Plant factors limiting roughage intake in ruminants

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Introduction

A debate on plant and other factors limiting roughage intake in ruminants is both relevant and timely. It is relevant because in the last decade we have learned a great deal more about it. It is timely because in the last decade or two it has been recognized, at least in countries in which environmental constraints (e.g. dry seasons and winters) cannot be buffered by high level of concentrate feeding, that static feed evaluation systems whether based on starch equivalents, total digestible nutrients, metabolizable energy or grain units have a limited relevance since none of them can predict voluntary feed intake. As a result these systems are of limited use for farmers who want to predict the production capacity of pastures or roughages and to assess their exchange rates to other forages. They are of limited value also for the planners of livestock production who need to know the potential feed intake of farm animals in order to predict if only approximately, the potential livestock production in a region from the available feed resources.

The problem of intake is of course not a new realization, many researchers have paid attention to this. Crampton (1957) attempted to predict intake from digestibility and chemical composition and found no good relationships and he suspected that degradation rate was an important factor though had no means of measuring it. Van Soest (1982) made a great contribution by attempting to divide the plants chemically in order to determine intake. While this was perfect within plants i.e. predicting intake at different stages of maturity, it was not accurate when divergent plants like legumes and grasses were involved. Balch (1969) attempted to predict intake by the number of chews required per unit of feed. Teller *et al*. (1993) advanced the hypothesis that the animals had a finite capacity to chew whether it be eating or rumination and that the total would not exceed about 16 h/day. Minson (1990) lists a whole range of factors plant and animal including grinding resistance to predict forage intake. Lechner Doll *et al*. (1991) described the importance of particle density in the rumen and its effect on rumen retention time which in turn could affect intake.

There are no doubt differences in the capacity of different ruminants to digest roughages. Ruminants that are most selective usually have the smallest rumen volume Hoffman (1989) Mould *et al*. (1982) demonstrated large differences between breeds of cattle in Bangladesh and Britain. Even within the same animals the gut volume is affected by pregnancy and lactation as discussed by Kay (1990). Hoffman (1989) discussed the seasonal variation in gut volume as response to quality of diets. Animal factors relating to intake will be discussed in more detail in another paper but here we must conclude that it is unlikely that description of plant factors can predict intake under all circumstances. One could hope that it would accurately predict ranking as there will be additional effects of season, breed, physiological state etc.

In this article I will review briefly the plant factors and plant dependent animal factors, which determine the intake and digestibility of roughages by ruminants and so the value of roughages in terms of animal production. This has been our main objective at the International Feed Resources Unit at the Rowett Research Institute. I will trace the stages by which, making full use of roughage degradability studies *in vitro* and *in vivo*, we have been able to define a feed potential index which provides a simple integrated measure of the value of roughage for animal production.

Rumen Environment

Definition of conditions

In order to pursue these lines of thoughts we have found it most rational to assume that the rumen environment for cellulolysis was as far as possible optimal i.e. adequate N, S, minerals etc. and optimal pH conditions. In other words intake would be limited by the plant factors which affected fill and subsequent removal. While in practise it may not always be possible to achieve optimal rumen conditions we found it most convenient to express the value of a feed under optimal conditions. The feeds may also contain antinutritive factors which may not only inhibit degradation of the feeds themselves but also affect degradation of accompanying feeds. Some of these factors will be referred to later. Antinutritive factors can both inhibit rumen microbes or affect the host animal.

In the following some of the characteristics of roughages that influence fill and removal are discussed below. They are solubility (A) the insoluble but fermentable fraction (B), the rate constant (C) the rate at which long particles are reduced to small particles (D), the rate of removal of small particles (E), and the rumen volume (F). It will be immediately apparent that A + B are the potential digestibility and by definition:

100-(A + B) will be totally indigestible.

Solubility (A)

The best hay is made during dry weather because with rain a proportion of soluble material contained inside plant cells will be washed off and both intake and digestibility will be decreased. The soluble material consisting largely of soluble carbohydrate and protein occupies little space in the rumen and is also rapidly fermented in the rumen. For both reasons it is a very important factor relating to roughages.

The soluble content can be determined in several ways. The simplest is to wash the roughages with water for a given period and measure the loss of dry matter. It can also be determined as that which is soluble in neutral detergent solution i.e. 100-NDF. It is also possible to measure the soluble organic matter which may be desirable in samples with high content of soluble ash. In our laboratory we often use the loss of dry matter or organic matter from samples contained in nylon bags that have been exposed to the washing procedure but not incubated in the rumen.

Insoluble but potentially fermentable fraction (B)
This is determined by extrapolating the exponential curve describing degradation of insoluble material to its asymptote. This potential or asymptote is seldom achieved in practice due to rumen retention time and the degradation rate (see later). It is clear that the fraction which is totally indigestible, 100-asymptote, will require space in the gut until it is eliminated in the faeces.

The rate at which the insoluble fraction B is digested (C)
It is clear that the importance to the animals of the B fraction is determined not only by its size but also by its potential rate of fermentation, as this will determine the amount of the B fraction that will be released within the time span limited by the rumen retention time. It follows that the B fraction and the C value should not be considered in isolation from each other.

The rate at which large particles are reduced to small particles (D)
This factor, depends on chewing rumination and microbial disintegration in the animal and is a very elusive parameter. Yet it is undoubtedly important for some feeds. If the rate at which the large particles are reduced to particles small enough to enter the liquid phase and be exposed to outflow is greater than the rate at which small particles flow out then it will be no constraint to feed intake. In our laboratory we measured this parameter by measuring outflow or rumen retention time of mordanted long or small hay particles. This is of course not totally realistic as the mordanted particles are completely undegradable and therefore not exposed to microbial disintegration. Some feeds, such as palm pressed fibre or sisal pulp, contain very tough fibre which is reduced to small particles at a rate much slower than the outflow of small particles.

Outflow of small particles (E)
This parameter depends in part on rumen motility and, differs substantially between roughages. There are very large differences in the outflow of small particles from ground fibrous roughages and of

protein supplements. Ørskov *et al*. (1988) showed that in circumstances in which the outflow of protein supplements was 0.06, the outflow of roughage was only 0.03. These differences reflect the length of time it takes for particles to traverse the solid mass of rumen contents and become suspended in the liquid phase from which outflow occurs. Outflow therefore depends on the shape and specific gravity of the small particles and on the hairiness which makes then cling and adhere to large particles in the solid phase. The specific gravity, is an elusive parameter as fermentation gases can be entrapped inside cell walls and make them less buoyant. There is still a great deal to learn about the factors affecting outflow of small particles. The question which we must address is whether the variation between fibrous roughages is sufficiently large to warrant a specific value to improve prediction of feed intake. There is no doubt variability in specific gravity between roughages and type of roughages and between small particles from seeds and roughages.

Rumen volume (F)
This factor is also extremely important but not a plant factor as such. The volume of the rumen, determines how much fermenting material can be accommodated at any one time. It is a factor which has been neglected in selection procedures for animals. Indeed in some countries it has probably been selected against as a high killing out percentage, i.e. carcass weight as a percentage of live weight, has been taken to be advantageous. It is undoubtedly genetic in origin (Ørskov *et al.* 1988). Animals selected on the basis of high or low outflow rate consistently showed differences in flow rates regardless of level and type of feed offered. Cattle in Bangladesh also have a much higher gut content (33%) (Mould *et al*., 1982) than normally reported for Friesian Cattle (Campling *et al*. (1961)).

Antinutritive factors
The identification of the above range of factors governing forage intake supposes that the animals will actually eat the diet. However, throughout evolution plants have developed survival strategies to prevent them being eaten by voracious herbivores or in some

instances also making use of them to spread their roots or seeds. During some growth stages the animals are discouraged from eating them while in others they may be encouraged. Different herbivores have also developed survival strategies, like the ability to select certain parts of the plants or to develop microbial populations capable of minimising antinutritive factors such as the microbial destruction of mimosine (Jones 1981) and some tannins from tanniferous plants (Brooker *et al* 1993).

Antinutritive factors are often associated with leguminous herbage shrubs or trees rather than gramineae. The recent interest in multipurpose trees has also stimulated research into simple techniques for the identification of antinutritive factors. Thus Khazaal and Ørskov (1993) used the simple yet effective gas evaluation technique of Menke and Steingass (1988) to identify microbial antinutritive factors. The difference in gas evolution with and without a compound which complexed antinutritive tannins provided a measure of the extent to which fermentation was inhibited.

