

# A critique of the Cornell Net Carbohydrate and Protein System with emphasis on dairy cattle.

## 1. The rumen model

**The late G. Alderman**  
**revised by J. France and E. Kebreab**

*The University of Reading, Department of Agriculture  
Earley Gate, Reading RG6 2AT, UK*

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### ABSTRACT

The Cornell Net Carbohydrate and Protein System (CNCPS) is primarily a nutrient supply model, since it does not model the utilisation of the absorbed nutrients, other than by using the NRC (1988) net energy and NRC (1985) available protein systems to calculate the animal's energy, protein and amino acid (AA) requirements. The model incorporates details of the metabolism in the rumen not found in other published models of energy and protein requirements, particularly rates of carbohydrate degradation, predicted rumen pH and rumen nitrogen and peptide balance. The model does not predict volatile fatty acid (VFA) proportions or methane production. Microbial growth is assumed to be dependent upon the rate of carbohydrate degradation, whereas other mathematical models of the rumen relate microbial growth to the concentration of nutrients in the rumen, and also require estimates of rumen volume and microbial mass. The microbial yield of structural carbohydrate (SC) bacteria is not limited or altered by the rumen ammonia supply, with the result that stoichiometrically unsound amounts of microbial protein and negative rumen ammonia levels can be predicted. Only estimated peptide supply modifies the growth of non structural carbohydrate (NSC) bacteria. Solid outflow rates adopted are low at higher levels of feeding compared to ARC (1984) and AFRC (1992), with the result that the proportion of OM digested in the rumen is predicted to be higher (c. 0.75) than the mean value 0.65 adopted by ARC (1980). The effects of liquid outflow rate upon the outflow of NPN, AA and soluble proteins, pectins, sugars, organic acids and VFA are ignored. Only peptides are affected by the liquid outflow rate in the model. The degradation rates for carbohydrate fractions A and B1 proposed are very high, exceeding the possible rate of microbial growth so that microbial synthesis does not respond to considerable variations in these high rates. The adopted maximum microbial yields of SC and NSC rumen bacteria are lowered by 20% to allow for the effects of protozoal predation, which has the effect of compensating for the high predicted microbial yields adopted, but the protozoa are not accounted as contributing to the microbial AAN

output. Starch disappearance in the rumen is not corrected for protozoal ingestion and its re-appearance in the intestine, nor is there any accounting for the protozoal contribution to fat uptake in the rumen. Predicted TDN values of forages are therefore sensitive mainly to the rate of cell wall degradation selected. Only one dietary parameter, effective neutral detergent fibre (eNDF%) defines or modifies maximum microbial yield, microbial maintenance, realised microbial yield, and rates of SC and NSC degradation. The consequence is that both energy and protein supply to the cow are affected by the parameter eNDF when values fall below 24.5% in diet DM.

KEY WORDS: CNPCS, dairy cows, lactation, rumen, metabolism, energy, protein, amino acids, supply

## GENERAL DESCRIPTION OF THE MODEL

Most current nutrient requirement systems for dairy cattle (Madsen, 1985; INRA, 1988; NRC, 1988; SCA, 1990; AFRC, 1993; Tamminga et al., 1994) describe protein metabolism in some detail, with the carbohydrate fractions of the diet featuring only as contributors to the overall energy exchanges in the rumen and absorption as ME, and subsequent utilisation as energy, not as defined energy supplying nutrients, VFA, glucose and fat. The need for nutrient requirement systems based on their fate in the animal's body has been recognised for over twenty years, with the rumen modelling efforts of Baldwin et al. (1977) and France et al. (1982), for example. Their models are complex, mechanistic and dynamic, originating at the biochemical level. They feature numerous equations of the Michaelis-Menten type, are written in a computer simulation language such as CSMP or C++, and require to be integrated over time to get results.

The Cornell Net Carbohydrate and Protein System uses a mixed empirical/mechanistic and non-dynamic model (i.e. not time dependent) to simulate the nutrient supply side of the ruminant animal, using standard spreadsheet software. Four sub-models are used, encompassing a great deal of published information on the characteristics of feeds, ruminant digestion and absorbed nutrients. It predicts steady state microbial fermentation, feed digestion and passage and end product formation. Further development of the model to remedy this situation has already been published (Pitt et al. 1995, 1996). The rumen model in version 3.0 form deals mainly with the adequacy and balance of the diet formulated in relation to the optimal nutrient supply to the rumen bacteria.

### *Ruminant feed description*

The CNPCS model relies almost entirely (with the exception of starch) upon the Goering and Van Soest (1970) acid and neutral detergent system of feed analysis both for carbohydrate and protein fractions. This means that most cell content

fractions other than starch (water soluble carbohydrates (WSC), organic acids and pectins) are not estimated separately, but their sum is computed from cell contents (CC) minus determined starch values. Neutral detergent insoluble N (NDIN) and acid detergent insoluble N (ADIN) are used to predict digestible and indigestible ruminally undegradable protein.

*Neutral Detergent Fibre, NDF.* By definition, carbohydrate fractions B2 and C together make up NDF, of which fraction B2 is titled 'available fiber', which is equivalent to 'digestible cell walls', or DNDF. Suggested ranges for the rates of degradation of the B2 (cell wall) fractions derived from published data using *in vitro* or *in situ* methods are given in Tables 4, 5 and 6 of Sniffen et al. (1992).

*Non Structural Carbohydrate, NSC.* Total carbohydrate is calculated by subtracting crude protein (CP%), ether extract (EE%) and ash (TA%) from 100, and then NDF% is subtracted to give NSC. NSC comprises sugar, pectins and organic acids (fraction A), and starch (fraction B1). Pectins and organic acids are not assigned a carbohydrate (CHO) fraction symbol, because they are not dealt with as separate fractions, the presumption apparently being that pectins ferment as fast as the sugar in fraction A, which is reasonable. However, pectins are known to yield an acetate dominated VFA pattern, not propionate, as for water soluble carbohydrates (WSC), so this will have to be corrected when attempting to predict VFA patterns as Pitt et al. (1995) have tried to do. Data for pectins are not given in any of the published tables of feed composition, although a method for pectin has been published (Faichney and White, 1983). The amounts of organic acids (mainly lactic acid) present in un-wilted grass silages and low dry matter maize silages can be of the order of 10% of the dry matter. Although they are either absorbed *de novo* or rapidly metabolised by rumen bacteria, contributing to the animal's energy supply, they do not contribute significantly to the microbial energy supply, and can be discounted as in AFRC (1992) and INRA (1988). The inclusion of organic acids in the calculated A1 CHO fraction unjustifiably increases the A1 fraction's contribution to microbial protein synthesis from most silage based diets.

*Proteins.* The CNCPS has five fractions (A, B1, B2, B3 and C) for protein compared to the four fractions of AFRC (1992), which are quickly degradable protein (QDP), slowly degradable protein (SDP), digestible undegradable protein (DUP) and indigestible undegradable protein (IUDP). The CNCPS B2 protein fraction is equivalent to SDP, whilst fraction B3 equates to DUP, and fraction C to  $100 - (a + b)$  of Ørskov and Mehrez (1977). The QDP fraction of AFRC (1992) requires correction for solid particulate matter, as Lopez et al. (1994), in order to compare it with the two CNCPS fractions, a non-protein nitrogen fraction (A) and true protein fraction (B1), precipitable by tungstic acid. Inasmuch as buffer soluble true protein can be a source of peptides to the NSC bacteria until they are washed out of the rumen by liquid outflow, this additional fraction is justified. The CNCPS assigns fixed rates of degradation (%/h) to each protein

fraction, which are independent of which feed they occur in, namely infinity, 200-300%, 5-15%, 0.10-0.15% and 0 for fractions A, B1, B2, B3 and C. This contrasts strongly with both the approach of AFRC (1992) and INRA (1988), which rely upon measurements of the degradation rate of SDP feed proteins in aggregate, using *in situ* or *in vitro* rumen liquor techniques.

