

## Ruminant nutrition research in South Africa during the decade 1985/1995

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Research on ruminant nutrition in South Africa is reviewed for the decade 1985/1995. The review covers the following topics: feed requirements and forage preferences in relation to carrying capacity, intake measurement and control/prediction, pasture utilization, protein digestion and metabolism, supplementation with carbohydrate, protein and fat, mineral nutrition, feed additives and treatments to improve nutritive value. Pointers to future endeavours also are discussed.

Herkouervoedingsnavorsing in Suid-Afrika vir die dekade 1985/1995 word in oënskou geneem. Die oorsig dek die volgende onderwerpe: voedingsbehoefte en -voorkeure soos dit verband hou met drakrag, meting en beheer/voorspelling van inname, weidingbenutting, proteïenvertering en -metabolisme, koolhidraat-, proteïen- en vetaanvulling, mineraal-voeding, voerbymiddels en behandelings wat voedingswaarde kan verbeter. Toekomstige behoeftes word ook bespreek.

**Keywords:** Research, ruminant nutrition, South Africa.

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### Introduction

A review has two limitations: (a) it cannot do justice to the vast amount of work done because, if it does, (b) the extent would discourage the reader from struggling through the information. Therefore, we highlighted primarily those issues which should also be regarded as harbingers of the future. This review is both timely and necessary, because it forces us to take stock of what has been achieved and where we should head with ruminant nutrition research. The reader will notice surprisingly good progress in some areas — a case in point is protein utilization in the dairy cow and the feedlot steer. In others, such as intake control and prediction with mechanistic approaches and food selection patterns, progress has been slow despite systematic and purposeful efforts, and in yet others such as mineral nutrition, research has declined. We addressed these topics under the headings indicated below.

### Feed requirements and forage preferences in relation to carrying capacity

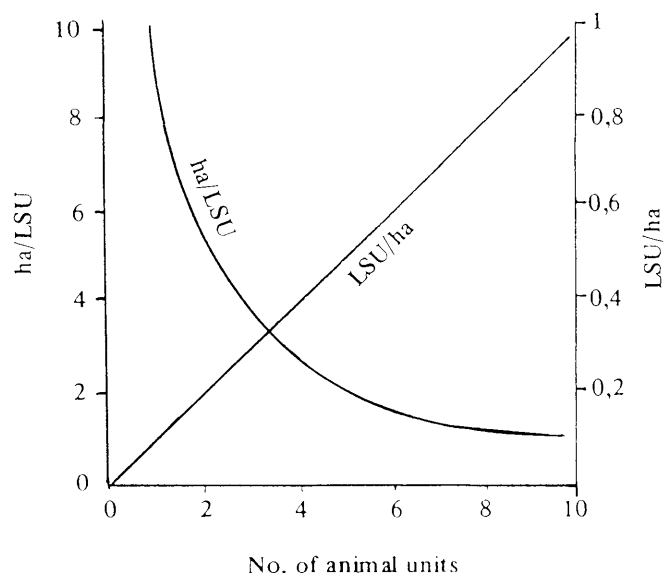
The animal unit (AU) (or large stock unit) as a norm or authoritative standard to estimate carrying capacity was developed in an effort to synchronize the requirements or intakes of animals with the supply of fodder from the veld (Meissner *et al.*, 1983). Officially, stocking rate has been expressed as the area of land per animal, that is, ha/AU. Recently Danckwerts (1989) aptly pointed out that this approach has serious conceptual and mathematical limitations:

1. The unit ha/AU decreases in magnitude with increasing animal numbers which is misleading, because a stocking rate of 2 ha/AU is heavier than one of 3 ha/AU.

2. The unit ha/AU is not linearly related to the number of animal units on an area of land whereas the unit AU/ha is (Figure 1).

Therefore, AU/ha should be used in preference to the traditional unit of ha/AU.

The AU as a norm has been criticized by ecologists and others as being either inadequate or irrelevant to estimate carrying capacity of biodiverse populations such as in game parks (Liversidge & Van Eck, 1993). They argue that in multiple-species systems interactions between grazers, browsers and



**Figure 1** Relationship of the units ha/AU and AU/ha with increasing animal units (0–10) on a 10 ha area of land (Danckwerts, 1989).

selective feeders are not easily predicted. One may find positive associations between grazers and browsers because they do not compete for the same fodder resource, whereas grazers and selective feeders do overlap in fodder preferences and therefore may impact negatively on each other. A case in point is that less sheep than cattle per AU should be stocked on sweet veld (Trollope *et al.*, 1992) in the Eastern Cape, whereas on sourveld in Kokstad Hardy (1994) showed that if the proportion of cattle in a mix with sheep was increased the stocking rate increased and the ratio widened in favour of cattle.

The criticism that the energy requirements of game species may be calculated inappropriately (Liversidge & Van Eck, 1993) appears unfounded. Direct measurements of intake on elephant (Meissner *et al.*, 1990), springbok (Vorster & Bigalke, 1991) and impala (Pietersen *et al.*, 1993) closely corresponded with the theoretical approach of Meissner (1982). To refine calculations of carrying capacity, however, it is essential to define requirements in terms of the herbage on offer, that is, measurement of the amount and quality of the herbage consumed by the grazing animal in addition to identification of the species composition of the selected diet (Meissner, 1994). In this regard, results on preference and quality of the diet selected have been reported from Döhne, Glen, Grootfontein, Upington and the Timbavati Nature Reserve.

The most recent reports, with interesting and far-reaching implications for stocking rate and veld management, are those of Meissner *et al.* (1992d), Ford (1994), Kok *et al.* (1994) and Du Toit & Blom (1995). Meissner *et al.* (1992d) showed that impala had equal intakes and selected a diet of similar quality in two habitats differing vastly in plant succession and botanical composition. This implies that impala may cause further destruction to already deteriorating veld. At Roodeplaat, Ford (1994) found no difference between Simmentalers, Ngunis and Afrikaners in selection of *Setaria sphacelata* and *Heteropogon contortus*, but Simmentalers selected less of the undesirable *Aristida congesta* than Ngunis and Afrikaners. These results suggest that indigenous stock may utilize veld more uniformly. Kok *et al.* (1994) found in the False Upper Karoo that Angora males selected differently than females and kids, whereas Du Toit & Blom (1995) showed in the neighbouring Noorsveld that the preference of Angoras corresponded more closely to that of two sheep breeds than to that of Boer goats. Their data imply that Angoras and sheep cannot always be stocked at higher rates than Angoras or sheep alone. The value of having data on what animals select has been demonstrated by Meissner (1994). He showed that if the difference in selection pattern of cattle and sheep is considered, the difference between them in stocking rate and therefore the impact on the vegetation could be 20%. Therefore, it is possible to predict AU ratios between cattle and sheep without necessarily having to resort to elaborate trials.

To further refine carrying capacity, the information discussed above should be integrated with veld condition score and other plant-based norms. This may require modelling. Carrying capacity is at best a dynamic equilibrium because it changes with season (Webber *et al.*, 1995) and is influenced by rainfall and many other variables. Multi-variable models have become possible by linking geographic information sys-

tems (GIS) with process information mathematical prediction models (Coughenour, 1993). Less sophisticated models may sometimes suffice. For example, the Glen group has been quite successful with the comparatively simple PUTU II model, showing application also in other areas (Howard & Kirkman, 1995).

