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Accounting for the effects of a ruminal nitrogen deficiency within the structure of the Cornell Net Carbohydrate and Protein System¹

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ABSTRACT: The Cornell Net Carbohydrate and Protein System (CNCPS) prediction of fiber digestion and microbial mass production from ruminally degraded carbohydrate has been adjusted to accommodate a ruminal N deficiency. The steps for the adjustment are as follows: 1) the ruminal available peptide and ammonia pools are used to determine the N allowable microbial growth; 2) this value is subtracted from the energy allowable microbial growth to obtain the reduction in microbial mass; 3) this mass reduction is allocated between pools of bacteria digesting fiber (FC) and nonfiber (NFC) carbohydrate according to their original proportions in the energy allowable microbial growth; 4) the reduction in fermented FC is computed as the FC bacterial mass reduction divided by its yield (g bacteria/g FC digested); and 5) this reduction is added to the FC

fraction escaping the rumen. Five published studies included information that allowed us to evaluate the response of animals to added dietary N. These evaluations compared observed and CNCPS-predicted ADG with and without this adjustment. The adjustment decreased the CNCPS overprediction of ADG from 19.2 to 4.7%, mean bias declined from .16 to .04 kg/d, and the r^2 of the regression between observed and metabolizable energy (ME) or metabolizable protein allowable ADG was increased from .83 to .88 with the adjustment. When the observed dry matter intake was regressed against CNCPS-predicted DMI with an adjustment for reduction in cell wall digestibility, the r^2 was increased from .77 to .88. These results indicated the adjustment for ruminal nitrogen deficiency increased the accuracy of the CNCPS model in evaluating diets of growing animals when ruminally degraded N is deficient.

Key Words: CNCPS, Microbial Growth, Modeling, Ruminal Nitrogen Deficiency

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Introduction

The rumen typically operates as an energy-limited system, but diets can be so low in degradable crude protein that microbial growth is limited by N. Ruminal bacteria respond differently to N sources and N limitation. Cellulolytic ruminal bacteria need ammonia as an N source, have little capacity to utilize amino N, are unable to ferment fiber when ammonia is depleted, and do not produce ammonia from amino N sources (Bryant and Robinson, 1961; Allison, 1969; Bryant, 1973). Some hemicellulose-digesting ruminal bacteria are stimulated by amino N, but even these species are primarily

dependent on ammonia as an N source (Gill and King, 1958). Many nonfiber digesting ruminal bacteria prefer amino N to ammonia (Allison, 1969; Van Kessel and Russell, 1996), and some can even produce ammonia from an amino N source (Bladen et al., 1961).

The Cornell Net Carbohydrate and Protein System (CNCPS) uses rates of carbohydrate fermentation to estimate microbial growth in the rumen (Russell et al., 1992). Growth yields are adjusted to accommodate maintenance energy expenditures, peptide availability, and pH, but the CNCPS does not have a provision for N limitation per se. Ruminal N limitation can decrease microbial flow (g bacteria/d) from the rumen (Satter and Slyter, 1974; Kang-Meznarich and Broderick, 1980; NRC, 1985), depress fiber fermentation (Russell et al., 1992), and reduce DMI (NRC, 1985, 1987; Van Soest, 1994, chap. 18 and 21), but the CNCPS did not have equations to accommodate these effects.

Most systems of ration formulation for cattle (ARC, 1980; NRC, 1989, 1996; CSIRO, 1990; INRA, 1989; AFRC, 1993) acknowledge the importance of supplying adequate N as well as energy. However, none of them has a systematic method of discounting ruminal activ-

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ity, microbial growth, and DMI when ruminal N is depleted.

Our objectives were 1) to devise equations that could quantify the impact of N limitation on microbial protein production, fiber digestion, and DMI and 2) to validate these CNCPS adjustments with experimental data with cattle responses to added dietary N.

Materials and Methods

Model Development

Figure 1 shows the algorithmic adjustments in the CNCPS structure used to improve predictions of microbial yield and cell wall digestion when ruminal N is deficient. The CNCPS microbial growth equations and their definitions as published by level 2 of the NRC (1996) model were used to adjust the rumen submodel. Definitions used for this submodel are shown in Table 1. In order to determine the total ruminal N balance, the first step is to compute the microbial growth from ruminally degraded fiber carbohydrate (**EFCBact**, g bacteria/d) and nonfiber carbohydrate (**ENFCBact**, g bacteria/d) when energy is limiting bacterial growth (**EAllowableBact**, g bacteria/d; Eq. [1]) as described by Russell et al. (1992):