## RUMEN MODEL TO PREDICT MICROBIAL GROWTH

The CNCPS model of rumen fermentation, described by Russell et al. (1992), divides the ruminal microbial ecosystem into two main groups of rumen bacteria, and the protozoa:

1. *SC bacteria* only ferment Structural Carbohydrates (cell walls, NDF), only use ammonia as their source of N, and do not ferment peptides or amino acids.
2. *NSC bacteria* ferment Non-Structural Carbohydrates (starch, pectin, sugars) and use ammonia or peptides and amino acids as their N sources, and can produce ammonia.
3. *Protozoa* are not considered in terms of their nutrient requirements, but their effects upon microbial protein synthesis are taken into account quantitatively.

### *Factors controlling microbial growth*

*Carbohydrate supply.* The CNCPS model assumes first order degradation characteristics [substrate limited, enzyme excess and specific rate constants (/h)] for the CHO fractions, whilst most other rumen models in addition modify carbohydrate degradation according to microbial mass present (Dijkstra and France, 1996). Rates of degradation ( $Kd_4$ ,  $Kd_5$ ,  $Kd_6$ ) for the CHO fractions are tabulated (often as ranges varying x 2) in Sniffen et al. (1992), Tables 4, 5 and 6. These 'logical rates' are stated to be based on *in vitro* or *in situ* work published earlier by numerous authors. However, the computer model issued (v 3.0) has single point values for each degradation rate rather than ranges. The origin of the listed ranges of A (sugar) and B1 (starch) CHO fraction degradation rates is obscure, although reference is also made to the unreliability of enzymatic studies.

The model can be criticised for its reliance on feed degradation data obtained from *in situ* or *in vitro* studies not calibrated against *in vivo* data, with the result that much faster rates of degradation for some fractions are used in the model than are observed in the rumen. Results from the *in vitro* rumen liquor gas pressure transducer technique have already confirmed that they may be an order of magnitude too high for some nutrients in the neutral detergent soluble (NDS) fraction (carbohydrate fractions A, B1) of feeds (Schofield and Pell, 1995).

No effects of microbial mass or N supply (other than peptide N) upon rates of CHO degradation are specified in the model. The tabulated degradation rates  $Kd_6$  for the B2 (cell wall) fraction by the SC fermenting bacteria are modified in the model by rumen pH predicted from effective NDF as defined by Mertens (1985). The proportion of the CHO fractions digested whilst in the rumen (RD) are calculated by equation (1), which includes rate of passage (Kp), which is affected by dry matter intake as described later:

$$RD = Kd / (Kd + Kp) \quad (1)$$

*Microbial yield.* Microbial yield (Y) in the rumen is predicted in the CNCPS by the use of the Pirt (1965) double reciprocal equation, which is rewritten as:

$$Y \text{ (g microbial DM/g CHO)} = 1 / [(KM/Kd) + (1/YG)] \quad (2)$$

where

KM is the microbial maintenance cost (0.05 and 0.15 g CHO/g microbial DM/h for SC and NSC bacteria),

$Kd_4$ ,  $Kd_5$ ,  $Kd_6$  are the rates of degradation (/h) of the A, B1 and B2 CHO fractions,

YG is the maximum microbial yield in the model initially set at 0.5 g microbial DM/g, CHO degraded, but reduced to 0.4 g/g after allowing for protozoal predation.

Using the microbial maintenance figures above, this equation becomes either:

$$Y1 = 1 / [0.05 / Kd_6 + 2.5], \text{ for SC bacteria} \quad (3)$$

or

$$Y2 \text{ or } Y3 = 1 / [0.15 / (Kd_5 \text{ or } Kd_4) + 2.5], \text{ for NSC bacteria} \quad (4)$$

which implies that microbial yield increases as Kd increases as shown in Figure 1.

It should be noted that with values for Kd greater than 1.0 /h (100% /h in the CNCPS model), little increase in microbial yield is predicted, so that the very high values for Kd of 100-400% for the A fraction (sugar) listed in Tables 4, 5 and 6 of Sniffen et al. (1992) give no significant increase in predicted microbial yield above those for much lower (less than 1.0 /h) rates of degradation. Schofield and Pell (1995), using gas pressure transducers, reported much lower rates of degradation, 0.15 to 0.19 /h for the NDS fraction (CHO fractions A and B1) of forages, than those used in the model.

The yield of NSC bacteria is stated to be increased by a maximum of 18% if peptide supply is not limiting, based on the work of Russell and Sniffen (1984). However, J. Dijkstra (personal communication) has pointed out that this conclusion was based on microbial yields calculated as g DM/g OM not per g CHO as in the CNCPS model. If the data are corrected for the trypticase additions (used as a

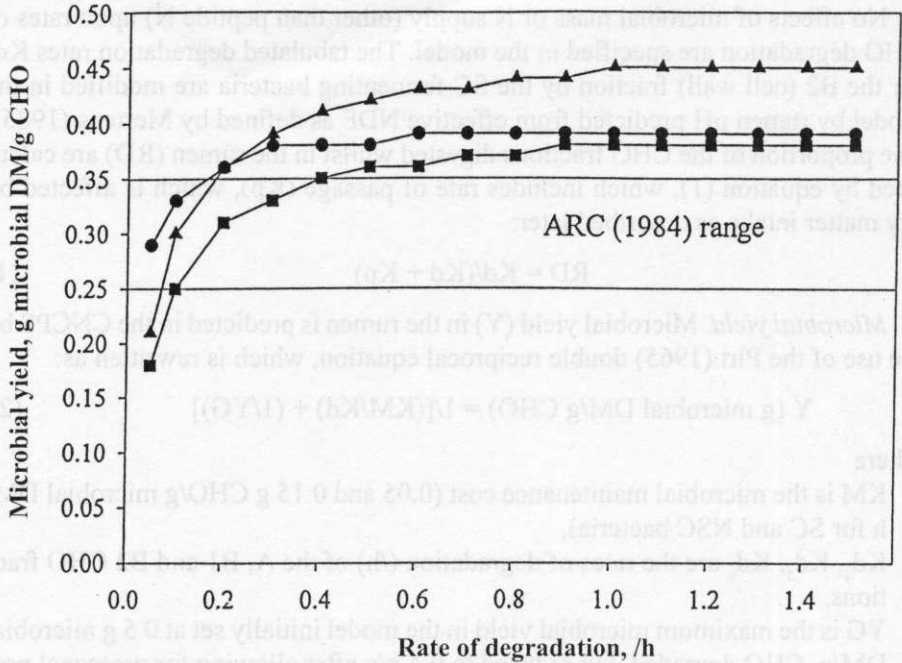


Figure 1. Predicted microbial yield in the CNCPS model compared with ARC (1984). Symbols: (●) Y1, equation (3) in text; (■) Y2 or Y3, equation (4) in text; (▲) Y2 or Y3, peptide supply non-limiting

source of peptide) an increase in microbial yield of about 50% is obtained, in line with other work (Baldwin et al., 1977, 77%; Dijkstra et al., 1992, 59%). Predicted microbial yields (allowing for an 18% improvement in NSC yields due to adequate peptide supply) in the region of 0.3 to 0.4 g microbial DM/g ruminally degraded carbohydrate (RDCHO) are predicted for feeds such as grass silage, wheat and soyabean, or 30 to 40 g N/kg RDCHO. Assuming that organic matter apparently digested in the rumen (DOMR) is 85% RDCHO (correcting for RDP and fat), this gives values of 26 to 34 g N/kg DOMR, comparable to the ARC (1984) values, ranging from 23 to 32 g N/kg DOMR.

