9311328
PN AAR-168
IDN-36679

Small Ruminant

Collaborative Research Support Program

Technical Report Series

Number

8

EFFICIENCY OF DIGESTION IN GOATS AND SHEEP

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1981

EFFICIENCY OF DIGESTION IN GOATS AND SHEEP[1/]

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Summary

Utilization of plant fiber by ruminants is a complex process. Simple measures of efficiency, such as average product per unit of feed input, can be misleading if they do not reflect critical points in the process of converting feed resources to animal product. The ultimate measure of efficiency must be economic as well as biological.

Ruminants are confronted with three protein subgroups: non-protein nitrogen, true protein, and bound (unavailable) nitrogenous substances. Each fraction influences the efficiency of protein utilization in the ruminant, in different ways.

Energy is derived from rapidly soluble substances (mainly carbohydrates) and slowly degradable cell-wall entities (mainly cellulose and hemicelluloses). The rate of degradation of the latter is influenced by lignification and other intrinsic factors, as well as certain management or processing factors. Intake of energy-providing dry matter is influenced by the presence of non-degradable cell-wall matter and its rate of passage through the digestive tract.

There is evidence that the goat, compared to sheep and cattle, has become adapted to a low-quality feed resource through his ability to selectively consume the more nutritious (less fibrous) plant parts, and to pass his digesta

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[1/] Presented at the First National Symposium on Tropical Goats and Sheep, Fortaleza, Ceará, Brazil, May 4-8, 1981.

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through at a faster rate. Critical evidence of higher digestibility of consumed fiber by the goat is lacking. If the faster rate of passage is indeed a fact, it could partially account for suggestions that the goat requires a higher level of dietary protein than sheep or cattle.

Several areas of research require diligent attention if the efficiency of small ruminant production in the tropics is to be improved appreciably.

Introduction

The ruminant occupies a special niche in Earth's ecology because of its foregut fermentation capacity. The small ruminant, especially goats and sheep, has a long history of contribution to man's food and fiber, mainly because it can live and produce from feed resources that man otherwise would have no way to utilize. The browse plants of the Caatinga and the crop residues from the agriculture of Brazil's Northeast are good examples.

Apart from the biological advantage, shared by all ruminants, the goat and the sheep have some special advantages in relation to cattle. In general, the capital requirements for efficient small ruminant production are less than for cattle. Also, their husbandry requirements are more easily met with family labor, and small producers can more easily convert one or two animals to cash through the local marketing system, to meet family or emergency needs.

It is no great surprise, then, that sheep and goats have come to be so important to the agricultural economy of Northeast Brazil. It is also of interest to note that cattle, sheep and goats each occupy their own special part of the Northeast, determined by rainfall and native vegetation variables as well as the relative possibility of improved forage cultivation. Although there is considerable overlap in geographic area, these three animal species are not entirely competitive with each other. Rather, each performs its own special function within the ecology of the region. This complementarity

of resource utilization is important to recognize before one enters a discussion of comparative efficiencies.

Biological Versus Economic Efficiency

In discussing the "efficiency" of a biological process such as digestion in ruminants, it is easy to fall into the trap of comparing average benefits, while ignoring a possible incremental economic benefit by producing at a different level of input. A simple example will serve to illustrate the point.

Let us imagine a hypothetical feeding trial in which lambs showed the following results:

Lot no.	1	2	3
Average daily gain, g	50	70	85
Feed per day, g	600	700	800
Feed/gain	12	10	9.4

Clearly, if one were to use the biological definition of efficiency, one would recommend ration 3 as being the most efficient. However, a simple economic analysis complicates the decision, and the outcome depends on relative prices. If the cost of 100 g of the above ration is set at 100, you would need a price-of-gain/cost-of-feed ratio of 7/1 to make it profitable to feed 800 g of feed, compared to 700 or 600. If the gain/feed price ratio were 6/1, 700 g per day would be the optimum feeding level. And if the gain/feed price ratio dropped to 4/1, 600 g/day would yield the most profit. At the 5/1 ratio, the decision is indifferent between 600 or 700 g. These results are illustrated below:

	Lot 2 over lot 1	Lot 3 over lot 2
Incremental feed	100 g	100 g
Incremental gain	20 g	15 g
Additional cost of feed	100	100

	Lot 2 over lot 1	Lot 3 over lot 2
Additional value of gain at gain/feed price ratios of		
7/1	140	105
6/1	120	90
5/1	100	75
4/1	80	60

Thus, because of the principle of diminishing marginal returns which applies to this biological function (as with many others), the economically most efficient decision is influenced by market prices and does not necessarily coincide with a narrow biological measure of efficiency.

A Conceptual Framework for Studying Digestive Efficiency

Feed digestion by ruminants is a very complex process, influenced by many different factors. It is therefore important that conditions be described very carefully when comparisons of relative efficiency are made.

In the conversion of feed resources to meat, milk, work, or fiber by animals, there are several inherent costs in the biological system. First of all there is an inevitable wastage of feed; in no situation do all available feed nutrients end up being consumed by animals.

Of the feed nutrients which do enter the digestive tract, some are totally unutilizable either directly by the animal or by the rumen microbial population. This obligate indigestible fraction is largely a function of plant cell-wall lignification. It is excreted in the feces along with other potentially digestible material which escapes digestion for various reasons. The difference between feed consumed and fecal material is called the "digestible" portion and is highly variable.

The losses of energy to methane and carbon dioxide gas from the rumen are more predictable, as are the losses in urine. The difference between the

digestible fraction and that lost to gasses and urine is called the "metabolizable" fraction.

Maintenance costs must also be accounted for. For animals which are homeotherms, these costs are high. For the individual animal, the metabolizable energy not needed for maintenance is available for a productive function such as growth, lactation, reproduction, or work, and is called the "net energy" fraction. On an energy equivalent basis (calory for calory) the efficiency of conversion of digestible energy to milk is much more efficient than its conversion to body tissue; therefore, the United States National Research Council has published separate values called "net energy for lactation" and "net energy for gain" in all recent tables of nutritive value of feedstuffs.

An additional overhead cost in the animal production enterprise is that represented by maintaining a breeding herd or flock. This cost is largely a function of two factors: reproductive efficiency and generation interval. The animal overhead cost can be greatly reduced by optimizing reproduction, mortality, and morbidity parameters in the herd.

It can be readily seen that the definition of "digestive efficiency" can change greatly, depending on which of the above costs are taken into account, and at which point in the production process one takes his measurement. The concept of a "digestibility coefficient," for example, which is the ratio of nutrients absorbed to nutrients consumed, is much different from considering an annual rate of meat production per hectare of land.

Protein Utilization

Modern advances in ruminant nutrition have shown that the traditional total kjeldahl nitrogen analysis of feed and feces, with the resultant estimate of "digestible crude protein," is not sufficient to describe the utilization of protein in ruminants. Rather, three separate fractions must be taken into account: The rapidly soluble fraction which is quickly available for rumen

microbial synthesis; the slowly degradable fraction which may escape rumen fermentation and be digested in the abomasum and duodenum; and the non-degradable fraction, either bound to lignin or present as the Maillard products of heat damage during processing.

The non-degradable fraction appears intact in the feces. It is of most concern in feeds which have been subjected to heat, either from fermentation (ensiling), drying, pelleting, or other processing procedures. A simple analytical test for heat-damaged protein is to determine kjeldahl nitrogen in the VanSoest acid-detergent fiber residue (VanSoest, 1965a.)

The NPN fraction is of considerable importance in silages and certain recycled waste feeds such as poultry manure. The degree to which it is utilized in the rumen depends on the presence of a carbohydrate source, available at approximately the same rate, to provide C chains for microbial amino acid synthesis. Starch has been shown to be an ideal carbohydrate to accompany NPN in the rumen (see the review by Reid, 1953).

True proteins are also utilized for microbial cell synthesis, but at differing levels of efficiency (Pichard and VanSoest, 1977). Slowly degradable proteins (those having a more complex molecular structure) may partially escape rumen degradation. The degree to which available protein and non-protein N enters microbial synthesis depends partly on the nature and vigor of the microbial population. For very high demands on daily protein production, such as during peak lactation in dairy animals, the daily rumen output of microbial protein may be insufficient, and some bypass of degradable dietary protein to the abomasum will be required.

Some special concerns exist with regard to the protein requirements of goats and sheep in the tropics. First of all, it is known that tannins can bind true protein, forming totally non-degradable leathers. Many browse feeds

such as the leaves of some deciduous trees and shrubs have a high tannin content. This could greatly complicate the efficiency of protein utilization by these animals. There is some evidence that goats, natural browsers, may have developed a predilection for a naturally high-protein diet (through judicious selectivity while browsing) as a means of combatting the tannin problem. Whether or not tropical hair sheep behave similarly is unknown. However, for the goat, the suggestions in the literature (Huston, 1978; Sands and McDowell, 1978) that dietary protein requirements, expressed as a ratio to utilizable dietary energy, are higher than for the sheep or the bovine, may have some fundamental basis in evolutionary adaptative strategy by which the goat deals with high tannin intakes.

A second concern is the naturally faster rate of passage of digesta in small ruminants. There is published evidence that goats have a faster rate of passage than larger ruminants, to compensate for their smaller rumen capacity relative to body size (Castle, 1956). A faster passage rate or shorter retention time could decrease the opportunity for complete utilization of slowly-degradable protein, in effect increasing the animal's total dietary protein requirement.

One additional factor needs to be mentioned when discussing the efficiency of protein use. When an animal absorbs more amine groups than it requires for its own amino acid synthesis, the extra amine groups are diverted to energy metabolism pathways and thus not wasted. This fact could lead to a false conclusion about protein efficiency if one is looking only at the nitrogen balance aspects.

Energy Utilization

When we say that ruminants can utilize "fiber" as an energy source, we are essentially saying that they can utilize cellulose and hemicelluloses. Or,

rather, that these fiber constituents can be degraded in the rumen by enzymes produced only by rumen microflora.

As long as sufficient fiber is in the diet to keep a healthy rumen environment, the ruminant can derive virtually all of its energy from non-fiber sources. Indeed this is the strategy which the cattle feedlots in the United States presently find to be most economical. Dairy farmers in North Carolina, likewise, feed sufficient "fiber" only to maintain normal rumen function and to avoid milk fat depression.

Morand-Fehr and Sauvant (1978) suggest that the minimum "fiber" requirement of the dairy goat is slightly higher than that of cattle. Again, this may be a function of reduced retention time in the rumen (Castle, 1956).

For goats and sheep in the tropics, any discussion of a bare minimum fiber requirement is quite irrelevant. The warm year-round temperatures of the equatorial region allow plants the luxury of diverting more of their energy to lignified structural tissue (Deinum and Dirven, 1974; DaSilva, 1981). Therefore, much of the feed that is available in the tropics is quite fibrous. Also, economic realities preclude the use of high levels of concentrates for most ruminant livestock production situations in the tropics.

The problem for the tropical ruminant, then, is to cope with feeds which have high cell-wall content. One coping mechanism for the free-grazing or browsing ruminant is selectivity. There is considerable evidence that the goat is able to selectively consume the more nutritious plants and plant parts when conditions are unfavorable, thus aiding in its survival (Van Dyne _et al._, 1980; Malechek and Provenza, 1981). This is consistent with the theory presented by VanSoest (1981) in his as-yet unpublished book, that small ruminants _must_ be more selective in terms of diet quality, compared to large ruminants, because of their shorter rumen retention time and higher metabolizable energy requirement in proportion to rumen capacity.

A second possible coping mechanism for the tropical small ruminant is a more efficient capacity to digest cellulose and hemicellulose. Devendra (1978) has suggested that the goat does indeed digest fiber more efficiently than sheep or cattle. Devendra (1975) earlier published digestibility coefficients for crude fiber in Pennisetum purpureum (napier or elephant grass) which were higher for goats than sheep; he has later reported similar results for pigeon pea forage (Devendra, 1979).

