Review

Supplementary feeding in ruminants - A physiological approach

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Received 18 May 1989; accepted 6 March 1990

Presented at the 28th Annual Congress of the South African Society of Animal Production, Ermelo, 11 April 1989

An alternative strategy for supplementing ruminants fed low-quality roughages is discussed. In this strategy, the quantity and quality of supplement are adjusted to constrain mass-loss to a limit compatible with the productive function of the animal. The limits to mass-loss for survival, reproduction, and wool growth are discussed in relation to winter mass-losses of unsupplemented animals in South Africa. The consequences of nutrient imbalances on feed utilization are discussed in the light of the requirements of the ruminant for individual nutrients. Possible benefits of manipulating the ratio of glucose: acetate in absorbed nutrients with rumen-stimulating supplements, bypass starch and protein, and protected fats are discussed.

'n Alternatiewe benadering tot die supplementering van herkouers wat laegraadse ruvoer vreet, word bespreek. Volgens hierdie strategie word die hoeveelheid en kwaliteit van 'n supplement gewysig om massaverlies te beperk tot 'n peil wat in ooreenstemming is met die dier se produksiefunksie. Norme vir oorlewing, reproduksie, en wolproduksie word bespreek in verhouding tot die winter-massaverliese van ongesupplementeerde diere in Suid-Afrika. Die gevolge van voedingstofwanbalanse op voerverbruik word bespreek in die lig van die behoefte van die dier vir individuele nutriente. Moontlike voordele om die glukose: asetaat-verhouding in geabsorbeerde nutriente te manipuleer deur middel van rumen-stimulerende supplemente, verbyvloei-stysel en -proteïen, en beskermde vette word bespreek.

Keywords: Acetate, fat, glucose, protein, ruminant, starch, supplement.

Supplementary feeding may be defined as the addition of catalytic amounts of strategic nutrients to the basal diet in order to increase the efficiency of feed utilization. Supplementary feeding strategies can only be addressed with any degree of scientific certainty if the deficiencies of feeds can be related to the requirements of the animal. Although it has been argued that research on supplementary feeding should be limited to trials conducted under field conditions (Engels, 1983), climatic and geographical factors vary so greatly that a sensible strategy can not be deduced from the mass of variable and conflicting results reported in the literature. Similarly, empirical strategies which rely on feeding a constant amount of a fixed supplementary mixture without regard to fluctuations in pasture quality do not address the realities of supplementary feeding. A responsible scientific approach to supplementary feeding strategies can only be advanced from a sound knowledge of the metabolism of individual nutrients such as glucose, acetate and individual amino acids, and their interactions.

Limits to animal production from native pastures

The first issue to be resolved before discussing the potential benefits of supplementary feeding in South Africa is to determine whether or not supplementary feeding should be regarded as a necessity. The term 'necessity' refers in the ultimate sense to animal survival, but economic necessity dictates that steps be taken to ensure that seasonal weight losses do not have permanent negative effects. Both these limits will be discussed in relation to the status quo of animals grazing native pastures in South Africa during winter.

Survival limits for cattle

To ensure survival, losses should not exceed 30% of live body mass for 18-month-old cattle and 40% of body mass for adult cattle (Pieterse, 1971). Although compensatory growth may or may not eliminate the effects of winter deprivation in growing castrates or in non-productive adult animals (Kreft, 1966; Reynecke, 1971; Schoeman & Lishman, 1965), reproductive ability may be affected in the case of breeding stock.

Limits for reproductive cattle

For pregnant cows of 500 kg mature live mass the survival limit is 315 kg (Pieterse, 1971) with the proviso that the calf is removed shortly after birth. At rates of live mass-loss which approach this limit (equivalent to 37%), the drain of lactation will affect both the growth rate of the calf and the ability of the cow to regain mass during the summer. Mature cows are, however, remarkably resilient and, provided that summer pastures are of such quality that the same mass can be maintained from autumn to autumn, a certain degree of winter mass-loss may be tolerated. Mature cows which lost 14% of mature mass produced as well as cows wintered so as to lose 10% of live mass (Pope, 1967).

Growth rate during the first winter after weaning is critical for heifers destined to calve at two years of age. Although winter deprivation may have only slight effects on mature size, it may have substantial effects on conception rate. Pope (1967) fed heifers to gain 1,6%, 19%, or 32% in live mass during the first winter following weaning. The proportion of heifers showing first heat at 15 months was 70%, 90%, and 100% respectively.

If heifers which conceive at 15 months of age are undernourished during the winter of their first pregnancy, fewer and lighter calves will be born and lighter weaning weights will be attained due to reduced milk production. This can reduce the mass of calf produced per cow bred by 25% (Pope, 1967). A mass-loss of less than 10% during the winter does not appear detrimental for pregnant heifers if sufficient nutritious summer grazing is available (Pope, 1967).

Mass-loss of grazing cattle in South Africa

Cattle may lose 22-25% of maximum summer weight during winter in the Eastern Highveld Region (Kreft, 1966; Reynecke, 1971), 13% in the Western Highveld Region (Kemm & Coetzee, 1964; Von la Chevallerie, 1965), 7% within 12 weeks in the Natal Bushveld Areas (Schoeman & Lishman, 1965), 6% over eight weeks in the Sourveld Regions of Natal, and 12% in the Eastern Cape Region (Bishop, Grobler & Smith, 1969). These results show that mass-losses of cattle grazing unsupplemented natural pastures can exceed the limits for successful reproduction as discussed above. The reality of the status quo in South Africa is evident from records obtained from the Highveld Agricultural Research Institute for the Afrikander stud over a 33-year period which show that only 53% of cows with first calves at foot re-calved within 15 months (Penzhorn & Kemm, 1973). The re-calving figure for cows calving for the first time - at an age of up to 3,5 years - was only 45%. The latter authors reported conception rates of 0-38% depending on the year in an experiment where animals received only a mineral supplement during winter. It is estimated that the mean calving percentage for cattle in South Africa is only 63%, and the intercalving period 499 days (personal communication: J.G. Cloete, 1989).

Survival limits for sheep

Survival masses for adult sheep have been defined as 40 kg for large-framed Merinos and 35 kg for small-framed Merinos and fine-woolled Merinos (Leng, 1986). This is equivalent to a mass-loss of 33% for large-framed (mass 60 kg) and 30% for small-framed Merinos (mass 50 kg). A mass-loss of 20% with South African Merinos was associated with mortalities of 10—30% (Cloete, 1971).

Limits for reproduction and wool growth in sheep

As with cattle, survival mass does not necessarily ensure that reproductive ability is not affected. Undernutrition of the pregnant ewe will reduce wool-follicle numbers in the lamb, but this disadvantage may be eliminated by good nutrition in early post-natal life (Corbett, 1979). The combined effects of pregnancy and lactation may reduce the annual fleece production of ewes by 10-14% (Corbett, 1979); a loss that will be exacerbated by undernutrition. The effects of undernutrition on the reproductive ability of ewes will follow the same pattern as those discussed above for cattle. Ewes, for example, which grazed Karoo shrub and lost 17 g/d during the last six weeks of pregnancy weaned only 50% of the lambs dropped (Cloete, 1969). Although undernutrition of young lambs may depress the number of wool-producing follicles, recovery is possible. Only under exceptionally severe conditions may recovery be limited (Corbett, 1979).

Wool growth rate is related to live mass-loss. A 24% loss in live mass decreased wool production by 22% and fibre diameter by 28% in Merino wethers (Swart, Van Schalkwyk, Hugo & Venter, 1963), while Dohne Merino ewes which lost 14% live mass produced 18% less wool of a fibre diameter 18% less than ewes fed at a maintenance level (Coetzee, 1964). Although loss of live mass and wool growth through winter may in some cases be recovered by compensatory growth during the following summer (Coetzee, Nel & Joubert, 1968; Jacobsz, Cronjé, Baard & Van Schalkwyk, 1971; Jacobz, Cronjé, Baard & Skea, 1971), the accompanying decrease in wool fibre diameter may result in tender fleeces. A significant proportion of adult Dohne Merino wethers developed tender fleeces after a mass-loss of only 14% in the study of Coetzee et al. (1968). This was accompanied by a reduction of 17—27% in wool growth rate.