This approach to microbial yield is in contrast to the direct effects of feeding level (and indirectly outflow rate) on microbial yield ( $y$ ) first suggested in ARC (1984) and subsequently redefined in AFRC (1992):

$$y = 7.0 + 6.0[1 - e^{-(0.35L)}] \quad (5)$$

where

$y$  is as g microbial CP (MCP)/MJ FME,

$L$  is ME intake as multiples of maintenance.

The NRC (1985) equation for microbial yield (Y) also implies an effect of feeding level, due to the presence of a constant term:

$$Y = 26.13\text{TDN} - 31.9 \quad (6)$$

where

Y is g microbial N/d,

TDN is kg/d.

Equation (6) which gives values for microbial N yields of 19.8 to 24.5 g N/kg TDN (= 198 to 245 g microbial DM/kg TDN, or 124 to 153 g MCP/kg TDN) as TDN intake increases from 5 to 20 kg/d, (equivalent to feeding levels  $L = 1$  to 4). However, the term TDN% used in NRC (1985), fermentable organic matter (FOM) in INRA (1988) and Tamminga et al. (1994), fermentable metabolisable energy (FME) in AFRC (1992), and digestible carbohydrate (DCHO) in Madsen (1985) all describe either the potentially fermentable or digestible energy supply. These estimates are not affected by outflow rate (as they are defined as measured at the maintenance level of feeding) and do not define the actual amounts of nutrients expected to be degraded in the rumen. An exception is ARC (1980), which took a mean value for the proportion of organic matter digested in the rumen (DOMR) of 0.65 of digested OM (DOM). The majority of these systems also specify fixed microbial protein yields per unit of fermentable matter, viz. 93 and 150 g MCP/kg FOM, and 106 g/kg DCHO, except AFRC (1992), which has a range of 8 to 12 g/MJ FME, dependent upon feeding level.

*Nitrogen supply.* The degradation of feed proteins is primarily a first-order process in the CNCPS model, but degradation of the resulting peptides is modified by the microbial mass of the NSC fermenting bacteria (NSCBACT) and the rumen liquid outflow rate (KI). Peptides not captured by the NSC bacteria are presumed to be degraded to ammonia, since there appears to be no computation of peptides escaping from the rumen in the liquid outflow and they are not included in the NAN outflow from the rumen. The CNCPS model does not take into account the effects of low N availability in the rumen in limiting microbial yield and rates of degradation, as reported by Oldham (1984). Consequently diets low in rumen degradable protein (RDP) can have predicted negative rumen ammonia levels which are biologically impossible (Dijkstra and France, 1996), and predicted amounts of microbial crude protein for which there is an inadequate supply of N. In contrast, the NRC (1985), INRA (1988) and AFRC (1992) models of microbial protein production all limit the amount of MCP synthesised to the estimated amount of N available to the rumen microbes, thus maintaining proper N stoichiometry in the rumen.

*Nitrogen recycling.* Endogenous N input into the rumen (urea and saliva proteins in saliva and urea absorption through the rumen walls) may be a significant factor when dietary N levels are low, but is only represented in a proportion of

rumen models (Dijkstra and France, 1996). The CNCPS model uses the NRC (1985) N recycling function (Yr), calculated as % of total dietary N intake, as shown in equation (7):

$$Yr = 121.7 - 12.01X + 0.3235X^2 \quad (7)$$

where

Yr is urea recycled (% of N intake),

X is intake of crude protein (% of diet DM).

This quadratic equation has a minimum value of 10% at 16% dietary crude protein in the dry matter, comparable to the values assumed by other models in their estimation of mean efficiency of N capture by rumen microbes. However, as dietary crude protein level rises above 16% (common in modern dairy cow diets) it predicts a reduction in N recycling, which is unrealistic. Urea recycling also features (as g N/d, not % of CP) in the calculation of rumen ammonia levels in an equation which can yield negative values. This is similar to the Scandinavian AAT (Madsen, 1985) and Dutch DVE (Tamminga et al., 1994) models which calculate and recommend optimal rumen N balances, but do not limit microbial protein synthesis by N supply. The presumption apparently is that deficiencies of rumen N supply in dairy cow diets in practice are rare, which can be questioned when maize silage and cereal based diets for cattle are in such widespread use. Recycling of microbial N, particularly by protozoa, does not feature in the CNCPS either, although Dijkstra (1994) has assembled a comprehensive model of protozoal N recycling.

*Rumen pH.* Although Russell et al. (1992) did not give a function to predict rumen pH, the CNCPS v.3.0 version of the CNCPS model predicts a drop in pH value below the norm of 6.46, based on Pitt et al. (1996):

$$\text{If cNDF} < 26.3\%, \text{ pH} = 5.46 + 0.038\text{eNDF}\%, \text{ otherwise pH} = 6.46 \quad (8)$$

Russell et al. (1992) did not adjust SC degradation rate when pH is lowered below their stated optimum of 6.725, but instead reduced maximum microbial yield (YG) for both NSC and SC bacteria when eNDF was below 20% in DM, using:

$$\text{New YG} = \text{YG} - 0.025(20 - \text{eNDF}\%) \quad (9)$$

Predicted rumen pH has subsequently been used in revisions of the model to modify microbial maintenance (KM), maximum microbial yield (YG), realised microbial yield (Y) and rate of CHO degradation Kd, as discussed later.

*Liquid and solid outflow rates.* Rumen modelling results are sensitive to the passage rates assumed. In most models, passage of material is assumed to be partly with the fluid phase and partly with the solid phase. The CNCPS assumes that



soluble sugars and acids are washed out with the particles, and calculates solid outflow rates (Kp) for forages and concentrates separately:

$$Kp[\text{forages}], \% / h = 0.388 + 0.02DMI/W^{0.75} + 0.0002(\text{forage \% in DM})^2 \quad (10)$$

$$Kp[\text{concentrates}], \% / h = -0.424 + 1.45Kp[\text{forage}] \quad (11)$$

where

DMI is in g/d,

W is in kg.

The coefficient 0.002 on DMI in the equation on p. 3567 of Sniffen et al. (1992) is confirmed by the senior author of that paper as an error, since it occurs as 0.02 in the spreadsheet, which then gives acceptable values for Kp[forages] as % /h. The corrected equation, equation (10), then gives the expected effect of significantly lower values for RD predicted by equation (1), as Kp (forages) and Kp (concentrates) increase with feed dry matter intake.

Both the calculated Kp values are adjusted for feed particle size by a correction factor (Af) using diet effective NDF (eNDF%) values:

$$Af [\text{forages}] = 100/(eNDF\% + 70) \quad (12)$$

$$Af [\text{concentrates}] = 100/(eNDF\% + 90) \quad (13)$$

The term eNDF% is defined in the footnotes to Tables 2 and 3 of Sniffen et al. (1992), p. 3569-3570 as 'the proportion of NDF that is effective in meeting the animal's fibre requirements', whilst the relevant columns of the tables are headed '% of NDF'. Values ranging from 60-98% for forages and 4-100% for concentrates are listed. However, use of that definition of eNDF results in Af values of the order of 0.6 for forages and large downward corrections to both Kp values. This definition is in conflict with the definition of eNDF% used in the equations which adjust rumen pH and microbial yield in subsequent revisions of the CNCPS model. Examination of the printed output from the model shows that the correct definition of eNDF% for use in equations (12) and (13) is eNDF as % of DM, which is the Tables 2 and 3 value times NDF % in DM. The senior author of Sniffen et al. (1992) has subsequently confirmed that this interpretation is correct.

