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Manipulation of fibre digestion in the rumen

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The nutritive value of fibrous feeds has usually been described in terms of digestibility and chemical composition. This description has many shortcomings, the main one being that it gives little indication of how much the animal will consume of the fibrous feeds. While in ruminants there is generally a positive relationship between digestibility and voluntary intake, this accounts for no more than about 0·5 of the variation in intake (Chenost *et al.* 1970). This description is also inadequate as a guide for the improvement of nutrition value as different components of the plant can be manipulated by different means.

In recent years much progress has been made by describing fibrous feeds by three important characteristics (Ørskov *et al.* 1988*b*), namely the soluble component, the insoluble but fermentable fraction and the rate at which the insoluble fraction is fermented. In the following the value of this approach for aiding the manipulation of fibre digestion is discussed in some detail.

MEASUREMENT OF FEED DEGRADABILITY BY INCUBATION IN RUMEN

In their simplest form all three characteristics can be described by defining the course of loss of dry matter with time from a feed sample incubated in porous nylon bags in the rumen, or for that matter in the caecum of hind-gut-fermenting animals. The findings generated from such information can be described using the exponential equation $p=a+b(1-e^{-ct})$, originally developed for the description of degradation of dietary protein (Ørskov & McDonald, 1979), where p is degradation at time t and a, b and c are constants. If the degradation of the insoluble material begins almost immediately on exposure to the rumen environment it follows that a represents the immediate soluble material which ferments rapidly, b represents the insoluble but fermentable material and c the rate constant of degradation of b. However, with fibrous feeds there is often a lag phase in the degradation of dry matter due to the time taken for adherence of cellulolytic organisms to the substrate and initially there may even be a slight increase in the dry matter content of the bag due to the weight of the adhering microbes. Consequently, the lag phase may give rise to negative values for a and very large b values, as defined by the equation of Ørskov & McDonald (1979), both of which are inappropriate for a biological understanding. As a result, a slightly different approach was adopted by McDonald (1981) and Ørskov (1989) in which a' is defined as the water-soluble organic or dry matter, and b' the insoluble but fermentable matter, where $b' = (a + b)-a'$. This is illustrated in Fig. 1 where the curve represents the course of degradation of a typical fibrous residue.

It will be appreciated that all these characteristics of fibrous feeds are important determinants of nutritive value and before discussing the manipulation of fibre digestion one needs to consider how these properties influence digestion and intake by the animal.

The soluble organic component consists mainly of sugars which are completely

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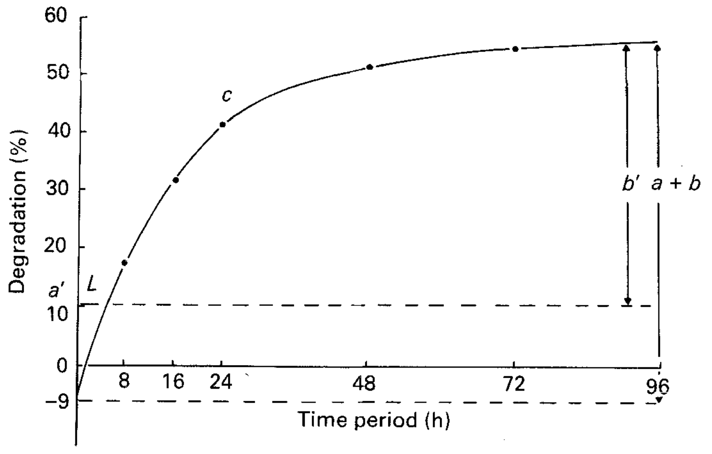

Fig. 1. Description of degradation characteristics of a typical fibrous residue using the expression $p = a + b(1-e^{-ct})$. If the soluble fraction is measured as a', the insoluble but fermentable fraction (b') is $(a + b) - a'$. L is the lag phase.

digestible. It will also include some organic components which are soluble but indigestible, such as phenolic materials released during chemical treatment (Chesson, 1981). In the ruminant it is important that the soluble organic component is contained within the plant cell, and so occupies little or no space in the rumen, and that it ferments rapidly.

