PHYSIOLOGICAL LIMITATIONS TO USING CONCENTRATES TO INCREASE THE DIGESTIBLE ENERGY INTAKE OF RUMINANTS GIVEN ROUGHAGE BASED DIETS

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Summary

The low intake and digestibility of low-quality roughages such as mature forages or crop residues often results in a digestible energy intake insufficient for a desired level of production. One alternative to increase digestible energy intake is to provide supplementary concentrates of high digestibility. Associative effects on forage fibre digestion may occur when roughage and concentrate are given together to ruminants. Positive associative effects may occur if the forage is deficient in a specific nutrient (e.g. fermentable N or S) and the concentrate supplement provides this nutrient in excess of the requirements for the fermentation of the concentrate in the rumen. More often negative associative effects are observed when the rumen fermentation of readily fermentable carbohydrates (RFC) in the concentrate reduces -the rate of rumen digestion of the forage cell wall constituents (CWC). This often causes reduced intake of the roughage i.e. substitution of concentrate for roughage occurs.

Reduced rumen digestion of CWC may be associated with a reduction in the number and activity of the bacteria which digest CWC, and also with a low rumen pH ($pH < 6.1$). Rumen pH is depressed principally by the VFA produced during the rapid fermentation of RFC, the extent of the pH depression depending on the buffering capacity of the rumen, the type and amount of RFC consumed and feeding management practices. Also rumen digestion of CWC may be severely reduced if fermentation of concentrates causes a deficiency of an essential substrate (e.g. N) for microbial fermentation of CWC.

It appears that it is roughages of low digestibility such as mature forages and crop residues and which have high contents of CWC and low contents of microbial substrates which are most severely affected by supplements containing RFC. An understanding of the physiological basis for associative effects and selection of appropriate management stratagies should lead to greater efficiency in feeding systems where low-quality roughages are supplemented with concentrates.

I. INTRODUCTION

In Australian grazing systems. animals frequently have to survive for . prolonged periods with mature pastures as their only source of nutrients. Low voluntary intake and digestibility lead to a low digestible energy intake which may be insufficient even to maintain liveweight. This may not be a major problem where animals are being kept primarily for production of offspring or wool and if mortality rates are acceptable, and if improved nutrition subsequent to the dry season or drought can compensate for such a period of low nutrition. However, there are many circumstances when it is worthwhile to consider providing supplements to avoid losses or to maintain production at a higher level than can be supported by mature pasture e.g. in the dairy industry. Also in recent years there has been increased interest in both Australia and elsewhere on the utilization of crop residues as animal feedstuffs. The physiological

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limitations to the utilization of such materials are likely to be similar in many respects to those with mature pastures; usually both are graminaceous species after senescence and possibly after deterioration due to leaching and microbial action.

To improve the situation it is obviously important to identify the sequence of limiting factors in the nutrition of the animal. It may be that there is a specific deficiency of minerals, of sulphur or of nitrogen (N) as either a substrate for rumen microorganisms (fermentable N) or amino acid N absorbed from the small intestine. Such nutrients may be provided as mineral supplements, non-protein-N or possibly as bypass protein supplements. As a first step to improve the nutrition of the animal provision of these types of nutrients is likely to be more cost-effective than taking measures to modify or supplement a basal feed resource to increase the digestible energy intake.

One alternative to increase the digestible energy intake of an animal consuming a fibrous diet is to include in the diet, or supplement the diet with a feedstuff of high digestibility i.e. a concentrated food or concentrate which is low in fibre and high in readily fermentable carbohydrate (RFC). The RFC contain large proportions of starch, sugar or occasionally lipid. In Australia only cereal grains and molasses are widely available, although by-products such as brans and citrus pulp may be important in specific areas. Oilseed meals may have a high lipid content depending on the technology used for the oil extraction process. Such materials are readily digestible in the rumen and contribute to the digestible energy intake of the animal, but by their physical nature do not make a large contribution to the rumen load of the animal to thereby decrease intake of a low-quality roughage.