### Intake measurement and control/prediction

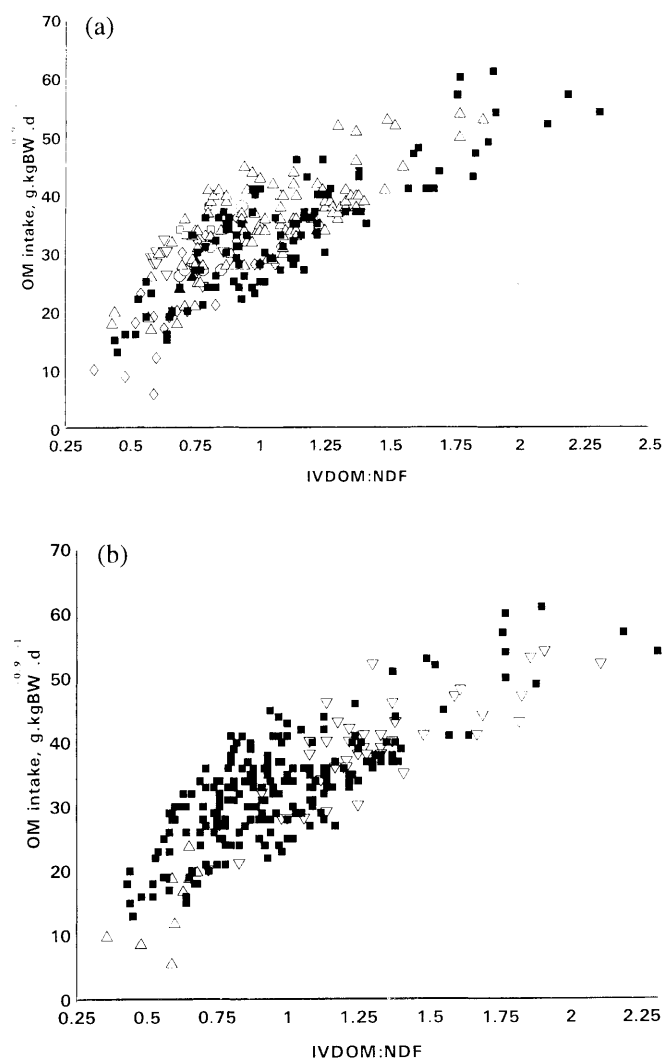
The control mechanisms and prediction of forage intake have been the subject of many studies. Factors investigated included physical structure of the plant in relation to palatability, chemical composition or quality constituents limiting intake, digestion and passage kinetics within the ruminant, and foraging behaviour. Some advances have been made in comprehension of intake control mechanisms and intake prediction, using both empirical and mechanistic approaches. These are summarized in this section.

Plant structural factors that relate to veld grass acceptability include tuft diameter, leaf percentage, leaf table height and stemminess (O'Reagain & Mentis, 1989). Acceptable species were leafy and non-stemmy with a high leaf table and leaves of low tensile strength. Avoided species generally were stemmy and had leaves containing low crude protein (CP), suggesting interaction between physical and chemical composition. This was also noticed by Teague (1989) with goats browsing *Acacia karoo* in the Eastern Cape. Browse intake was related positively to the leaf mass per unit length of the shoot and the ease of harvesting leaf material, but the relationship was modified by browse-induced tannin levels and the overall digestibility of leaves and shoots.

Chemical constituents that primarily limit intake of subtropical forages are those associated with the cell wall. In accordance with the preceding discussion on plant structure, subtropical grasses are generally more stemmy than temperate grasses and have a higher cell wall component. Cell wall constituents that have been shown to be correlated with intake include NDF (Meissner *et al.*, 1991), ADF (Cilliers & Van der Merwe, 1993) and ADL (Pietersen *et al.*, 1993). Meissner and his co-workers (1991) showed that intake is generally limited above NDF levels of 55 to 60% of DM, but not below. Most subtropical grasses at time of grazing would contain NDF above this indicator level, whereas NDF in most temperate grasses and legumes would be below it. An interesting empirical prediction equation of forage intake has been developed by Meissner & Paulsmeier (1995). They showed that intake of non-lactating ruminant species feeding on grasses, legumes, hays, silages, shrubs and even supplemented forages (Figure 2) can be predicted with the same relationship from the ratio between *in vitro* digestibility of organic matter (IVDOM) and NDF:

$$\text{OM intake (g/kg.W}^{0.9}\text{/day)} = 70 - 97e^{-0.975 \text{ (IVDOM/NDF)}} \\ r = 0.82; \text{ Error of estimate } 5 \text{ g/kg.W}^{0.9}\text{/day}$$

Two aspects feature prominently in the equation: the body mass of the animal is raised to the power of 0.9 instead of the usual 0.75 or 1.0, and the equation conforms to the law of diminishing returns. Mass raised to the power of 1.0 is appropriate if intake is primarily controlled by physical constraints within the digestive tract, whereas mass raised to the power of 0.75 is appropriate when intake is rather controlled by absorbed nutrients or energy balance. Intake of most forages



**Figure 2** Relationship between intake (g OM.kg.BW<sup>-0.9</sup>.d<sup>-1</sup>) and the ratio of IVDOM:NDF (Meissner & Paulsmeier, 1995) for:

(a) animal species

- sheep
- △ cattle
- ◇ goats
- ▽ blue wildebeest
- ▲ red deer
- impala
- blesbok

(b) grasses and legumes plus shrubs

- grasses
- ▽ legumes
- △ shrubs

will be controlled by a combination of physical limiting factors and chemical constituents sensed in the blood or at the tissue level. Therefore, mass raised to the power of 0.9 generally may be more applicable. One also suspects that the law of diminishing returns should feature, as intake will be severely limited at low ratios of IVDOM to NDF (i.e. low digestibility and high cell wall), less so at medium ratios and even negligible at high levels (i.e. high digestibility and low cell wall).

An advantage of the equation is that it can be used to distinguish between cell wall induced and other limiting factors. Meissner & Paulsmeier (1995) showed that if intake of a forage falls below the IVDOM/NDF predicted value minus the

error of estimate, other factors in addition to cell wall induced factors may be limiting intake. Identified non-cell wall factors include high phenolic compounds in shrubs (Meissner & Paulsmeier, 1995), low DM content (Meissner *et al.*, 1992c) and high ash content (Meissner & Paulsmeier, 1995) in ryegrass, high soluble N, nitrate and oxalate contents in kikuyu (Pienaar *et al.*, 1993) and a poor N to energy ratio which, in turn, limit microbial protein production in the rumen of animals consuming ryegrass, other temperate species (Meissner *et al.*, 1993) and kikuyu (Marais *et al.*, 1990). Toxic compounds and legume bloat are, of course, further potent factors limiting intake.

The empirical approach of Meissner & Paulsmeier (1995) complies with the notion that feed intake of forages is controlled by physical constraints, primarily rumen fill and the rate of removal of digesta from the rumen (Roux & Meissner, 1984). Removal of digesta is a function of fermentation rate and the rate of outflow from the rumen. A mechanistic model approach to predict intake therefore would have to include these rates in a combined equation. Pienaar *et al.* (1980) used first-order equations together with other variables to predict intake, but found significant deviations from first-order kinetics for both fermentation and outflow. The deviations consist of a phase of increasing activity at the onset, which since has been effectively accommodated by a gamma function (Pienaar & Roux, 1989). In practice, all that is measured is fermentation through *in vitro* gas production and potential digestibility. Passage rate is estimated from the observed fermentation rate. The gamma function has proved useful in predicting intake for the evaluation of forage germplasm (Pienaar *et al.*, 1994) and, surprisingly, also with more concentrated feedstuffs in a feed evaluation system (Pienaar, 1994).