$$EAllowableBact = EFCBact + ENFCBact \quad [1]$$

Because the FC and NFC bacteria are assumed to contain 10% N (Russell et al., 1992) by the CNCPS model, **EAllowableBact** multiplied by .1 gives the bacte-

ria requirement for N. If the ruminal N balance is negative (the requirement is higher than the sum of dietary supply and recycled N), microbial growth is decreased (ARC, 1980). Nitrogen-allowable bacterial growth (**NAllowableBact**, g bacteria/d; Eq. [2]) is the sum of ruminally degraded true protein N (**PeptideUptakeN**, g N/d), nonprotein N from the diet (**DegradedDietN**, g N/d), and recycled N (**RecycledN**, g N/d) divided by the bacterial nitrogen concentration (10%):

$$NAllowableBact = \frac{(PeptideUptakeN + DegradedDietN + RecycledN)}{.1} \quad [2]$$

If fermentable energy is the first-limiting nutrient, microbial protein production is dictated by energy, not N, available in the rumen, and there is no need to reduce microbial yield. However, if N is limiting then microbial yield is reduced (**BactRed**, g bacteria/d) by the difference between the energy allowable and the protein allowable bacterial growth (Eq. [3]):

$$BactRed = EAllowableBact - NAllowableBact \quad [3]$$

Some ruminal bacteria can continue to ferment carbohydrates even if N is limiting and growth is not possible (Van Kessel and Russell, 1996). Energy spilling can be caused by futile cycles of potassium, ammonium, or protons through the cell membrane (Russell and Cook, 1995). Continuous culture studies with N-limited mixed ruminal bacteria indicated NFC bacteria fermented abnormally large amounts of glucose or starch, but FC bacteria could not spill energy (Van Kessel and Russell, 1993). Because NFC bacteria can “spill energy” when N is limiting, NFC digestion is not affected, but N limitation has a negative effect on FC digestion (Russell, 1998).

Within the CNCPS, the overall FC digestion is dependent on FC digestion rate of each feed; therefore, the effect of the nitrogen deficiency must be determined for each feed in the diet. The reduction in bacterial yield for the j^{th} feed (Eq. [4]) is computed using the **EBactRatio** _{j} (Eq. [5]).

$$NAllowableBact_j = NAllowableBact \times EBactRatio_j \quad [4]$$

$$EBactRatio_j = \frac{EFCBact_j + ENFCBact_j}{EFCBact + ENFCBact} \quad [5]$$

where **EFCBact** (g bacteria/d) is the sum of **EFCBact** _{j} and **ENFCBact** (g bacteria/d) is the sum of **ENFCBact** _{j} for all feeds.

Then, the bacterial yield reduction for each feed (**BactRed** _{j} , g bacteria/d) (Eq. [6]) is computed for each feed from its energy allowable growth of FC (**EFCBact** _{j}) and NFC (**ENFCBact** _{j}), and N allowable growth (**NAllowableBact** _{j}).

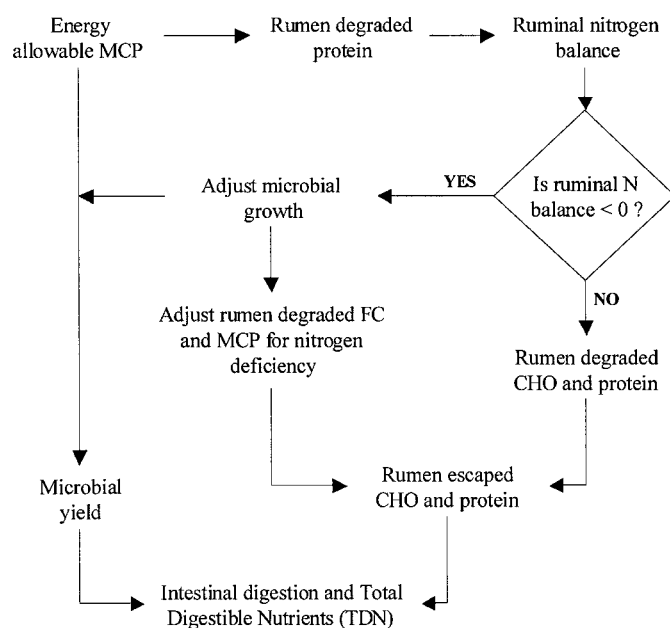


Figure 1. Process for adjusting microbial crude protein (MCP) yield and ruminal degradation of fiber carbohydrate predictions for a ruminal N deficiency. CHO = carbohydrate and FC = fiber carbohydrate.