Russell et al. (1992) use a term for liquid outflow rate (Kl) in the following equation for peptide uptake (PEPUP):

$$PEPUP = (KUP \times NSCBACT)/[RDPEP(KUP \times NSCBACT + Kl)] \quad (14)$$

where

Kl is % /h for a steady state rumen.

The companion paper which is referred to (Sniffen et al., 1992) gives no guidance on the calculation of Kl other than saying that it is an input to the model. However, Pitt et al. (1996) dealing with the prediction of VFA and rumen pH, quote a function for Kl attributed to Fox et al. (1990):

$$Kl (/d) = 1.059 + 0.0458DMI/W \quad (15)$$

where

Kl is as a decimal per day for a steady state rumen,

DMI is as g/d,

W is in kg.

The values obtained for solid ( $K_p$ ) and associated liquid ( $K_l$ ) outflow rates for diets of various forage:concentrate proportions are shown in Table 1 and those for  $K_p$  in Figure 2, where they are compared with the solid outflow rates of AFRC (1993).

TABLE 1  
Solid outflow rates ( $K_p$ , /h), for forage (F) and concentrates (C), and liquid outflow rates ( $K_l$ , /h) in the CNCPS model compared to AFRC (1993)

DMI kg/d	xM L	Liquid outflow Kl	Solid outflow rate $K_p$ for forage % diet DM								60%F, AFRC	
			40%		60%		80%		100%	40%C	(1993)	
			F	C	F	C	F	C	F	Mean	F + C	
6	1	.063	.017	.026	.021	.026	.027	.017	.034	0.023	.019	
12	2	.082	.027	.041	.031	.041	.037	.031	.044	0.035	.052	
18	3	.101	.037	.055	.041	.055	.046	.046	.054	0.047	.077	
24	4	.120	.047	.069	.051	.069	.056	.060	.064	0.058	.096	

Predicted liquid outflow rates are about three times the solid outflow rates at low feeding levels, reducing to twice at higher feeding levels. For typical dairy cow diets with 40 to 60% of forage, the solid outflow rates ( $K_p$ ) range from 0.017 to 0.069 /h in Table 1. The weighted means are 0.6 to 0.7 of the AFRC (1993) diet outflow rates, except at the maintenance feeding levels. Note should also be taken of the adoption of fixed solid outflow rates for dairy cows of 0.06 /h in INRA (1988) and Tamminga et al. (1994), and 0.08 /h in Madsen (1985). These differences in rumen solid outflow rates have important theoretical implications for the amount of dry matter required to be held in the rumen and the volume of the rumen at different feed intakes, when a steady state is assumed.

The low outflow rates also affect the predicted digestibility of feed fractions in the rumen (RD), defined by equation (1). For a typical  $K_d$  value of 0.1 /h for the cell wall or B2 protein fraction, and a diet of 60:40 forage to concentrates, RD is predicted to be 0.73 to 0.61 for feeding levels  $L = 1$  to 4 times maintenance, comparable with the ARC (1980) mean value for DOMR of 0.65. When  $K_d = 0.2$  /h, as for starch, then RD varies from 0.84 to 0.76. This prediction of a higher proportion of OM digested in the rumen could be a contributory cause of the high levels of predicted VFA production found by Pitt et al. (1996).

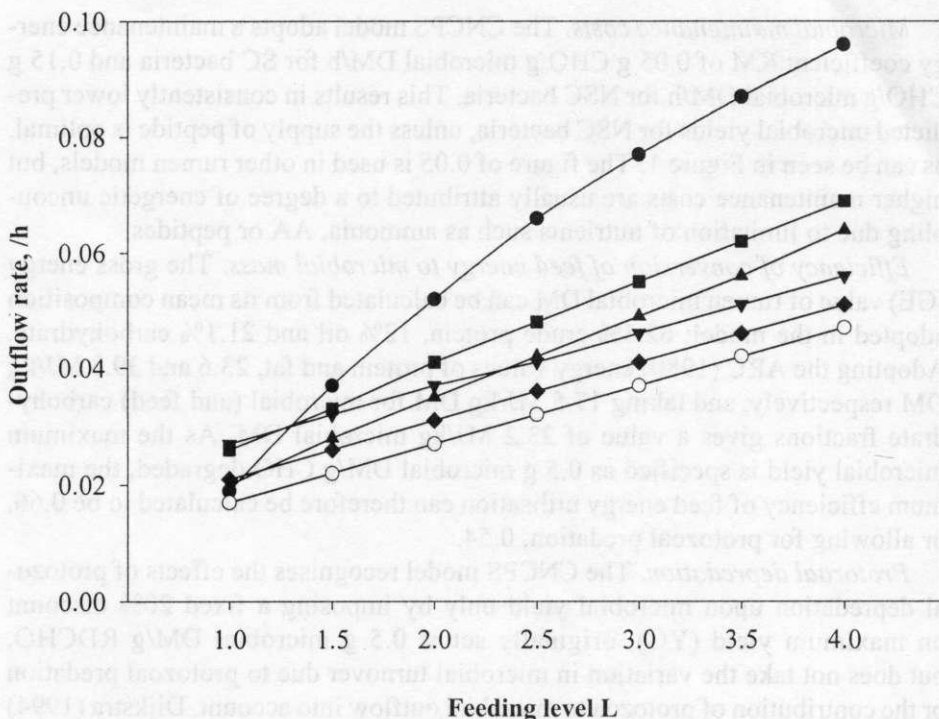


Figure 2. Solid outflow rates in the CNCPS model compared with AFRC (1993). Symbols (see Table 1): (■) C40%; (▲) C60%; (○) F40%; (◆) F60%; (▼) F80%; (●) AFRC

In steady state situations, and in the absence of microbial engulfment and lysis, microbial growth rate equals the solid outflow rate. The CNCPS model assumes that the fractional growth rate of SC and NSC rumen bacteria is equal to the fractional degradation rate of SC and NSC respectively, which presents some biological problems (Dijkstra and France, 1996). They pointed out that the tabulated fractional degradation rate of SC can be as low as 0.02 /h (Sniffen et al., 1992, Tables 4, 5 and 6) which is likely to be lower than the lowest particle outflow rate, so that the survival of SC bacteria would require their attachment to newly ingested particles with a low probability of passage. The highest tabulated degradation rate, 350% /h, for the A fraction of NSC (sugar) is higher than the maximum growth rate of rumen bacteria and is therefore biologically impossible. These contradictions arise from the adoption of the simplifying assumption that microbial growth is dependent upon the rate of CHO degradation, whereas the latter is the result of microbial activity leading to microbial growth, as in other models of the rumen.

*Microbial maintenance costs.* The CNCPS model adopts a maintenance energy coefficient KM of 0.05 g CHO/g microbial DM/h for SC bacteria and 0.15 g CHO/g microbial DM/h for NSC bacteria. This results in consistently lower predicted microbial yields for NSC bacteria, unless the supply of peptide is optimal, as can be seen in Figure 1. The figure of 0.05 is used in other rumen models, but higher maintenance costs are usually attributed to a degree of energetic uncoupling due to limitation of nutrients such as ammonia, AA or peptides.