A major difficulty with the efficient use of concentrates by ruminants is that as the amount of concentrates given increases, the intake of roughages may decrease i.e. 'substitution' of concentrate for roughage occurs. 'Secondly, the digestion of the fibrous components of cell wall constituents (CWC) of the diet may be depressed by the dietary concentrates. Both of these factors, but especially the former will reduce the amount of digestible energy the animal obtains from the roughage. In some situations the overall effect of concentrate supplementation may be to replace low-cost roughage in the diet with high-cost concentrates with little increase in digestible energy intake or of production by the animals.

It may be desirable for dietary concentrates not to be fermented in the rumen but to be digested and absorbed from the small intestine. This would be expected to reduce energetic losses due to the rumen fermentation, allow absorption of digestible energy as glucose rather than VFA and avoid the detrimental effects of RFC on fibre digestion. Some starches (e.g. maize and sorghum) are only slowly fermented in the rumen and an appreciable proportion may escape rumen fermentation (Sutton 1980). Also considerable amounts of starch in rice bran have been reported to reach the duodenum of cattle (Elliott et al. 1978). However, many of the RFC such as molasses and ground cereal grains are rapidly fermented in the rumen, and no means are presently available to increase the proportion of RFC bypassing rumen fermentation but digested in the small intestine.

II. SUBSTITUTION EFFECTS OF CONCENTRATES

When ruminants are given a fibrous roughage ad libitum the addition of concentrates have in various experiments been reported to cause an increase, no change or a decrease in intake of the roughage. The most frequently observed effect when low-quality roughage is supplemented with concentrates high in RFC is represented in the results of Mullholland et al. (1976) where oat straw was supplemented with various levels of concentrate. Total dry matter (DM) intake and digestible organic matter (OM) intake increased, but intake of straw decreased linearly (Figure 1). Similar results have been reported in numerous experiments when low-quality roughages have been supplemented with concentrates high in RFC (Elliott 1976 a b; Fick et al. 1973; Henning et al. 1980; Dixon 1984; Rodenas and Dixon 1985).

The decrease in roughage DM intake per unit of supplement DM given is known as the substitution rate. This substitution rate may be negative where the supplements stimulate roughage intake. When supplements high in RFC are given the substitution rate will usually range from approximately 0 where the concentrate has no effect on roughage intake to 1.0 where the roughage intake decreases by an amount equal to the concentrate given. In some experiments substitution rate has been reported to exceed 1.0.

In experiments where the roughage consisted of cereal straw or low-quality hays, stimulation in roughage intake by supplements can usually be attributed to addition of another nutrient such as N in the supplement. For example Crabtree and Williams (1971 a) found that a concentrate containing 3.1% N stimulated intake of oat straw containing 0.6% N by sheep, but a subsequent experiment (Crabtree and Williams 1971 b) indicated that the increased intake was due to the addition to the diet of N rather than of RFC. Similarly an increase in intake of low-quality tropical grass hay occurred due to molasses supplementation, but this was subsequently shown to be due to the sulphur content of the molasses (Kennedy and Siebert 1972). In these situations it would probably be more economical to provide the specific nutrient required as non-protein-N or a source of sulphur.

A decrease in roughage intake with RFC supplementation may be due to the animal receiving sufficient energy from a highly digestible diet to satisfy its energy requirements (Weston 1983). However, decreases in roughage intakes are also often observed even when the diet is based on low-quality roughage and the digestible energy intake is apparently much less than the potential of the animal to utilize energy e.g. even when the animal is losing liveweight. In such situations the decrease in intake is more likely to be due to interactions in digestion in the animal, one of the most important of which is a reduction in the rate of rumen microbial digestion of the CWC. One of the primary limitations to intake of low quality roughage is the amount of digesta contained in the reticulo-rumen undergoing digestion or the 'rumen load' (Weston 1983). If the rate of microbial digestion of fibre in the rumen is decreased, then for a fixed rumen load size a longer time will be required to eliminate from the rumen a given quantity of fibrous material and voluntary intake of the fibrous material may decrease. Hence a decrease in roughage intake may occur due to a decreased rate of digestion in the rumen of the fibrous constituents of roughage. The ingestion of concentrates (Dixon 1985) and a deficiency of specific microbial substrates (Hunter and Siebert 1985) have been shown to decrease the rate rather than the extent of rumen digestion of fibrous materials.

III. EFFECTS OF CONCENTRATES ON DIGESTIBILITY OF CWC

If increasing proportions of a highly digestible concentrate are given with a roughage of low digestibility, it might be expected that there should be a linear increase in DM digestibility in proportion to the amount of concentrate. However, mouth-to-rectum DM digestibility often increases more slowly than should occur on the basis of the digestibilities of the individual roughage and

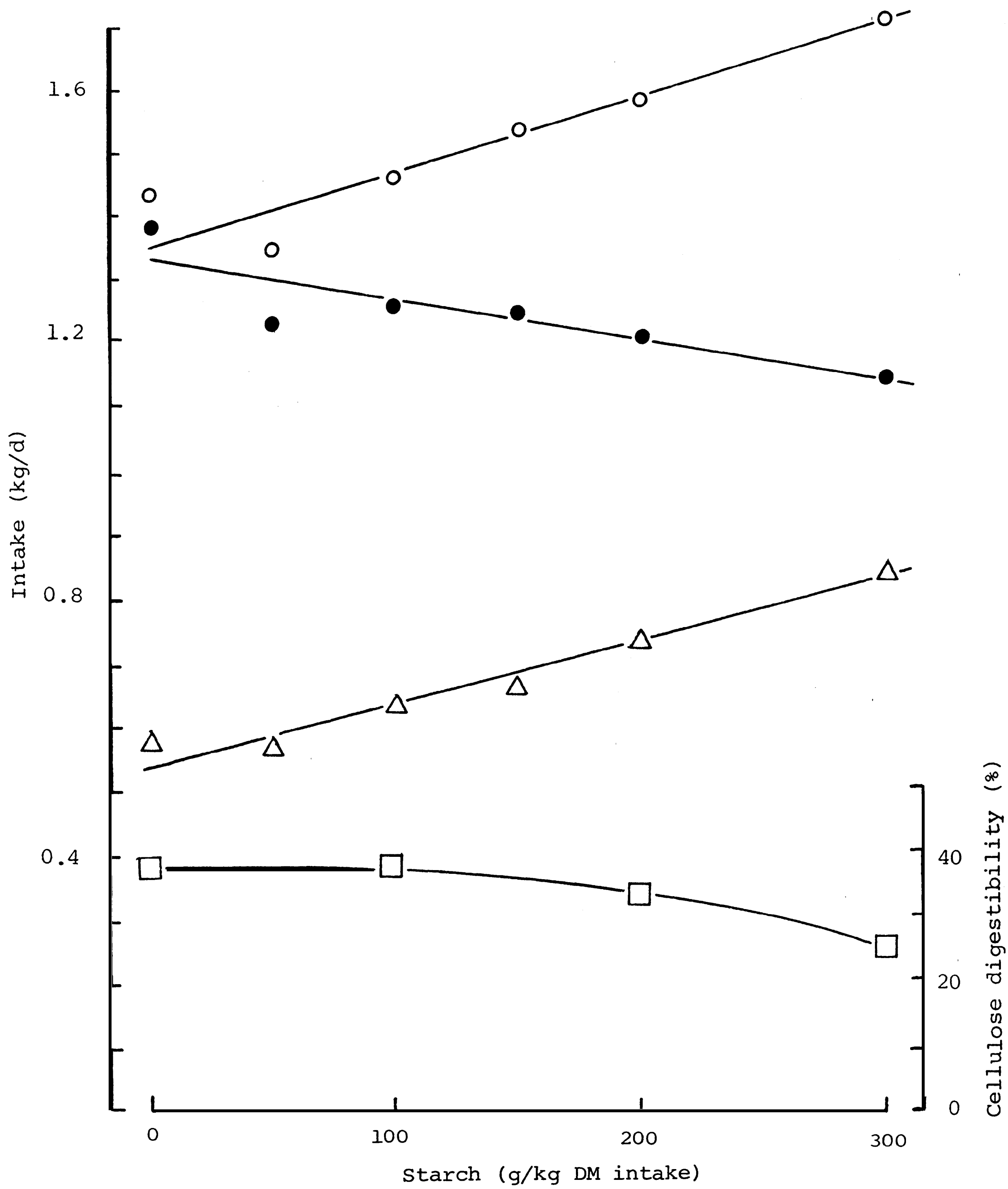

Fig. 1 Intakes of total DM (O-O), straw DM (●-●) and digestible OM (△-△) and cellulose digestibility (□-□) by sheep given ground oat straw and various levels of starch (Mullholland et al. 1976)

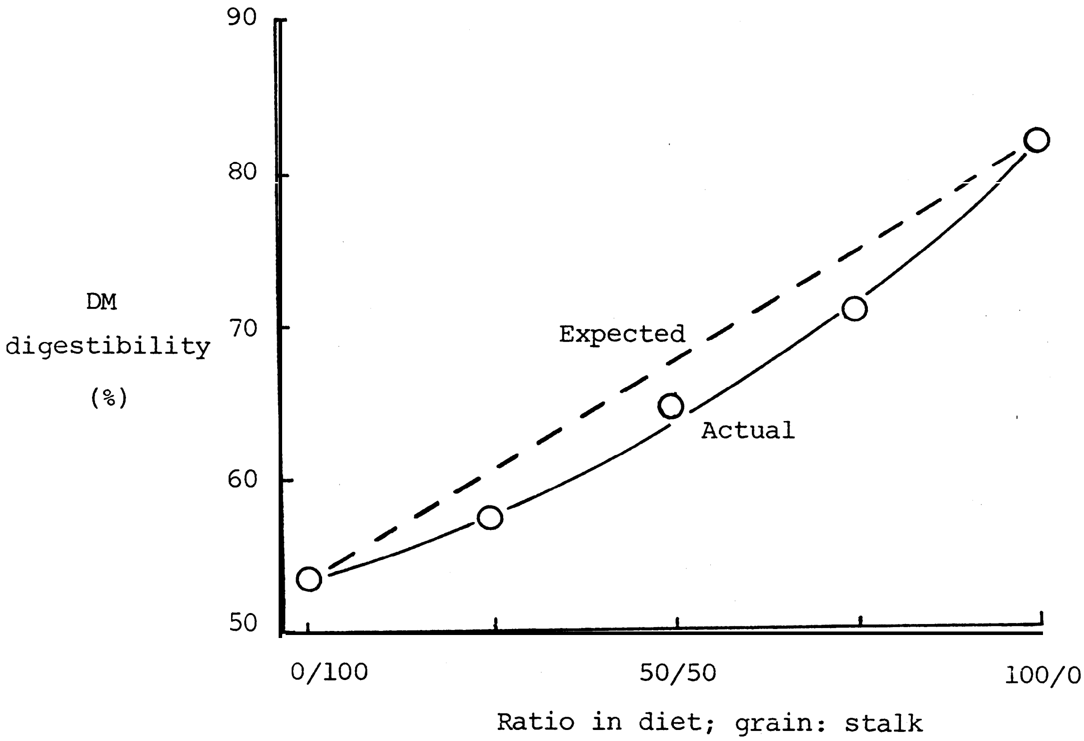

Fig. 2 Change in DM digestibility as corn grain replaced corn stalk in diets for cattle (McDonnell et al.1979)

concentrate ingredients (Figure 2). This is due to negative associative effects between the digestion of the concentrate and the CWC (hemicellulose and cellulose) of the roughage, where the rate of digestion in the rumen of CWC is decreased by the ingestion of the concentrates.

The effects of a reduction in CWC digestibility in the rumen may not be observed in digestibility in the entire digestive tract but have detrimental effects on roughage intake. For example in one experiment barley grain supplements for a grass hay reduced the cellulose disappearance from nylon bags incubated in the rumen, but did not reduce cellulose digestibility between the mouth and the rectum. Nevertheless a decrease occurred in intake of the hay (Lamb and Eadie 1979). It appears that a reduced rate of cellulose digestion was associated with an increased retention time of fibrous residues in the rumen, and this caused the decrease in the hay intake. Also it has been shown that as cellulose digestion in the rumen is decreased by RFC, the proportion of cellulose digestion occurring in the caecum and colon increases (MacRae and Armstrong 1969); this may also partly explain why a depression in digestion of CWC in the rumen may not be observed over the entire digestive tract.