Brown (1981) has recently completed a review of literature in which direct comparisons of fiber digestibility were reported in sheep and goats. Of nine papers reviewed, in only one (Jones et al., 1971) was the digestibility of cellulose reported. This was with temperate forage species. No significant difference was found in cellulose digestibility between goats and sheep. In a second paper (Wilson, 1976), goats had a slight advantage over sheep in the digestibility of the neutral-detergent and acid-detergent fiber fractions.

The other seven papers all reported digestibility of crude fiber. In three of them, including the two by Devendra (1975, 1979) cited above, digestibility was slightly higher in the goat. One author (Chenost, 1972) reported slightly higher digestibility of Digitaria decumbens (pangola grass) by sheep than goats. In four papers, no difference was found (including the same report by Chenost, 1972, pertaining to temperate forage species; also Ademosun, 1970; Adeyanju, 1975; El Hag, 1976).

All of these research reports failed to make any mention of possible species differences in selective intake. Failure to report or discuss the chemical composition of feed refused in experiments of this type is a serious oversight, and in effect renders meaningless the comparisons of digestibility data. It is quite possible - in fact highly probable - that the higher apparent digestibility of crude fiber is a result of selective refusal of the more fibrous portions of the ration.

Evidence of such selectivity of intake in a digestibility trial is presented by Brown (1981). She fed three levels of chopped wheat straw (35, 50 and 65% of the ration dry matter) combined with a ground corn/soybean meal mixture, to temperate breeds of goats and sheep. Although offered the same rations, the diets actually consumed by the goats were 1-2 percentage units lower in neutral-detergent fiber (NDF) than those consumed by thesheep. Digestibility of NDF was slightly higher in the goats consuming the low fiber ration (50 vs. 49%) but was lower in goats than sheep for the high fiber ration (44 vs. 51%). Digestibility of cellulose showed an identical pattern.

Careful examination of the intake data from the same experiment tells us more about the possible adaptive mechanism of the goat to low quality diets. All animals in this experiment were allowed ad libitum intake. The results are shown below; intake is expressed as g per kg body weight$^{.75}$ per day.

Performance criteria	Percent wheat straw			
	35		65	
	goats	sheep	goats	sheep
% Digestibility of DM	71	70	52	57
Dig. DM intake, g/kg$^{.75}$	42	44	25	27

Even though the goats showed a lower dry matter digestibility than the sheep, on the high fiber diet, their intake of digestibile dry matter was maintained almost equal to that of the sheep. The only plausible explanation for these results is a faster relative rate of passage and shorter retention time for the goats on the high fiber diet, compared to the sheep. This is assuming no dietary influence on relative rumen volume.

The apparent shorter retention time for the goat on a low quality diet would necessitate a lower apparent digestibility, because it is unlikely that the rate of digestion would increase. However, the faster rate of passage appears to allow a higher level of intake per day, which compensates for the lower digestibility and evens out the difference in digestible dry matter

(or energy) intake, relative to the sheep.

Intake Regulation

Variability among individuals of ruminant species is much greater with respect to voluntary intake of dry matter, than in the utilization of either energy or protein. For energy intake regulation, the ruminant is concerned with three categories of dry matter: the very rapidly digestible, the slowly degradable (cellulose and hemicelluloses), and the indigestible or highly lignified. The first fraction is solubilized almost immediately and has little effect in controlling the total amount of feed consumed. The second fraction will disappear from the rumen either through digestion or through passage; both rates, then, help determine intake capacity. The third, indigestible fraction, will disappear only by passage, and is of considerable interest in controlling voluntary intake.

Intake by free-ranging animals is influenced by available herbage, grazing pressure or stocking rate, forage palatability, animal selectivity, and time available for grazing. The recent review by Malechek (1981) discusses these factors with relation to goats. The discussion below is limited to the situation where neither feed availability nor animal feeding time are limiting factors, and selectivity is ignored. It addresses only the issue of how much of a given selected diet will be consumed.

When the consumed ration contains a high proportion of plant cell-wall components (cellulose, hemicelluloses, lignin) the physical capacity of the digestive tract becomes a factor limiting intake. Several reports have demonstrated this phenomenon in cattle. For example, Conrad, Pratt, and Hibbs (1961) reported that fecal dry matter output was a constant 1.2% of body weight in cattle, when the diet was an alfalfa/brome grass mixture of widely varying quality (fiber concentration). VanSoest (1965b.) showed that the NDF fraction of temperate forages was highly correlated ($r = -.7$) with voluntary intake by cattle.