Mass- and wool losses of grazing sheep in South Africa

Live mass-losses of sheep grazing natural pastures in winter have been recorded at 15—30% of maximum summer mass in the Western Highveld Region (Pieterse, Kemm & Coetzee, 1965; Coetzee et al., 1968), 17% in the Eastern Cape (Nel & van Niekerk, 1970), and 24% in the Central Orange Free State Region (Swart et al., 1963). There is little doubt that these values are in some cases very close to the limits for survival as discussed above, and exceed the limit for tender fleeces. Tender fleeces in unsupplemented grazing sheep in the Orange Free State and Western Highveld Regions have been known to constitute 58—66% of the woolclip (Bosman, Nieman, Swart & Cronjé, 1967; Coetzee et al., 1968).

Variation in the nutritive value of native pastures

The above results illustrate the consequences of exceptionally severe conditions, and it would be foolhardy to formulate empirical supplementation regimes on the basis of these extremes. Seasonal variations are such that the nutritive value of natural pastures such as those discussed above may improve to the extent that supplementation is unnecessary, or may even support mass gains. Natural pastures in the Western Highveld Region have been known to support masslosses of as little as 1% during winter in younger sheep (Kemm & Coetzee, 1967) and even mass gains of 4% in adult wethers (Coetzee & Jaarsma, 1970). In contrast, Coetzee et al. (1968) reported mass-losses in sheep of up to 30% at the same Research Institute, while mass-loss during the following winter was only 16%. During this period, the corresponding occurrence of tender fleeces improved from 58% to 0%. The considerable variation in nutritive value and composition of natural pastures renders any empirical strategy based on feeding a constant amount of a supplement of fixed composition of little practical value. This is evident from the variable and often conflicting nature of responses to supplementation carried out under pasture conditions.

Variation in responses to supplementation

An experiment conducted by Henning, Compaan & Grobler (1984) with Dohne Merino ewes grazing natural pasture in the Eastern Cape Region illustrates the complexities arising from climatic variations. High- and low-protein supplements

were made available to the animals during three consecutive winters. The high-protein supplement was more effective in restricting weight loss during the two years of highest rainfall, but this trend was reversed in the year of lowest rainfall when the low-protein supplement realized the most favourable results. The mean intake of the low-protein supplement varied from 56—137 g/d depending on the year, and that of the high-protein supplement varied from 148—458 g/d. In both instances the lowest intake was obtained during the year of lowest rainfall. Although Henning et al. (1984) have thoroughly discussed the reasons for these results, this experiment nevertheless serves to illustrate the complex interactions between climate, intake and response to supplements. Interpretation of reports in the literature is further complicated by variations in stocking rate, selective grazing, and pasture type and composition. When these variables are considered, it is evident that the results of trials carried out under uncontrolled field conditions are of little predictive value. Any attempt to distil justifiable recommendations from the plethora of conflicting reports on the subject is not likely to succeed.

A flexible approach to supplementation

The variable nature of pasture quality necessitates a more realistic approach in order to maintain a constant level of animal production efficiency from year to year. Although the limits for animal production discussed above are intended merely as guidelines, they *are* relatively constant. By defining a target winter mass-loss (which may vary according to herd structure, breed, and price ratios), the amount and type of supplement fed may be adjusted accordingly by monitoring the rate of mass-loss as the season progresses. This approach allows for variations in pasture quality and

provides flexibility in terms of mass-loss for different physiological states, and the type and amount of supplement. Having defined what is required in terms of animal production, the second step is to define what the animal requires to achieve this.

Limits to efficient metabolism

The principal nutrients absorbed by the digestive tract of the ruminant are acetate, propionate, amino acids and glucose. In the case of animals grazing roughages such as those discussed above, acetate constitutes the main energy source (Preston & Leng, 1987). Less propionate is produced in comparison with diets of higher digestibility, and little glucose (5—10 g/d) is absorbed (Leng, 1970). The amino acid supply from such roughages is typically low, and microbial protein production is limited by low microbial growth efficiencies (Leng, 1984). The balance of absorbed nutrients arising from roughage fermentation is therefore characterized by a low supply of glucogenic energy sources (propionate, starch, amino acids) relative to the quantity of energy available as acetate.