The relative effects of RFC on the digestion of hemicellulose and cellulose are not well defined, and may well vary with the roughage. When maize stover was fed with a range of levels of maize grain, Henning et al. (1980) observed that the digestion of hemicellulose and cellulose were depressed equally. In contrast Romero et al. (1985) observed greater depression in the digestion of cellulose than of hemicellulose of *Pennisetum purpureum* forage when sorghum grain or maize grain supplements were given.

A decrease in either the intake or digestibility of the CWC will reduce the digestible energy the animal derives from the roughage component of the diet, although due to the higher digestibility of the concentrate component digestible energy intake is not likely to actually decrease. The important point is that it may not increase to the extent expected from the level of concentrates given.

Several factors are thought to be associated with the depressions in rumen microbial digestion of CWC.

(a) Effects of concentrates on the rumen microbial population

The fermentation of CWC in the rumen occurs by the action of an active microbial population which is able to produce an array of enzyme systems to hydrolize these constituents. It follows that obtaining a maximum rate of microbial fermentation of the CWC of the diet depends directly upon maintaining a rumen environment suitable for those microbial species which are most active in hydrolysing CWC.

Several authors have shown that as the proportion of concentrate in a diet increases, there is an increase in the numbers of microbes which are known to digest and utilize RFC, and a decrease in the number of cellulotyic micro-organisms (El-Shazly et al. 1961). This is likely to reduce the potential for production of cellulase by the microbial population, and hence reduce the rate of cellulose digestion. Henning et al. (1980) observed a decrease in the number of cellulotyic bacteria but not of the hemicellulolytic bacteria, even though digestion of hemicellulose and cellulose were equally depressed.

The addition of concentrates containing sugar or starch to the diet may be associated with large increases in the numbers of protozoa in the rumen. It has been postulated that large populations of certain species of protozoa may be detrimental to the animal by reducing the supply of microbial protein to the small intestine (Bird and Leng 1983) and by reducing the rumen digestion of poor-, quality fibre by anaerobic fungi (Soetanto 1985). Alternatively large protozoa1 populations may be advantageous since the protozoa have the capacity to ingest and store large amounts of starch and sugar shortly after these materials enter the rumen; this may avoid rapid fermentation of these substrates and a decrease in rumen pH which is detrimental to rumen digestion of CWC.

(b) The pH of the rumen environment

The rumen pH is of importance to rumen CWC digestion since the pH optima of the CWC digestion is in the range pH 6.6-7.0. It has been shown in vitro (Terry et al. 1969; Stewart 1979) and in vivo by infusing acids into the rumen (Mould and Ørskov 1983/84) that cellulase activity and hence fermentation of fibre decreases with a reduction in pH, and is negligible when pH is less than pH 6.0.

The pH in the rumen is the end result of a number of factors each of which will influence the rumen pH. Fermentation processes produce VFA end-products which tend to reduce the pH if production occurs more rapidly than absorption from the rumen. Alternatively ruminant saliva is alkaline (Kay, 1966) and the amount of each type of saliva secreted depends on the feedstuffs ingested and the duration of rumination. Furthermore forages have some buffering capacity (Playne and MacDonald 1966). Among temperate forage species, the buffering capacity of grasses is less than that of legumes, and decreases with increasing maturity of the grass (Greenhill 1964). However, no information appears to be available on the buffering capacity of senesced forages.

(c) The effect of diet and feeding practices on rumen pH

In general the rumen pH of an animal consuming only long roughage of low quality will be in the range pH 6.2-7.0, and consequently is sufficiently high not to reduce the rate of CWC digestion. However, the fermentation of RFC in the rumen may reduce rumen pH since the rate of production of VFA is likely to be greater than the rate of absorption from the rumen, and the buffering capacity of the rumen fluid may be exceeded.