The extent of digestion of the insoluble component depends on its lignin content and on the nature of the lignin. For instance, lignin in leaf and stem are different (Boon, 1989) and even stems of similar lignin content can show differences in extent of digestion. The rate at which digestion takes place and the amount which is potentially degradable together determine how much of the material will be digested during the time the materials are exposed to fermentation in the rumen or hind-gut. It can be seen, therefore, that it is the rate and potential extent of digestion which together will influence the rumen volume occupied during fermentation.

MANIPULATION OF SOLUBILITY

While the content of soluble sugars or carbohydrates in straw has a beneficial effect on its nutritive value it is of course also important that as much as possible of the soluble carbohydrate is translocated to the grain before harvesting. Increasing the soluble content in the crop residues by selection or other means is likely to influence grain yield negatively. It has been observed, for instance, that crops force-ripened by drought or deficiencies generally produce straw of high nutritive quality due to inefficient translocation of the soluble content.

Harvesting conditions. In earlier times when straw was used as a major feed for cattle it was customary to harvest the crop, particularly oats, slightly before ripening, but ripening took place in the stook in the fields. There is no information available but it is quite likely that this method of harvesting produced a more nutritive straw with a high content of soluble organic matter, but then it is also likely that grain yield was lower. In some instances unthreshed sheaves of oats were fed to cattle and horses, in which case of course the efficient translocation of solubles into the grain would not matter. For maize

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Table 1. *Effect of cellulase enzyme mixtures on degradation characteristics of stem leaf sheath and leaf blade from barley straw*

Botanical fraction	Cellulase addition (g/kg)	pH	Solubility (g/kg)	48 h loss (g/kg)	Potential (g/kg)	Rate constant (fraction/h)
Stem	0	5·6	135	299	403	0·0244
	5	4·7	174	293	383	0·0212
Leaf sheath	0	5·0	185	680	812	0·0347
	5	4·8	290	677	832	0·0276
Leaf blade	0	5·2	227	775	851	0·0454
	5	4·8	461	789	834	0·0484

harvesting in many developing countries the maize cob with the grains is harvested while the crop is still quite green. The green crop then contains sufficient soluble sugars to produce sufficient lactic and other volatile fatty acids to preserve the stovers as silage.

Effect of external treatment on content of solubles. Almost all chemical treatments used in practice so far, namely alkali (ammonia or sodium hydroxide) or oxidative methods (e.g. hydrogen peroxide), cause only small increases in the soluble materials. However, this is likely to be due in part to the release of indigestible phenolic compounds associated with lignin; cellulose itself is not hydrolysed by the treatment but merely made more accessible. Treatment with cellulase enzymes on the other hand is able to solubilize cellulose. This effect was apparent in the work of Nakashima *et al.* (1988) which showed clearly that the degradability of straw was increased to such an extent that the resulting fermentation of the solubilized sugars gave pH conditions (pH 4–5) suitable for stable straw silage (see Table 1). It is, thus, possible to use this method to preserve wet straw. The botanical component most influenced by enzyme treatment is that of the leaf blade. On the other hand the total extent of digestion was changed only little, if at all. The large effect on the digestibility of leaf blade could perhaps in the future be used to make straw leaf a suitable feed even for some simple-stomached animals or hind-gut fermenters. First, however, a technique must be developed for separation of straw into leaves for animal feeding and stems for industrial use (Rexen & Munck, 1984).

MANIPULATION OF POTENTIAL DEGRADABILITY OF THE INSOLUBLE FRACTION

Chemical treatment. It is in the improvement of the degradability of the insoluble fraction that chemical treatments have been most successful (Sundstøl, 1988). Some examples of the effect of alkali treatment are given in Table 2, from Ørskov (1989). Here it can be seen that the improvement is largely associated with the *b* value, potential degradability, and so with improving the accessibility of bacteria to the substrate. Different chemical treatments act in different ways. For instance, Grenet (1989) showed some excellent examples of swelling of the secondary cell wall which in turn increases accessibility to substrate. While the chemically determined lignin content sometimes decreases slightly, this is by no means consistent. Ramanzin *et al.* (1986) showed only very small changes in lignin content between treated and untreated materials. Oxidative treatments such as