$$\text{BactRed}_j = (\text{EFCBact}_j + \text{ENFCBact}_j) - \text{NAllowableBact}_j \quad [6]$$

The reduction in FC bacterial yield (**FCBactRed_j**, g bacteria/d) due to a ruminal N deficiency is then computed (Eq. [7]) for each feed from the reduction in bacteria produced allocated to the feed and the **EFCBactRatio_j** when N is not limiting (Eq. [8]).

$$\text{FCBactRed}_j = \text{BactRed}_j \times \text{EFCBactRatio}_j \quad [7]$$

$$\text{EFCBactRatio}_j = \frac{\text{EFCBact}_j}{\text{EFCBact}_j + \text{ENFCBact}_j} \quad [8]$$

As discussed before, N limitation is likely to decrease carbohydrate fermentation as well as FC bacterial growth. *Fibrobacter succinogenes* was unable to ferment “excess cellobiose” when N was limiting (Maglione and Russell, 1997), and mixed-culture studies indicated

that organic matter digestion was also reduced by N limitation (Milton et al., 1997a,b). To account for this effect, **FCBactRed_j** is multiplied by the inverse of its yield (**Y_{1j}**, g bacteria/g FC digested) to estimate the amount of FC for each feed that is not degraded (**FCRed_j**, g FC/d) (Eq. [9]):

$$\text{FCRed}_j = \frac{\text{FCBactRed}_j}{Y_{1j}} \quad [9]$$

In this case, we have simply used the reduction in FC bacteria to estimate additional FC passage from the rumen. The reduction in FC bacteria was computed in Eq. [7], and it dictates the FC escape (not the converse).

The last step is to adjust the ruminally degraded carbohydrate B2 (**RDCB_{2j}**, g/d; Eq. [10]) and ruminal escape carbohydrate B2 (**RECB_{2j}**, g/d; Eq. [11]). The **RDCB_{2j}** and **RECB_{2j}** were calculated as described by Pitt et al. (1996). No feedback adjustment is performed

Table 1. Description of the acronyms used in the nitrogen adjustment submodel

Acronym	Description
BactRed	Total amount of bacteria growth reduction due to ruminal N deficiency, g of bacteria/d
BactRed _j	Amount of bacteria growth reduction due to ruminal N deficiency for the j th feed, g of bacteria/d
DegradedDietN	Amount of ruminally degraded N provided by the diet, g of N/d
EAllowableBact	Total bacteria growth allowable by ruminal available energy, g of bacteria/d
EBactRatio _j	Proportion of fiber carbohydrate and nonfiber carbohydrate bacteria for the j th feed to the total diet bacteria based on energy availability in the rumen
EFCBact	Total diet energy allowable fiber carbohydrate bacteria growth, g of bacteria/d
EFCBact _j	Energy allowable fiber carbohydrate bacteria growth for the j th feed, g of bacteria/d
EFCBactRatio _j	Proportion of fiber carbohydrate bacteria to the total bacteria growth for the j th feed based on energy availability in the rumen
ENFCBact	Total diet energy allowable nonfiber carbohydrate bacteria growth, g of bacteria/d
ENFCBact _j	Energy allowable nonfiber carbohydrate bacteria growth for the j th feed, g of bacteria/d
FCBactRed _j	Amount of fiber carbohydrate bacteria growth reduction for the j th feed, g of bacteria/d
FCRed	Total fiber carbohydrate not degraded due to fiber carbohydrate bacteria reduction growth, g of fiber carbohydrate/d
FCRed _j	Fiber carbohydrate not degraded due to fiber carbohydrate bacteria reduction growth for the j th feed, g of fiber carbohydrate/d
FCRedRatio	Proportion of fiber carbohydrate not degraded because of N limitation, %
NAllowableBact	Total bacterial growth allowable by diet ruminal degradable N intake, g of bacteria/d
NAllowableBact _j	Bacterial growth allowable by ruminal degradable nitrogen intake for the j th feed, g of bacteria/d
PeptideUptakeN	Amount of nitrogen from degraded peptide used by ruminal bacteria, g of N/d
RDCB _{2j}	Rumen degraded carbohydrate B2 for the j th feed, g of carbohydrate/d
RECB _{2j}	Rumen escaped carbohydrate B2 for the j th feed, g of carbohydrate/d
RecycledN	Amount of nitrogen recycled through the blood as ammonia, g of N/d
Y _{1j}	Microbial yield for fiber carbohydrate bacteria for j th feed, g bacteria/g fiber carbohydrate digested in the rumen

Table 2. