessment typically is both expensive and laborious, quick, easy, accurate and precise methods to estimate forage quality are needed. Prediction of nutritive value is being largely covered in two other chapters in this volume; one by Mould using forage

chemistry and bioassays and one by Stuth et al. for the use of near-infrared reflectance spectroscopy. Prediction of intake will be emphasized in this paper and the reader is referred to a more complete review of the topic by Poppi (1996).

With any attempt to predict forage quality by indirect methods, the method and the mathematical relationships derived from it must be evaluated using an independent data set. Evaluation samples must not be part of the ‘calibration’ data set. Otherwise, the equations have limited robustness.

Traditionally, standards of acceptance include statistics of the goodness of fit (r^2 and S.E.) between quality (intake or digestibility) and the independent variables (biological assays, chemistry or physico-chemistry). While these are useful to determine if a relationship exists, variability among animals given the same feed is often rather substantial, and provides the upper limit to the precision with which forage quality can be predicted. The collective S.E. for a group of predicted values can never be as good as the S.E. for the reference method upon which the relationship is based. Redshaw et al. (1986) found that prediction errors were about twice as large as the error for measured intake and digestibility.

4.1. Feed chemistry

Many attempts have been made to predict intake from simple chemical values (Rohweder et al., 1978). Most of these were empirical equations based on one or more chemical components, and typically are useful only for feeds of the same population on which they are based. Failures result because variation in the statistical relationship among the analytes and forage quality exists due to season, weather, location and many other variables, many of which are unknown. Rational or mechanistic equations have been developed on theoretical bases, either proven or unproven (Mertens, 1985; Weiss et al., 1992; Van Soest, 1994), that theoretically are more robust.

4.1.1. Simple relationships

Scientists have seldom attempted to predict performance directly from feed chemistry, but normally attempt to predict the components of forage quality, intake and digestibility. Conventional wisdom suggests a strong relationship between intake and digest-

ibility (i.e., Conrad et al., 1964; Freer and Jones, 1984), yet Minson (1990) and Moore and Coleman (2001) reported correlations between intake and digestibility from the literature ranging from -0.30 to 0.78 . Therefore, intake cannot be reliably predicted from estimates of digestibility, often easily obtained with simple bioassays, such as the *in vitro* technique (Tilley and Terry, 1963).

Routine forage quality analyses frequently include determinations of CP, neutral detergent fiber (NDF), and acid detergent fiber (ADF). Within forage species these values vary in a consistent manner, usually with increasing maturity, and may be used to rank quality. Cell walls and their derivatives, ADF and hemicellulose, have been used either alone or with other chemical entities to predict both intake (Table 2) and digestibility (Mertens, 1985; Minson, 1990; Moore et al., 1996). Rohweder et al. (1978) found that correlations between intake and NDF content lacked consistency and were generally low for subtropical species. Different equations relating intake to NDF were proposed for legumes and grasses. Moore et al. (1996) concluded that simple prediction equations must be different for temperate and tropical grasses. They found that at the same digestibility, intake of tropical grasses was higher than that for temperate grasses.

4.1.2. Multiple regression

Moore and Kunkle (1999) used a diverse group of both temperate and tropical forage species, fed to non-lactating cattle either alone or with supplement, to develop and test equations for intake and digestibility based on forage chemistry. Multiple regression equations were developed using CP, ADF, and *in vitro* digestibility to predict intake and *in vivo* digestibility. With the validation dataset, the difference between predicted DMI and actual DMI was within 10% of the mean observed DMI for 54% of the observations (acceptable), and an additional 39% were between 10 and 20% of the mean (marginal). Only 7% of the differences were greater than 20% of the mean (unacceptable).

Several multiple regression and multivariate techniques are available to assist in modeling relationships of chemistry to forage quality. Rook et al. (1990) described principal component and ridge regression analyses to relate several attributes of silage, including acids, pH and chemistry, to intake.

Table 2
Prediction of voluntary intake with NIR spectroscopy or by various conventional chemistry methods

Forage type and measure	Species	Method	Calibration			Validation			Reference
			N	R ²	SEC ^a	N	R ²	SEV ^a	
Mixed C ₃ and C ₄ forages (g MBS ^{-1b})	Sheep	NIRS	76	0.64	8.6	38 ^c	–	7.9	Norris et al. (1976)
Mixed C ₃ forages (g MBS ⁻¹)	Sheep	NIRS	30	0.71	8.2	30	0.49	10.6	Eckman et al. (1983)
Mixed grass and forbs (g MBS ⁻¹)	Cattle	NIRS	21	0.72	9.6	–	–	–	Ward et al. (1982) ^d
Mixed grass and legume (g kg ⁻¹ BW)	Cattle	NIRS	53	0.70	1.7	17	0.73	1.7	Redshaw et al. (1986)
	Sheep	NIRS	44	0.60	3.1	15	0.71	2.8	
Mixed hay and diets (g kg ⁻¹ BW)	Sheep	CP, ADF, DOM ^e	85	0.72	3.1	46	0.76	2.8	Moore and Kunkle (1999)
Mixed grass and legume (g kg ⁻¹ BW)	Goats	NDF, lignin	20	0.56	2.1	–	–	–	Coleman et al. (2001) ^f
		Retention time	20	0.70	1.6	–	–	–	

^a SEC: standard error of calibration; SEV: standard error of validation with random subset.

^b MBS: animal weight^{0.75}.

^c Odd samples of the original 76 were used for calibration and the even samples for validation.

^d Intake measured with grazing animals.

^e DOM: in vivo organic matter digestibility.

^f Adapted from the data.

4.2. Physico-chemical methods

4.2.1. Biomechanical

Voluntary intake below the energy demand of the animal often occurs because the forage is resistant to breakdown during chewing. Slow rate of particle comminution, long retention times of residues in the rumen (Balch and Campling, 1962), and potentially extended ruminating time are consequences. This resistance to breakdown by chewing has been attributed to the physical strength of the material (Mackinnon et al., 1988). An early study by Troelson and Bigsby (1964) demonstrated that intake was highly correlated ($r = 0.94$) with the particle size index obtained from an artificial masticator. Subsequent measures of 'resistance' included grinding energy ($r = 0.90$; Chenost, 1966), tensile strength ($r = -0.47$; Henry et al., 1996), and shear strength (Mackinnon et al., 1988). These estimates of the resistance of plant material to breakdown not only directly have an impact upon particle size reduction and passage from the rumen, but influence the surface area available for microbial enzymes to attack the residual lignified cellulose tissues. Retention time was more useful for predicting intake of hay by goats than forage chemistry (Table 2; Coleman et al., 2001).

4.2.2. Near-infrared reflectance spectroscopy

Near-infrared reflectance spectroscopy (NIRS) is a method of analysis that can perform all three steps in

feed evaluation quickly and accurately (Murray, 1996). It has been used to identify plant species (qualitative analysis; Coleman et al., 1990), and predict chemistry and quality of forages (quantitative analysis and nutritional analysis; Norris et al., 1976). The early work of Norris et al. (1976) not only demonstrated that NIRS could be used for estimation of chemical composition of forages; they also showed a relationship between NIRS spectra and animal intake and digestibility. Following this work, several researchers reported direct calibrations for digestibility (Barber et al., 1990) and intake (e.g., see Table 2). Stuth et al. (this volume) reviews this topic in more detail.

Because NIRS has the potential to directly predict intake and digestibility, the use of two equations, one for predicting chemistry with NIRS, and another for predicting intake or digestibility with NIRS chemistry, should not be used when one equation could suffice. One would assume additive errors by using the two equations. Some argue that if NIRS is used to predict intake and digestibility directly, it is difficult to monitor the equations to determine if they fit the unknowns of interest. However, before 1976 when NIRS was first introduced for forage analysis, the use of validation and monitoring equations was not practiced. The same problem of monitoring exists when forage chemistry is used to predict intake and digestibility.

Direct prediction of digestibility using NIRS is in most cases more precise than the use of chemistry

(Barber et al., 1990; Givens et al., 1997; Coleman et al., 1999). Intake is more difficult both to measure and to predict than is digestibility, largely because intrinsic properties of the feed only partially explain variability in intake (Heaney et al., 1968; Heaney, 1970; Coleman and Windham, 1989). However, several reports are summarized in Table 2 in which the residual S.E. approximates 10% of the mean of actual intake, and are similar to other published results using chemistry or chewing behavior. The report of Ward et al. (1982) suggested elevated residual variability, but the S.E. was higher because indirect methods were used as the reference method to estimate intake. These results suggest that NIRS spectra certainly contain information related to intake and can provide a very useful tool for predicting animal response when they are fed forages as the sole diet.

