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EVALUATION OF STRAWS IN RUMINANT FEEDING

Edited by
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EVALUATION OF STRAWS IN RUMINANT FEEDING

Proceedings of a workshop held in Perignat-les-Sarlièves, Aubière (France) from 2 to 4 June 1987 under the auspices of COST (European Cooperation in Scientific and Technological Research)—COST 84 bis, organised with the support of the Commission of the European Communities by INRA, Research Centre of Clermont-Ferrand, Theix.

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INTRODUCTION

The Workshop reported in this volume is the third of a series sponsored by the Commission of the European Communities, Directorate-General for Science, Research and Development (DG XII), under the Concerted Action Project COST 84 bis, entitled "Use of lignocellulose containing by-products and other plant residues for animal feeding".

Three topics were treated:

- In-vivo methods for measuring intake and digestibility
- Feeding trials with producing animals - long term effects
- Advances in predicting straw digestibility and intake.

The papers were circulated among the participants in advance and were discussed in the eleven sessions of the workshop, a rapporteur summarizing the discussions in each session. Dr. E.R. ØRSKOV of the Rowett Research Institute, Aberdeen, UK, led the opening and concluding discussions and formulated the recommendations of the workshop.

There is a widening gap in staple food supplies between "South" and "North" in the present-day world. While lignocellulosic crop residues, such as cereal straw, are posing problems concerning their disposal and environmental pollution in developed countries, they are a badly needed source of animal feed in developing countries, as they represent a vast reservoir of nutrients. These nutrients can be either extracted within the rumen - a genuine natural fermentor - or a by using industrial processes.

As a "new" source of feed for ruminants, straw does not compete with richer feeds, such as cereal grains and oil cakes, suitable for the nutrition of monogastrics, which include man. Research in the field of ruminant digestion clearly demonstrated that straw could supply a major part of the diet of low-productivity animals at a given physiological life cycle or of animals lacking other sources of feed e.g. in developing countries, and that it could also provide a small part of the feed of high production animals.

While the potential nutritive value of straws is unquestioned, it can vary over a wide range according to variety, strain and growth conditions. The elaboration of satisfactory feeding systems requires, therefore, an accurate as possible measurement and prediction of the straw feeding value.

These measurements can help in choosing appropriate supplements to straw as the basic component of the diet, or in deciding whether or not one should resort to pretreatments to improve its feeding characteristics. But they can also lead to suggestions for the improvement of straw feed values through appropriate plant breeding programmes.

As straw is composed of very complex polysaccharides bound with lignin, the appraisal or prediction of its feed value requires the use of refined new techniques in this case. The traditional series of chemical analysis have been shown to be inappropriate, if not useless.

The aim of the present workshop which is to review the "state of the art" of the methodologies and techniques which are available now or foreseeable in the near future in order to assess and evaluate the actual feed value of a given straw, should be seen in this context.

CONDITIONS FOR OPTIMIZING CELLULOLYTIC ACTIVITY IN THE RUMEN

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Summary

In order to optimize rumen digestion of straw-based diets the following microbial-related factors are discussed : micro-or-ganisms involved and their interaction, effect of carbohydrate supplement and of pH, supply of microbial nutrients and absence of toxic substances. The required amounts of degradable nitrogen (N), sulphur (S), phosphorus (P) and magnesium should be expressed in terms of digestible organic matter (OMD). Total nitrogen requirement approximates 26 g N/kg OMD. Contribution of recycled N may reduce these figures by to 10 to 40% depending on straw treatments. 1.8 g S/kg OMD should be available. S availability in straw would not exceed 0.3. About 5 g soluble P/kg OMD are required in the rumen. They are supplied by salivary secretion when dietary P concentration and absorbability are adequate. Branched chain fatty acids and vitamin B may stimulate fibre digestion. Crossfeeding among microbes contributes to their supply. In addition to urea, a small proportion of protein may enhance the cellulolytic activity. The pH should be prevented from falling below 6.0 and all the required nutrients should be supplied along with cell-wall degradation which is a slow process. It is concluded that more research should be directed towards stimulation of ruminal implantation of fungi and quantification of endogenous N supply.

