Ruminal and postruminal digestion of dietary protein and starch in steers: 2. Multivariate model prediction of non-ammonia nitrogen and starch passage and digestibility

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Multivariate prediction models were developed from the results of three divergent trials with multicannulated steers. Diets differed in composition and physical structure. Energy contents varied from 10 to 13 MJ ME/kg DM, starch from 20 to 62%, CP from 102 to 155 g/kg DM and RDP from 60 to 85%. In the first trial, diets were compiled from byproducts of the milling industry; in the second, maize meal was the major component and in the third high and normal lysine maize cultivars were fed either whole or rolled. Feeding levels were controlled or *ad libitum*, varying between 65 to 95 g DM/kg$W^{0.75}$/d. With more starch in the diet, proportionally more passed to and was digested in the lower digestive tract. More starch tended to pass into the duodenum with lower RDP in the diet, but the effect was indirect through a reduction in the proportion OM which was apparently digested in the rumen (OMD_R). NAN passage and digestion in the lower digestive tract were negatively associated with starch content of the diet. This effect was apparently rumen pH related, where high starch fermentation in the rumen lowered pH probably to the detriment of microbial protein production. NAN passage to the duodenum was associatecl positively with N intake or protein content of the diet and negatively with OMD_R. RDP level in the diet *per se* did not affect the amount of NAN passing to the duodenum, but its interaction with OMD_R was highly significant. Thus, with lower RDP levels, OMD_R was less, resulting in more NAN passing to the duodenum. Multivariate models predicted NAN and starch passage to the lower digestive tract with an r^2 between 0.89 and 0.97 and *SD*s of 15 g NAN/d and 60 g starch/d. Non-intake associated differences between steers in amino acid and glucose availability at the duodenum was substantial, explaining partly the vast difference in feedlot performance of individual steers.

Meervoudige-veranderlike voorspellingsmodelle is ontwikkel vanaf resultate van drie uiteenlopende proewe met rumen- en duodenaalgefistuleerde osse. Die diëte het in samestelling en fisiese vorm verskil. Energie-inhoud het tussen 10 en 13 MJ ME/kg DM gevarieer, stysel tussen 20 en 62%, RP tussen 102 en 155 g/kg DM en RDP tussen 60 en 85%. Die diëte in die eerste proef is saamgestel met neweprodukte van die maalbedryf, die in die tweede proef het mieliemeel as die hoofkomponent bevat en in die derde proef is hoë en normale lisien mielietipes heel of gerol gevoer. Voedingspeil het tussen 65 en 95 g DM/kg $W^{0.75}$/d gevarieer, laasgenoemde was *ad libitum*. Op diëte wat meer stysel bevat het, het verhoudelik meer stysel na die laer spysverteringskanaal gevloei en daar verteer. Op diëte met laer RDP % was daar 'n neiging tot meer styselvloei na die duodenum, maar die effek was indirek, veroorsaak deur 'n afname in persentasie OM wat skynbaar in die rumen verteer het (OMV_R). NAN-vloei en -vertering in die laer spysverteringskanaal was negatief gekorreleerd met styselinhoud van die dieet. Dit kan skynbaar toegeskryf word aan lae rumen pH met hoë styselvertering wat mikrobe-proteïenproduksie benadeel. NAN-vloei na die duodenum was positief gekorreleerd met N-inname en proteïeninhoud van die dieet, maar negatief met OMV_R. RDP-persentasie in die dieet *per se* het nie NAN-vloei na die duodenum beïnvloed nie, maar wel die interaksie tussen RDP en OMV_R. Byvoorbeeld, by laer RDP-waardes was OMV_R laer, wat NAN-vloei na die duodenum bevoordeel het. Meervoudige-veranderlike modelle het NAN- en styselvloei na die laer spysverteringskanaal voorspel met 'n r^2 van tussen 0.89 en 0.97 en *SA*'s van 15 g NAN/d en 60 g stysel/d. Nie-inname verwante verskille tussen osse in aminosuur- en glukosebeskikbaarheid by die duodenum was groot, wat onder andere die groot verskille tussen individue in voerkraalprestasie verklaar.

Keywords: Prediction model, non-ammonia nitrogen, starch, digestion, steers

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Introduction

Although the volatile fatty acids (VFA) produced in the rumen are important contributors to the energy supply for growth of feedlot steers, amino acid and glucose uptake from the small intestine may be quantitatively and qualitatively even more important. This results firstly because, since amino acids are utilized for protein synthesis and gluconeogenesis, amino acid availability in the small intestine correlates better with growth rate than VFA availability in the rumen (MacRae & Ulyatt, 1974). Secondly, glucose is used 10 to 40% more efficiently when absorbed from the small intestine rather than as VFA from the rumen (Leng, 1982; Owens *et al.*, 1984), although results in practice do not always support this (Theurer, 1986). Thus, the availability of amino acids and glucose in the small intestine and the factors influencing it, are of interest.

More amino acids are expected to be available in the small intestine when ruminal degradation of dietary protein is lower (Meissner & Du Plessis, 1992), however, this is not always true (Meissner & Du Preez, 1996). Depending on the feedstuffs used, ruminal pH and ruminal turnover, the amount of microbial amino acids produced on a diet with higher RDP may be higher than on a diet with lower RDP; the net result is similar amounts at the duodenum. Meissner & Du Preez (1996) found N intake and the proportion OM fermented in the rumen (an inverse function of rumen turnover) were the major factors affecting non-ammonia nitrogen (NAN) passage to the duodenum, whereas protein degradation (60% vs 70% RDP) did not have a significant effect. With more starch in the diet, proportionally more starch was digested postruminally. Meissner & Du Plessis (1992) furthermore found that starch passage to the duodenum was increased by lower RDP in the diet. Hence, effective prediction of NAN and starch availability in the small intestine requires a multifactorial approach with extensive data sets. The data sets of Meissner & Du Plessis (1992) and Meissner & Du Preez (1996) were therefore supplemented with those of Leeuw and Coetzer (unpublished) in order to obtain divergent dietary conditions which could allow robust tests and to develop reliable prediction equations.