Lippke and Barton (1988) demonstrated excellent correlation of a single wavelength (1696 nm) with DDMI and ADG. The utility of the equation has since been validated with samples not included in the original calibration (Lippke et al., 1989). The wavelength was chosen a priori for its association with ADF, not by multiple regression with 700 data points available. Birth (1985) showed that with small data sets, the probability of obtaining high correlations with random numbers was very high when the number of X variables (NIR wavelengths) was 50–100 times greater than the number of samples.

Poppi (1996) argued that NIRS was the method of the future for prediction of intake, and that large databases could be established by collection of spectra as intake trials were conducted and response variables could be added later. He suggested that improvements in predictability could be accomplished by utilizing sophisticated population structuring and local equations. The recent advent of single-sample calibrations (Isaksson and Naes, 1991) could make this possible, provided a library of sufficient samples can be established.

The problem with predicting *in vivo* measurements with routine chemistry or NIRS has been in obtaining sufficient numbers of samples for which reference data were obtained under carefully controlled and defined conditions. More rigorous statistical procedures and larger sample sets may help overcome problems of developing broadly based robust equations.

5. Supplemental concentrates and forage utilization

Forages, stovers and crop residues normally fail to support adequate production. This is particularly true in developing countries where much of the tropical forages are fed (Leng, 1990; Orskov, 1996). In these cases, supplementation to meet the requirements for deficient nutrients may be provided to attain the desired performance. The subject of supplementation of forages has been often studied and reviewed (Horn and McCollum, 1987; Poppi and McLennan, 1995; Moore et al., 1999). Despite a voluminous amount of data on the subject, the response of ruminants fed mixtures of forage and supplements is anything but uniform (Horn and McCollum, 1987). In general, a positive response may be observed if the supplement contains a usable form of the most limiting nutrient.

While there is a great void in our ability to accurately predict intake and production, it is likely that the inclusion of supplements in the diet will further exacerbate the problem. A major difficulty is in the interaction of nutrients and nutrient sources, *i.e.*, starch on fiber digestion. For a feed evaluation system to work, the prediction of forage quality must be separated from the interaction of feed sources. This would involve three steps: (1) determine or predict the quality of the base feed; (2) determine or predict the nutritive value of the supplement; (3) model the associative effects for the complete diet (Moore et al., 1999). An attempt to predict from feed (forage) characteristics how the feed would perform in a mixed diet cannot be accomplished in a single step due to the multitude of interactions involved.

6. Summary and conclusion

Animal variation due to preference, physiological state or genetic potential for production, and thus demand, contributes to errors in measurements of forage quality. This variation leads to errors in prediction models and makes it difficult to predict nutritive potential with sufficient accuracy. For plant breeders, precision in ranking different ecotypes may be more important than absolute accuracy.

A database must be developed containing sufficient samples of feeds and forages with intake and

digestibility data determined under relatively uniform conditions. Because of the diversity of vegetation types and conditions, it will be difficult for a single laboratory to conduct such rigorous determinations over a wide population of samples that represent the diversity required. Large databases with in vivo digestibility have been developed over time in Europe, particularly the UK (Baker and Barnes, 1990; Barber et al., 1990; Givens et al., 1997), but the forage species were limited to temperate species, often ryegrass (*Lolium perenne*) and ryegrass/clover (*Trifolium* spp.) mixtures, and all were fed at a restricted intake. No known comprehensive databases exist for voluntary intake of forages and fodder crops fed as the sole source of the diet, and on which complete characterization (e.g., chemical analysis and NIRS spectra) has been conducted.

Collaboration is needed in parts of the world where low quality tropical forages and feed/crop by-products and residues comprise large portions of the diet for ruminant animals. Databases could be constructed with information on intake and digestibility obtained under rigorous standards and on which extensive chemical composition and NIR spectra are known.