An intricate mechanistic approach to describe foraging behaviour in kudu has been developed by Owen-Smith (1993). He tested the linear programme model (LPM) of Belovsky with modifications from the classical or contingency model (CM). Food choice was between the herbaceous and woody plant components for the LPM and among plant species or categories for the CM. Constraints considered were consumption rate, foraging time and digestive capacity. The LPM estimated the overall diet of kudu fairly accurately and distinguished between habitats, but the animals accepted a wider dietary range than predicted optimal by the CM. This primarily results because neither foraging time nor digestive capacity formed an effective constraint. Where more constraints, including thermal tolerance, were included, predictions still suggested no consistent ranking of feed types. As a result, Owen-Smith (1993) concluded that, whereas dynamic programme models offer a solution to predicting and understanding complex foraging behaviour, the challenge is clearly formidable. With reference to the gamma function of Pienaar & Roux (1989), it is evident that digestion and passage kinetics offer but one solution to a series of functions that need to be solved before we will be able to understand and predict foraging behaviour.

Apart from forages, intake prediction is important in feedlots because feed costs may account for 70% or more of total costs. Logically, it could be expected that an increase in intake would increase ADG and the feed/gain ratio should

benefit. Therefore, the question could be posed whether it would be profitable to manage for increased intake. Unfortunately, the relationship between feed intake and ADG or the feed/gain ratio in the feedlot is generally poor (Meissner *et al.*, 1986; 1994; 1995). The low correlation between intake and ADG partially results because a positive relationship exists below but not above an ADG of 1.5 kg/day (Meissner *et al.*, 1995). Faster growing steers (ADG of > 1.8 kg/day) often do not gain at their high rate because of high intake. High intakes may increase maintenance requirements and fat deposition to the detriment of efficiency (Slabbert *et al.*, 1992). Therefore, it is not surprising to see results where efficiency was equal to that of *ad libitum* or even benefitted if intakes were slightly restricted (Meissner & Roux, 1984; Slabbert *et al.*, 1992). The results suggest, firstly, that energy requirements of fast-growing feedlot steers are lower than predicted from NRC or ARC equations (Table 1) and, secondly, that feedlot managers may not benefit by striving for higher intakes.

The concept of high maintenance requirements and fat deposition with high intakes on concentrate diets also are indirectly illustrated by two South African studies on compensatory growth. Both the studies of Greeff *et al.* (1986) and Marais and his co-workers (1991) showed progressively improved efficiencies with realimentation after increasing severity of restriction. With increased restriction, maintenance requirements are reduced and less fat is produced, advantages which are 'carried over' for a period of time during realimentation.

### Pasture utilization

Utilization of veld has largely concentrated on carrying capacity and management studies. From a plant production point of view, studies have included the effect of defoliation

on regrowth and total dry matter (DM) yield. From an animal nutrition point of view, few results have been documented in the past decade.

Selection patterns of oesophageally fistulated animals have resulted in the identification of preferred plant species and demonstration of major differences in quality between animal-selected and hand-clipped samples. Oesophageal collection techniques have improved to the extent of using remote-controlled cannulae to determine selection patterns without disturbing the grazing behaviour of the animal (Raats & Clarke, 1991).

Considering the quality of herbage selected by non-lactating cattle and sheep, reasonable levels of animal production may be expected, even during winter. Previous data, however, showed that herbage intake by Merino wethers on veld at Glen was barely sufficient to meet maintenance requirements during winter, even though the CP and DOM content of the diet appeared satisfactory (Engels & Malan, 1978; De Waal, 1986). Veld samples, incubated *in situ* (De Waal, 1986), showed a considerably slower fermentation in winter than in summer (26 vs. 49% DM disappeared/24 h). The slow fermentation, in conjunction with selective grazing behaviour resulting in much walking, is responsible for a reduction in intake (De Waal, 1986) and therefore production.

Seasonal changes of veld quality also have been measured in the Natal Sourveld (O'Reagain & Mentis, 1988) where *Hyparrhenia*, *Eragrostis* and *Sporobolus* grass species dominate. Average CP selected was highest (10%) during spring and declined towards summer and autumn. *In vitro* digestibility increased from spring to summer but declined sharply going into autumn and winter. Both dietary CP and digestibility were positively related to percentage leaf selected but negatively to percentage dead material.

Another interesting facet of the O'Reagain & Mentis (1988) study was the decline in CP concentration in selected pasture material as the length of stay in a camp increased from day 1 to day 14. As expected, CP content was the highest on day 1 and lowest on day 14. The decline, however, was greatest between days 1 and 7 with a small and insignificant decline between days 7 and 14. Considering the protein requirements of beef steers at maintenance, it appears that on average, dietary CP levels in the Natal sourveld should be sufficient for production until late autumn. However, the decline in dietary CP from day 1 to 14 does not support this assumption. It is evident that from summer onwards, cattle in a rotational grazing system in this area experience lengthening periods of sub-maintenance dietary CP and, in winter, maintenance requirements are not satisfied on even the first day of occupation. Consequently, unsupplemented cattle will be protein deficient and will have difficulty maintaining body mass from at least early autumn. Results like these would enable better strategic supplementation of veld.

Another interesting aspect of veld utilization is the difference observed with different cattle breeds. Ngunis have been found to maintain condition during winter and they maintain higher blood urea levels than Bonsmaras or Herefords. In a further study, Linington and Osler (1992) determined whether blood metabolites change breed-specific as the veld deteriorates. In mid-winter, blood urea was higher in Nguni than in Bonsmara or Brahman cows and glucose was lower in spring.

**Table 1(a)** Estimates of ME intake (MJ/day) of feedlot steers at different body masses and ADG

Body mass (kg)	ADG (kg/day)			
	1.0	1.5	2.0	2.5
200	77	87	87	-
300	91	103	103	97
400	108	122	122	-

**Table 1(b)** ME requirements of medium frame steers calculated for ADG between 1.0 and 2.0 kg/day (average of ARC, 1984 and NRC, 1984)

Body mass (kg)	ADG (kg/day)		
	1.0	1.5	2.0
200	52	71	100(8.3*)
300	69	94	129(10.8)
400	85	114	137(13.1)

\* DM intake (kg/day) required if ME content of diet is 12 MJ/kg (Meissner *et al.*, 1995)

Further investigations are in progress to establish whether the ability of Ngunis to adapt to poor nutritive conditions is due to selective grazing or some physiological adaptive mechanism. Behaviour studies indicated that Simmentaler bulls walked less than Afrikaner or Nguni bulls and tended to consume less of the unpalatable grasses during winter (Osler, unpublished).

Animal production results on cultivated pasture have increased during the past ten years to complement existing data, which largely concentrated on the *in vitro* digestibility and CP content of pasture samples as indicators of energy and/or protein value. More studies also paid attention to anti-nutritional factors that may limit production.

Nitrogen content in forages depends on fertilizer regime and form of fertilizer applied. High levels of N fertilizer applied on grass pastures give rise to concern about the composition of CP subsequently formed in the plant and its effect on plant composition and animal production. For example, high N application on kikuyu (*Pennisetum clandestinum*) decreased the bio-availability of Ca, since 95% of the Ca present was in the form of calcium oxalate which would be unavailable to ruminants (Marais, 1990). According to Pienaar *et al.* (1993), oxalates, high soluble N and nitrate contents are higher in young, actively growing kikuyu than in older material. These quality factors and high fibre content may limit voluntary intake of sheep grazing kikuyu.