Procedures

Data sets

The experiments of Meissner & Du Preez (1996), Meissner & Du Plessis (1992) and Leeuw and Coetzer (unpublished) are referred to in the text as Exp. 1, 2 and 3, respectively.

In Exp. 1, eight ruminal and duodenally fistulated steers were fed in a Latin square design. In the first 4 × 4 Latin square two protein contents (i.e., 105 and 125 g CP/kg DM) were fed, each at 60 and 70% RDP. The dietary energy concentration was 10.0 MJ ME/kg DM. In the second 4 × 4 Latin square the dietary energy concentration was 12.5 MJ ME/kg DM, the two protein contents were raised to 135 and 155 CP/kg DM respectively, to obtain the same protein to energy ratios as in the first trial. The RDP levels were also 60 and 70%. All diets were fed in four equal portions each day at a level of 100 g air dry feed per kg metabolic mass ($W^{0.75}$). The diets consisted of different proportions of sorghum, maize, maize and wheat byproducts, cottonseed hulls, lucerne pellets, salt, minerals, vitamins, $CaCO_3$ as buffer, an antibiotic and an ionophore. More details are given by Meissner & Du Preez (1996).

Protein degradability was determined by nylon bag technique. Digesta passage was measured by the double marker technique with Na-dichromate as particulate and Co-EDTA as fluid marker, respectively. Passage and disappearance of OM, N, starch and NAN were determined between mouth and duodenum and between duodenum and faeces. Measurements in the rumen included pH and NH_3-N concentration.

In Exp. 2, twelve steers were fistulated in the rumen and duodenum and allocated factorially to one of three dietary treatments. The treatments differed in daily supply of CP and RDP, effected by the following protein supplements: 1.44% urea (117 g CP/kg DM; 74% RDP), 0.96% urea (102 g CP/kg DM; 70% RDP) and 0.47% urea plus 5.7% fish meal (118 g CP/kg DM; 62% RDP). The remainder of each diet consisted of 11% cottonseed hulls, about 80% maize meal, molasses, a premix containing vitamins, trace minerals, salt, $NaHCO_3$, KCl, an ionophore and an antibiotic, and $CaCO_3$. The ME content of the diets was approximately 11.7 MJ/kg DM and the diets were fed in four equal portions each day at a level of 80 g DM/kg $W^{0.75}$.

The same markers and measurements as described for Exp. 1 applied for Exp. 2. See details in Meissner & Du Plessis (1992).

In Exp. 3, eight steers were fitted with ruminal, duodenal and ileal cannulae. They were allocated to one of four dietary treatments in a Latin square design and fed *ad libitum*. The dietary treatments consisted of different maize cultivars. These were a high-lysine cultivar, which was fed either whole or rolled, a soft normal-lysine cultivar fed whole, and a hard normal-lysine cultivar fed whole. The diets consisted of 87% maize to which was added 30 g/kg of a urea-mineral mixture, 50 g/kg molasses and 50 g/kg maize-crop residue. The urea-mineral mixture consisted of urea, $CaCO_3$, DiCaP, salt, $NaHCO_3$, K_2SO_4, vitamins, trace minerals, an antibiotic and an ionophore. The CP content of the diets averaged 138 g/kg DM, about 30% was contributed by urea, and the ME content, calculated from the apparent digestibilities, was > 13 MJ/kg DM.

Chrome oxide was used as an indigestible marker to determine digesta flow and purine to distinguish microbial N in total duodenal N. RDP values of whole maize cannot be effectively determined by nylon bag technique; these were estimated from the proportion of microbial N in total N at the duodenum (range 70 to 85%). As with Exp. 1 and 2, passage and disappearance of OM, N, starch and NAN were calculated between mouth and duodenum and between duodenum and faeces. Rumen pH and NH_3-H also were measured.

The most prominent differences between experiments were in feedstuffs and physical structure of the diets, ME contents (10 to > 13 MJ/kg DM), starch contents (20 to 62%), CP contents (102 to 155 g/kg DM) and RDP levels (60 to 85%).

Statistical analyses

Differences between treatments within experiments were established by the General Linear Models (GLM) Program of SAS (1985), employing the prescribed methods for Latin squares and factorial designs. NAN and starch passage to the duodenum and postruminal digestion were predicted by multivariate model building, where the contribution of factors and their interaction were tested with the stepdown procedure of GLM. Since significant contributions to the overall variation in dependent variable accounted for were very small at $p \leq 0.05$, only contributions at $p \leq 0.01$ were included in the final models. Prediction models of NAN passage were scrutinized in plots of observed data points *vs* predicted data points.

Results

Intake, passage and disappeareance of OM, starch and NAN in the digestive tract are displayed in Tables 1, 2 and 3 for Exp. 1, 2 and 3, respectively. Intake of OM did not differ sig-

Table 1 Intake, passage and disappearance of OM, starch and nitrogenous substances in the digestive tract of steers fed diets of byproducts of the milling industry, and formulated to contain two levels of respectively energy, crude protein and RDP (Exp. 1)

	ME MJ/kg DM		Crude protein,%		RDP, %		
Item	12.5	10.0	14.0	12.0	70	60	*SD*
Intake							
OM, kg/d	8.02	8.09	8.06	8.05	8.13	7.99	0.22
Starch, kg/d	2.12^b	1.80^a	1.81^c	2.11^d	1.90	2.02	0.16
N, g/d	207^b	164^a	199^d	172^c	187	183	6.09
Rumen pH	6.23^a	6.41^b	6.33	6.31	6.63^f	6.28^e	0.11
Rumen NH_3-N, mmol/l	8.37^b	7.08^a	8.03	7.42	8.74^f	6.75^e	1.14
Disappearance before duodenun							
OM, kg/d	4 59^a	5.39^b	4.89	5.09	5.09	4.89	0.29
OM, % of intake	57.2^a	66.6^b	60.7	63.2	62.6	61.0	2.57
Starch, kg/d	1.71	1.56	1.51^c	1.77^d	1.61	1.67	0.16
Starch, % of intake	80.7^a	86.7^b	83.4	83.9	84.7	82.7	3.81
N, g/d	41.2	35.5	40.1	36.6	42.0	34.7	11.2
N, % of intake	19.9	21.6	20.2	21.3	22.5	19.0	5.28
Passage to duodenum							
OM, kg/d	3.43^b	2.70^a	3.17	2.96	3.04	3.09	0.20
Starch, kg/d	0.41^b	0.24^a	0.30	0.34	0.29	0.35	0.07
NAN, g/d	164^b	125^a	154^d	133^c	143	145	8.29
Disappearance after duodenum							
OM, kg/d	1.68^b	0.96^a	1.41	1.23	1.31	1.33	0.20
OM, % of intake	20.9^b	11.9^a	17.5	15.3	16.1	16.6	2.59
Starch, kg/d	0.29^b	0.12^a	0.18	0.23	0.18	0.22	0.07
Starch, % of intake	13.7^b	6.67^a	9.94	10.9	9.47	10.9	3.68
NAN, g/d	119^b	83.1^a	112^d	90.1^c	100	102	9.38
NAN, % of N intake	57.5	50.7	56.3	52.4	53.5	55.7	5.28

Values with different superscripts between energy contents (a,b), protein contents (c,d) and RDP levels (e,f) differ ($p \leq 0.05$)

Table 2 Intake, passage and disappearance of OM, starch and nitrogenous substances in the digestive tract of steers fed maize diets differing in crude protein and RDP of the supplement (Exp. 2)

Item	1.44% urea (74% RDP)	0.96% urea (70% RDP)	0.47% urea; 5.7% fish meal (62% RDP)	SD
Intake				
OM, kg/d	5.68	5.70	5.51	0.21
Starch, kg/d	3.49	3.50	3.22	0.13
N, g/d	118^b	103^a	116^b	4.42
Rumen pH	5.99	6.00	5.87	0.15
Rumen NH_3-N, mmol/l	17.4^b	16.1^{ab}	10.5^a	1.68
Disappearance before duodenum				
OM, kg/d	2.97^{ab}	3.30^b	2.55^a	0.19
OM, % of intake	52.3^{ab}	57.9^b	46.3^a	1.54
Starch, kg/d	2.96^b	2.91^b	2.46^a	0.14
Starch, % of intake	84.8^b	83.1^b	76.4^a	1.95
N, g/d	24.6^{ab}	33.5^b	16.3^a	3.98
N, % of intake	20.8^{ab}	32.5^b	14.1^a	3.50
Passage to duodenum				
OM, kg/d	2.71^{ab}	2.39^a	2.98^b	0.11
Starch, kg/d	0.52^a	0.59^{ab}	0.76^b	0.06
NAN, g/d	89.6^{ab}	68.5^a	98.5^b	8.40
Disappearance after duodenum				
OM, kg/d	1.36	1.04	1.70	0.13
OM, % of intake	23.9^{ab}	18.2^a	30.9^b	2.67
Starch, kg/d	0.32^a	0.38^a	0.57^b	0.08
Starch, % of intake	9.17^a	10.9^a	17.7^b	2.43
NAN, g/d	62.4^{ab}	45.7^a	67.4^b	7.96
NAN, % of N intake	52.9^{ab}	44.4^a	58.1^b	7.43

^{a,b} Values in the same line with different superscripts differ ($p \leq 0.05$)

nificantly between energy and protein contents in Exp. 1, as planned (Table 1). Starch intake differed because the starch contents of the 12.5 MJ ME/kg DM (high energy) diets were higher than the starch contents of the 10.0 MJ ME/kg DM (low energy) diets. Intake also differed between protein contents because feedstuffs (energy sources) with higher protein contents often have lower starch contents owing to starch extraction. Nitrogen intakes differed between energy and protein contents but not between RDP-values as planned. In the rumen, pH was lower with the high energy diets and the lower RDP-values. The latter may be explained by lower NH_3-N concentrations for the 60% RDP *vs* the 70% RDP diets.

Proportionally more OM and starch disappeared before the duodenum on the low energy diets. Protein contents and RDP % did not have a significant effect on OM disappearance or on starch disappearance if corrected for differences in starch intake. Nitrogen disappearance before the duodenum was not significantly affected by either energy content of the diet, protein content or RDP % (Table 1). In contrast, the amount of NAN flowing to the duodenum was higher on the high energy diets and higher protein contents, whereas RDP% did not have a significant effect. Both OM and starch passage to the duodenum was higher on the high energy diet; that coincided with more OM and starch (kg and %) being digested in the lower digestive tract. Passage of OM and starch and their disappearance after the duodenum were, however, not significantly affected by protein content or RDP%. More NAN was digested in the small intestine on the higher protein diets, but that could be explained hy the higher N intake. Again, RDP% did not have a significant effect on NAN digestion or on the digestion of OM and starch.

In Exp. 2 (Table 2), N intake was similar on the high urea (1.44%) diet and the fish meal diet, but N intake, as intended, was significantly lower with the low urea (0.96%) diet. The difference in N intake and RDP % was reflected in the rumen NH_3-N levels, where the fish meal diet (62% RDP) had the lowest level. Intake of OM and starch did not differ significantly between treatments. Also, rumen pH was similar.

Less OM, starch and N disappeared before the duodenum on the fish meal diet than on the urea diets (Table 2), although only the difference between the fish meal diet and the low urea diet was significant. As a result, more OM, starch and

Table 3 Intake, passage and disappearance of OM, starch and nitrogenous substances in the digestive tract of steers fed different maize cultivars (Exp. 3)

	Maize cultivar				
	High-lysine		Soft normal	Hard normal	
Item	whole	rolled	whole	whole	*SD*
Intake					
OM, kg/d	5.58	5.63	5.52	5.65	0.45
Starch, kg/d	3.64	3.58	3.53	3.55	0.33
N, g/d	128	123	133	132	11.6
Rumen pH	5.72	5.66	5.71	5.72	0.14
Rumen NH_3-N, mmol/l	5.21	5.85	4.64	4.64	0.58
Disappearance before duodenum					
OM, k./d	3.69	3.61	3.30	3.87	0.25
OM, % of intake	66.1	64.1	59.8	68.5	2.85
Starch, kg/d	2.74	2.63	2.44	2.77	0.29
Starch, % of intake	75.3	73.5	69.1	78.0	3.40
N, g/d	60.7	54.1	46.4	54.2	8.70
N, % of intake	47.4	44.0	34.9	41.1	5.20
Passage to duodenum					
OM, kg/d	1.88	2.02	2.22	1.78	0.29
Starch, kg/d	0.87	0.94	1.06	0.78	0.14
NAN, g/d	63.4	64.9	81.7	78.2	7.97
Disappearance after duodenum					
OM, kg/d	1.20	1.24	1.52	1.10	0.16
OM, % of intake	21.5	22.0	27.5	19.5	1.01
Starch, kg/d	0.67^a	0.70^a	0.91^a	0.60^a	0.11
Starch, % of intake	18.4	19.6	25.8	16.9	0.94
NAN, g/d	44.1	44.2	59.3	52.0	5.60
NAN, % of N intake	34.5	35.9	44.6	39.4	4.92

[a,b] Values in the same line with different superscripts differ ($p \leq 0.05$)

NAN passed to the duodenum on the fish meal diet than the urea diets and more were apparently digested. Noteworthy is the significant difference in starch digestion between the fish meal diet and the urea diets, whereas for NAN digestion the fish meal diet only differed significantly from the low urea diet. As with the results of Exp. 1 (Table 1), these results indicate that the major effect on NAN passage and digestion is due to protein level and not the degradability of protein.

In Exp. 3 (Table 3), more starch disappeared after the duodenum on the soft normal-lysine treatment, but the result was no longer significant when adjusted for difference in starch intake. There also appears to be a small difference between the high-lysine and normal-lysine cultivars in N transactions. Rumen NH_3-N concentrations tended to be lower on the normal-lysine cultivars, with correspondingly lower N disappearance before the duodenum but more passage of NAN to the duodenum and digestion in the lower digestive tract.

In view of the main goal of the investigation *i.e.*, to define factors influencing NAN and starch availability at the duodenum, it is of interest to compare results between experiments. The results show that with more starch in the diet, proportionally less is digested before the duodenum and more in the lower digestive tract: In Exp. 1 (Table 1), the low energy diet contained 20% starch; 86.7% was digested before the duodenum and 6.67% thereafter. The high energy diet contained 24% starch, 80.7% was digested before the duodenum and correspondingly 13.7% thereafter. In Exp. 2 (Table 2), the diets contained about 55% starch, and between 76 and 85% starch was digested before the duodenum and between 9.2 and 18% thereafter. The relatively small difference as compared to Exp. 1 may be due to comparatively lower intakes and therefore slower passage to the duodenum in Exp. 2. Noteworthy also is the higher starch digestion in the lower digestive tract on the fish meal (62% RDP) diet compared to the urea (70–74% RDP) diets. In Exp. 3 (Table 3), the diets contained 58 to 62% starch, 69 to 78% was digested before the duodenum and correspondingly 16.9 to 26% thereafter.

The difference in NAN digestion in the lower digestive tract shows the opposite trend to that of starch, although the relationship is not close, presumably owing to differences in protein level, RDP, intake and physical form of the diet. In Exp. 1, an average of 54 NAN as a percentage of N intake was digested in the lower digestive tract, in Exp. 2, 52% and in Exp. 3, 39%. Of further significance to NAN availability at the duodenum is rumen pH, because that may affect microbial growth and protein production. Rumen pH was higher in Exp. 1 (6.32) than in Exp. 2 (5.95) and in Exp 3. (5.70). If the daily trend in rumen pH is considered (Figure 1), it is noteworthy that in Exp. 1 rumen pH never declined to below 6, in Exp. 2 it did for about 9 h, and in Exp. 3 rumen pH was always below 6.

Tables 4 and 5 show the prediction models for NAN passage to the duodenum as obtained by the stepdown procedure. Model A (Table 4) is based on N and starch intake, whereas Model B (Table 5) is based on protein and starch content of the diet. The final prediction models are those based on the combined data of Exp. 1, 2 and 3, but the corresponding equations for Exp. 1 only and for Exp. 1 and 2 combined, are also shown to illustrate that the partial contributions of influencing

Table 4 Prediction model A with data successively analysed for Exp. I, Exp. 1+2 and Exp. 1+2+3. Dependent variable NAN passage to the duodenum (g/d)

Exp.	Parameter	Value ± *SD*	*t*-value	PR ≥ F	
Exp. 1	Intercept	135.6 ± 37.81	3.59	0.0013	$n = 32$
	N intake (g/d)	0.573 ± 0.103	5.57	0.0001	$r^2 = 0.727$
	Starch intake (kg/d)	-5.51 ± 7.679	-0.717	0.4793	*SD* = 15.9g/d
	$RDP.OMD_R$ (%)[1]	-0.017 ± 0.004	-3.927	0.0005	*CV*% = 11.01
Exp 1 + 2	Intercept	116.4 ± 28.90	4.03	0.0003	$n = 43$
	N intake (g/d)	0.654 ± 0.075	8.73	0.0001	$r^2 = 0.831$
	Starch intake (kg/d)	-10.78 ± 4.334	-2.49	0.0172	*SD* = 15.6g/d
	$RDP.OMD_R$ (%)	-0.014 ± 0.003	-4.47	0.0001	*CV*% = 12.07
Exp 1 +2 + 3	Intercept	118.1 ± 15.22	7.76	0.0001	$n = 74$
	N intake (g/d)	0.724 ± 0.046	15.78	0.0001	$r^2 = 0.885$
	Starch intake (kg/d)	-12.70 ± 1.885	-6.74	0.0001	*SD* = 15.5g/d
	$RDP.OMD_R$ (%)	-0.017 ± 0.002	-8.13	0.0001	CV % = 15.19

[1] $RDP.OMD_R$ = Interaction between RDP (%) and OM fermented in the rumen as a % of total OM digested (OMD_R)

Table 5 Prediction model B with data successively analysed for Exp 1, Exp 1+2 and Exp 1+2+3. Dependent variable NAN passage to the duodenum (g/d)