1. INTRODUCTION

Rumen fermentation of lignocellulosic feeds occurs in a complex system that is influenced by dynamic interactions among the animal, the diet and the microbial population. It is known that animal factors such as feed intake, rumination and chewing times and rate of passage of digesta affect the relative amount of ruminal digestion of plant cell-walls. Dietary factors such as intrinsic characteristics of the fibre including chemical and physical structure also affect the rate of digestion. The indigestible fraction of fibre is known to be closely related to the lignin content of forages. Delignification processes (chemical, biological or physical) improves the rate of fermentation. Grinding and alkali treatments can increase surface area for microbe attachment and/or accessible to enzymes. However, these animal and feed aspects have recently been discussed elsewhere (1,2) and will not be examined here.

The aim of the present paper is to review the conditions directly related to microbial activity which are required to optimize rumen digestion of straw-based diets. They concern the balance between microbial species and populations, physico-chemical characteristics of the environment such as pH, and dietary factors like the effect of carbohydrate supplement, the supply of nitrogen, minerals and growth factors and the absence of toxic substances.

2. MICROORGANISMS INVOLVED AND IMPORTANCE OF MICROBIAL INTERACTIONS

2.1. Fibrolytic microorganisms

Demeyer (3) reported that plant tissue particles entering the rumen are colonized within 5 min by bacteria, within 15 min by protozoa and within 2h by fungal sporangia and rhizoids. Up to now cellulolytic bacteria have been considered to carry out the major part of fibre digestion in the rumen. Bacteroides succinogenes a gram-negative rod, Ruminicoccus flavefaciens and Ruminicoccus albus gram-positive cocci are the most important cellulolytic species. The first two species synthesize the most active cellulases (4). They are attached to, or associated with, plant cell walls. They also degrade hemicellulose but do not always utilize the products of hydrolysis : xylan or pentose. Hemicellulases are also produced by non-cellulolytic species such as Bacteroides ruminicola and Butyrivibrio fibrisolvens. Most cellulolytic and hemicellulolytic bacteria can also degrade pectin but some do not use the uronic acids released.

Protozoa are also involved in rumen degradation of cellulose and they have frequently been reported to possess cellulases and hemicellulases and to engulf plant cell walls (5). Experiments with defaunated animals (removal of protozoa) generally indicate that overall fibre digestibility is decreased (3,6) although some contradictions are now apparent : defaunation may enhance plant cell-wall digestion of tropical forages supplemented with molasses (Jouany, personal communication). These discrepancies could be due to relative changes in bacterial and fungal populations : the removal of protozoa might be detrimental to some cellulolytic bacteria species but beneficial to cellulolytic fungi.

The phycomycete fungi are a recently discovered group of rumen microorganisms. At least 3 species are known and all ferment plant cell-wall polysaccharides as sole sources of carbon and energy. Their numbers are larger on a high fibre diet than on a high concentrate diet (7). They attach to lignified vascular tissues and degrade extensive amounts of sclerenchyma tissue. Recently Fonty et al. (8) isolated strains of Neocallimastix frontalis from the rumen of sheep. In vitro they colonize straw tissues, degrade cellulose and xylan and ferment several monoses with production of acetate, ethanol, lactate and H_2.

The presence of fungi in the rumen allows more tissues to be disrupted and increases the surface area exposed to bacterial enzymes (E. Grenet, personal communication). Therefore, factors which may stimulate fungi implantation may also improve the digestibility of straw-based diets.

2.2. Microbial interactions in the rumen

The many interactions between or within rumen populations have recently been reviewed (4,9,10,11). Of special importance is the synergism between fibrolytic species and non fibrolytic species. An efficient degradation of plant cell-wall can only be achieved by the activi-

ties of various populations : hydrolytic, fermentative and methanogenic.

The majority of non-fibrolytic bacteria in the rumen of animals fed high roughage diets are associated with plant material. They hydrolyze the non structural carbohydrates, starch and fructosans and protein and may ferment cellulose fragments, xylan, cellobiose and pentose (Butyrivibrio fibrisolvens, Selenomonas ruminantium...). They are in close association with fibrolytic species. They may increase fibre degradation by disposing of products such as pentose or succinate (ex : S. Ruminantium and B.succinogenes), thus alleviating catabolic repression and by providing the cellulolytic bacteria with amino acids and growth factors.