Increased N fertilization increased total N and nitrate-N ( $\text{NO}_3\text{-N}$ ) levels in ryegrass herbage (De Villiers & Van Rysen, 1991), whereas the level of non-structural carbohydrate and DM content of the herbage decreased. Similarly, in *Panicum maximum* cv Gatton, Van Niekerk *et al.* (1993) found that an increase in N application from 0 to 150 kg N/ha increased the N content by 38%, whereas the  $\text{NO}_3\text{-N}$  concentration doubled to concentrations which could become critical. Water-soluble carbohydrate concentrations decreased with increasing N fertilizer levels. This drop may be to the detriment of efficient N utilization in the rumen, cause a slower digestion rate and thus a decline in intake at the highest N fertilization level (Van Niekerk *et al.*, 1993). The slower digestion may also result because of nitrate accumulation (Marais *et al.*, 1988) as discussed below.

On kikuyu containing high levels of nitrate, nitrite which accumulated during the reduction of nitrate to ammonia reduced digestibility *in vitro* (Marais *et al.*, 1988). Nitrite reduced the microbial population with a concomitant reduction in cellulase and xylanase activity of the digesta. The growth of four major rumen cellulolytic bacteria was depressed severely by nitrite, whereas some other rumen bacteria were relatively insensitive to nitrite. Owing to the sensitivity of some rumen bacteria to nitrite, digestibility and therefore animal performance could be affected even before clinical symptoms of nitrite toxicity become apparent.

Theoretically, cultivated pastures should have a high nutritive value with N levels ranging between 2.6 and 4.2% in low, medium and high N fertilizer applications; however, generally the growth rate of lambs is poor. This can be attributed to low DM content of the pastures (Meissner *et al.*, 1992c) and thus an inability of the animal to consume sufficient material. It can be also ascribed to negative effects of the form of nitrogen (e.g. nitrate) on digestibility. To counteract these problems, a

plant breeding programme is under way at Cedara to select ryegrass lines with high DM and total non-structural carbohydrate (TNC) content. Total non-structural carbohydrates in forages improve the palatability and intake as well as growth characteristics of the grass (Marais *et al.*, 1995). It is, however, important that selection for a specific trait does not negatively influence other desirable traits. According to Marais and his co-workers (1995), the selection for increased DM and TNC content in *Lolium multiflorum* did not adversely affect cell wall composition and digestibility.

Inclusion of legumes into grass pastures (e.g. lucerne into *Eragrostis curvula* or clovers into ryegrass) can save greatly on fertilizer costs and enhance animal production. Volatile fatty acid (VFA) concentrations in the rumen generally are higher in animals grazing legumes than when grazing grass (Kriek, 1993; Paulsmeier & Meyer, 1993). This could be responsible for higher microbial protein production which is reflected in higher post-ruminal non-ammonia N (NAN) flow and absorption on lucerne (Kriek, 1993), and on ryegrass/Persian clover intercrop (Paulsmeier & Meyer, 1993). In addition, a favourable protein:energy intake may be responsible for higher lamb growth rates on legumes or grass/legume combinations.

The use of leguminous shrubs recently has received attention through supplementation of hay with tagasaste (*Chamaecytisus palmensis*) (Van Niekerk *et al.*, 1995) and the supplementary grazing of beef steers on *Leucaena leucocephala* (Zacharias *et al.*, 1991). Tagasaste supplemented to sheep fed three hay qualities increased DOM and intake of low and medium quality hays. These advantages could be attributed to enhanced rumen fermentation which resulted in higher VFA and ammonia ( $\text{NH}_3$ ) concentrations in the rumen. A higher NAN flow to the abomasum might have been responsible for the higher OM intake of the groups supplemented with tagasaste (Van Niekerk *et al.*, 1995). In Natal, a grazing study with beef steers was conducted to compare the performance of beef steers grazing kikuyu foggage and given limited access to *Leucaena leucocephala* (3 h/day) with steers grazing only kikuyu foggage during autumn and early winter (Zacharias *et al.*, 1991). For three seasons the animals grazing *Leucaena* performed significantly better and gained c. 25 kg per animal more over 90 days than those on kikuyu alone.

The risk of bloat on irrigated lucerne and clover (*Trifolium* spp.) largely prevents producers from including these legumes in their fodder flow programme. Specific gravity measurements of rumen contents of sheep grazing ryegrass, clover or the intercrop of ryegrass and clover showed a significantly higher presence of foam in the rumen on pure clover than on ryegrass or the mixture (Paulsmeier & Meyer, 1993). The bloat risk with cattle on legumes generally is higher. An experiment with Bonsmara steers on ryegrass and/or Persian clover showed severe incidences of bloat with the pure clover treatment in comparison to ryegrass or the intercrop.

A screening procedure for bloat risk is being developed for lucerne cultivars based on qualitative forage aspects including protein solubility, foam formation, chlorophyll release and plant-anatomical parameters. Foam formation measured *in vitro* on these lucerne cultivars could have led to decreased DM intake, but it was not related to N solubility (Meissner *et al.*, 1994). Generally, to develop the screening test, the varia-

tion found within a species was too small (Meissner *et al.*, 1994). Currently a broader range of clovers and non-bloating legumes, such as *Lotus corniculatus*, are being included in the study.

Environmental factors play a major role in the development of foam *in vitro*. Maximum temperature the day prior to measurement and wind speed were responsible for 75% of the variation in foam produced (Paulsmeier *et al.*, 1994). Cell wall thickness and ease of rupture with release of chlorophyll from the cell may play a role, although leaves incubated in rumen fluid *in vitro* were shown to have no remaining cell content even when the cell wall was not ruptured (Robbertse, unpublished).

### Protein digestion and metabolism

Ideal dairy cow diets should combine a balanced source of undegraded protein (UDP) with a source of non-protein N (NPN) or degradable protein (RDP) to supply the required ammonia N for optimal rumen microbial growth (Erasmus *et al.*, 1988). Inclusion of NPN in the form of urea has been met with scepticism by many farmers, yet results of Erasmus and his co-workers (1986) with 1 to 1.6% urea in complete diets containing 16% CP have been promising. The proviso is that the urea is mixed with the correct level of UDP, that is, a level of UDP exceeding 40% of CP for high producers. Undegraded protein sources preferably should include fish meal, otherwise limiting amino acids may augment the inability to manufacture milk protein. From their work, at least 1% urea in the diet can be recommended.

The quest for good UDP sources has led to the development of protein degradation databases. Following upon the initial work of Cronjé (1983) with *in situ* nylon bag studies, protein sources and other feedstuffs have been categorized for dairy cattle (Erasmus *et al.*, 1988; 1990a; 1990b) and feedlot cattle diets (Meissner *et al.*, 1992a). Surprisingly, values corresponded well at similar fractional outflow rates, despite vastly different rumen fermentation media (Table 2). In a study to investigate the effect of rumen fermentation medium, Cronjé (1992c) designed an experiment with three widely different dietary energy concentrations and imposed three NH<sub>3</sub> con-

**Table 2** Protein degradability values of feedstuffs with the fermentation substrate dairy cattle diets<sup>a</sup> or feedlot cattle diets<sup>b</sup>