*Efficiency of conversion of feed energy to microbial mass.* The gross energy (GE) value of rumen microbial DM can be calculated from its mean composition adopted in the model: 62.5% crude protein, 12% oil and 21.1% carbohydrate. Adopting the ARC (1980) energy values of protein and fat, 23.6 and 39.3 MJ/kg DM respectively, and taking 17.5 MJ/kg DM for microbial (and feed) carbohydrate fractions gives a value of 23.2 MJ/kg microbial DM. As the maximum microbial yield is specified as 0.5 g microbial DM/g CHO degraded, the maximum efficiency of feed energy utilisation can therefore be calculated to be 0.66, or allowing for protozoal predation, 0.54.

*Protozoal depredation.* The CNCPS model recognises the effects of protozoal depredation upon microbial yield only by imposing a fixed 20% discount on maximum yield (YG), originally set at 0.5 g microbial DM/g RDCHO, but does not take the variation in microbial turnover due to protozoal predation or the contribution of protozoa to microbial outflow into account. Dijkstra (1994) and Dijkstra et al. (1997) have shown that the effects of protozoa in the rumen on nutrient utilisation and N recycling can be modelled, and take into account many aspects of their activity in the rumen not incorporated in the CNCPS rumen model.

*Metabolism of fats and long chain fatty acids.* The CNCPS model assumes that no long chain fatty acids (LCFA) are taken up by microbes, and that 100% of dietary fat escapes degradation in the rumen, thus implying that no glycerol is released in the rumen. However, it is known that feed lipids are rapidly hydrolysed and hydrogenated by rumen microbes to glycerol and saturated LCFA (Dijkstra and France, 1996). The glycerol released is normally assumed to be degraded in the rumen at a rate similar to sugar. LCFA are only metabolised slowly by rumen microbes, but some are taken up (Bauchart et al., 1990). Consequently, the total flow of LCFA to the intestines is the sum of LCFA arising from feed and microbial matter, i.e. it is normally greater than the dietary fat input because of de novo fat synthesis by the rumen bacteria.

*Variations in composition of rumen microbes.* The chemical composition of mixed rumen bacteria, as reviewed by Clark et al. (1992), was found to be highly variable, with crude protein varying from 30-66%, with inverse variation in bacterial polysaccharides. The amino acid composition of the bacterial protein was fairly constant, except for variations in histidine and methionine. The composi-

tion of protozoa is also known to differ from that of rumen bacteria (Czerkawski, 1976), whilst the proportion of protozoa in the microbial population varies with the diet. The nucleic acid content of microbial cell dry matter in the CNCPS is taken as 15%, based on Purser and Buechler (1966). Nucleic acids are taken to have an N content of 15%, equivalent to 93.75% crude protein. This represents a deduction of about 16% for nucleic acids from microbial protein, compared to 25% in AFRC (1992) based on a 1992 EEC Ring Test.

The microbial storage polysaccharide content is probably the most variable component of microbial dry matter (Storm and Ørskov, 1983; Dijkstra and France, 1996) and it is an important component of NSC bacterial outflow from the rumen. Dijkstra et al. (1992) varied the microbial polysaccharide level according to dietary characteristics. Yet most published rumen models (including the CNCPS) have assumed a constant composition of microbial non-protein organic matter. The CNCPS model recognises the effects of protozoal depredation upon microbial yield, but does not then take the contribution of protozoa to microbial outflow into account.

#### DEVELOPMENTS IN THE RUMEN MODEL SINCE 1992

Since its publication in 1992, the CNCPS model, as applied to beef cattle, has been adopted in the NRC (1996) publication *Nutrient Requirements of Beef Cattle*. The latter publication has been used to cross check the core rumen equations, resulting in subsequent modification and updating of the model. Pitt et al. (1996) also proposed a number of modifications to the model. These were primarily concerned with the effects of low rumen pH (possibly due to the low fibre diets used in US beef feed lots) upon rumen microbial efficiency, but equations were also suggested for the prediction of both the proportions and amount of VFA produced, and the amounts of methane and carbon dioxide produced (not included in CNCPS v.3.0). A current research version of the model (CNCPSREV) was made available to the author by Dr D.G. Fox of Cornell University. This incorporates some of the equations proposed by Pitt et al. (1996). Subsequently, an updated model (version 3.1) of the CNCPS was promulgated as part of the software package CPM Dairy, made available in the autumn of 1998. This was a joint activity by Fox and co-workers at Cornell University, Chalupa at Pennsylvania University and Sniffen at the W.H. Miner Agricultural Research Institute, Chazy NY. The other component of that software package is a modified NRC (1988) dairy cow model. The package was written in computer code, rather than utilising a standard spreadsheet as the CNCPS did. These developments, which mostly affect the supply model, are reviewed below.

*Central role of effective NDF*

In version 3.0 of the CNCPS, the maximum microbial yield of the SC bacteria ( $Y_G \leq 0.4$  g microbial DM/g CHO fermented) is corrected downwards by equation (9) by 0.025 g/g per 1% of eNDF when less than 24.5% of diet dry matter, implying an effect of pH as well as that due to SC:NSC substrate proportions. However, as eNDF is now used in CNCPSREV (as suggested by Pitt et al., 1996) and CPM Dairy to predict rumen pH, eNDF also affects the values of KM1, YG1, Y1, Y2 and Y3. Reductions in the values of Y also lead to the calculation of reduced values for Kd for all types of carbohydrate. This means that eNDF% (for values below 24.5% in diet DM) is affecting directly ruminally degraded CHO (RD) and hence energy supply (as TDN, DE, ME and net energy) and microbial protein (and metabolisable protein) supply to the animal. Such an over reliance upon one dietary parameter in a rumen metabolism model seems unwise, particularly as the routine determination of eNDF presents some difficulties. However, Mertens (1997) reviewed the subject of measuring the physical structure of feeds for cows and redefined his original definition of eNDF (Mertens, 1985) to become physically effective NDF (peNDF), which has been adopted in the CPM Dairy version of the CNCPS. The new definition results in values which average 3% above the eNDF values in the earlier CNCPS v.3.0 Feed Library (W. Chalupa, personal communication). As a consequence, some of the equations which are driven by eNDF have had to be adjusted.

*Particle size adjustment to solid outflow rates.* Predicted outflow rates of forage and concentrate particles are adjusted according to their eNDF content by means of equations (12) and (13). Because of the form of these equations, the effect of an increase of 3 percentage units by replacing eNDF% by peNDF% will be a very small reduction in Af of the order of only 0.03. Consequently, equations (12) and (13) are retained unchanged in the CPM Dairy version of CNCPS.

*Prediction of rumen pH.* The CNCPS v.3.0 version of the model predicts a drop in pH value below the norm of 6.46 when eNDF is less than 26.3% of diet dry matter using equation (8) published subsequently by Pitt et al. (1996). Russell et al. (1992) did not adjust SC degradation rate when pH falls below their stated optimum of 6.725, but predicted that parameter direct from diet eNDF%. However, the NRC (1996) beef model and the latest version examined (CNCPSREV) use a slightly modified equation (8) to predict rumen pH, which uses a lower eNDF% limit:

$$\text{If eNDF} < 24.5\%, \text{ rumen pH} = 5.425 + 0.04229\text{eNDF}\% \quad (16)$$

which still implies a maximum (and normal) rumen pH of 6.46 as in Pitt et al. (1996). To accommodate the revision of feed and diet eNDF% values to the higher peNDF% adopted in the CPM Dairy version, the minimum level at which equation

(16) to predict rumen pH comes into action has been raised from 24.5 to 27.5%, according to the CPM Dairy Help file. However, a listing of the equations in CPM Dairy (W. Chalupa, personal communication) has the following equations for the prediction of rumen pH from peNDF expressed as a decimal:

$$\text{Rumen pH} = (1 - G) * (5.25 + 4.229 \text{peNDF}) + 6.47G \quad (17)$$

where

$$G = 1 / \{1 + \exp[-20 * (\text{peNDF} - 0.2639)]\} \quad (18)$$

Equation (17) is curvilinear, but over the range for peNDF values of 15 to 26%, (equivalent to 12 to 23% eNDF) gives predicted pH values quite close to the equation due to Pitt et al. (1996), (Figure 3), and thereafter deviates, becoming asymptotic at pH = 6.47 for peNDF values of 32-33%, whereas the linear equation (16) ceases at a value of 24.5% eNDF% (= 27.5% peNDF). Equation (16), which has an upper limit, made the running of optimising procedures for diet formulation difficult, so the continuous function, equation (17), was derived to solve this problem.