Interspecies transfer of hydrogen to methanogens in order to keep a low partial pressure of hydrogen in the medium is particularly important for many bacterial species. It allows more acetate and thus more energy production during fermentation through the production of ATP by substrate-level phosphorylation (SLP) with decreased amounts of propionate and lactate (3,12,13). Such hydrogen transfer also takes place between methanogens and populations of protozoa and fungi. Physical associations between entodiniomorphs and methanogens have been observed (3). The activity of fungal enzymes is enhanced by co-culture with methanogenic bacteria (5). Piromonas communis and Sphaeromonas communis degrade more cellulose and produce more acetic acid and less ethanol and lactate when co-cultured with a methanogenic bacteria (14).

Interspecies H_2 transfer allowing disposal of H_2 by the reduction of fumarate to succinate, sulphate to sulphide and nitrate to nitrite coupled to anaerobic electron transport phosphorylation (ETP) has been recently emphasized (15). Synthesis of ATP via ETP may play a vital role in some fibrolytic rumen bacteria such as B. succinogenes and B. fibrisolvens which may derive 50 and 26%, respectively, of their total substrate from ETP.

An optimized digestion of high straw diet relies on the right balance between microbial populations involved. Supplementation with other types of cabohydrates, inadequate nutrient supply and use of some additives can result in proliferation of organisms at the expense of fibrolytic species.

3. SUPPLY OF EASILY DEGRADABLE CARBOHYDRATES AND EFFECT OF pH

A stimulatory effect of low amounts of easily degradable carbohydrates (5-10% of the substrates) on cellulolysis has been reported in vitro (3). Only few in vivo experiments support these observations. Silva and Orskov (16) have recently shown that addition of 15% of sugar beet pulp in an untreated straw diet could increase straw dry matter disappearance from nylon bags by about 6-10%. Degradable β glucans present in pulp might be more effective than starch or molasses. However, degradation of ammonia-treated straw was not improved by beet pulp addition in Rusitec (17). Treated straws may contain sufficient amounts of available β glucans to allow for the synthesis of adhering glycocalyx fibres of G+ cellulolytic bacteria.

The inclusion of starchy concentrates in mixed diets has long been found to reduce fibre digestion (18). The reduction becomes significant when the diet contains about 30 to 40% grain (9) or even with lesser amounts. Henning et al. (19) observed that the digestibility of cellulose and hemicellulose declined linearly as the proportion of maize grain (in a diet based on maize straw) increased above 7.8%. The reduction of cellulolytic activity can be due to decreases 1) in number of cellulo-

lytic bacteria and/or their growth rates, 2) in rate of cellulases synthesis and 3) in enzyme activity. Both a decline of pH down to values below 6.2-6.0 often observed with grain supplementa-tion and the presence of easily degradable carbohydrates can exert at least one of these effects.

In vitro, in batch cultures, degradation of pure cellulose was much reduced by the presence of starch and cerelose which lowered the pH from 6.5 to below 5.5. This effect was not observed when the pH was maintained at the control level (20). When pure cultures of cellulolytic bacteria were grown in cellobiose-limited chemostats the cultures washed out at pH values ranging from 5.7-6.0, whereas non cellulolytic bacteria were resistant to lower pH (4). The sensitivity of cellulolytic bacteria to low pH might be related to a reduction in ATP synthesis from ETP (15). Proton motive force across the cell membrane can be dissipated at low pH (4).

In vivo, Mould et al. (21,22,23) clearly demonstrated that a decrease in pH below 6.0 was involved in the depression of cellulolysis. Offering roughage in a long form which stimulates the salivation, or inclusion of additional buffering material in the diet could help to maintain the pH above 6.0, thus reducing the negative associative effects of mixed feeds. The administration of dietary buffers such as sodium bicarbonate is largely utilized in that respect (24,25). However, buffers in some experiments only partially alleviate fibre depression (22) and a carbohydrate effect independent of pH appears to be involved.

Van Gylswyk and Schwartz (9) reported that the addition of starch increases the lag time in the degradation of grass fibre in vitro and that strains of B. succinogenes which can use both starch and cellulose preferentially digest starch. Production of cellulase by the latter bacteria can be decreased when grown on glucose instead of cellulose. This inhibitory effect of glucose on cellulase synthesis supports the fact that the number of cellulolytic bacteria does not change greatly when part of the forage is replaced by increasing amounts of readily fermentable carbohydrates (9). In vivo, there might be a selection for less pH sensitive strains or for strains which preferentially use starch or glucose.

It can be concluded, in conformity with Sutton (18), that in order to maintain cellulolytic activity when straw diets are supplemented 1) pH should be prevented from falling below 6.0 and 2) starchy concentrates with slow rates of degradability (such as whole grains rather than ground ones) or concentrates based on fibrous by-products should preferentially be used.

4. SUPPLY OF NITROGEN

4.1. Amount of nitrogen required

Most cellulolytic bacteria require ammonia (NH_3) as N source for incorporation into cell protein. Ammonia is supplied by deamination of feed and endogenous protein amino acids or by degradation of dietary and endogenous non protein N (NPN) such as urea. The amount of N required can be related either to the concentration of NH_3 in the rumen medium or to the potentially degradable organic matter.

Ammonia concentration is only indicative as it reflects the balance between production, absorption and utilization. Levels of NH_3-N for maximum activities range from about 50 to 280 mg N/l although pure cultures generally require much lower ammonia concentration for growth (<1,4

mg N/l). These wide variations can be explained by different requirements for growth and fermentative activities and also by the different pathways of NH_3-incorporation, i.e. glutamine synthetase and glutamate dehydrogenase. These enzymes differ in their affinity for NH_3. The first pathway predominates at low NH_3 level in the environment, whereas the second acts at high NH_3 levels (26).

The type of substrates also influences NH_3 requirement. It was recently shown that the minimum NH_3-N concentration required to maximize the degradation of barley (125 mg/l) was greater thant that for degradation of maize (61 mg/l) (27). Orskov (28) reported that only 20 mg/l of ammonia were required for maximal rate of digestion of alkali treated barley straw. Nevertheless, it seems reasonable to consider that values below 50 mg NH_3-N/l indicate N limitation.

Numerous determinations of the amount of N incorporated into microbes in relation to the organic matter apparently digested in the rumen (N/kg OMDR) or fermented (N/kg OMF), (efficiency of microbial protein synthesis or yield) have been carried out in vivo. Mean figures used in systems for feed protein evaluation (29,30,31) are around 30-34 g N/kg OMDR although wide variations between experimental conditions are shown. Values for high roughage diets and particularly for alkali-treated straws reported in (32) and recently by Vérité et al. (personal communica-tion) are within 28-36 g N/kg OMDR. Therefore, it seems correct to adopt a mean requirement of about 32 g available N/kg OMDR or of about 21 g available N/kg of organic matter digestible in the total digestive tract (OMD) assuming that 0.65 OMD is digested in the rumen (29,31).

The efficiency of capture of degradable N is not known precisely but should be around 0.8 for non protein N (31). Therefore total requirement for available N approximates 40 g/kg OMF or 26 g/kg OMD. In in vitro experiments, using continuous culture systems (ex : Rusitec) these values represent the minimum amounts required to optimize straw degradability.

In vivo, the amount of N being recycled into the rumen may contribute significantly to fulfil microbial requirements. The processes of nitrogen recycling have been reviewed recently (33). It is suggested that 4-12 g of protein N/d enter the forestomach of sheeps coming from muco-proteins in saliva and keratinized protein in cells sloughed from the rumen wall. However, the extent of fermentation of these forms of N is not known.

Urea enters the rumen via saliva and diffusion through the rumen wall. The recycling of urea in saliva is function of saliva flow rate and urea concentration which is positively related to plasma urea concentration. The overall amount depends on factors which affect flow rate such as ruminating and chewing time. The rate of passage of urea through the rumen wall is inversely related to rumen NH_3 concentrations and is positively influenced by feeding readily fermented carbohydra-tes. Increased permeability of rumen wall may be due to butyrate production which may act either on the wall-attached microbial activity or on epithelial cell division.

In sheep, saliva contributes to 0.5-2 g urea-N/d and passage across rumen wall to 1-2 g up to 13 g N/d under diverse dietary circumstances. With sheep fed on dried grass (34) the total daily recycled urea amounted to 3.5 g N/d, representing 11.2 g N/kg OMDR as 0.39 kg OM were digested in the rumen. In this case 28% of the requirement could be provided by recycled N. Some of the systems account for N recycling directly. For instance it has been proposed to relate recycled N (RN) to ingested N

(IN), with RN=0.15 IN for lactating cows (35). Such a relationship might underestimate RN when IN is low. In the PDI system (36) it is considered that the entry of endogenous N balances a true efficiency of capture of 1. N recycling may also be underestimated by this way. However, certain small apparent deficits of ruminal degradable N are allowed.

With straw-based diet, supply of salivary urea might be maximal, but transfer through the wall rather limited by the absence of readily fermented carbohydrates, especially when straw is untreated. In sheep fed this type of diet, it can be assumed that about 4 g of available N are recycled daily. It is clear that the contribution of recycled N to microbial requirement will be more significant with untreated straw than with treated straw, especially when diet is fed ad libitum. A rapid calculation indicates that for untreated or alkali-treated straws recycled N could represent 37 or 10% respectively of the microbial requirements.

It should be noted that with high straw diets, goats appear to be more efficient than sheep in nitrogen recycling to the rumen : in the absence of N supplementation, ruminal NH_3 concentration, VFA concentration and fibre degradation in nylon bags in situ are much larger for goats than for sheep (37).

4.2. Source of nitrogen

Recent evidence indicates that the proportion of rumen microbial N which is derived from NH_3-N may be as low as 20% and varies with dietary protein content (3). Bacterial population attached to solid particles were recently shown to incorporate a larger proportion of N derived from amino acids or/and peptides than bacteria associated with the liquid phase of a Rusitec (46% vs 19%) (38).

Although direct amino acid or peptide incorporation does not decrease the energy cost of cell formation it may decrease transport energy expenditure (32). Furthermore some strains of cellulolytic bacteria require small amounts of amino acids and peptides. Amino acids can serve as precursors for branched chain fatty acids (BCFA) which are growth factors for a number of bacterial species including cellulolytic organisms (39).

In most practical diets, sufficient degradable protein is normally present together with an extensive turnover of microbial protein and supply of endogenous protein to meet any specific needs for preformed peptides, amino acids and BCFA (31). This is particularly true when the provision for sulphur is adequate. However, with straw diets with a low degradable protein content it would be important to determine whether preformed amino acids are required or not to optimize cell wall degradation.

Positive responses to protein supplementation have been observed and will be reported in detail in a subsequent paper by Hvelplund (40). Several trials indicate that fishmeal addition stimulates fibre digestion. Some recent results, showing that rates of digestion of ammonia-treated straw in nylon bag in situ were significantly increased when fishmeal was added to the basal diet of sheep (41) corroborate previous observations. Therefore it can be suggested that, adding together with urea a small proportion of slowly degraded protein, providing a steady supply of peptides and/or amino acids would favour cellulolytic activity in straw-based diets.

Replacing urea by a slow release NPN source may help to adjust the rate of release of NH_3 to that of cell-wall degradation which is a rather

slow process. However, these late release compounds (biuret-IBDU-glucosyl-urea...) are often swept out of the rumen before they are fully metabolized but this nitrogen may be partly recycled to the rumen after absorption. When urea can be mixed thoroughly with straw, use of such compounds does not seem to be necessary. If this cannot be achieved, the use of slow release NPN sources might be advantageous.

5. MINERAL SUPPLY

The essentiality and role of mineral elements in rumen microbe metabolism have recently been emphasized in reviews dealing with sulphur (42,43) or with other minerals and trace elements (24,44). With straw-based diet, an adequate supply of the required elements is of particular significance as mineral content or/and availability in straw can be very low.

In this report we shall consider the requirements for sulphur (S), phosphorus (P) and magnesium (Mg) in terms of digestible organic matter rather than in terms of in total dry matter content or as optimal concentrations in the environment as already suggested (25). This approach is particularly advisable for straw based diets, their digestibility differing within treatments.

The direct effect of sodium (Na), potassium (K) and calcium (Ca) as "nutrients" is difficult to distinguish from their indirect effect on the physicol-chemical characteristics of the environment : buffering capacity, dilution rate and osmolality. These characteristics are important for optimizing cell-wall degradation. The effect of pH was already discussed. An excess of Na intake may increase dilution rate and thus reduce the time allowed for cellulose fermenta-tation. It may also increase the osmolality in such a manner that rumination, salivation and fermentation may be depressed. However, these aspects have been dealed with elsewhere (24,44) and will not be discussed further here.

Trace elements which may have a direct effect on microbes will be briefly considered.

5.1. Sulphur

The main function of S is to support the synthesis of sulphur-amino acids, methionine and cystine needed for the elaboration of microbial protein. Some microorganisms are capable of reducing sulphate into sulphide which is also produced from protein degradation. Sulphide (S^{2-}) is then incorporated into amino acids. However, sulphide which is not used for protein synthesis is absorbed very rapidly through the rumen wall and some is lost with the flow. Sulphide absorption is much faster than for ammonia and is a function of sulphide concentration.

Smith (43) calculated the amount of available S required in the rumen taking into account losses and recycling. The latter author considered a mean S:N ratio of 0.06 in rumen microbes and from the average efficiency of microbial protein (around 32 g N/kg OMF), sulphur microbial uptake was assumed to be around 2.0 g/kg OMDR or 1.3 g/kg OMD. However, even in vitro the efficiency of uptake is not total. In order to optimize protein synthesis in batch cultures, the optimal amount was above 1.6 g S/kg OMD (25).

In vivo, sulphide losses and the amount of recycled S would represent about 0.5-0.8 and 0.1-0.2 respectively of the true requirement. Therefore, total requirements for available S (Sa) should range around 2.8 g/kg OMDR or 1.8 g/kg OMD.

In vitro, when using the Rusitec technique the supply can be somewhat lower : 2.5 g S/kg OMF or 1.6 g S/kg OMD.

S-availability in some forages is rather low and particularly in straws. This was recently demonstrated using the Rusitec technique (Stevani et al., unpublished results). The same batch of straw (1.3 g S/kg DM), either alkali-treated or untreated, was either supplemented or not with sulphate. The addition of sulphate to the medium increased all the fermentative parameters with treated straw. With the non-treated one only volatile fatty acids were slightly increased (table I). Therefore, a supply of 3.6 g S/kg OMF or 2.3 g/kg OMD in treated straws is well below microbial needs, whereas 5.7 g/kg OMF or 3.7 g/kg OMD in untreated straw, is only slightly deficient. This trial shows that alkali treatment apparently does not increase the availability of straw S which may be strongly associated with cell walls. The same trend was observed in vivo in sheep for protein synthesis (45). Sulphate supplementation of alkali-treated straw plus urea increased bacterial total amino N from 10.6 to 16.7 g/d.

With natural diets, the dietary S levels for which positive responses in fibre digestibility to S addition are obtained, may vary considerably between less than 2.5 to 5.7 g/kg OMD (25). The optimal dietary supply depends on the amount and rate of S release in the rumen in order to match microbial activity. With natural feeds it is likely that the S fraction associated to protein follows protein degradability which varies widely with feedstuffs.

However, with some particular forages such as tall fescue, S availability (Sa) appears to be very low. This might apply to straws in which Sa would not exceed 0.3. Therefore, if the S content of untreated straw is assumed to be around 1.2 g/kg DM, it can be calculated that it should be supplemented with 0.4 g Sa/kg DM. With the same straw but alkali-treated the supply should be about 0.6 g Sa/kg DM.

With discontinuous feeding, slow-release S compounds, such as elemental sulphur or methionine, which minimize sulphide loss from the rumen ought to be used preferentially to fast release compounds such as sulphate.

However, the supply should not exceed the requirements as excessive S intake upsets animal zinc absorption and copper availability.

5.2. Phosphorus

Phosphorus (P) is a constituent of primary cell metabolites such as nucleotides, coenzymes, teichoid acids of the cell walls of Gram-positive (G+) bacteria and phospholipids. Bacterial P:N ratios vary from one author to another. The assumed P:N ratios in rumen microbes (0.188 (24) and 0.145 (43)) result in P incorporation estimates of 5.7 and 4.3 g P/kg OMF respectively.

A series of assays using either semi-continuous (Rusitec) (46,47,48) or entirely continuous (49) culture systems were undertaken to examine the effect of P on the principal parameters associated with degradative and synthetic processes and to ascertain more precisely the minimal phosphorus requirements for each of these processes. The mean results are summarized in table II. Compared to a P-supplemented medium, levels of P lower than 3.0 g/kg OMF drastically reduced degradative activities. In every assay, cellulose was much more affected than hemicellulose degradation and volatile fatty acid (VFA) production.

It has been shown that cellulases isolated from mixed rumen bacteria have specific P requirements (50). Phosphorus is probably an impor-