Calorimetric experiments have shown that the efficiency of utilization of acetate is low when fed as the sole energy source (Armstrong & Blaxter, 1957), and that efficiency is improved when acetate is supplemented with small amounts of propionate or protein (Armstrong & Blaxter, 1957; Johnson, 1972; Lobley & McRae, 1986). Since both these substrates are glucose precursors, it has been proposed that the improvement may be due to the relief of some rate-limiting effects of glucose in the metabolism of acetate to fatty acids (Hovell, Greenhalgh & Wainman, 1976). Interactions between glucose and acetate are shown in Figure 1.

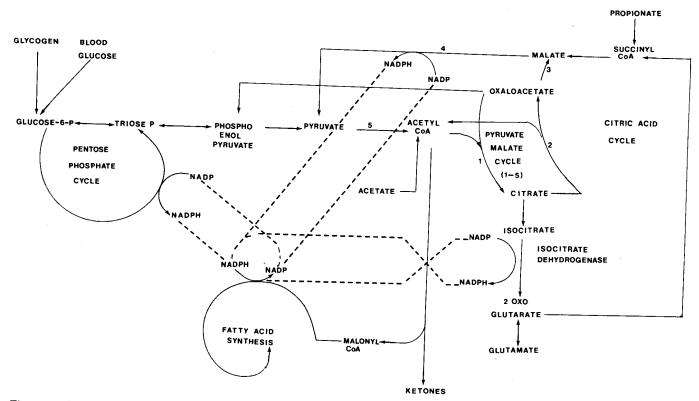


Figure 1 Interactions between glucose and acetate metabolism in the ruminant.

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From Figure 1 it is evident that the utilization of acetate for fatty acid synthesis will be limited if the supply of NADPH is insufficient. Fourteen mol NADPH is required for the synthesis of 1 mol palmitate from acetate. Theoretically, NADPH may be generated from glucose via the pentose-phosphate pathway, via the pyruvate-malate cycle, or from acetate via the isocitrate-dehydrogenase pathway. One mol of glucose can theoretically be completely oxidized to yield 12 mol NADPH in the pentose-phosphate cycle, but 1 mol glucose will yield only 2 mol NADPH in the pyruvatemalate cycle. It follows that if the carbons of fatty acids are derived not from glucose, but from acetate as is the case in ruminants (Hanson & Ballard, 1967), NADPH would be most efficiently produced by oxidation of glucose in the pentose-phosphate pathway. This is confirmed by the low activity of pyruvate-malate cycle enzymes and the high activity of pentose-phosphate pathway enzymes (Hanson & Ballard, 1967; Baldwin, Reichl, Louis, Smith, Yang & Osborne, 1973). Although NADPH may be derived from acetate by the isocitrate-dehydrogenase pathway (Vernon, 1981), theoretical calculations indicate that the extent to which this pathway is used may be limited by the ability of adipocytes to utilize excess ATP (Preston & Leng, 1987). These calculations suggest that at least 70% of NADPH production is probably derived from glucose via the pentosephosphate pathway. This implies that 0,65 g glucose will be required per gram fat synthesized. Although the dependence of acetate metabolism on glucose availability has been demonstrated indirectly by the results of calorimetric experiments (Armstrong & Blaxter, 1957) and in vitro tissue incubations (Yang & Baldwin, 1973), and may be inferred from numerous experiments where sources of bypass protein have been fed (e.g. Kemm, 1965), the subject remains contentious. In some calorimetric experiments no responses to additional glucose precursors were obtained (Hovell et al., 1976; Ørskov, Grubb, Smith, Webster & Corrigal, 1979), but the relatively high level of amino acids supplied to the sheep may have provided sufficient glucose precursors. Although other factors such as the supply of oxaloacetate (Armstrong & Blaxter, 1957) and effects of insulin (Vernon, 1981; Abdul-Razzaq & Bickerstaffe, 1989) may also play a role, many of the observed effects of glucose precursors can be explained by the NADPH theory.