Exp.	Parameter	Value ± SD	*t*-value	PR ≥ F	
Exp 1	Intercept	45.73 ± 58.28	0.785	0.4395	*n* = 32
	Protein (%)	9.766 ± 1.793	5.447	0.0001	$r^2 = 0.742$
	OM intake (kg/d)	7.706 ± 4.842	1.591	0.1232	*SD* = 15.7g/d
	Starch (%)	-0 599 ± 0.683	-0.877	0.3881	*CV*% = 10.92
	RDP.OMD$_R$ (%)	-0.015 ± 0.005	-3.259	0.0030	
Exp 1+2	Intercept	28.18 ± 48.44	0.582	0.5641	*n* = 43
	Protein (%)	10.15 ± 1.647	6.163	0.0001	$r^2 = 0.842$
	OM intake (kg/d)	8.458 ± 4.150	2.038	0.0485	*SD* = 15.3g/d
	Starch (%)	-0.756 ± 0.329	-2.296	0.0273	*CV*% = 11.48
	RDP.OMD$_R$ (%)	-0.013 ± 0.004	-3.623	0.0008	
Exp 1+2+3	Intercept	93.36 ± 24.67	3.78	0.0003	*n* = 74
	Protein (%)	6.075 ± 1.127	5.39	0.0001	$r^2 = 0.902$
	OM intake (kg/d)	10.66 ± 1.893	5.63	0.0001	*SD* = 14.5g/d
	Starch (%)	-1.169 ± 0.155	-7.56	0.0001	*CV*% = 14.7
	RDP.OMD$_R$ (%)	-0.017 ± 0.002	-8.80	0.0001	

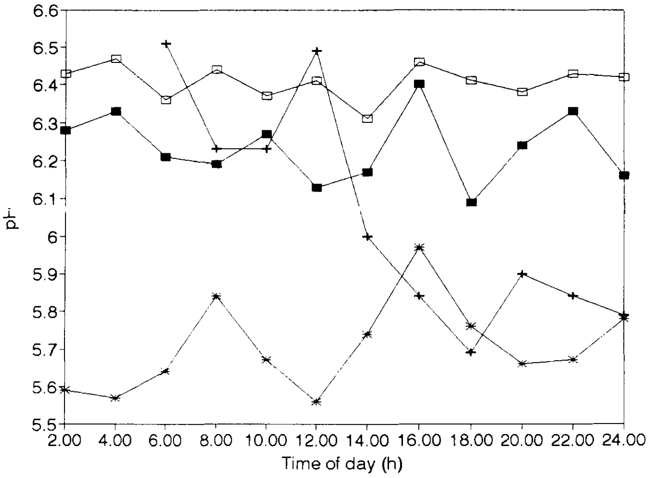

Figure 1 Daily variation in rumen pH. —■— Exp. 1 HE; —□— Exp. 1 LE; —+— Exp. 2; —*— Exp. 3.

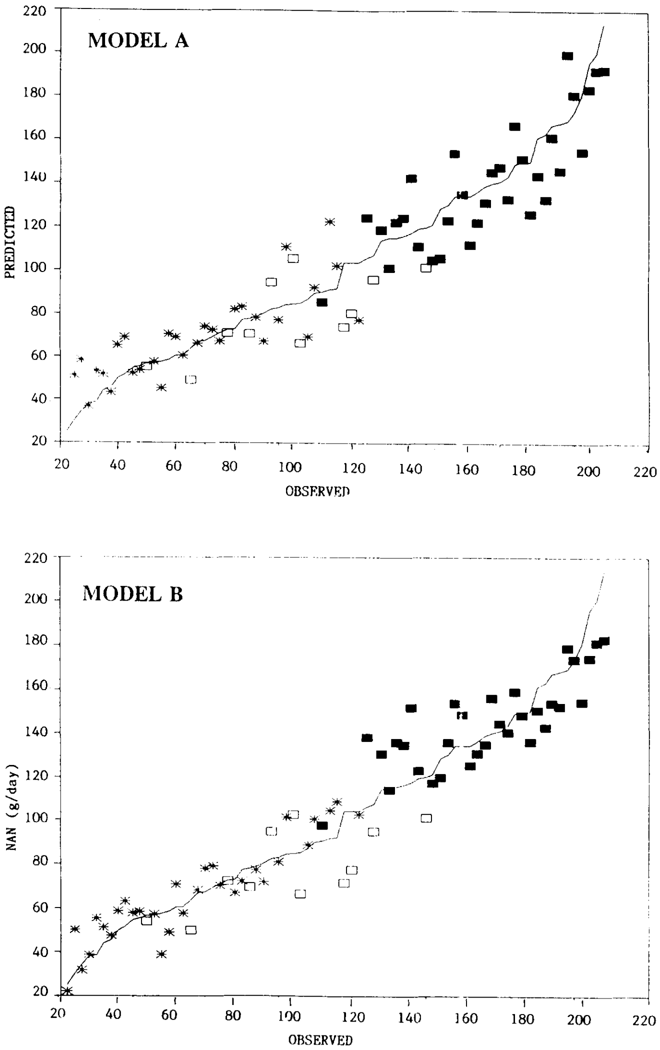

Figure 2 Predicted NAN (g/d) *vs* measured NAN observations. Model A is based on N and starch intake (see Table 4). Model B is based on dietary protein and starch contents and OM intake (see Table 5). — Observed ■ Exp. 1; □ Exp. 2; * Exp. 3.

variables are similar, although not always significant owing to an insufficient degrees of freedom. For example, in Model A starch intake was negatively associated with NAN passage for all three sets of data (Table 4). The regression coefficient of Exp. 1 data was, however, not significant, clearly because of insufficient degrees of freedom.

The r^2 and standard deviations (*SD*) of Model B were marginally better than those of Model A. Model B also is the preferred prediction equation because it is easy to determine the protein, starch and RDP contents of any particular feedlot diet and one can usually also anticipate the OM intake with comparative ease. Judging from the *t*-values, N intake or protein percentage and the interaction between RDP and percentage OM fermented in the rumen are the main contributors to the variation in NAN passage accounted for. It is of interest to note that the ME content of the diet and RDP % *per se* or their interactions with other variables were not significantly associated with NAN passage. Thus, it appears that the influence of protein degradability was through its effect on rumen fermentation. With lower RDP levels proportionally less OM was digested in the rumen which apparently allows more protein to pass through to the duodenum (see also Table 8). Starch content or intake as suggested, might have been negatively associated with NAN passage to the duodenum because of the resulting lower pH (Figure 1) which presumably could depress microbial growth.

Generally, prediction models A and B of the combined data of Exp. 1, 2 and 3 fitted the data satisfactorily with an r^2 of about 0.9 and an *SD* of 15 g NAN/day. The fit also was unbiased as indicated by the plots of observed *vs* predicted NAN in Figure 2. Of concern, however, was the fact that RDP of whole maize in Exp. 3 could not be measured effectively by the nylon bag technique and therefore had to be predicted from microbial N at the duodenum. Hence, predictions from the models could be skewed. Therefore, the robustness of the regression coefficients was tested if the RDP values in Exp. 3 were firstly decreased by 10 percentage units and secondly, again decreased by 10 percentage units but also allowing a

20% increase in NAN passage to the duodenum (Table 6 and Figure 3). These changes did not alter the regression coefficients significantly if the numerical value ± *SD* of the regression coefficients in Table 6 are compared with the corresponding regression coefficients in Tables 4 and 5. The changes also did not have a major effect on the r^2 and *SD*, and the resulting alternative models still fitted the data sets satisfactorily (Figure 3). The test, therefore, suggests that the prediction models are robust and relatively accurate, and that the parameters contributing to the variability in NAN passage to the duodenum have a strong influence.

Table 6 Prediction Models A and B (Exp. 1+2+3) when in Exp. 3 RPD values (Alternative model 1) were decreased by 10%, and RDP and NAN values (Alternative model 2) were respectively decreased by 10% and increased by 20%. Dependent variable NAN passage to the duodenum (g/d)

Model	Parameter	Value ± *SD*	*t*-value	PR ≥ F	
Model A					
Altern. 1	Intercept	112.6 ± 17.81	6.32	0.0001	$n = 74$
	N intake (g/d)	0.762 ± 0.051	15.06	0.0001	$r^2 = 0.858$
	Starch intake (kg/d)	-15.19 ± 2.086	-7.28	0.0001	*SD* = 17.2g/d
	RDP.OMD$_R$ (%)	-0.016 ± 0.003	-6.31	0.0001	*CV*% = 16.91
Altern. 2	Intercept	108.7 ± 16.08	6.076	0.0001	$n = 74$
	N intake (g/d)	0.744 ± 0.046	16.30	0.0001	$r^2 = 0.869$
	Starch intake (kg/d)	-10.52 ± 0.046	-5.59	0.0001	*SD* = 15.6g/d
	RDP.OMD$_R$ (%)	-0.016 ± 0.002	-7.116	0.0001	*CV*% = 14.50
Model B					
Altern. 1	Intercept	118.5 ± 28.30	4.186	0.0001	$n = 74$
	Protein (%)	5.020 ± 1.234	4.067	0.0001	$r^2 = 0.880$
	OM intake (kg/d)	10.59 ± 2.093	5.24	0.0001	*SD* = 15.4 g/d
	Starch (%)	-1.371 ± 0.162	-8.44	0.0001	*CV*% = 15.14
	RDP.OMD$_R$ (%)	-0.018 ± 0.002	-7.70	0.0001	
Altern. 2	Intercept	72.46 ± 26.06	2.780	0.0001	$n = 74$
	Protein (%)	6.400 ± 1.137	5.63	0.0001	$r^2 = 0.888$
	OM intake (kg/d)	12.69 ± 1.863	6.81	0.0001	*SD* = 14.2g/d
	Starch (%)	-0.982 ± 0.150	-6.564	0.0001	*CV*% = 13.25
	RDP.OMD$_R$ (%)	-0.018 ± 0.002	-8.153	0.0001	

Prediction models for starch passage to the duodenum and postruminal starch digestion were even more convincing than the NAN prediction models (Table 7), with r^2 of 0.97 + and CV of 6 to 13%. Rumen degradation of protein had a prominent influence in both models, as a factor *per se* and through an interaction with the proportion of starch digested in the rumen. As with NAN passage though, the effect of RDP was predominantly through its influence on rumen fermentation, indicating that with lower RDP more starch in general would be available in the lower digestive tract (see also Table 8). With these models, in contrast to the NAN models, ME content of the diet did make a significant contribution to the variation accounted for in starch passage or starch digestion. This may be explained partly by the fact that the higher ME diets also contained higher levels of starch.