References

- Abrams, S.M., Harpster, H.W., Wangness, P.J., Shenk, J.S., Keck, E., Rosenberger, J.L., 1987. Use of a standard forage to reduce effects of animal variation on estimates of mean voluntary intake. *J. Dairy Sci.* 70, 1235–1240.
- AFRC, 1992. Technical committee on responses to nutrients, Report No. 9. Nutritive Requirements of Ruminant Animals: Protein. *Nutr. Abst. Rev., Series B* 62. CAB International, Wallingford, Oxon, pp. 787–835.
- ARC, 1980. The Nutrient Requirements of Ruminant Livestock. Commonwealth Agriculture Bureau, Farnham Royal, pp. 73–119.
- Baker, C.W., Barnes, R.J., 1990. The application of near infrared spectrometry to forage evaluation in the Agricultural Development and Advisory Service. In: Wiseman, J., Cole, D.J.A. (Eds.), *Feedstuff Evaluation*, No. 50. Nottingham Easter School in Agricultural Science, Butterworths, London, pp. 337–351.
- Balch, C.C., Campling, R.C., 1962. Regulation of voluntary intake in ruminants. *Nutr. Abstr. Rev.* 32, 669–686.
- Barber, G.D., Givens, D.I., Kridis, M.S., Offer, N.W., Murray, I., 1990. Prediction of the organic matter digestibility of grass silage. *Anim. Feed Sci. Technol.* 28, 115–128.
- Birth, G., 1985. Evaluation of correlation coefficients obtained with a stepwise regression analysis. *J. Appl. Spec.* 39, 729–732.
- Blaxter, K.L., Wainman, F.W., Wilson, R.S., 1961. The regulation of food intake by sheep. *Anim. Prod.* 3, 51–61.
- Broderick, G.A., 1994. Quantifying forage protein quality. In: Fahey Jr., G.C., Moser, L.E., Mertens, D.R., Collins, M. (Eds.), *Forage Quality, Evaluation, and Utilization*. ASA, CSSA, and SSSA, Madison, WI, pp. 200–228.
- Burns, J.C., Pond, K.R., Fisher, D.S., 1994. Measurement of forage intake. In: Fahey Jr., G.C., Moser, L.E., Mertens, D.R., Collins, M. (Eds.), *Forage Quality, Evaluation, and Utilization*. ASA, CSSA, and SSSA, Madison, WI, pp. 494–532.
- Castler, M.D., 1997. Breeding for improved forage quality: potentials and problems. In: *Proceedings of the XVIII International Grassland Congress*, vol. 3, June 8–19, 1997. Winnipeg, Man. and Saskatoon, Sask., Canada, pp. 323–330.
- Chalupa, W., Sniffen, C.J., Fox, D.G., Van Soest, P.J., 1991. Model generated protein degradation nutritional information. In: *Proceedings of the Cornell Nutrient Conference*, Ithaca, NY, p. 44.
- Chenost, M., 1966. Fibrousness of forage: its determination and its relation to feeding value. In: *Proceedings of the X International Grassland Congress*, Helsinki, Finland, July 7–16, 1966, pp. 406–411.
- Cochran, R.C., Galyean, M.L., 1994. Measurement of in vivo forage digestion by ruminants. In: Fahey Jr., G.C., Moser, L.E., Mertens, D.R., Collins, M. (Eds.), *Forage Quality, Evaluation, and Utilization*. ASA, CSSA, and SSSA, Madison, WI, pp. 613–643.
- Coleman, S.W., Barth, K.M., 1977. Utilization of supplemental NPN and energy sources by beef steers consuming low-protein hays. *J. Anim. Sci.* 45, 1180–1186.
- Coleman, S.W., Windham, W.R., 1989. In vivo and in vitro measurements of forage quality. In: Marten, G.C., Shenk, J.S., Barton II, F.E. (Eds.), *Near Infrared Reflectance Spectroscopy (NIRS): Analysis of Forage Quality*, Agriculture Handbook, No. 643. USDA-ARS, Brooksville, FL, pp. 83–95.
- Coleman, S.W., Neri-Flores, O., Allen, R.J., Moore, J.E., 1978. Effect of pelleting and of forage maturity on quality of two subtropical forage grasses. *J. Anim. Sci.* 46, 1103–1112.
- Coleman, S.W., Christiansen, S., Shenk, J.S., 1990. Prediction of botanical composition using NIRS calibrations developed from botanically pure samples. *Crop Sci.* 30, 202–207.
- Coleman, S.W., Lippke, H., Gill, M., 1999. Estimating the nutritive potential of forages. In: Jung, H.G., Fahey Jr., G.C. (Eds.), *Nutritional Ecology of Herbivores*. In: *Proceedings of the V International Symposium on Nutrient Herbivores*, San Antonio, TX, pp. 647–695.
- Coleman, S.W., Hart, S.P., Sahl, T., 2001. Prediction of intake of hay differing in species and maturity by goats. In: *Proceedings of the XIX International Grassland Congress*, São Paulo, Sao Paulo, Brazil, February 10–21, 2001, pp. 366–367.
- Conrad, H.R., Pratt, A.D., Hibbs, J.W., 1964. Regulation of feed intake in dairy cows. I. Change in importance of physical and physiological factors with increased digestibility. *J. Dairy Sci.* 27, 54–62.
- Crampton, E.W., 1957. Interrelations between digestible nutrients and energy content, voluntary dry matter intake and overall feeding value of forages. *J. Anim. Sci.* 16, 546–552.

- Crampton, E.W., Donefer, E., Lloyd, L.E., 1960. A nutritive value index for forages. *J. Anim. Sci.* 19, 538–544.
- Dhiman, T.R., Kleinmans, J., Tessmann, N.J., Radloff, H.D., Satter, L.D., 1995. Digestion and energy balance in lactating dairy cows fed varying rations of alfalfa silage and grain. *J. Dairy Sci.* 78, 330–341.
- Dove, H., 1996. The ruminant, the rumen and the pasture resource: nutrient interactions in the grazing animal. In: Hodgson, J., Illius, A.W. (Eds.), *The Ecology and Management of Grazing Systems*. CAB International, Wallingford, Oxon, pp. 219–246.
- Eckman, D.D., Shenk, J.S., Wangness, P.J., Westerhaus, M.O., 1983. Prediction of sheep responses by near infrared reflectance spectroscopy. *J. Dairy Sci.* 66, 1983–1987.
- Freer, M., Jones, D.B., 1984. Feeding value of subterranean clover, lucerne, phalaris and Wimmera ryegrass for lambs. *Aust. J. Exp. Agric. Anim. Husb.* 24, 156–164.
- Givens, D.I., De Boever, J.L., Deaville, E.R., 1997. The principles, practices and some future applications of near infrared spectroscopy for predicting the nutritive value of foods for animals and humans. *Nutr. Res. Rev.* 10, 83–114.
- Goto, I., Minson, D.J., 1977. Prediction of the dry matter digestibility of tropical grasses using a pepsin–cellulase assay. *Anim. Feed Sci. Technol.* 2, 47–253.
- Greenhalgh, J.F.D., 1982. An introduction to herbage intake measurements. In: Leaver, J.D. (Ed.), *Herbage Intake Handbook*. British Grassland Society, Hurley, pp. 1–10.
- Heaney, D.P., 1970. Voluntary intake as a component of an index to forage quality. In: Barnes, R.F., Clanton, D.C., Gordon, C.H., Klopfenstein, T.J., Waldo, D.R. (Eds.), *Proceedings of the National Conference on Forage Quality, Evaluation, and Utilization*, Lincoln, NE, pp. C1–C10.
- Heaney, D.P., Pritchard, G.I., Pigden, W.J., 1968. Variability in ad libitum forage intakes by sheep. *J. Anim. Sci.* 27, 159–164.
- Heaney, D.P., Pigden, W.J., Minson, D.J., 1969. Indoor feeding trials for estimating digestibility and intake. In: Campbell, J.B. (Ed.), *Experimental Methods for Evaluating Herbage*, Publication No. 1315. Canada Department of Agriculture, Swift Current, Sask., Canada, pp. 185–199.
- Henry, D.A., Macmillan, R.H., Simpson, R.J., 1996. Shear and tensile fracture properties of leaves of pasture grasses. *Aust. J. Agric. Res.* 47, 587–603.
- Holmes, J.H.G., Franklin, M.C., Lambourne, L.J., 1966. The effects of season, supplementation, and pelleting on intake and utilization of some sub-tropical pastures. *Proc. Aust. Soc. Anim. Prod.* 6, 354–363.
- Horn, G.W., McCollum, F.T., 1987. Energy supplementation of grazing ruminants. In: *Proceedings of the First Grazing Livestock Nutrient Conference*, Jackson, WY, USA, pp. 125–136.
- Hvelplund, T., Weisbjerg, M.R., 2000. In situ techniques for the estimation of protein degradability and postrumen availability. In: Givens, D.I., Owen, E., Axford, F.F.E., Omed, H.M. (Eds.), *Forage Evaluation in Ruminant Nutrition*. CABI Publishing, Wallingford, Oxon, pp. 233–258.
- Isaksson, T., Naes, T., 1991. Segmented calibration. In: Murray, I., Cowe, I. (Eds.), *Making Light Work: Advances in Near Infrared Spectroscopy*. VCH, Cambridge, pp. 140–146.