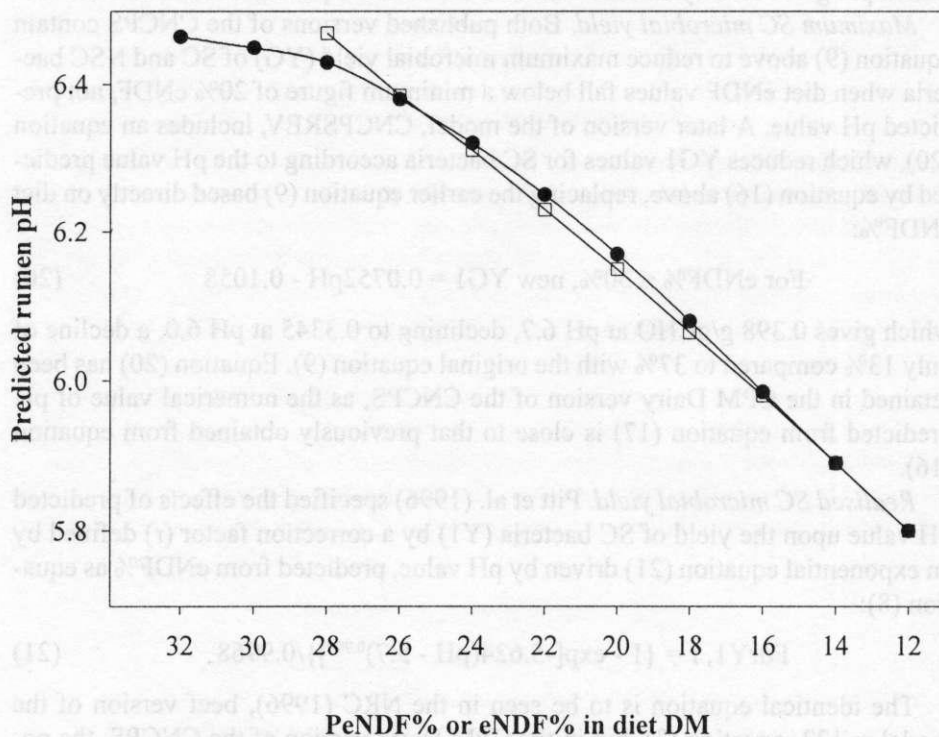


Figure 3. Prediction of rumen pH from eNDF% as Pitt et al. (1996) (□) and peNDF% as CPM Dairy (1998) (●)

*Effect of rumen pH upon rumen microbial parameters*

Predicted rumen pH has subsequently been used to modify maximum microbial yield (YG1) of NSC bacteria, instead of using eNDF% directly. Adjustments to microbial maintenance (KM1) and realised microbial yield (Y) based on predicted rumen pH suggested by Pitt et al. (1995) have been adopted, and also consequential corrections to the degradation rates  $Kd_4$ ,  $Kd_5$  and  $Kd_6$  for both SC and NSC CHO.

*SC microbial maintenance.* Pitt et al. (1996) suggested a linear equation (19) to modify slightly microbial maintenance (KM1) for SC bacteria according to predicted pH value from equation (8):

$$\text{New KM1} = 0.1409 - 0.0135\text{pH} \quad (19)$$

Declines in rumen pH value increase KM1 slightly from 0.05 at the normal pH 6.7, rising to 0.064 at pH 5.7. This equation has been retained unmodified in the CPM Dairy version of CNCPS, as the revised equation (17) for the prediction of rumen pH gives closely similar values to the earlier equation based on cNDF%.

*Maximum SC microbial yield.* Both published versions of the CNCPS contain equation (9) above to reduce maximum microbial yield (YG) of SC and NSC bacteria when diet eNDF values fall below a minimum figure of 20% eNDF, not predicted pH value. A later version of the model, CNCPSREV, includes an equation (20), which reduces YG1 values for SC bacteria according to the pH value predicted by equation (16) above, replacing the earlier equation (9) based directly on diet eNDF%:

$$\text{For eNDF\%} \leq 30\%, \text{ new YG1} = 0.0752\text{pH} - 0.1058 \quad (20)$$

which gives 0.398 g/gCHO at pH 6.7, declining to 0.3345 at pH 6.0, a decline of only 13% compared to 37% with the original equation (9). Equation (20) has been retained in the CPM Dairy version of the CNCPS, as the numerical value of pH predicted from equation (17) is close to that previously obtained from equation (16).

*Realised SC microbial yield.* Pitt et al. (1996) specified the effects of predicted pH value upon the yield of SC bacteria (Y1) by a correction factor (r) defined by an exponential equation (21) driven by pH value, predicted from eNDF% as equation (8):

$$\text{For Y1, } r = \{1 - \exp[-5.624(\text{pH} - 5.7)^{0.909}]\} / 0.9968 \quad (21)$$

The identical equation is to be seen in the NRC (1996), beef version of the model, p.122, equation (3), but in the CPM Dairy version of the CNCPS, the power factor of 0.909 has been omitted from the term (pH - 5.7), where pH is now predicted from peNDF% as equation (17), whilst the other constants are retained.



The effect is very small ( $<0.01$ ) but shifts the pH value at which a decline in Y1 starts to 6.7 not 6.9 as previously.

*Realised NSC microbial yield.* Pitt et al. (1996) also specified the effects of predicted pH value upon the yield of NSC bacteria (Y2 and Y3) by their equation (7), similar in structure to that given for SC bacteria, equation (21), but with different constants:

$$\text{For Y2 and Y3, } r = \{1 - \exp[-0.693(\text{pH} - 4.5)^{1.732}]\} / 0.9373 \quad (22)$$

This equation predicts a curvilinear reduction in Y2, Y3 values to 0.7 of their starting value at pH 6.7, but does not appear to feature in the CPM Dairy version of the CNCPS. Correction factors ( $r$  for Y1, Y2), modified microbial maintenance (KM1) and maximum microbial yields (YG1, YG2), using the relevant functions for SC and NSC bacteria, are shown in Figure 4.