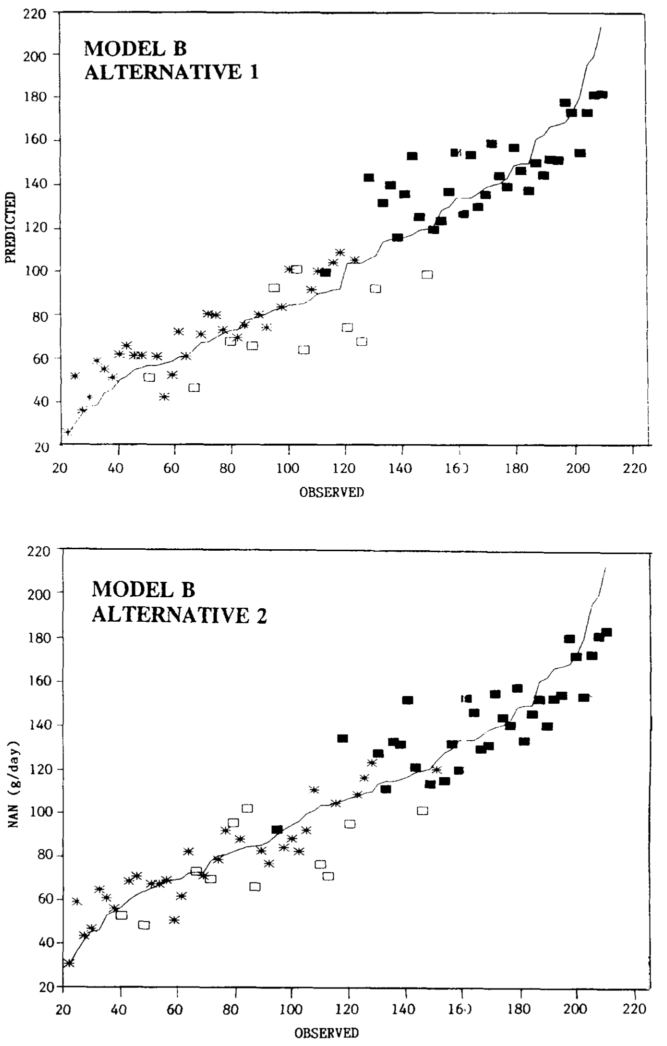

Figure 3 Predicted NAN (g/d) *vs* measured NAN observations. Model B: Alternative 1 — RDP levels were decreased by 10%. Alternative 2 — RDP levels and NAN values were respectively decreased by 10% and increased by 20% (see Table 6). —— Observed ; ■ Exp. 1; □ Exp. 2; ∗ Exp. 3.

Using the prediction models for NAN and starch passage to the duodenum, predictions were made for typical scenarios expected with feedlot diets (Table 8). The ME content of the diet was set at 12 MJ/kg DM and the OM intake at 8 kg/day, but the other variables were varied according to what might be encountered in different feedlot dietary compositions. The protein content was varied from 11 to 13%, starch content from 20 to 35 and to 50%, the RDP from 60 to 70%, the OMD$_R$ from 60 to 80% and the St.D$_R$ from 70 to 90%. The predictions indicate that within protein and starch contents, the highest availability of amino acids and starch at the duodenum can be expected with either 60 or 70% RDP at 60% OMD$_R$ and at 70% St.D$_R$. The amino acid contribution to the total will be more with 60% RDP than with 70% RDP, but this will be compensated for by more starch with the 70% RDP diet. Thus, provided amino acid availability is not limiting, one can expect similar growth performance on these two scenarios.

Across dietary starch contents, the maximum amino acid plus starch availability of the 11% protein and 35% starch diet (1.63 and 1.61 kg/day) may give better performance than

Table 7 Prediction models for starch passage to the duodenum (kg/d) and postruminal starch digestion (% of starch intake)

Independent variable	Parameter	Value ± *SD*	*t*-value	PR ≥ F	
Starch passage (kg/d)	Intercept	0.267 ± 0.103	2.609	0.0111	$n = 74$
	ME (MJ/kg)	-0.020 ± 0.009	-2.234	0.0254	$r^2 = 0.97$
	RDP (%)	0.032 ± 0.001	22.730	0.0001	SD = 60g/d
	Starch intake (kg/d)	0.152 ± 0.009	17.525	0.0001	CV% = 13.11
	RDP.St.D$_R$ (%)[1]	-0.0004 ± 0.00001	-34.064	0.0001	
Starch digested (%)	Intercept	12.95 ± 1.571	8.241	0.0001	$n = 74$
	ME (MJ/kg)	0.346 ± 0.135	2.562	0.0126	$r^2 = 0.991$
	RDP (%)	1.156 ± 0.021	54.20	0.0001	SD = 0.96%
	RDP.St.D$_R$ (%)	-0.014 ± 0.0002	-76.62	0.0001	CV% = 6.12

[1] RDP.St.D$_R$ = Interaction between RDP (%) and starch fermented in the rumen as % of total starch digested (St.D$_R$)

the maximum amino acid and starch availability of the 11% protein -50% starch diet (1.72 and 1.70 kg/day), because amino acids in the combined availability of the latter diet may be insufficient (126 and 116 g NAN/d *vs* 143 and 133 g NAN/d — Table 8).

Table 8 Prediction of NAN and starch available for postruminal digestion. Assumption: OM intake of steer is 8 kg/d and the dietary energy content is 12 MJ ME/kg DM

Protein %	Starch %	RDP %	OMD$_R$ %	St.D$_R$ %	NAN g/d	Starch$_D$ kg/d	[1]AA + Starch$_D$ kg/d
11	20	60	60	70	161	0.535	1.54
			80	90	140	0.055	0.93
		70	60	70	151	0.575	1.52
			80	90	127	0.015	0.81
13	20	60	60	70	173	0.535	1.62
			80	90	153	0.055	1.01
		70	60	70	163	0.575	1.59
			80	90	139	0.015	0.88
11	35	60	60	70	143	0.735	1.63
			80	90	123	0.255	1.02
		70	60	70	133	0.775	1.61
			80	90	109	0.215	0.90
13	35	60	60	70	156	0.735	1.71
			80	90	135	0.255	1.10
		70	60	70	145	0.775	1.68
			80	90	122	0.215	0.98
11	50	60	60	70	126	0.936	1.72
			80	90	105	0.456	1.11
		70	60	70	116	0.976	1.70
			80	90	91.8	0.416	0.99
13	50	60	60	70	138	0.936	1.80
			80	90	118	0.456	1.19
		70	60	70	128	0.976	1.78
			80	90	104	0.416	1.07

[1] AA + Starch$_D$ = Amino acids (NAN × 6.25) plus starch availability at the duodenum

During the statistical analysis, it became evident that individual variation in NAN and starch passage to the duodenum was substantial. Consequently, individual variation was investigated further, using the data of Exp. 3 where treatment differences mainly were not significant. The fermentation of OM in the rumen as proportion of the total OM digested (OMD$_R$) was used as reference. This is a function of rumen retention time which is partly determined by individual variation. Because rumen retention time affects OMD$_R$, intake is expected to also affect OMD$_R$, but in Exp. 3 the correlation ($r^2 = 0.007$) was not significant. Therefore, the differences in OMD$_R$ were apparently largely the result of inherent variability (Table 9). OMD$_R$ was significantly negatively associated with NAN ($r^2 = 0.37$) and starch ($r^2 = 0.77$) passage to the duodenum, *i.e.*, more NAN and starch passed to the duodenum when proportionally less OM was fermented in the rumen. The net effect of the variation between animals on the same diet was that more than double the amount of amino acids and starch were in some animals available for absorption than in others (Table 9).