Excess acetate may be diverted to inefficient substrate cycles and energy dissipated as heat if the supply of glucose is insufficient. The activities of acetyl-CoA synthetase and acetyl-CoA hydrolase, which together constitute a substrate cycle for acetate with concomitant hydrolysis of ATP, were higher in adipose tissue from sheep fed a fibrous diet than from sheep fed a starchy diet (Scollan, Brisbane & Jessop, 1988). This theory is also supported by the high values for heat increment obtained by Armstrong & Blaxter (1957) when acetate was fed to sheep in the absence of glucose precursors.

In situations where glucose supply is deficient, a certain amount of dietary protein may be diverted to glucose production, reducing the amount of amino acids available for protein deposition. Evidence in support of this is to be found in studies which have shown increased nitrogen excretion when excess acetate was added to the diet (Tyrell, Reynolds)

& Moe, 1979). Other studies have shown that this effect may be alleviated by increased supply of glucose precursors (Girdler, Thomas & Chamberlain, 1985; Lobley & McRae, 1986).

Feed intake may also be decreased if the imbalance of acetate to glucose is sufficiently great. Several studies have linked acetate supply to the regulation of voluntary intake (Egan, 1964; Egan, 1977). The stimulation of voluntary intake sometimes observed in response to supplementation with bypass protein may be related to this observation.

The requirement of acetate metabolism for glucose can, on the one hand, be satisfied by supplementation with bypass protein and starch. Alternatively, the requirement for glucose may be decreased by supplementing with bypass fatty acids. Dietary fatty acids are largely incorporated directly into tissue lipids (Scott & Cook, 1975). Supplementation with fatty acids may decrease the synthesis of fatty acids from acetate, thereby alleviating the drain on glucose and glucose precursors such as amino acids for NADPH production. The sparing of amino acids thus affected may promote a reduction in protein breakdown. Yang, Baldwin & Garrett (1978) found that *in vitro* incorporation of acetate into fatty acids or oxidation to CO₂ was lowered in tissue from lambs fed a protected fat supplement, and oxidation of glucose was also depressed.

In conclusion, a strong body of evidence suggests that a low ratio of glucose to acetate may not only limit the efficiency of energy utilization, but also the efficiency of protein synthesis if amino acids are used for gluconeogenesis. While the relative importance of these factors will depend on the productive function of the animal, it is significant to note that Preston & Leng (1987) listed glucose as the first-limiting nutrient in ruminants fed roughage diets for growth (fattening), puberty, conception, pregnancy, lactation and work, and amino acids as the second-limiting nutrient for puberty, conception, pregnancy and lactation.

It is self-evident that supplements should be evaluated in terms of glucogenic potential and not simply crude protein or metabolizable energy. Carbohydrate and protein sources will differ in their glucogenic potential. Although glucose entry rate in lambs was increased by the supplementation of a roughage diet with either bypass protein or sodium propionate, the sources were not used with equal efficacy for this purpose (Cronjé, 1987). Acetate clearance rate was, however, significantly related to glucose entry rate irrespective of supplement. This technique could be used to determine the glucogenic potential of supplements, and could play an important role in the design of future supplementary feeding strategies.

Rumen-stimulating supplements

The initial step in any supplementation programme should be to increase the efficiency of microbial fermentation in the rumen by supplying sources of readily fermentable nitrogen or combinations of fermentable nitrogen and carbohydrate. Firstly, this may increase the potential supply of energy to the animal via a greater conversion of low-quality roughage to utilizable nutrients, and also via an increased intake resulting from a faster flow of nutrients through the gut. Secondly, protein supply may be increased via an increased

outflow of microbial biomass to the lower gut. Any improvement in the efficiency of rumen microbial fermentation will increase the ratio of protein to energy (i.e. glucose precursor: acetate) in the digesta flowing into the small intestine (Preston & Leng, 1987). This may increase the efficiency with which acetate is utilized by body tissues.