It is clear from the above description of factors affecting intake of roughages that only the A, B and C values are strictly speaking plant factors. Although affected by plants, D and E are also affected by animals in so far that the actions of chewing and rumination are involved. In the following I would like to examine the extent to which feed intake and feed utilization can be predicted from a description of feed characteristics. Here the nylon bag technique has been extremely useful, with degradation characteristics supplemented by the exponential equation $p = a + b(l-e-ct)$ developed by Ørskov and McDonald (1979). This equation was originally developed for protein supplements in which the intercept was also an approximate expression of solubility. However this is not necessarily the case for roughages due to the occurence of a lag phase or a period in which there is no net disappearance of the insoluble but fermentable substrate B. Accordingly A was defined as the laboratory determination of solubility and B as the insoluble but fermentable substrate, defined here as $(a + b)-A$, i.e. the asymptote less the solubility. The rate constant C is as in the original equation. The major plant factors affecting intake can now be derived from this relatively simple description in the absence of antinutritive factors.

The ability of these plant factors to predict intake and animal performance has been tested in four separate trials in different parts of the world with different feed resources. The first trial was reported from our group using different types and varieties of straws with and without ammonia treatments. A total of ten straws with A values of 12-24, B values of 26-48 and C values of 0.0304-0.0481 were tested. The results are given in Table 1 below.

Table 1. Accuracy of Estimating Digestibility, Dry matter Intake, Digestible Dry Matter Intake and Growth Rate of Steers from Feed Degradation. Characteristics, as Indicated by the Multiple Correlation Coefficients (r) between Factors of the Degradation Equation and these Parameters. (Ørskov and Ryle 1990).

Factors Used in Multiple Regression Analysis	Digestibility	Dry Matter Intake	Digestible Dry Matter Intake	Growth Rate
(A + B)	0.70	0.83	0.86	0.84
(A + B) + c	0.85	0.89	0.96	0.91
A + B + c	0.90	0.93	0.96	0.95
Index value	0.74	0.95	0.94	0.96

The use of the asymptote (A + B) was superior to the use of metabolizable energy concentration to predict intake. Adding to the rate constant (C) significantly improved the prediction which again was further improved by separately using A, B and C as defined earlier.

The same principle was used in a trial by Kibon and Ørskov (1993) in which six browse species from the North of Nigeria were fed to goats. Table 2 shows very similar results to those shown in Table 1 except that the prediction from asymptote (A + B) was not so good.

Khazaal *et al*. (1993) obtained almost similar accuracy for determining feed potential when ten leguminous herbages from Portugal, were fed to sheep (see Table 3). As in the previous work the addition of the rate constant significantly improved the accuracy of prediction.

Table 2. Accuracy of Prediction of Digestibility, Dry Matter Intake, Digestible Dry Matter Intake and Growth Rate from the Factors of the Exponential Equation and the Index Value as Indicated by the Multiple Correlation Coefficients (Kibon and Ørskov, 1993)

Factors Used in Multiple Regression Analysis	Digestibility	Dry Matter Intake	Digestible Dry Matter Intake	Growth rate
(A + B)	0.65	0.57	0.15	0.41
A + B + c	0.88	0.99	0.92	0.99
Index value	0.75	0.90	0.88	0.81

Table 3. Accuracy of Estimation of Digestibility and Intake of Hay by Sheep from Degradation Characteristics of Leguminous Forages as Indicated by the Multiple Correlation Coefficients. (Khazaal et al., 1993)

Factors	Digestibility	Dry Matter Intake
(A + B)	0.82	0.77
(A + B) + c	0.86	0.88
A + B + c	0.95	0.88

Table 4. The Estimation of Digestibility Dry matter Intake, Digestible Dry Matter Intake and Growth Rate of Steers from the Feed Degradation Characteristics as Indicated by Multiple Correction Coefficients (r) (Shem and Ørskov 1993).

Factors Used in Multiple Regression Analysis	Digestibility	Dry Matter Intake	Digestible Dry Matter Intake	Growth rate
(A + B)	0.85	0.83	0.84	0.80
(A + B) + c	0.95	0.84	0.88	0.90
A + B + c	0.98	0.90	0.93	0.93
Index value	0.95	0.90	0.92	0.89

Finally similar results were obtained in a large trial reported by Shem and Ørskov (1993) in which 17 different feeds, including several types of maize stover, banana leaves, bean straws and Napier grass, grown on the slopes of Mount Kilimanjaro were given *ad libitum* to steers (Table 4).