Discussion

The results are discussed across experiments and in the context of the multivariate models rather than the findings in

Table 9 Animal variation in proportion of OM fermented in the rumen (OMD$_R$) and its effect on NAN and starch passage to the duodenum. Average of the four treatments in Exp 3.

Steer No.	OMD$_R$ %	NAN g/d	Starch kg/d	AA + Starch[1] kg/d
15	85.0^{c}	51.7^{ab}	0.34^{a}	0.66
5	80.5^{bc}	37.4^{a}	0.49^{ab}	0.72
3	76.1^{abc}	44.0^{a}	0.55^{abc}	0.83
13	72.7^{abc}	70.1^{bc}	0.79^{bc}	1.23
9	72.1^{abc}	65.2^{bc}	0.67^{abc}	1.08
10	71.8^{abc}	90.8^{d}	1.00^{c}	1.57
8	70.7^{a}	67.7^{bc}	0.84^{bc}	1.26
12	66.4^{a}	78.4^{cd}	0.96^{c}	1.45
SD	1.43	2.26	0.05	–

[1] AA + Starch = Amino acids (NAN × 6.25) plus starch

[a,b] Values in the same column with different superscripts differ ($p \leq 0.05$)

Exp. 1, 2 and 3 *per se*.

With more starch in the diet more passed to the duodenum and a higher percentage of dietary starch was digested in the lower digestive tract. This agrees with the reports of Owens *et al.* (1986) and Hill *et al.* (1991). They found linear relationships between starch entering the duodenum and starch digested in the small and large intestine. The relationship in the present study was also linear, with postruminal starch digestion increasing from 50% when 0.24 kg entered the duodenum on the low energy diet in Exp. 1 (Table 1) to 86% on the soft normal-lysine cultivar in Exp. 3 (Table 3) when 1.06 kg entered the duodenum. More starch is expected to pass to the duodenum on whole maize than milled maize (Hale, 1973; Galyean *et al.*, 1981); therefore, the differences between Exp. 1, 2 and 3 in the proportion of starch entering the duodenum are not solely accounted for by differences in dietary starch contents, but may also be due to differences in starch sources and processing methods.

Whereas starch passage to the duodenum and postruminal starch digestion increased with more starch in the diet, NAN passage to the duodenum decreased. Postruminal NAN digestibility was not affected by any factors measured, and averaged 69 ± 1.5% across diets. This corresponds with NAN digestibilities reported by Streeter & Mathis (1995). They showed a slight increase in NAN digestibility to about 72% when fish meal is part of the escape protein; the results in Exp. 2 (Table 2) of Meissner & Du Plessis (1992), however, do not correspond, but their results are consistent with the contention of Owens *et al.* (1984).

NAN passage to the duodenum on high quality forage diets is 1 to 2 g/MJ ME intake (Beever *et al.* 1987). This figure is usually lower with high energy (feedlot) diets, because of reduced ruminal dilution rate (Owens *et al.*, 1984). In the present investigation NAN passage decreased from 1.6 g/MJ ME intake on the two diets in Exp. 1 (Table 1) to about 1.2 g/MJ ME intake on the diets of Exp. 2 (Table 2) and to 0.9 g/MJ ME intake for the diets in Exp. 3 (Table 3). The decline in NAN passage is apparently associated with lower microbial protein production on the higher starch diets.

Ruminal pH was found to decline in association with the higher starch fermentation in the rumen (Figure 1). The pH in Exp. 3 was consistently lower than 6 even though buffers were included in the diets. Henning *et al.* (1993) showed that low pH depresses microbial growth and efficiency.

The negative effect of high starch contents on NAN passage to the duodenum is illustrated further in the prediction models of Tables 4 and 5. It would appear that for NAN optimization, starch in maize-based feedlot diets should not exceed 50%, although the degree of maize processing will have a modifying effect. The calculations in Table 8 support this contention as they indicate that NAN availability may become limiting unless the CP % in the diet is increased.

The prediction models (Tables 4 and 5) indicate that N intake and therefore protein content of the diet are the primary supporters of high NAN passage. In contrast, RDP% within the limits of practical South African feedlot diets, have little or no effect on NAN passage. The results of Meissner & Du Plessis (1992), Streeter & Mathis (1995) and Meissner & Du Preez (1996) apparently support this conclusion. The effect of RDP is apparently rather through its effect of changing rumen fermentation and thereby affecting the proportion of OM that is apparently digested in the rumen. Lower RDP levels will tend to decrease rumen fermentation, thereby allowing more protein unfermented through to the duodenum. In the present investigation this effect resulted in 10 g NAN/day more (Table 8). Because the proportion of OM and therefore starch that is apparantly fermented in the rumen is reduced, more starch will also pass to the duodenum as predicted by the models in Table 7 and shown in Table 8. Whether these alterations in OMD_R and $St.D_R$ coincide with a change in rumen retention time should be investigated, but it seems highly probable.

Individual variation in rumen retention time and, as a result OMD_R, may be substantial (Orskov *et al.*, 1971; Smuts *et al.*, 1995). It also is a heritable characteristic (Smuts *et al.*, 1995). The results in Table 9 indicate that steers with low OMD_R may benefit from the availability of more amino acids and starch in the small intestine, if it is assumed that starch digestion in the small intestine is beneficial, which is not generally true (Theurer, 1986). With more absorbed amino acids and glucose, both the supply to and efficiency of utilization of these nutrients at the tissue level should be improved (Leng, 1982; Owens *et al.*, 1984). Meissner and co-workers (1995) showed that feedlot steers, gaining in excess of 2 kg/day resulting in a feed conversion ratio of 4 kg DM/kg gain, rarely have high feed intakes. Perhaps these animals have short rumen retention times which enhances postruminal nutrient supply and absorption. Future work should address this hypothesis.

The models to predict NAN and starch availability at the duodenum both proved satisfactorily accurate (Figure 2) and robust (Table 6, Figure 3), and because they resulted from divergent feeding systems, should apply across most feeding systems used in southern Africa. The extended data set of the three trials also confirmed the pointers from the first paper (Meissner & Du Preez, 1996).

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