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Table 2. *Effects of dry matter degradation characteristics of straws on intake of dry matter and on growth rate in steers*

Straw Type	Straw Variety	Untreated (U) or ammonia treated (A)	Solubility (g/kg)	Potential (g/kg)	Rate constant (fraction/h)	Dry matter intake in steers (kg/d)	Growth rate (kg/d)
Winter barley	Gerbel	U	125	388	0·0359	3·43	0·11
		A	160	623	0·0257	4·70	0·36
	Igri	U	136	433	0·0389	3·56	0·13
		A	159	532	0·0350	4·82	0·33
Spring barley	Corgi	U	160	521	0·0481	5·16	0·40
		A	190	667	0·0457	5·86	0·61
	Golden Promise	U	150	555	0·0304	4·43	0·20
		A	201	613	0·0377	4·93	0·60

Table 3. *Potential degradability and the rate constant of dry matter (DM) loss of wheat straw and maize stover, sprayed with or without hydrogen peroxide before ammonia treatment, determined by incubation in rumen nylon bags*

Treatment (g/kg straw)	Potential (g/kg DM)		Rate constant (fraction/h)	
	Wheat straw	Maize stover	Wheat straw	Maize stover
Untreated	599	677	0·0430	0·0487
NH_3-treated	722	741	0·0450	0·0537
10 g H_2O_2 + NH_3	754	760	0·0478	0·0540
50 g H_2O_2 + NH_3	773	794	0·0471	0·0576
100 g H_2O_2 + NH_3	802	815	0·0561	0·0691
SED	15·9	7·1	0·0029	0·0023

SED, standard error of difference.

alkaline H_2O_2 on the other hand appear to act by selectively oxidizing lignin, thus removing the protective barriers in a dissimilar manner to alkali treatment. As a result the effect of alkali and oxidative treatment can be additive. Thus, incubation of H_2O_2-treated wheat straw and maize stover in a closed chamber with 30 g ammonia/kg at 90° for 24 h led to the results shown in Table 3 (Adebowale *et al.* 1989). It must be remembered that H_2O_2 is only effective at alkaline pH (Gould, 1985). It can be seen that H_2O_2 caused substantial increases in the extent of degradation.

Enzyme treatment. As referred to previously the greatest effect of enzyme treatment appears to be that of solubilizing sugars from cellulose which in turn ferment to yield fermentation acids, an effect more evident in leaves than in stems. When fermentation of

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the released sugars was prevented by addition of propionic acid, Nakashima & Ørskov (1989) observed small but significant increases in the extent of rumen degradation of the enzyme-treated straw. This was further increased with use of xylanase (*EC* 3.2.1.32) as the enzyme (Smith *et al.* 1990) and further research in this area may well establish methods whereby degradability can be further increased with use of suitable enzymes. The use of enzymes to upgrade straw rather than chemicals is most desirable from an environmental point of view.

Improvement by genetic selection. A vital advance in our appreciation of fibrous feeds as feedstuffs, arising from the definition of degradability characteristics, is the realization that different species and cultivars vary widely in nutritive value (Pearce, 1983; Kernan *et al.* 1984; Tuah *et al.* 1986; Bainton *et al.* 1987). This can be seen also in Table 2 where the four different varieties of barley straw studied showed large differences in nutritive value. The variation in the nutritive value of the straw is generally not associated with the yield and quality of grain (Tuah *et al.* 1986), although Capper (1990) working in Syria did observe a small negative relationship between grain yield and straw quality.

MANIPULATION OF DEGRADATION RATE

The manipulation of the potential extent of degradation cannot be seen in isolation from effects on the rate of degradation. An increase in potential degradability would be of little advantage to the animal if the degradation rate was so low that the increased potential could not be realized during the time the feed was retained in the rumen. Degradation rate due to its effect on intake is indeed very important and an improved rate can be extremely useful even though the potential may not be increased. Thus, for instance, the differences between Corgi and Golden Promise (Table 2) were almost entirely due to differences in degradation rate which caused substantial differences both in digestibility in vivo and in growth rate of the steers, which differed by about 200 g/d. As a result, treatments which mainly or only affect degradation rate would be of advantage, particularly in feeding systems where voluntary food intake was the limiting factor.