The rate of fermentation of different RFC can vary widely. Where different sugars were added to in vitro fermentations, virtually all (97-100%) of sucrose, glucose and fructose were fermented within 2 h, but only 42-56% of galactose, xylose and arabinose (Sutton 1968; 1969). Starches from different sources (e.g. barley versus maize) have different physical characteristics and different rates of fermentation, and the treatment of starch with moist heat or fine grinding will greatly increase the rate of rumen fermentation. The manner of processing of barley grain has a major effect on the depression in rumen pH and fibre digestion (Ørskov and Fraser, 1975; Ørskov et al. 1978). Barley grain when ground and pelleted reduced roughage intake and fibre digestion much more than when given as whole grain or when less severely processed, and this was apparently due to the more rapid fermentation and production of VFA by the pelleted barley supplement reducing rumen pH to a greater extent. The same principle appears to apply when comparing various sources of RFC. Romero et al. (1985) observed a more severe depression in digestion of cellulose' from *Pennisetum purpureum* forage due to a supplement of ground sorghum grain than an equal amount of maize bran,and this was associated with a greater rate of rumen fermentation and depression in rumen pH with the former supplement. Similarly Vaamonde et al. (1983) observed a lower rumen pH when 40% of a diet based on NaOH-treated maize cobs consisted of ground sorghum grain rather than wheat bran. Some temperate grasses at early stages of growth may contain sufficiently high levels of RFC as sugars to cause depression in rumen pH (Beever et al. 1981), but this is not likely to occur with mature forages with their generally low soluble carbohydrate content.

The level of RFC in the diet obviously influences the amount of RFC ingested. with diets consiting principally of RFC rumen pH may be as low as pH 5.5 for prolonged periods. with lower levels of dietary RFC the reduction in rumen pH has in some experiments been linearly related to the amount of RFC ingested (Cohen and Dixon 1983; Mould et al. 1983/84 a). In some other experiments no depression in rumen pH was observed until quite large amounts of RFC were included in the diet (Henning et al. 1980). Given the number of independent factors which may influence rumen pH, such differences between , experiments might be expected.

The manner in which the RFC are ingested by the animal may have a major influence on the depression in rumen pH and consequently on fibre digestion. For example sheep fed once per day a mixed roughage concentrate ration had a rumen pH depressed to pH 5.8 several hours after feeding, and this gradually increased again (Moir and Somers 1957). However, in sheep receiving the same ration in four meals throughout the day, rumen pH was maintained at greater than pH 6.7. Kaufmann (1976) obtained similar results for dairy cows fed two or 14 times per day.

It may be possible to reduce the effects of the depression in rumen pH by giving the concentrates once each several days rather than daily on the basis that

CWC digestion will be severely affected on the day of giving the supplement but can proceed on the days on which supplements are not given. In a recent experiment (F. Fredericks' and R.M. Dixon, unpublished results) weaner sheep grazing mature pasture only maintained liveweight when oat or triticale grain supplements were given each day, and tended to gain liveweight and produce more wool when the same amounts of the same supplements were given one each three days.

(d) The effect of maintaining rumen pH to remove the depressing effect of RFC

If the depression in CWC digestion associated with dietary RFC is due to a depression in pH, it is to be expected that maintenance of high rumen pH should eliminate this depressant effect. In vitro experiments indicated that the effect of additional RFC occurred principally due to the pH depression (Terry et al. 1969 ; Stewart 1977). When rumen pH was maintained in vivo by infusion of buffers Mould et al. (1983/84 a) found on average for a range of concentrates and roughages that approximately half of the depression was removed, suggesting that a major part of the reduction in rate of microbial digestion of fibre could be attributed to affects other than those of rumen pH. Inclusion of buffers into the diet has been reported to have beneficial effects on CWC digestion in the rumen (Osbourn et al. 1969) and on OM digestibility in diets containing ground but not long hay, presumably because with long hay saliva output was sufficient to maintain the rumen pH (Mould et al. 1983/84 b).