One feed (*Banana pseudostems*) was excluded because the intake was far less than expected, possibly because it contained 95% of water; intake could therefore have been limited by the rate at which the water was excluded or by other unidentified factors.

The results summarized in Table 1 to 4 are promising and indicate that for many roughages a reasonably precise estimate of feed potential can be obtained from simple studies using nylon bags incubated in the rumen of sheep or cattle. A similar, though not quite as precise, estimation based on the dynamic gas evolution technique has been reported by Blummel and Ørskov (1993). No doubt there will be exceptions, as with *banana pseudostem* and possibly with feeds containing extremely tough fibre such as palm pressed fibre and sisal pulp.

From both a practical and conceptual point of view of feed potential, it would be desirable to create one value, as was attempted from the work described in Ørskov and Ryle's book of 1990. The multiple regression equation intake $Y = X_1A + X_2B + X_3C$ was divided by X_1, so the value for A was 1. For the experiment referred to, X_2/X_1 was 0.4 and X_3/X_1 was 200. In other words a straw having an A value of 15, a B value of 30, and a C value of 0.04 would have an index or feed potential value of 15 + 12 + 8 = 35. This value has of course no biological meaning but can indicate the potential consumption and therefore the potential performance of the animals. In this work a potential value of 33 enabled the animals to consume sufficient for their maintenance need. The above results also illustrate that the value of a feed can be improved by improving A, B or C. An improvement in the A value relative to B may have no effect on overall digestibility yet still enable the animals to consume more. The accuracy is quite surprising, probably because the degradation rate constant may be positively correlated with for instance D and E, thus making it less important to know the values for these parameters.

The concept appears to be correct and the future feed evaluation table may well take the form of Table 5. The concept of feed potential also needs to be developed for pasture evaluations so that the expected performance of grazing animals in different seasons can be predicted.

Table 5. Description of Feeds in Terms of the Factors of the Exponential Equation and the Index Value

Type of Feed	A	B	c	L	Index Value
Spring barley straw (Celt	10.3	33.8	0.0466	4.8	33.1
Spring barley straw (Corgi)	12.8	37.1	0.0580	6.7	39.2
Spring barley straw (Doublet)	10.9	39.9	0.0495	5.8	36.8
Winter barley straw (Gerbel)	6.6	39.1	0.0247	3.3	27.2
Oat straw (Ballad)	11.4	38.2	0.0240	2.7	31.5
Rice straw (Sasanisiki)	17.1	36.0	0.0399	4.2	39.5
Maize stover	15.6	46.7	0.0356	12.8	41.4
Barley leaf blade	15.6	70.2	0.0672	5.0	57.1
Barley stems	13.5	36.4	0.0406	7.3	26.2
Oat leaf	11.3	49.4	0.0352	3.9	38.1
Oat stems	12.4	29.8	0.0152	1.5	27.1
Rice leaf	15.1	37.2	0.0340	5.2	36.8
Rice stems	30.0	33.5	0.0484	4.7	53.1
Maize cob	12.5	41.5	0.024	16.1	33.9
Maize leaf	19.7	38.0	0.041	14.2	41.5
Maize stem	14.1	36.9	0.032	11.2	35.5
Hay	21.5	49.6	0.037	3.2	59.0

E.R. Ørskov and W. J. Shand (unpublished). L = lag phase

These new concepts have already given rise to new perspectives.

1. The concept of feed potential in different regions can be of value for planning the most appropriate type of animal production commensurate with the feed resource. Thus reproduction, milk production and fattening can be allocated to separate areas. It also

helps to avoid the problems for both humans and animals when exotic high-producing animals are imported into areas in which there is a total mismatch between animal and feed potential. I have seen appalling malnutrition in thousands of European and American Holstein cows in South America, Asia and Africa. Application of the concept of feed potential could prevent such mistakes happening again.