*Liquid outflow rate and peptide uptake.* Equation (15) for liquid outflow rate was omitted from NRC (1996), as equation (14) for peptide uptake (PEPUP) was simplified to  $\text{PEPUP} = \text{RDPEP}$ . Equation (15) has been retained in the CPM Dairy

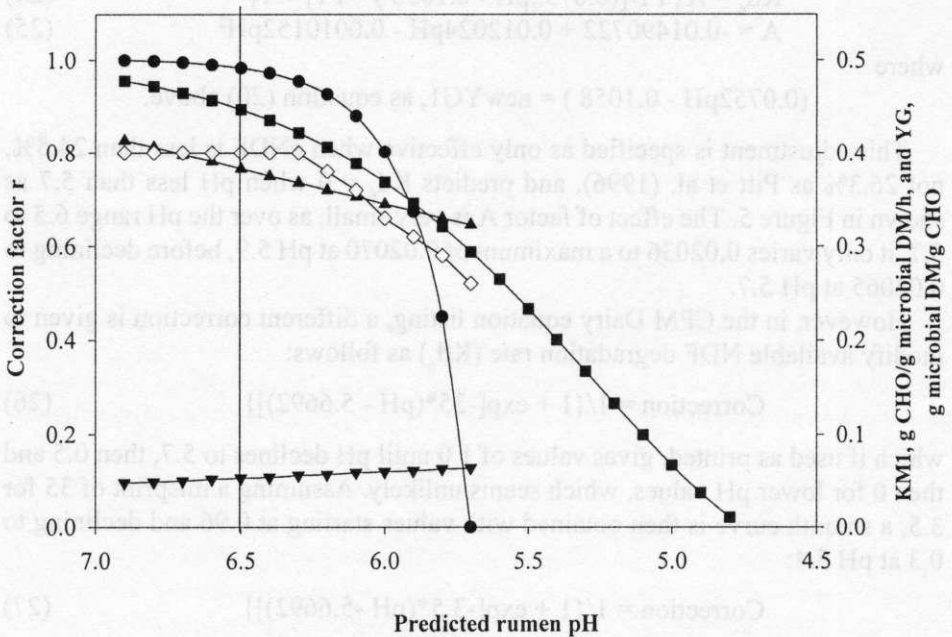


Figure 4. Effect of predicted pH upon microbial yields. Symbols: (●) correction factor for yield of SC bacteria as Pitt et al. (1996); (■) correction factor for yield of NSC bacteria as Pitt et al. (1996); (▼) SC microbial maintenance as Pitt et al. (1996); (▲) maximum microbial yield as CNCPSREV, equation (20) in text; (◇) maximum microbial yield from eNDF < 20%, as Russell et al. (1992) and NRC (1996), equation (9) in text

version of the CNCPS, although recalculated to give percent per hour (%/h), not decimal per day.

*Rate of carbohydrate degradation.* Because of the effects of rumen pH on microbial maintenance and maximum and realised microbial yield described above by equations (19) - (22), the effective rates of degradation of the SC ( $Kd_6$ ) and NSC ( $Kd_4$  and  $Kd_5$ ) carbohydrate fractions must be adjusted to match these new values. This can be done by substituting in a rearranged equation (2), as follows for the SC CHO fraction:

$$Kd_6 = (KM1*Y1*YG1)/(YG1 - Y1) \quad (23)$$

Equation (4) of Pitt et al. (1996) has added the term  $KM1*YG1$  to equation (23), which is not explained. As  $KM1$  is set at 0.05 and  $YG1$  at 0.40, the value of that term is  $0.05*0.4 = 0.02$ , identical to an unexplained term of 0.02 in equation (2) of NRC (1996), p.122.

For eNDF values greater than 24.5%, both NRC (1996) and CNCPSREV give two equations to modify  $Kd_6$  according to predicted rumen pH:

$$Kd_6 = A \{ Y1 / [(0.0752pH - 0.1058) - Y1] + 1 \} \quad (24)$$

$$A = -0.01490722 + 0.012024pH - 0.0010152pH^2 \quad (25)$$

where

$$(0.0752pH - 0.1058) = \text{new}YG1, \text{ as equation (20) above.}$$

This adjustment is specified as only effective when eNDF is less than 24.5%, not 26.3% as Pitt et al. (1996), and predicts  $Kd_6 = 0$  when pH less than 5.7 as shown in Figure 5. The effect of factor A is very small, as over the pH range 6.5 to 5.7, it only varies 0.02036 to a maximum of 0.02070 at pH 5.9, before declining to 0.02065 at pH 5.7.

However, in the CPM Dairy equation listing, a different correction is given to modify available NDF degradation rate ( $Kd_6$ ) as follows:

$$\text{Correction} = 1 / \{ 1 + \exp[-35*(pH - 5.6692)] \} \quad (26)$$

which if used as printed, gives values of 1.0 until pH declines to 5.7, then 0.5 and then 0 for lower pH values, which seems unlikely. Assuming a misprint of 35 for 3.5, a smooth curve is then obtained with values starting at 0.96 and declining to 0.3 at pH 5.4:

$$\text{Correction} = 1 / \{ 1 + \exp[-3.5*(pH - 5.6692)] \} \quad (27)$$

Assuming a maximum value for  $Kd_6$  of 0.06 /h, the effect of this correction is also shown in Figure 5. The curve does not now have an unlikely maximum of 0.073 at pH 6.3 nor does it decline to zero at pH 5.7 as predicted by the NRC (1996) function, but predicts a value for  $Kd_6$  of 0.03 /h (0.5 of start value) at pH 5.7, reaching a value of nearly zero at pH 4.3.

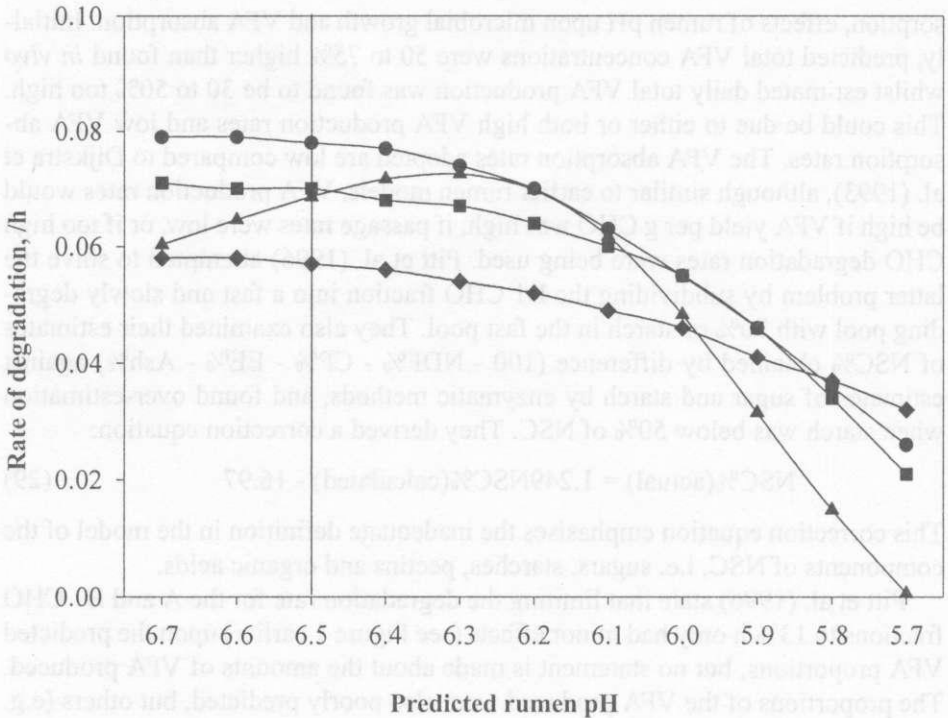


Figure 5. Effect of rumen pH on rate of degradation (Kd6) of cell walls (SC), with the original value of Kd6 taken as 0.06. Symbol: (●) Pitt et al. (1996) equations (1), (2), (3) and (4); (■) CNCPSREV spreadsheet ex Cornell as at 10/97; (▲) NRC (1996), p. 122, equations (1), (2), (3), (4) and (5); (◆) CPM Dairy equation listing, equation (26) in text