(e) Competition among microbial groups for essential nutrients

A consequence of the changes in the microbial species present in the rumen is that the microorganisms digesting CWC will have to compete for essential substrates with the microorganisms digesting RFC (e.g. for ammonia, peptides, S, #minerals, branched-chain VFA, vitamins). In general it is the rate at which ATP energy from substrate becomes available to the microorganisms that limits the rate of microbial growth in the rumen. Since CWC are hydrolyised slowly in comparison with the RFC, it follows that ATP energy for microbial growth becomes available more slowly for the microorganisms dependent on CWC as energy sources, Following ingestion of a meal of roughage and RFC it may be that the essential nutrients available are rapidly and completely utilized by the microorganisms fermenting the RFC, and there will subsequently be a deficiency of these essential substrates for the microorganisms digesting the CWC constituents. If for example a certain microbial substrate such as fermentable N is less than that required by the population of microbes, the ingested dietary N to provide this fermentable N is likely to be largely used within a few hours by the RFC fermenters or absorbed from the rumen and there is likely to be a shortage of fermentable N for the CWC digesting microbes. El-Shazly et al. (1961) and Fick et al. (1973) demonstrated both in vitro and in vivo that cellulose digestibility is depressed much more than the overall OM digestibility by a deficiency of fermentable N for microbial growth (Table 1).

It will often be difficult to conclude whether adequate amounts of all essential microbial substrates are available. Firstly, even if the contents of the various microbial substrates in the feedstuffs are known, the rate and the extent to which individual substrates become available in the rumen are often illdefined (Playne et al., 1972; Durand and Kawashima 1980). Secondly, the requirements of the microorganisms for various substrates are often not known and will vary with the microbial species. Thirdly, the supply of various substrates by recycling within the rumen due to lysis of microorganisms or by recycling from the blood cannot be predicted with confidence. For example most experimental work has been carried out on fermentable N but there is still doubt about the actual rumen ammonia concentrations required by microorganisms and if in animals consuming diets based on mature forages low in nitrogen the addition of RFC to the rumen will stimulate endogenous urea transfer to the rumen (Kennedy 1980; Norton et al. 1982). Similarly it has been shown in several experiments with animals fed diets based on purified cellulose or poor-quality hays (Hemsley and Moir 1963; Cline et al. 1966; Hume et al. 1970) that responses can be obtained to supplementation of the rumen with branched-chain VFA, although these substrates are also available in the rumen from degradation of dietary true protein and microorganisms.

The content of nutrients in the forage may also be important. It is known that much of the digestion of fibrous material in the rumen is due to the action of microorganisms either attached to or in close physical association with the particulate matter. Microorganisms attached to forage material rich in the. essential nutrients required may be able to obtain at least the majority of these nutrients directly from the plant particle to which it is attached. In contrast, microorganisms attached to material containing low levels of the essential nutrients will presumably have to obtain these nutrients from the rumen fluid and will have to compete to a greater extent with other microbial species such as the RFC fermenters present in the rumen fluid. Alvarez et al. (1984) demonstrated that this occurred when there was a deficiency of fermentable N for the rumen microorganisms; digestion of maize cobs of low N content was depressed much more than that of *Pennisetum purpureum* forage by low fermentable N availability.

Table I Effects of starch supplements for *Digitaria decumbens* hay on in vivo organic matter and cellulose digestibility in sheep (Fick et al. 1973)

Digestibility (%)	NPN supplement (g N/d)	Starch supplement (g/d) 50	100	200
Organic matter	0	57	52	51
	10	51	56	60
Cellulose	0	54	55	34
	10	56	53	49

(f) Differences among feedstuffs in the extent of depression in digestion

In a number of experiments the depression in rumen digestion due to RFC has been greater for some feedstuffs than for others. Burroughs et al. (1949) observed in vivo that maize cobs DM digestibility was depressed from 57% to 35% by supplementation with 0.6% liveweight of starch, whereas lucerne hay DM digestibility was not affected. Similarly in experiments where rumen digestion was measured using nylon bags, dietary RFC reduced the rate of DM disappearance of NaOH-treated maize cobs by 46-75% but that of tropical grasses forages by 15-23% (Dixon and Parra 1984). Maize bran supplementation of *Cynodon dactylon* hay caused depressions in the rate of DM digestion of three tropical grasses but not for two legumes (*Canavalia* leaf and lucerne) or sweet potato forage, suggesting that differences may occur between graminaceous and non-graminaceous species (Cohen and Dixon 1983). Molasses supplements decreased the rate of rumen digestion of sisal pulp three-fold but that of *Leucaena* forage and sunflower meal by only 21% and 22% respectively (Herrera et al. 1981), while in a similar experiment molasses supplements depressed DM digestion of sugar-cane tops and *Pennisetum purpureum* forage by 26-30%, but that of Leucaena and sweet potato forage by only 12-14% (Encarnacion and Hughes-Jones 1981).