As mentioned in the introduction, the expression of feed potential refers to feeds that are consumed under conditions in which the rumen environment is optimal. Less than optimal conditions will prevent the feed potential from being expressed as both intake and nutrient extraction may be limited. Some of these deficiencies can be overcome by addition of urea or the specific limiting factor. Problems of pH can be largely overcome by limiting processing of concentrate and by feed management. Some problems cannot be rectified economically and sometimes less than the feed potential has to be accepted in practice.

2 The concept also clearly illustrates that roughages can be upgraded by chemical, biological or physical means or by genetic selection by concentrating on any of the three factors A, B and C. For instance chemical treatment has the greatest effect on the B value. Enzymic treatment affects mainly the A value. Genetic selection can be aimed at any of them; it does not need to enhance digestibility as long as feed intake is the limiting factor.

3. The index or feed potential can help planners predict potential livestock production in different regions and, last but not least can provide farmers for the first time with an exchange rate for their roughage feeds.

Are feed potentials additive? To my knowledge, this has not been adequately tested but there appears to be no reason why they should not be. Basically, I think they are, if the utilization is expressed as work or as energy deposited or retained. However it is most likely that the daily work involved in chewing and rumination is similar whether the index value is 20 or 60. This would mean in effect that if the work in chewing activity is reasonably constant then the energy available for other purposes should increase with increasing index value; this perhaps brings us back to the general observation that concentrates are more efficiently utilized than roughages. In other words, while intake of digestible energy will be linearly related to feed potential, the animal's performance will show a small but consistent non-linear effect, whereby energy available for maintenance, protein and fat deposition will increase per unit increase in absorbed energy. This needs now to be investigated.

I would finally like to pay tribute to the great Canadian scientist E.W. Crampton. He had great visions of events and depth of understanding. He wrote in 1957 that the extent of voluntary consumption of a forage is limited primarily by rate of digestion of its cellulose and hemicellulose rather than by contained nutrients or the completeness of their utilization. He continued to say "Rate of digestion may be retarded by any one of numerous circumstances which interfere with the numbers or activity of rumen microflora. These include excessive lignification from advanced maturity, practical starvation of flora from nitrogen or specific mineral deficiency or the presence of excess of bacteriostatic agents". Had he continued on that line and been able to determine rate of digestion as we now can, he would surely have been well ahead of us now. He must surely be considered as one of the giants of ruminant nutrition.

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Postscript

The concepts need further elaboration but it would appear that simple measurements such as the A, B and C value provide a much better description of feed value than digestibility and metabolizability and considerably cheaper.

There will be exception or feeds which are consumed in lesser quantities than predicted. One feed isolated here was banana pseudostem which was consumed in much less amounts than predicted probably due to its higher moisture content (95%). Other feeds contain antinutritive factors which reduce feed intake.

Finally the concept emphasises that feed potential or feed value can be improved both by A, B and C values. Generally in the old systems improvements in feed value is taken to be improvement only in digestibility. Feeds which have similar digestibility can have substantial differences in feed potential. This means that genetic selection for improved crop residues can be aimed at improving any of the three characteristics and likewise upgrading procedures.

Breeds and types of animals will no doubt be different. Indigenous animals can probably consume more roughage than exotic animals but this is not a great problem. It could perhaps be used to describe differences between breeds and types of animals.

The best laboratory measurements which come close to predicting feed potential is the dynamic gas evaluation technique which has the further advantage that it can detect phenolic related antinutritive factors. Chemical analysis are very poor and I think we all agree that we need to be very critical about spending time and resources on that. NIR where it is available and can be calibrated to predict the feed characteristics hold some promise for rapid determination.

Comments on optimising rumen environment

Several authors have commented on the importance of optimising rumen environment for maximal rate and extent of degradation of cellulosic roughages. I would like to draw attention to some interesting work carried out by ILRI. Niger and ILRI IBADAN (Nigeria) where fistulated animals were grazing or offered the seasonally available feeds. About every two weeks a standard cellulosic material was incubated in their rumen and the degradability determined. Using this approach it is possible to identify periods in which the basal feeds are underutilized and the limiting factors can be identified and if possible rectified by appropriate supplements. This approach ensures also that scare supplements e.g. brans, tree leaves etc. are utilized most efficiently as they support utilization of basal feeds as well as being utilized as a source of energy or protein in their own right. I would finally add that while the feed characteristics can be determined in any rumen in which cellulolysis is optimal trials aimed at optimising rumen environment can only be done in the area and with the feeds to which it applies.