- Jarrige, R., Demarquilly, C., Dulphy, J.P., Hoden, A., Robelin, J., Beranger, C., Geay, Y., Journet, M., Malterre, C., Micol, C., Petit, M., 1986. The INRA “fill unit” system for predicting the voluntary intake of forage-based diets in ruminants: a review. *J. Anim. Sci.* 63, 1737–1758.
- Johnson, C.R., Reiling, B.A., Mislevy, P., Hall, M.B., 2001. Effects of nitrogen fertilization and harvest date on yield, digestibility, fiber, and protein fractions of tropical grasses. *J. Anim. Sci.* 79, 2439–2448.
- Jones, D.I.H., Hayward, M.V., 1973. A cellulase digestion technique for predicting dry matter digestibility of grasses. *J. Sci. Food Agric.* 24, 1419–1426.
- Kenney, P.A., Black, J.L., 1984. Factors affecting diet selection by sheep. I. Potential intake rate and acceptability of feed. *Aust. J. Agric. Res.* 35, 551–563.
- Leng, R.A., 1990. Factors affecting the utilization of ‘poor-quality’ forages by ruminants particularly under tropical conditions. *Nutr. Res. Rev.* 3, 277–303.
- Leng, R.A., 1996. Evaluation of tropical feeds. In: Speedy, A.W., Dalibard, C., Sansoucy, R. (Eds.), *Tropical Feeds and Feeding Systems*. In: *Proceedings of the First FAO Electronic Conference on Feed Evaluation*. FAO, Rome, 17 pp. <http://www.fao.org/WAICENT/FaoInfo/Agricult/AGA/AGAP/FRG/Default.htm>.
- Lippke, H., 1980. Forage characteristics related to intake, digestibility and gain by ruminants. *J. Anim. Sci.* 50, 952–961.
- Lippke, H., Barton II, F.E., 1988. Near infrared reflectance spectroscopy for predicting intake of digestible organic matter by cattle. *J. Dairy Sci.* 71, 2986–2991.
- Lippke, H., Barton II, F.E., Ocumpaugh, W.R., 1989. Near infrared reflectance spectroscopy for estimation of digestible organic matter intake and body weight gain. In: *Proceedings of the XVI International Grassland Congress*, Nice, France, pp. 893–894.
- Mackinnon, B.W., Easton, H.S., Barry, T.N., Sedcole, J.R., 1988. The effect of reduced leaf shear strength on the nutritive value of perennial ryegrass. *J. Agric. Sci. (Camb.)* 111, 469–474.
- Marten, G.C., 1970. Measurement and significance of forage palatability. In: Barnes, R.F., Clanton, D.C., Gordon, C.H., Klopfenstein, T.J., Waldo, D.R. (Eds.), *Proceedings of the National Conference Forage Quality, Evaluation, and Utilization*, Lincoln, NE, USA, pp. D1–D55.
- McDowell, L.R., 1985. *Nutrition of Grazing Ruminants in Warm Climates*. Academic Press, New York, 443 pp.
- Mertens, D.R., 1973. Application of theoretical mathematical models to cell wall digestion and forage intake in ruminants. Ph.D. Thesis. Cornell University, Ithaca, NY (Diss. Abstr. AAD74-10882).
- Mertens, D.R., 1985. Factors influencing feed intake in lactating cows: from theory to application using neutral detergent fiber. In: *Proceedings of the 1985 Georgia Nutrient Conference*, February 13–15, 1985, Atlanta, GA, USA, pp. 1–18.
- Millford, R., Minson, D.J., 1965. The relation between the crude protein content and the digestible crude protein content of tropical pasture plants. *J. Br. Grassl. Soc.* 20, 177–179.
- Minson, D.J., 1990. *Forage in Ruminant Nutrition*. Academic Press, New York, 483 pp.