The observed differences between feedstuffs may be at least partly due to a greater content of CWC in the roughages of lower quality being associated with a greater depression in rumen DM digestion. Secondly, the rate and extent of digestion of the hemicellulose and cellulose constituents can vary widely between forages (Van Soest 1975) and it is therefore not surprising if the effects of RFC on their rumen digestion may also vary. Thirdly, differences may be associated with varying buffering capacities of the roughages. Correlations have been observed between the depression in CWC digestion of various forages and their buffering capacity (Osbourn et al. 1981). Possibly the greater depression in in vivo DM digestion of maize cobs than of lucerne observed by Burroughs et al. (1949) was at least partly because rumen pH was maintained at a higher level in the cattle given lucerne hay than maize cobs due to the high buffering capacity of lucerne (Osbourn et al. 1981). Experiments are needed to examine these interactions and to identify the relative importance of various factors such as rumen pH, the contents and characteristics of cellulose and hemicellulose, the buffering capacity of the roughage and concentrate feedstuffs, the deficiency of specific substrates for the microbial fermentation and the possibility of differences between graminaceous and non-graminaceous species.

IV. IMPLICATIONS FOR SUPPLEMENTATION OF LOW-QUALITY ROUGHAGES

From the foregoing discussion it is clear that the level of concentrate supplementation at which depression of CWC digestibility commences may vary depending upon many factors. If experiments are considered where diets based on grass hays or fibrous crop residues were fed, in some experiments depression in in vivo CWC digestion occurred where concentrates constituted less than 10% of the total DM intake (Faichney 1965; Fick et al. 1973). In other experiments depression has been observed when concentrates constituted 10-20% of total DM intake (Mullholland et al. 1976; Henning et al. 1980), or only more than 30% of DM intake (Chappell and Fontenot 1968; Lamb and Eadie 1979). In general it appears that for diets based on such roughages CWC digestibility over the entire digestive tract will not be appreciably reduced when concentrates comprise less than perhaps 25% of DM intake. An important exception will occur if the concentrate is severely deficient in a microbial substrate such as fermentable **N**.

The intake of low-quality roughage is likely to be more sensitive than CWC digestibility to concentrate supplementation, and is likely to be more important in determining digestible energy intake. The substitution rate may vary widely depending on a number of factors related to:-

a) Type and quantity of roughage given.
b) Type and quantity of concentrate given.
c) Management of the animal and the feeding system used.
d) The physiological status of the animal (A.R. Egan, unpublished results).

Due to the effect of the rate of rumen CWC digestion upon roughage intake, it is to be expected that those roughages whose rumen digestion is most affected by concentrates will show the highest roughage substitution rates due to **dietary** concentrates. That is, those'roughages which do not stimulate salivation to maintain a high rumen pH, which have a low buffering capacity, which are deficient in many microbial substrates and which are slowly digested in the rumen are likely to be most affected. Mature forages and fibrous crop residues will tend to have these characteristics. It is of interest that if experiments are considered where hay was supplemented with cereal grain up to 40% of DM intake, substitution rates were inversely related to hay digestibility (Torres and Boelcke 1978).

When RFC supplements have comprised less than 10% of DM intake most experiments have found no change or a tendency for an increase in roughage intake (Andrews et al. 1972; Fick et al. 1973; Elliott 1967a; Henning et al. 1980; Rodenas and Dixon 1985). When RFC supplements have comprised up to 20% of DMI decreases in roughage intake were found in a number of these experiments, and when RFC have comprised more than 20% of DMI decreased roughage intake has often been observed.

CONCLUSIONS

Concentrates which are fermented slowly rather than rapidly in the rumen, which contain adequate microbial substrates and which do not cause a severe reduction in rumen pH are to be preferred as supplements to roughages. Manipulation of feeding management and inclusion of buffers in the diet may be beneficial. The optimum level of concentrate will depend on the response curve of output of the required animal product for various levels of concentrate input, which will have to be determined for the feeding system of interest. However, understanding of the physiological limitations to increasing digestible energy intake by dietary concentrates should assist determination of optimum feeding stratagies.

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