A wide range of voluntary intake responses to supplementation with rumen stimulants has been reported in the literature. Intake of wheat straw was increased by 230% (Louw, 1978), that of ground maize stalks by 25% (Grey & Franck, 1970), oat straw by 50% (Greeff, Van der Merwe & Swart, 1963), sugar-cane tops by 38% (Van Niekerk & Jacobs, 1985), and *Eragrostis curvula* hay by 28—36% (Pieterse, Lesch, Oosthuizen & Le Roux, 1966; Pieterse & Lesch, 1964). Intake responses to supplementation of winter native pasture have varied from no response (Coetzee & Dyason, 1968) to increases of 17—52% (Lesch, Pieterse & Oosthuizen, 1963; Lesch & Van Schalkwyk, 1967). Increases of digestibility of crude fibre of 27% have been recorded by Greeff *et al.*, 1963.

Rumen-stimulating supplements will decrease the live mass-loss of roughage-fed animals considerably (Reynecke, 1971; Kreft, 1966; Pieterse, 1962; Kemm & Coetzee, 1964; Van Niekerk & Jacobs, 1985; Lishman, 1965). However, the best improvement that can be expected is prevention of live mass-loss or, at best, a slight gain in live mass (Louw, Steenkamp & Van der Merwe, 1972; Schoeman & Lishman, 1965; Van Niekerk & Van der Merwe, 1966). Rumen stimulants do not appear to be effective in reducing the loss of wool growth to any appreciable extent (Kemm & Coetzee, 1967; Coetzee & Pieterse, 1966). Although seasonal variations undoubtedly influence the magnitude of responses to rumen stimulants, several trials in which no responses were found were ascribed to low and variable intake of supplement (Swart & Bosman, 1964; Van Niekerk, Basson & Mulder, 1967; Kemm & Coetzee, 1964; Swart & Van der Linde, 1966). Nolan, Norton, Murray, Ball, Roseby, Rohan-Jones, Hill & Leng (1975) showed that 20-50% of sheep with access to a liquid molasses mixture under extensive farming conditions did not consume the supplement at all, while Leng (see Preston & Leng, 1987) found that 20% of cattle did not consume supplements in the form of molasses/ urea blocks.

Urea-based supplements should include a source of readily fermentable carbohydrates where a ratio of 1:13 of urea: maize meal (Pieterse et al., 1966) or 1:8-10 of urea: molasses (Von la Chevallerie, 1965; Lishman, 1965; Coetzee, 1969) would appear to give good results. Molasses fed alone will generally give little response, and may even increase mass-loss (Greeff et al., 1963; Kreft, 1966; Von la Chevallerie, 1965; Van Niekerk & Jacobs, 1985). The inclusion of excess maize meal has been shown to depress intake and will be discussed in a later section. The optimum intake of urea will depend on the characteristics of the roughage in question and is difficult to predict. Pieterse et al. (1966) fed various combinations of urea and maize to wethers as a supplement to E. curvula hay and found the optimum increase in voluntary intake to occur with a combined intake of 8 g/d urea and 100 g/d maize meal. Lesch & Van Schalkwyk (1967) sprayed urea onto mature veld hay in varying amounts

and observed that the highest intake by steers was obtained with 52 g/d urea. Since the optimum levels of urea intake may vary considerably, the only accurate index of intake is rumen ammonia concentration, which should be above 5 mg NH₃-N/100 ml rumen fluid (Satter & Slyter, 1974). Urea is toxic in excess and intake should therefore not exceed 14 g/d for sheep and 112 g/d for cattle (Van der Merwe, 1974).

Bypass starch supplements

Bypass starch supplements represent a source of glucose precursors to the animal. Maize is commonly used as a supplementary feed in South Africa. Although maize does provide a certain amount of bypass starch, a considerable amount of fermentation also occurs in the rumen (Cronjé, 1983). The presence of excessive, readily fermentable starch in the rumen may lead to a shift in the microbial ecology of the rumen at the expense of fibre-digesting organisms resulting in a depression of intake (Gilchrist & Schwartz, 1972). Depression of intake has also been reported by Pieterse *et al.* (1966), Nel & Van Niekerk (1970), Swart, Nieman, Engels & Biel (1971), and Van Niekerk & Jacobs (1985).

Bypass protein supplements

Sources of protein resistant to breakdown in the rumen not only supply amino acids, but represent a potential source of glucose. Supplementation of roughage diets with a source of bypass protein has been shown to increase glucose production rate by 72% in lambs (Cronjé, 1987). This supports the hypothesis that amino acids may be used to increase gluconeogenesis, thereby illustrating the futility of evaluating supplements in terms of crude protein and metabolizable energy.

Supplementing with bypass protein has, in many instances, increased voluntary intake. For example, Swart et al. (1971) reported an increased intake of 37% when fishmeal was given at 0,667 g/kg live mass to Merino wethers fed low-quality *Themeda triandra* hay, whereas Kemm (1965) recorded increases of 45% and 93% in intake of poor-quality *E. curvula* hay when Dorper wethers were given 20 or 65 g/d fishmeal respectively. Reasons for these effects include slow release of amino acids, sulphur, and energy in the rumen, and provision of glucose and amino acids at tissue level (Kellaway & Leibholz, 1983; Preston & Leng, 1987).

There is little doubt that supplementation with bypass protein will reduce mass-loss of animals fed roughage diets to zero or may even support a mass gain (Kemm, 1964; Kemm, 1965; Pieterse et al., 1965; Van Niekerk & Van der Merwe, 1966; Kemm & Coetzee, 1967; Coetzee & Jaarsma, 1970). Bypass protein supplementation will stimulate wool growth (Coetzee & Jaarsma, 1970) and is clearly superior to maize and urea in this respect (Coetzee & Pieterse, 1966; Kemm & Coetzee, 1967; Coetzee & Dyason, 1968; Nel & Van Niekerk, 1970). Increases of up to 44% have been recorded with fishmeal (Coetzee & Dyason, 1968), and increases of 14% with groundnut oilcake (Coetzee & Jaarsma, 1970).

In conclusion, bypass protein can be used, when necessary, to give mass and wool gains over and above those obtained using rumen-stimulatory urea/molasses supplements.

Bypass fat

Dietary fat may be included in ruminant diets up to a level of 5—7%, after which intake is depressed (Scott & Cook, 1975; Thornton & Tume, 1984). This effect is due to a depression of 13—59% in fibre digestion (Jenkins & Palmquist, 1984; Palmquist, 1984). This effect may, however, be avoided by the formation of complexes which protect fat from degradation in the rumen, but which dissociate at the acidic pH of the lower gut.

Supplementation of ruminants fed low-quality diets with protected fat may decrease the requirement for glucose and spare amino acids from breakdown for gluconeogenesis. In experiments with growing heifers fed ammoniated rice straw and formaldehyde-treated cottonseed meal, supplementation with 200 g/d protected fat improved growth rate by 30% (see Perdok, 1987). Van Houtert & Leng (1986) showed that the growth rate of sheep fed rice straw could be increased by 44% when protected fat was fed at a level of 25 g/d, and by 56% when 50 g/d was fed. Supplementation of the diet of grazing ruminants with protected fat during winter is a novel concept which, with the exception of the above two studies, has not been explored in detail yet.

Conclusions

Physiologically justifiable limits to mass-loss form the framework of the supplementary feeding strategy discussed in this paper. This offers the flexibility necessary to accommodate different target mass-losses as dictated by breed, herd structure, economic constraints, etc. Climatic and geographical variations in the nutritive value of natural pastures may be accommodated by varying the amount of supplement fed. In this way, a constant level of animal production may be achieved once a target mass-loss has been defined for a particular situation. Mass changes must be monitored regularly so as to predict the end-of-season target. If supplementation appears to be necessary, a rumenstimulating supplement should be supplied as the first step. If the predicted end-of-season mass-loss still exceeds the target, nutrients of high glucogenic potential should be added to the supplement and incremented until the target is achieved. Supplementation of roughage-fed ruminants with protected fats is an exciting new development and justifies an increased research effort.

Little research has been done on developing a scientific basis for supplementary feeding strategies in terms of the requirements of the host animal for specific nutrients. The measurement of acetate clearance rate as an index of the balance of dietary acetate to glucose could provide a means of evaluating supplements in terms of their glucogenic potential.

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