- Minson, D.J., Harris, C.E., Raymond, W.F., Milford, R., 1964. The digestibility and voluntary intake of S22 and HI ryegrass, S170 tall fescue, S48 timothy, S215 meadow fescues and Germinal cocksfoot. *J. Br. Grassl. Soc.* 19, 298–305.
- Moore, J.E., Coleman, S.W., 2001. Forage intake, digestibility, NDF, and ADF: how well are they related? *Proc. Amer. Forage Grassl. Council* 10, 238–242.
- Moore, J.E., Kunkle, W.E., 1999. Evaluation of equations for estimating voluntary intake of forages and forage-based diets. *J. Anim. Sci.* 77 (Suppl. 1), 204.
- Moore, J.E., Burns, J.C., Fisher, D.S., 1996. Multiple regression equations for predicting relative feed value of grass hays. In: *Proceedings of the 1996 American Forage and Grassland Council*, Vancouver, BC, pp. 35–139.
- Moore, J.E., Brant, M.H., Kunkle, W.E., Hopkins, D.I., 1999. Effects of supplementation on voluntary forage intake, diet digestibility, and animal performance. *J. Anim. Sci.* 77 (Suppl. 2), 122–135.
- Mott, G.O., Moore, J.E., 1970. Forage evaluation techniques in perspective. In: Barnes, R.F., Clanton, D.C., Gordon, C.H., Klopfenstein, T.J., Waldo, D.R. (Eds.), *Proceedings of the First National Conference on Forage Quality, Evaluation, and Utilization*. Lincoln, NE, USA, pp. L1–L10.
- Murray, I., 1996. The value of traditional analytical methods and near-infrared (NIR) spectroscopy to the feed industry. In: Haresign, W., Cole, D.J.A. (Eds.), *Recent Advances in Animal Nutrition*. Butterworths, London, UK, pp. 87–108.
- Nolan, J.V., 1993. Nitrogen kinetics. In: Forbes, J.M., France, J. (Eds.), *Quantitative Aspects of Ruminant Digestion and Metabolism*. CAB International, Wallingford, Oxon, pp. 123–143.
- Norris, K.H., Barnes, R.F., Moore, J.E., Shenk, J.S., 1976. Predicting forage quality by infrared reflectance spectroscopy. *J. Anim. Sci.* 43, 889–897.
- NRC, 1989. *Nutrient Requirements of Dairy Cattle*, 6th ed. National Academy Press, Washington, DC, pp. 5–10.
- NRC, 1996. *Nutrient Requirements of Beef Cattle*, 7th ed. National Academy Press, Washington, DC, pp. 3–21.
- Orskov, E.R., 1996. Plant factors limiting roughage intake in ruminants. In: Speedy, A.W., Dalibard, C., Sansoucy, R. (Eds.), *Tropical Feeds and Feeding Systems, Proceedings of the First FAO Electronic Conference on Feed Evaluation*. FAO, Rome. <http://www.fao.org/WAICENT/FaoInfo/Agricult/AGA/AGAP/FRG/Default.htm>.
- Orskov, E.R., Reid, G.W., Kay, M., 1988. Prediction of intake by cattle from degradation characteristics of roughages. *Anim. Prod.* 46, 29–34.
- Poppi, D.P., 1996. Predictions of food intake in ruminants from analyses of food composition. *Aust. J. Agric. Res.* 47, 489–504.
- Poppi, D.P., McLennan, S.R., 1995. Protein and energy utilization by ruminants at pasture. *J. Anim. Sci.* 73, 278–290.
- Raymond, W.F., 1969. The nutritive value of forage crops. *Adv. Agron.* 21, 1–108.
- Redshaw, E.S., Mathison, G.W., Milligan, L.P., Weisenburger, R.D., 1986. Near infrared reflectance spectroscopy for predicting forage composition and voluntary consumption and digestibility in cattle and sheep. *Can. J. Anim. Sci.* 66, 103–115.
- Rohweder, D.A., Barnes, R.F., Jorgensen, N., 1978. Proposed hay grading standards based on laboratory analyses for evaluating quality. *J. Anim. Sci.* 47, 747–759.