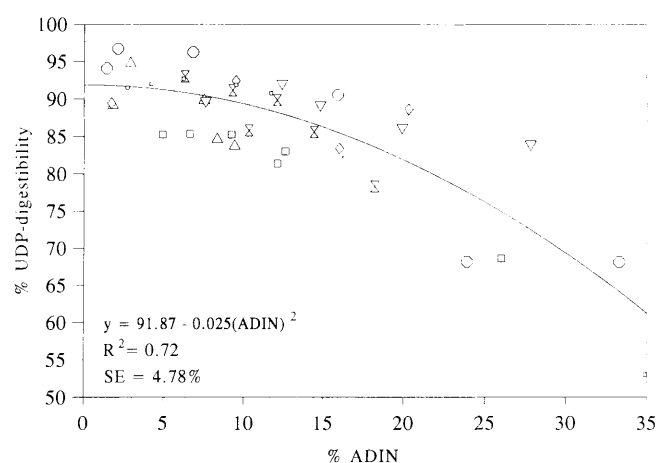
Feedstuffs	Ruminal fractional outflow rate		
	0.05 <sup>a</sup>	0.04 <sup>b</sup>	0.06 <sup>b</sup>
Fish meal (local)	40.3	41.4	39.2
Maize gluten 20	83.3	86.3	84.3
Maize gluten 60	31.0	31.9	29.8
Hominy Chop	73	70.6	66.6
Maize	63	70.4	66.6
Sorghum	60	61.2	54.5
Wheat bran	87	89.9	87.3

<sup>a</sup> Erasmus *et al.*, 1988; 1990a

<sup>b</sup> Meissner *et al.*, 1992a

centrations on each of these. Ammonia concentration did not affect degradation. However, dietary energy concentration had a differential effect on the degradative potential of the feedstuffs tested. He concluded that expression of the basal diet effect appears to be governed by several factors which include the potential rate and extent of degradation of the test feedstuff and the prevailing rate of flow of particles from the rumen.

To increase the UDP fraction of highly degradable protein sources, both microwave and drum-roasting have been used. Smith & Vosloo (1994a) decreased protein degradation of whole cottonseed from 54 to 30% at a fractional outflow rate of 0.08/h. Treatment was effected in a microwave oven operated at 155 °C for 20 min, apparently without affecting the absorption of lysine and methionine in sheep fed diets containing the treated whole cottonseed. Schroeder (1994) drum-roasted the main plant protein sources and found the optimal treatment exposure 150 °C for 30 min. This exposure time apparently maximizes amino acid availability in the small intestine of the dairy cow. In the Schroeder study, the acid detergent insoluble nitrogen (ADIN) content of the treated protein sources showed a high correlation with the digestibility of the UDP fraction (Figure 3). Heat treatment was not sufficiently below 12 to 15% ADIN, but UDP digestibility decreased markedly when ADIN exceeded this level.



**Figure 3** Relationship between acid detergent insoluble nitrogen (ADIN) as a percentage of total N and UDP digestibility of various heat-processed plant protein sources (Schroeder, 1994).

Tannins in sainfoin and sheep's burnet also depress rumen degradation of plant protein (Meissner *et al.*, 1993), but they increase NAN passage to the small intestine. Meissner *et al.* (1993) showed that NAN passage to the small intestine improved from 75% of N intake for temperate grasses plus lucerne and triticale, to 97% for tropical forages and to 112% for tannin-containing forages and artificially dried grass. The advantage of the tannin forages, however, is partially offset by a lower intestinal digestibility ( $64 \pm 6\%$ ) of the protein compared to other forages ( $76 \pm 2\%$ ).

Depending upon milk production, diets for dairy cows should contain between 40 and 50% of dietary protein in the form of UDP (Erasmus *et al.*, 1986). Levels of 35 to 40% appear optimal in feedlot diets (Meissner *et al.*, 1992b). The latter researchers also showed substantial cost savings when

the total CP in the feedlot diet was decreased progressively from 14 to 10% of DM towards the end of the fattening period, compared to maintaining a constant level of 12% of DM. Meissner & Du Plessis (1992), in conjunction with these studies, indicated that the advantage of the 35 to 40% UDP diets can be explained by an increase in amino acids reaching the duodenum and more starch digestion in the small intestine. They concluded that the amino acid profile at the duodenum of the feedlot steer is unlikely to change significantly, even at 35 to 40% UDP in the CP, because of the overwhelming effect of the microbial amino acid composition. This contrasts with the dairy cow where, because of high intake, substantial alterations are possible (Erasmus *et al.*, 1994b) (Table 3).

Contradictory results obtained with the RDP-UDP system led to the realization that protein sources with low ruminal N degradation, that is, high UDP content, also may have low and variable availability of protein in the small intestine. This prompted Erasmus *et al.* (1994a) to compare the chemical composition and UDP digestibility of unfermented feedstuffs isolated from polyester bags or from duodenal digesta. They found a good correlation. They also showed that the factor for UDP digestibility used in some protein evaluation systems was too high. This demonstrated a need for a system to provide specific UDP digestibilities for different feedstuffs, or at least groups of feedstuffs.

The change in amino acid composition, which may occur during rumen incubation of proteins, and the subsequent availability of these amino acids to the host animal were investigated by Erasmus *et al.* (1994a). They found that the absorbable amino acid profile of UDP measured by the mobile bag technique closely reflected the amino acid profiles of rumen incubated residues. This suggests that in dairy cows rumen degradation has a greater influence on the post-ruminal provision of specific absorbable amino acids than post-ruminal digestion.

Undegraded protein sources are expensive. Therefore, more emphasis should be put into increasing microbial protein production in the rumen (RMP) and to optimize microbial growth efficiency (MOEFF). These issues have been recently addressed at Irene.

Kernick (1991) did a series of experiments to determine whether supplying peptide-N instead of NPN would improve MOEFF and hence RMP production. Results showed that the

response to peptide supplementation was affected by microbial growth rate, level of N supplied and the specific substrate fermented. With both straw and starch as substrates, the response at lower dilution rates, that is, slow specific growth rates, was small whereas at higher dilution rates MOEFF and RMP production increased. If N was limiting, as with maize straw, there was no significant response to peptide supplementation whereas the response was positive when N was adequate. Kernick (1991) concluded that the lack of response to peptide supplementation on ryegrass was due to sufficient protein to meet the N and peptide requirements of the bacterial population.

The results of Kernick (1991) demonstrate stimulatory effects of peptides over a range of microbial populations. The response apparently is not only due to the supply of branched chain fatty acids, because MOEFF increased with peptide supplementation on maize straw and starch, even though branched chain fatty acids were adequate. A negative observation in these experiments was that increased protein synthesis was offset partially by an increased deamination of the additional amino acids supplied by the peptides, resulting in a decreased overall efficiency of protein utilization. Thus, whereas these experiments demonstrated beneficial effects to RMP and MOEFF with peptide supplementation, practical guidelines for supplementation are not yet possible.

In another series of experiments, Henning *et al.* (1991; 1993) investigated whether RMP production can be increased if energy and N release in the rumen are synchronized more closely. Previous studies world-wide have been inconclusive. Henning and co-workers in both *in vitro* and *in vivo* studies supplied the same daily amount of urea-casein as readily available N, and glucose or maltose as readily available energy, but according to different patterns, that is, pulse dosed or continuously infused. Both *in vitro* and *in vivo* studies showed no advantage to MOEFF or RMP production with improved synchronization. What did transpire, however, was that in the *in vivo* study the constantly infused energy was utilized 17% more efficiently for microbial growth than the same amount of energy given as pulse dose. This coincided with lower rumen pH for energy pulse dose treatments. Henning *et al.* (1993) consequently concluded that if the rumen energy supply to the rumen was more gradual, MOEFF should improve. Therefore, diets should be formulated to promote uniform fermentation.

With this in mind, Henning (1991) determined fermentation patterns of energy sources by measuring the change in gas production rate over time. The incubations gave distinct and repeatable fermentation patterns for the various energy sources and also suggested that feedstuffs can be combined to obtain more even fermentation patterns. Recently, Henning and co-workers (1995) demonstrated a curvilinear relationship between fermentation rate and MOEFF *in vivo*, indicating an optimum fermentation rate to attain maximum MOEFF. This is exciting, because if fermentation rates of mixtures of energy sources can be predicted with confidence, it should also be possible to predict maximum MOEFF.

Evidence of decreased fitness and adaptability to harsh conditions (Wentzel *et al.*, 1979; Fourie *et al.*, 1986) in high wool and mohair producers, as well as abortions in Angora goats, prompted the question whether selection for high fibre pro-

**Table 3** Effect of protein supplement in dairy cattle diets on selected amino acids in duodenal digesta

Amino acid (g/100g essential AA)	Protein supplement			
	Blood meal	Maize gluten 60	Blood + gluten 60	Sunflower oilcake
Histidine	6.59 <sup>b</sup>	4.57 <sup>a</sup>	5.69 <sup>ab</sup>	4.49 <sup>a</sup>
Isoleucine	7.45 <sup>a</sup>	9.77 <sup>bc</sup>	8.32 <sup>ab</sup>	10.4 <sup>c</sup>
Leucine	21.7 <sup>a</sup>	27.0 <sup>b</sup>	25.0 <sup>ab</sup>	22.5 <sup>ab</sup>
Lysine	14.8 <sup>c</sup>	10.7 <sup>a</sup>	12.4 <sup>ab</sup>	13.2 <sup>bc</sup>
Methionine	4.71 <sup>a</sup>	5.81 <sup>b</sup>	5.19 <sup>a</sup>	5.78 <sup>b</sup>

<sup>a,b,c</sup> Means in the same row with different superscripts differ ( $p \leq 0.05$ ) (Erasmus *et al.*, 1994b)

duction actually increases the efficiency of N utilization, or whether the selection merely favours partitioning of nutrients (N, glucose, etc.) to fibre production. A further question is whether this occurs to the detriment of other essential body functions. Cronjé at Irene addressed these questions in a series of experiments. Using the Angora and Boer goat as models of high vs. low fibre producers respectively, Cronjé (1992a) showed that in comparison to the Boer goat, Angoras retained 33% more N, partitioned 62% vs. only 48% of urea N flux to recycling, and excreted only 38% vs. 52% of that flux. He suggested that higher N retention and urea recycling in the Angora could be an adaptive mechanism developed to satisfy the demand for amino acids via selection for hair production. As a result of the high demand of amino acids for hair production, amino acids are apparently partitioned away from gluconeogenesis, even to the extent that the Angora goat may be unable to mobilize sufficient endogenous protein reserves rapidly enough during times of stress (Cronjé, 1992b). In a subsequent experiment with high and low wool producers, Cronjé & Smuts (1994) showed that higher wool production was achieved by partitioning a greater percentage of N consumed to wool, and not because N and energy retention was increased. These results confirm the findings on the Angora goat and, because of decreased ability to mobilize amino acids for gluconeogenesis when suddenly required, excessive selection for fibre production alone must be guarded against.

#### Supplementation with carbohydrate, protein and fat

Supplementation of forages with grain (carbohydrate) is intended to increase overall energy intake and availability to the animal. Often, however, cell wall digestibility and intake of the forage are depressed, with the result that digestible energy intake is increased only marginally or not at all. Local results show depressions in sheep intake of straw supplemented with 200 g whole maize (Cronjé & Weites, 1990), of *Eragrostis curvula* supplemented with pulse doses of glucose twice per day in either the rumen or abomasum or starch in the rumen (Meissner & Todtenhöfer, 1989), of lucerne and maize cob leaves but not straw when starch was infused over 12 to 24 h into the rumen (Pienaar *et al.*, 1990) (Table 4), and of early season (immature) ryegrass but not mid-season (mature) ryegrass when 200 g maize meal was supplemented twice daily through the rumen cannula (Meissner *et al.*, 1991). Both Pienaar *et al.* (1990) and Meissner *et al.* (1991) showed that a decrease in rumen pH was not responsible for the depression in fibre digestion, in contrast to general belief (Henning *et al.*, 1980; Mould *et al.*, 1983). In subsequent experiments, Meissner and his co-workers (1991) found that the depression of cell wall digestibility and intake of higher quality forages was more severe than for lower quality forages, a result also borne out by the difference between straw vs. lucerne and maize cob leaves in the study of Pienaar *et al.* (1990). As a generalization, Meissner *et al.* (1991) showed that intake depressions are likely to occur when between 150 and 300 g maize meal per day are supplemented to sheep consuming forages with less than 55 to 60% NDF (cell wall), whereas intake depressions are of less concern with forages containing more than 55 to 60% NDF.

**Table 4** Voluntary OM intake (g/day) of roughages and substitution (g/g) during starch infusion (600 g/sheep/day)

Treatment	Roughage		
	Lucerne	Maize cob leaves	Straw
Zero starch infusion	1293 <sup>b</sup>	1160 <sup>b</sup>	622
Starch infused over 12 h	1025 <sup>a</sup> (-0.45*)	655 <sup>a</sup> (-0.84**)	689 (0.11 NS)
Starch infused over 24 h	1018 <sup>a</sup> (-0.46*)	1093 <sup>b</sup> (-0.11 NS)	593 (-0.05 NS)

<sup>a,b</sup> Means in the same column with different superscripts differ ( $p \leq 0.05$ )

\*\*, \*\* Substitution rate significant at  $p = 0.05$  and  $p = 0.01$ , respectively;

NS = not significant

(Pienaar *et al.*, 1990)

Pienaar *et al.* (1990) explained the depression in forage fibre digestion and intake by starch as being primarily due to a reduced rate of fibre digestion. This supports the theory of Varga (1987) who showed that the overall rate is slower because the attachment of cellulolytic bacteria to fibrous material is delayed. Other factors advanced by Hoover (1986) as being responsible for the decreased fibre digestion include insufficient nutrients, especially iso-acids, to promote fibre digestion. This may explain partially why cell wall digestion and ryegrass intake was not reduced when 100 g maize meal in the supplements of Meissner *et al.* (1991) was replaced by 100 g fish meal per day and why the substitution rate of barley supplementation of an oaten hay/lucerne mixture was reduced when part of the barley was replaced by lupins or fish meal (Coetzee *et al.*, 1995).

A further advantage of fish meal and other high UDP sources is promotion of amino acid uptake from the small intestine, which is known to enhance forage intake (Egan, 1965; Leng, 1984). This was demonstrated further by Cronjé & Weites (1990) when, in contrast to whole maize supplementation, cottonseed oilcake meal increased straw intake and in the study of Meissner & Todtenhöfer (1989) when casein was pulse-dosed into the abomasum instead of glucose or starch. Of interest to protein utilization in this regard, are the results of Cronjé *et al.* (1992a; 1992b) who showed that, with protein supplementation of wheat straw diets to lambs, the flux, oxidation and incorporation of lysine, leucine and methionine into body protein were increased. Despite the fact that the supplements included large proportions of UDP, including meat meal, it was apparent that methionine was limiting for protein synthesis in lambs, even with protein supplementation at 200 g/day.

Including fat in diets containing substantial amounts of roughage may decrease fibre digestion. The depression is greater with polyunsaturated fats, as occur in oils, than with saturated fats (Macleod & Buchanan-Smith, 1972). Smith & Vosloo (1990) reported depressions of fibre and other constituents, apart from ether extract, when up to 20% whole cottonseed was included in the diets. The depressions were relieved partly when lanolin was included as emulsifier. Despite the depressions in digestibility, N retention in sheep was improved with whole cottonseed inclusion, possibly because of improved microbial protein synthesis (Smith & Vosloo, 1990) or possibly because of more UDP with whole cottonseed. Subsequently, Smith & Vosloo (1994a) showed that the degradation of whole cottonseed in the rumen can be



decreased by heat treatment. This should be advantageous to the dairy cow, both by increasing UDP and enhanced inertia of fat in the rumen.

The studies of Smith & Vosloo (1990; 1994a) were followed up by studies with whole cottonseed in dairy cow diets (Smith & Vosloo, 1994b). The results showed advantages in milk and milk fat yield for diets containing whole cottonseed, whole cottonseed with lanolin and heat-treated whole cottonseed. The heat-treated whole cottonseed treatment tended to give the best results. Milk protein was not affected, but milk fatty acid composition was altered in relation to the degree of saturation of the fatty acids. Including up to 25% whole cottonseed in complete dairy cow diets should benefit milk production and fat yield. Since including 39% whole cottonseed in diets of dairy bulls did not affect sperm production and viability, the free gossypol at these inclusion levels probably was detoxified effectively in the rumen (Smith *et al.*, 1991).

Fat inclusion in the form of tallow to increase milk production (Smith *et al.*, 1993) and in the form of the rumen inert Ca soaps also may have potential, in the latter case as roughage supplement (Cronjé & Oberholzer, 1990). Rumen active fat supplements, in the form of cotton acid oil and fish soapstock, killed all rumen protozoa, reduced intake and caused rumen stasis. Calcium soaps in contrast, had no effect on these variables, and doubled lamb growth.

### Mineral nutrition

Mineral nutrition has received limited attention during the past decade. Reports dealt with Mn, S, Cu, Zn and Se supplementation to cattle, sheep and Angora goats and the mineral content of poultry manure. Noteworthy is the finding that Se (as selenomethionine) degradation in the rumen follows the same trend as that of the protein of feedstuffs, suggesting that Se availability to the rumen microbes and the animal is determined partially by ruminal degradation (Van Ryssen *et al.*, 1995).

After the extensive studies of Read *et al.* (1986) on P deficiencies and supplementation at Glen and Armoedsvlakte, little else has come forth on this important, but still much-debated issue. Predicting P status of grazing animals and P deficiencies apparently remains an unrealizable goal. Using faecal analysis for this purpose has been met with scepticism,

but recently Grant *et al.* (1995) showed some useful results in non-lactating game species. They showed that faecal P and N could effectively distinguish between landscapes, season, and grazing, browsing and selective feeding animal species. They showed also that P and N concentrations in the fodder were predicted better from a combination of P and N concentration in the faeces rather than from either concentration alone. This may be expected because of the close association of N and P at the tissue level. In a calibration study, Wrench (unpublished) confirmed the interaction between faecal P and N to predict feed N but not feed P (Table 5). She also showed that the prediction equation for feed P may apply across grazing ruminant species.

Some concern has been directed at high intakes of salt (NaCl) through supplements. De Waal *et al.* (1989a, 1989b) showed decreased production of young sheep following excessive intake of salt through licks, whereas Spangenberg *et al.* (1995) reported aphosphorosis in cows supplemented with P owing to high salt intake. The mechanisms may be related to (a) interference with normal  $N^+/K^+$  transport across membranes resulting in increased (maintenance) energy expenditure, (b) sensitivity of neuronal receptors to dissolved solutes (NaCl) and specific ions such as  $Na^+$  in the liver (Lautt, 1980), and (c) depressed intake by sheep due to high NaCl-induced ruminal osmotic loads (Ternouth & Beattie, 1971; Grovum, 1994). The evidence points to the fact that the use of salt to control lick intake is questionable and should receive urgent attention, especially where water intake may be limited and/or water quality is poor. Maybe research again should address alternative approaches such as lick blocks and water-based licks.

### Feed additives

Ionophores as feed additives have proved to be effective and versatile. Their effects in feedlot diets are well documented. Recently, Casey and his co-workers (1994) reported that alternating monensin-Na and salinomycin may be more effective in improving feed efficiency than using either alone. This suggests that the rumen microbes or animals may adapt to a particular ionophore after a period of time. Monensin-Na also has been used in pasture supplements where it has proved to control coccidiosis in lambs (B.D.H. van Niekerk, pers.

**Table 5** Prediction equations of feed P and CP% from faecal analyses in impala and other game species. Animals were non-pregnant and non-lactating

Species	Y	X <sub>1</sub>	X <sub>2</sub>	Intercept/ Constant	Regression coefficient 1	Regression coefficient 2	R <sup>2</sup>	SE of estimate
Impala	Feed P (%)	Faecal P (%)	–	0.019 ± 0.025 <sup>b</sup>	0.369 ± 0.042	–	0.73	0.037
All species <sup>a</sup>	Feed P (%)	Faecal P (%)	–	0.028 ± 0.009 <sup>b</sup>	0.336 ± 0.023	–	0.51	0.056
Impala	Feed CP (%)	Faecal CP (%)	–	–5.79 ± 1.96	1.37 ± 0.17	–	0.70	1.45
Impala	Feed CP (%)	Faecal CP (%)	Faecal P (%)	–4.44 ± 1.66	0.91 ± 0.19	6.80 ± 1.81	0.79	1.19
All species	Feed CP (%)	Faecal CP (%)	–	1.99 ± 0.45	0.640 ± 0.057	–	0.40	2.05
All species	Feed CP (%)	Faecal CP (%)	Faecal P (%)	1.12 ± 0.36	0.425 ± 0.067	5.44 ± 1.10	0.67	1.47

<sup>a</sup> Impala (no browse), blesbok and blue wildebeest

<sup>b</sup> If the intercept is computed to be zero at x(0), y(0) the regression coefficient (slope) becomes 0.400 for impala and 0.403 for all species, indicating that feed P is 40% of faecal P within the range of experimental values, that is, 0.13 to 0.87% faecal P. (Unpublished data of J.M. Wrench).

comm.) and decreased milk urea in cows grazing kikuyu with high degradable N content (Van der Merwe *et al.*, 1995). With the advent of a monensin rumen bolus which slowly releases its contents, legume bloat also may be controlled (Henning, 1994).

A relatively new development is that ionophores are being tested in dairy cow rations. During early lactation, many high producing cows in negative energy balance develop elevated ketone bodies which may affect production and health adversely. Because the ionophores increase glucose precursors in the form of propionate (Deacon & Meissner, unpublished), the theory is that ionophores can reduce the incidence of subclinical ketosis. This has been confirmed by Erasmus *et al.* (1993) for monensin-Na (Table 6). Their results, together with those of Deacon & Meissner (unpublished), indicate that milk production is increased 1 to 2 l/day with 15 mg monensin-Na per kg DM, with no major differences in milk composition.

Yeast culture is a further additive of benefit to the dairy cow. Erasmus *et al.* (1992) showed that DM intake, CP and ADF digestibilities were higher whereas peak lactic acid concentrations in the rumen were lower. In addition, both milk production and NAN flow to the duodenum tended to be higher in yeast-supplemented cows. The duodenal amino acid profile, including higher methionine levels, also was more favourable, suggesting that yeast culture may change the microbial population. Supplementation appears optimal at 10 g/cow/day.

#### Treatments to improve nutritive value

Ammoniation of low quality roughages with or without NaOH treatment has proved to increase digestibility, particularly of cell wall constituents. Brand and his co-workers at Elsenburg have investigated various treatment options: anhydrous ammonia by the stack and oven methods, urea treatment and urea treatment plus NaOH. They also have included moisture levels, level of treatment and time exposed as variables in an effort to optimize treatment. Brand & Cloete (1988) showed that digestibility and intake with oven-ammoniated straw were higher than urea and anhydrous ammonia treatment in the stack. A large proportion of the added N was accounted for as ADIN, suggesting that the available N for rumen fermentation probably still is limiting. Brand *et al.* (1989a) found better hydrolysis of urea to ammonia with moisture levels of 400 g/kg straw than 250 g/kg straw; treatment efficiency improved with time exposed. The urea level should be at least 50 g/kg straw to be effective. In a subsequent trial (Brand *et al.*, 1989b), a combination of urea and NaOH was compared with urea or NaOH treatment alone. The 400 g/kg straw moisture level was confirmed as being optimal. Addition of NaOH to urea accelerated hydrolysis but also reduced urea degradation. The IVDOM of the combined treatment was substantially higher than the IVDOM of the urea and NaOH treatments, which suggests synergism.

Following upon their studies of optimal treatment conditions, Brand and his co-workers investigated the replacement value of treated straw in hay-based diets for lambs, wethers, and ewes in late pregnancy and lactation. In diets of growing lambs, lucerne hay was progressively substituted with urea-ammoniated straw (Brand *et al.*, 1990). Feed intake, ADG, fat

**Table 6** Concentrations of ketone bodies in blood and milk of dairy cows one to six weeks postpartum, receiving either 0, 10 or 20 mg/kg DM monensin-Na

Ketone body concentration (mg/100 ml)	Treatment				SE <sub>m</sub>
	0 + BST*	0	10	20	
Blood $\beta$ -OH-butyrate	5.61	5.42	4.27	4.75	0.50
Blood acetoacetate	0.76 <sup>a</sup>	0.57 <sup>ab</sup>	0.45 <sup>b</sup>	0.44 <sup>b</sup>	0.08
Milk acetone	0.95 <sup>a</sup>	0.63 <sup>ab</sup>	0.26 <sup>b</sup>	0.27 <sup>b</sup>	0.15

\* BST (Bovine somatotropin) was injected as from 12 weeks postpartum.

<sup>a,b</sup> Figures in the same row with different superscripts differ ( $p \leq 0.05$ ) (Erasmus *et al.*, 1993)

deposition and feed conversion efficiency could not be maintained as levels of urea-ammoniated straws increased. Higher cell wall content in straw-based than in lucerne-based diets increased bulkiness which was responsible primarily for lower feed intake. In a similar lucerne substitution experiment with wethers (Brand *et al.*, 1992), intake declined with progressive increases in untreated, urea-enriched and urea-ammoniated wheat straw, but the quadratic response indicated a positive associative effect between straw and lucerne hay. Nitrogen retention corrected for N intake was not significantly different between the lucerne and straw-based diets, but VFAs were higher on the lucerne diets. Ammoniation in comparison with untreated straw improved digestibility of all constituents and feed intake, and decreased rumen retention time. If fish meal was used to supplement urea-supplemented or urea-ammoniated wheat straw, feed intake increased by 13%. Maize meal supplementation did not alter straw intake (Brand *et al.*, 1991). This indicates a deficiency in amino acid absorption from the small intestine on ammoniated straws which was confirmed by lower concentration of milk protein from ammoniated straw-based diets than from lucerne-based diets (d'Hangest d'Yvoi & Botha, 1995). Both fish meal and maize meal supplementation and their combination in the Brand *et al.* (1991) study improved digestibility of OM, but the maize meal diets tended to depress the digestibility of cell wall. This could be expected from our earlier discussion of the effects of carbohydrate on fiber digestion. Nitrogen balance generally was improved in wethers receiving diets containing urea-ammoniated wheat straw and fish meal alone or combined with maize meal. Body mass of ewes during late pregnancy receiving either urea-supplemented wheat straw diets or urea-ammoniated wheat straw diets was not affected by treatment, but during lactation urea-ammoniated wheat straw diets resulted in higher ewe body masses (Brand *et al.*, 1988) and 10% higher birth masses of their lambs. Urea-ammoniation, however, produced no advantage in lamb growth and survival rate.

Other notable experiments on ammonia and NaOH treatment are those conducted by Swiegers *et al.* (1988) and Swiegers & Meissner (1988) on common reed and Snyman *et al.* (1991) on different fractions of maize residues.

Alkaline hydrogen peroxide treatment is a development showing promising results because lignin apparently is dissolved (Gould, 1984). In a preliminary investigation, Brand *et al.*

al. (1989c) showed between 57 and 81% improvements in straw intake provided the treated material was supplemented with urea. The major effect apparently was ascribable to the alkalinity (NaOH), because peroxide alone did not affect intake. This was confirmed by Meeske *et al.* (1993). They, in fact, showed that results may be better with NaOH treatment than NaOH plus H<sub>2</sub>O<sub>2</sub>, because NAN flow to the duodenum and ME intake by wethers receiving NaOH treated diets were higher than by wethers receiving alkaline hydrogen peroxide-treated diets. Thus, in contrast to theory, there seems to be no particular advantage to peroxide.

### Conclusions and future needs

To refine estimates of carrying capacity, animal requirements will have to be defined in relation to the constraints of the environment, that is, veld condition and yield as they are affected by season and rainfall. The information required to integrate necessitates modelling which should form the basis of future approaches. The same need applies to studies of intake control and prediction where mechanistic models probably always will have to be supported by empirical data. Empirical relationships often are useful because they may indicate the direction towards the mechanism — a case in point is the IVDOM/NDF relationship of Meissner & Paulsmeier (1995) to predict intake across animal species and forage types. With intake control in the feedlot, the results of Meissner *et al.* (1994, 1995) regarding fast-growing steers have been surprising. These steers did not grow fast because of high intake and because they were not of superior genetic make-up — the question is why they grew faster and more efficiently than their compatriots.

Protein digestion in the dairy cow and the feedlot steer has been studied extensively, resulting in the establishment of valuable databases categorizing protein sources in terms of RDP and UDP, and UDP digestibilities and amino acid profiles in the small intestine. Often, though, the efforts to increase post-ruminal digestion neglect or depress microbial protein production. Therefore, the effort at Irene (Henning, 1991) to study microbial growth efficiency in relation to carbohydrate source and complementary fermentation patterns should be welcomed and enhanced. Cronjé and his co-workers (Cronjé, 1992a, 1992b; Cronjé & Smuts, 1994) have studied nitrogen partitioning between fibre and non-fibre producing animals extensively. Similar efforts to study differences between indigenous stock (Nguni) and others have commenced. Differences in metabolic rate and nutrient partitioning or recirculation may explain differences in adaptability. Therefore, this work should be encouraged.

Pasture utilization and species differences should be studied in terms of ability to provide nutrients in the digestive tract for absorption. This ability then may be related to characteristic chemical constituents which can be utilized by plant breeders to improve current germplasm. More effort should be put into this approach with emphasis on legumes and forage species with low nutrient and water requirements which can be cultivated on degraded soils.

Research on supplementation with carbohydrate, protein and fat and the reasons for interaction have made some progress. Fat supplementation through whole cottonseed (Smith & Vosloo, 1994b) and other means, that is, rumen

inert fats, remains important to improve the energy balance and milk production of the high-producing dairy cow. The possible role of ionophores to enhance glucogenesis at the critical periods of negative energy balance and reconception is also encouraging. Mineral supplementation and mineral nutrition in general have been neglected the past decade in South Africa. While progress in this field is difficult and experiments are laborious, the need remains to demarcate the locations of deficiency and toxicity. Efforts in the past also have not adequately taken into account the selective and seasonal feeding patterns of animals.

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