External manipulation of degradation rate of fibrous residue. In general, chemical treatments, either alkaline or oxidative, have tended to increase potential degradability without any consistent effect on degradation rate. The limited amount of information on combinations of alkali and oxidative treatment reported by Adebowale *et al.* (1989) indicate that this procedure may increase both potential degradability and degradation rates. However, even when only potential is increased an unchanged degradation rate will refer to a larger fraction and, thus, in general both food intake and digestibility will be increased. Due to the increased intake there will generally also be an increase in outflow rate of small particles from the rumen. As a result the differences in digestibility in vivo between untreated and chemically upgraded materials with *ad lib.* feeding is generally less than expected from static estimates of digestibility such as in vitro or 48 h *in sacco* methods. For enzyme treatment in which a part of the most easily accessible cellulose is solubilized (Nakashima & Ørskov, 1989, 1990) the degradation rate of the insoluble residue is generally decreased.

Increasing degradation rate by genetic selection. The concept of characterizing roughages in terms of the three factors described earlier is new so the possibility of increasing degradation rate by genetic selection can only be speculative. Nevertheless the

Table 4. *Effect of botanical fractions of different types of cereals on degradation characteristics of dry matter*

Type of straw	Fraction	48 h degradation (g/kg)	Potential degradability (g/kg)	Rate constant (fraction/h)
Oats	Leaf	501	607	0·0353
	Stem	271	421	0·0152
Wheat	Leaf	615	734	0·0423
	Stem	330	448	0·0259
Spring barley	Leaf	705	853	0·0383
	Stem	284	377	0·0248
Rice	Leaf	435	525	0·0341
	Stem	596	638	0·0487

straws of the cereal varieties examined so far show substantial differences in degradation rate, indicating there may be a selectable genetic component. In Table 2, as mentioned previously, the only substantial difference between the varieties Corgi and Golden Promise was in degradation rate. More collaboration between nutritionists and plant breeders is required to see what progress can be made in this direction. In part, varietal differences in degradation rate may be explained by differences in leaf:stem ratio since the leaf possesses not only a substantially higher potential degradability but also a much higher degradation rate than stem, except for rice straw (Shand *et al.* 1988; Table 4).

EFFECT OF RUMEN ENVIRONMENT

So far it has been assumed that degradation rate has been determined under conditions in which rumen environment was optimal for cellulolysis. To define whether a rumen environment is optimal is presently not easy. Silva *et al.* (1989) found that even when pH and ammonia concentrations were optimal cellulosis could sometimes be increased by addition of easily digestible cellulosic material, particularly if the basal diet consisted of untreated straw supplemented with urea. For example, they observed a 20% increase in intake of untreated straw by sheep when 15% of the diet consisted of sugar-beet pulp.

In many intensive feeding systems in which rapidly degraded substrates such as starch and sugars are given, the rumen pH is often reduced to levels well below the optimum for cellulases. Mould *et al.* (1982) showed that if rumen pH was reduced below about 6·2 cellulolysis was reduced. This problem of reduced degradation rate was shown to result in up to 40% reduction in digestibility of hay. Fahmy *et al.* (1984) showed that the digestibility of ammoniated straw could be reduced from 53 to 23% when the diet was changed from one of ammoniated straw only to one of 300 g ammoniated straw and 700 g rolled barley/kg. While the soluble part of the straw and its potential degradability are relatively constant attributes of the diet, its degradation rate can be greatly reduced by an unfavourable rumen environment with the expected consequences of reduced intake and reduced digestibility in vivo.

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Table 5. *Mean intake, rumen outflow rate of small particles and apparent digestibility in two groups of Friesian cattle previously selected on the basis of low outflow (LO) and high outflow (HO); effects of feeding low- or high-roughage diets at restricted or* ad lib. *levels*

	Low roughage		High roughage		Pooled standard error of column means
	Ad lib.	Restricted	*Ad lib.*	Restricted	
Dry matter intake (g/kg $W^{0.75}$ per d)					
LO	148·7	105·8	107·4	76·0	
HO	145·6	103·5	106·1	74·8	6·2
Fractional outflow rate (per h)					
LO	0·0298	0·0257	0·0275	0·0254	
HO	0·0323	0·0309	0·0302	0·0316	0·0010
Dry matter digestibility (g/kg)					
LO	688	731	657	655	
HO	674	696	636	640	6·2
Organic matter digestibility (g/kg)					
LO	710	751	673	670	
HO	696	714	651	656	6·3