- Rook, A.J., Dhanoa, M.S., Gill, M., 1990. Prediction of the voluntary intake of grass silages by beef cattle. 2. Principal component and ridge regression analyses. *Anim. Prod.* 50, 439–454.
- Rymer, C., 2000. The measurement of forage digestibility *in vivo*. In: Givens, D.I., Owen, E., Axford, F.F.E., Omed, H.M. (Eds.), *Forage Evaluation in Ruminant Nutrition*. CABI Publishing, Wallingford, Oxon, pp. 113–134.
- Sniffen, C.J., O'Connor, J.D., Van Soest, P.J., Fox, D.G., Russell, J.B., 1992. A net carbohydrate and protein system for evaluating cattle diets. II. Carbohydrate and protein availability. *J. Anim. Sci.* 70, 3562–3577.
- Tamminga, S., Chen, X.B., 2000. Animal-based techniques for the estimation of protein value of forages. In: Givens, D.I., Owen, E., Axford, F.F.E., Omed, H.M. (Eds.), *Forage Evaluation in Ruminant Nutrition*. CABI Publishing, Wallingford, Oxon, pp. 215–232.
- Tilley, J.M.A., Terry, R.A., 1963. A two-stage technique for the *in vitro* digestion of forage crops. *J. Br. Grassl. Soc.* 18, 104–111.
- Troelson, J.E., Bigsby, F.W., 1964. Artificial mastication—a new approach for predicting voluntary forage consumption by ruminants. *J. Anim. Sci.* 23, 1139–1142.
- Tudor, G.D., Minson, D.J., 1982. The utilization of the dietary energy of pangola and setaria by growing beef cattle. *J. Agric. Sci. (Camb.)* 98, 395–404.
- Van Soest, P.J., 1994. *Nutritional Ecology of the Ruminant*, 2nd ed. Cornell University Press, Ithaca, NY.
- Varga, G.A., Tyrrell, H.F., Huntington, G.B., Waldo, D.R., Glenn, B.P., 1990. Utilization of nitrogen and energy by Holstein steers fed formaldehyde- and formic acid-treated alfalfa or orchardgrass silage at two intakes. *J. Anim. Sci.* 68, 3773–3791.
- Ventura, M., Moore, J.E., Ruelke, O.C., Franke, D.E., 1975. Effect of maturity and protein supplementation on voluntary intake and nutrient digestibility of Pangola digitgrass hays. *J. Anim. Sci.* 40, 769–774.
- Waldo, D.R., 1970. Factors influencing the voluntary intake of forage. In: Barnes, R.F., Clanton, D.C., Gordon, C.H., Klopfenstein, T.J., Waldo, D.R. (Eds.), *Proceedings of the First National Conference on Forage Quality, Evaluation, and Utilization*, Lincoln, NE, pp. E1–E22.
- Waldo, D.R., Smith, L.W., Cox, E.L., 1972. Model of cellulose disappearance from the rumen. *J. Dairy Sci.* 55, 125–129.
- Waldo, D.R., Varga, G.A., Huntington, G.B., Glenn, B.P., Tyrrell, H.F., 1990. Energy components of growth in holstein steers fed formaldehyde- and formic acid-treated alfalfa or orchardgrass silages at equalized intakes of dry matter. *J. Anim. Sci.* 68, 3792–3804.
- Ward, R.G., Smith, G.S., Wallace, J.D., Urquhart, N.S., Shenk, J.S., 1982. Estimates of intake and quality of grazed range forage by near infrared reflectance spectroscopy. *J. Anim. Sci.* 54, 399–402.
- Weiss, W.P., Conrad, H.R., St. Pierre, N.R., 1992. A theoretically-based model for predicting total digestible nutrient values of forages and concentrates. *Anim. Feed Sci. Technol.* 39, 95–110.
- Weston, R.H., 1996. Some aspects of constraint to forage consumption by ruminants. *Aust. J. Agric. Res.* 47, 175–197.