#### Prediction of VFA production

The current CNCPS model does not include a quantitative representation of VFA in the rumen, although the well recognised acronym VFA appears in an equation defining the quantitative sum of ruminally degraded carbohydrate (RDC) fractions A, B1 and B2:

$$\text{VFA} = \text{RDCA} + \text{RDCB1} + \text{RDB2} \quad (28)$$

This equation can easily be misunderstood, as it omits the substantial losses of carbon dioxide and methane arising from microbial fermentation of both SC and NSC carbohydrates. Pitt et al. (1995; 1996) have developed a VFA sub-model of the CNCPS model using the same feed description and inputs. Their sub-model predicts acetate, propionate, butyrate, lactate and methane production, VFA ab-

sorption, effects of rumen pH upon microbial growth and VFA absorption. Initially, predicted total VFA concentrations were 50 to 75% higher than found *in vivo* whilst estimated daily total VFA production was found to be 30 to 50% too high. This could be due to either or both high VFA production rates and low VFA absorption rates. The VFA absorption rates adopted are low compared to Dijkstra et al. (1993), although similar to earlier rumen models. VFA production rates would be high if VFA yield per g CHO was high, if passage rates were low, or if too high CHO degradation rates were being used. Pitt et al. (1996) attempted to solve the latter problem by subdividing the B1 CHO fraction into a fast and slowly degrading pool with 70% of starch in the fast pool. They also examined their estimates of NSC% obtained by difference (100 - NDF% - CP% - EE% - Ash%) against estimates of sugar and starch by enzymatic methods, and found over-estimation when starch was below 50% of NSC. They derived a correction equation:

$$\text{NSC\%}(\text{actual}) = 1.249\text{NSC\%}(\text{calculated}) - 16.97 \quad (29)$$

This correction equation emphasises the inadequate definition in the model of the components of NSC, i.e. sugars, starches, pectins and organic acids.

Pitt et al. (1996) state that limiting the degradation rate for the A and B1 CHO fractions to 13%/h only had minor effects (see Figure 1 earlier) upon the predicted VFA proportions, but no statement is made about the amounts of VFA produced. The proportions of the VFA produced were also poorly predicted, but others (e.g. Neal et al., 1992) have encountered the same problem. This may be due to reliance on the stoichiometric relationships of Murphy et al. (1982) and Murphy (1984). Pitt et al. (1996) also concluded that the CNCPS model was using estimated ruminal B1 degradation rates substantially greater than actual degradation rates. Gas production *in vitro* estimates of nutrient degradation rates (Schofield and Pell, 1995) also suggest lower rates of fermentation for the A and B1 fractions of carbohydrate than adopted in the model. However, lowering the B1 fraction degradation rate significantly would lower predicted NSC microbial synthesis in the CNCPS model.

#### *Prediction of methane production*

The original series of papers and the current software version of the CNCPS model do not predict methane or carbon dioxide outputs from the rumen, although methane losses are included (plus urine losses) in the calculation of diet ME values from DE value. After total digested organic matter (or in this case TDN) has been calculated, TDN is converted to DE by using 4.4 kcal/g TDN, and then to ME by applying a DE/ME coefficient of 0.82 to allow for losses of both methane and urine. Pitt et al. (1996) have published a first attempt at including such a sub-model. The stoichiometric procedure of Wolin (1960) was used, based on the cal-

culated production of propionate from the microbial degradation of A, B1 and B2 CHO fractions. This was then adjusted for rumen pH value, on the basis that at pH 6.0, methane production was found to be nil by Strobel and Russell (1986). Calculated methane production was within  $\pm 15\%$  of the levels measured by the latter workers at a rumen pH of 6.7. The amounts of propionate were calculated using the empirical stoichiometric relationships of Murphy et al. (1982) and Murphy (1984) commented on in the discussion of prediction of VFA production above.

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## STRESZCZENIE

### Krytyka „Cornell Net Carbohydrate and Protein System” ze szczególnym odniesieniem do bydła mlecznego. 1. Model żywca

Cornell Net Carbohydrate and Protein System (CNCPS) jest przede wszystkim modelem określającym podaż składników pokarmowych, ponieważ nie uwzględnia wykorzystania wchłoniętych składników pokarmowych i różni się od systemów energii netto NRC (1988) i białka dostępnego NRC (1985) do obliczania zapotrzebowania zwierząt na energię, białko i aminokwasy (AA). Model CNCPS uwzględnia czynniki dotyczące przemian żwaczowych, których nie uwzględniają inne opublikowane modele określające zapotrzebowania na energię i białko, zwłaszcza tempo rozkładu węglowodanów, przewidywanego pH oraz bilansu azotu i peptydów w żwacu. Model nie określa proporcji lotnych kwasów tłuszczowych (VFA) ani produkcji metanu. Zakłada on, że rozwój mikroorganizmów zależy od tempa rozkładu węglowodanów, podczas gdy inne modele matematyczne odnoszą wzrost masy bakteryjnej w żwacu do stężenia składników pokarmowych w płynnej treści żywca i wymagają określenia objętości żywca i masy drobnoustrojów. Wydajność produkcji drobnoustrojów rozkładających strukturalne węglowodany (SC) nie jest ograniczona lub uzależniona od ilości dostępnego w żwacu amoniaku, w wyniku czego obliczenia stechiometryczne mogą prowadzić do otrzymania niepewnych ilości białka drobnoustrojów i ujemnego poziomu amoniaku w żywa-

czu. Tylko określona ilość dostarczanych peptydów modyfikuje wzrost bakterii rozkładających niestrukturalne węglowodany (NSC). Przyjęte tempo przepływu cząstek stałych jest niskie przy wysokim poziomie żywienia w porównaniu z ARC (1984) i AFRC (1992), w wyniku czego oszacowany udział masy organicznej strawionej w żwaczu jest większy (około 0,75) niż średnie wartości 0,65 przyjęte przez ARC (1980). Model ten nie uwzględnia wpływu tempa przepływu płynnej treści żwacza na wypływ NPN, AA i rozpuszczalnego białka, pektyn, cukrów, kwasów organicznych i VFA. W tym modelu przyjęto, że jedynie peptydy zależą od wypływu płynnej treści ze żwacza. Proponowana szybkość rozkładu węglowodanów frakcji A i B1 jest bardzo duża, przewyższająca możliwe tempo wzrostu drobnoustrojów, a więc synteza mikroorganizmów nie odpowiada znacznej zmienności przy takim wysokim tempie rozkładu. Przyjęta maksymalna wartość wydajności produkcji mikroorganizmów z węglowodanów strukturalnych i niestrukturalnych obniża wartość produkcji bakterii żwaczowych o 20% na potrzeby wzrostu pierwotniaków, jednakże pierwotniaki nie są wliczane do puli wypływającego azotu AA mikroorganizmów. Do wartości ubytku skrobi w żwaczu nie wprowadzono poprawek na ilość skrobi pobieranej przez pierwotniaki i jej ponowne pojawienie się w jelicie; nie uwzględniono też udziału pierwotniaków w przemianach tłuszczu w żwaczu. Przewidywana wartość TDN dla pasz zielonych jest powiązana głównie z tempem rozkładu ścian komórkowych roślin. Tylko jeden czynnik dotyczący diety, efektywny rozkład neutralnego włókna detergentowego (eNDF%), definiuje bądź modyfikuje maksymalną produkcję mikroorganizmów i ich utrzymanie, rzeczywistą wydajność mikroorganizmów i tempo rozkładu SC i NSC. Konsekwencją tego jest to, że na ilość dostarczonej krowie energii i białka wpływa parametr eNDF, kiedy zawartość suchej masy w diecie wynosi poniżej 25%.