MANIPULATION OF FIBRE DIGESTION BY SELECTION OF MOST SUITABLE ANIMALS

It can be seen from Fig. 1 that animals which retain the feed for a longer time than others are also able to extract more nutrients from it. Since rumen retention time depends on rumen volume, it suggests ruminant breeds dependent on poor roughages should be selected for greater rumen volume. In some limited work Mould *et al.* (1982) observed that the rumen volume of small Zebu cattle (*Bos indicus*) that were traditionally maintained on rice straw in Bangladesh was far greater relative to live weight than normally observed in European animals. They also ate more straw than the voluntary intake expected from temperate animals. Moran & Wood (1982) showed that mature swamp buffaloes (*Bubalus bubalis*) had higher rumen volume and thus lower dressing percentages (carcass weight as a proportion of live weight) than the Zebu cattle with which they were compared and that differences in dressing percentage between cattle and buffaloes were almost entirely due to differences in gut volume. One may ask whether cattle in the USA and north-west Europe may have been selected against gut volume and so against efficient digestion of roughage by using dressing percentage as a positive index for cattle breeding. In order to assess the variability between animals in rumen retention time, Ørskov *et al.* (1988*a*) examined a herd of Friesian cattle and observed considerable variation which could almost account for individual variability in digestibility. Three animals selected for low fractional outflow from the rumen (high retention time) and three selected for high outflow (low retention time) were subsequently given two different diets at two levels of feeding to see whether the differences were consistent. The results are given in Table 5. It can be seen that while voluntary intake did not differ between the two groups, digestibility was consistently higher in the cows selected for low fractional outflow, and they also showed a consistently higher digestibility for different intakes and diets, suggesting that such characteristics could be selected for. It is, thus, possible that animals could be selected to extract more nutrients

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from fibrous roughages without at the same time selecting for low voluntary food intake. Weyreter & Engelhardt (1984) showed that sheep traditionally pastured on heather moorland had such a large rumen volume that they could eat enough wheat straw for maintenance whereas sheep breeds selected under intensive management and with a smaller rumen were unable to eat sufficient straw or digest it well enough. These authors also make an interesting comparison between types of ruminants in environments of different resource quality. More information is needed to determine the heritability of gut volume as this could have important consequences for utilization of fibrous roughages.

MANIPULATION OF RUMEN MICROBES FOR MORE EFFICIENT DIGESTION

It seems most unlikely that bacteria could be engineered to enhance potential extent of degradation. Theoretically it may be possible to produce organisms which may enhance degradation rate or introduce the capacity to produce cellulase enzyme into non-cellulolytic rumen organisms. Introduction of cellulase enzymes into organisms which survive at lower rumen pH than the present known cellulolytic organisms may also prove possible. These developments have recently been discussed by Flint *et al.* (1989), Ørskov & Flint (1990) and Stewart *et al.* (1990). The general consensus seems to be that the long-term survival of manipulated strains of microbes in the rumen will present problems and that not much progress will be made by this route. On the other hand this area of investigation is rapidly developing and the continuous inoculation with engineered organisms may be more likely to succeed (Wallace, 1989).

CONCLUSION

Utilization of fibrous diets by ruminants can be manipulated in various ways. Digestibility and intake can be improved by increasing the potential degradation of the insoluble but fermentable fraction and by increasing degradation rate. While extent of degradation of straw can be enhanced by chemical treatment, both extent and rate of degradation show a considerable genetic variation between cereal cultivars which shows little or no correlation with the yield and quality of grain. An improved utilization of straw can also be achieved in animals which, due to a large rumen volume, can both eat more and retain it longer and, thus, extract a greater amount of nutrients. Manipulation by developing superior micro-organisms is now being attempted but progress is likely to be limited. Presently the greatest progress can be made by selecting plant cultivars which, apart from producing the desired quality and quantity of main products, also produce crop residues of a high nutritive value.

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