Earlier studies at North Carolina State University (Johnson and Rodriguez, 1977) have shown a high degree of correlation ($r = -.8$) between the non-digested cell-wall fraction and voluntary intake, over a wide range of fiber concentrations (40 to 60% NDF) in rations for dairy steers. It was suggested that the non-digested cell-wall fraction, which represents the sum of the totally non-degradable portion and the potentially digestible portion which escapes digestion, represents a practical ceiling limiting intake. Over the range of diets studied, the non-digested cell-wall intake was virtually a constant.

This concept was examined further by Brown (1981) in the previously cited experiment with wheat straw in sheep and goats. For goats consuming rations with 35, 50, and 65% wheat straw (34, 44 and 56% NDF in the feed consumed), the intake of non-digested NDF was 10, 13 and 13 g/day, per kg body weight$^{.75}$. For sheep offered the same rations (35, 46, and 58% NDF in the feed consumed) the respective non-digested NDF intakes were 11, 12 and 13 g/kg$^{.75}$/day. Thus it appears that non-digested cell-wall material provides a ceiling to intake in goats and sheep, as well as in cattle. On the basis of data available to date, this principle is especially operative with diets that are relatively high in fiber content, as with the 50 and 65% wheat straw diets in Brown's experiment.

Needs for Further Research

The relationships between digestibility and intake need further clarification in small ruminants. It is still not clear whether rumen physiology is basically the same among goats, sheep, and cattle, or if basic differences do indeed exist. It is important to know whether data about nutrient requirements or nutritional value of feeds is applicable across species or only within species. Of particular interest with regard to fiber utilization are the interrelationships among rate of digestion, rate of passage, and level of intake as they influence net apparent digestibility; and how these same parameters interact to influence the voluntary intake capacity of the animal.

For small ruminants in the tropics, it is as yet quite impossible to recommend an optimum feeding strategy. This is the ultimate goal toward which applied research should be directed. It involves attention to the nutritional requirements of the animals, the nutritive value of feedstuffs, and the effect of the tropical environment on both the animals and the plants upon which they feed.

The tropical hair sheep is really an enigma. One could speculate that the hair sheep is closer to the tropical goat than his temperate wooled cousin, with respect to basic rumen physiology and dietary preferences. The probability of a genetic adaptation to the environment would lead to this hypothesis. However, the data by which to prove the point do not exist.

Goats in the tropics tend to be smaller in body size than European dairy breeds. If VanSoest's theories of the relation of ruminant body size to feeding strategy (VanSoest, 1981) are correct, it would follow that the tropical goat is even less tolerant of high fiber diets, and even more selective in his feeding habits, than temperate breeds. As we consider possible dry season supplementation strategies for the goat, this possible basic difference should be looked for.

The interaction between reproductive management and nutritional strategies should be obvious. Is there one or more "best" times of year for breeding, and hence parturition and lactation, to occur? What are the specific supplementary feeding needs during periods of highest nutritional stress, such as post-weaning, late gestation, and peak lactation? Do these requirements differ between tropical sheep and goats?

On the feed evaluation side, the old proximate analysis will no longer suffice. We need, as a minimum, the following analyses:

Total cell-wall (NDF)
Cellulose
Hemicellulose (NDF - ADF)

Lignin

In vitro dry matter and fiber digestibility

Crude protein (kjeldahl N)

Acid-detergent nitrogen (Maillard products)

Major minerals

Laboratories involved in routine feed analysis should re-tool themselves for these procedures.

Finally, we need to be concerned with the entire productive cycle of the animal and its special requirements at each critical stage. Livestock production in the caatinga is an extensive enterprise. Animals, however, are individuals, with changing individual needs. If improvements are to be made in the productive efficiency of our tropical small ruminants, we must learn how to feed them better throughout their entire life cycle. If these improvements are to be economical, their cost must be less than the expected return. If we as animal scientists fail in this research mission, the relative importance of small ruminants will only decline. We must not fail.

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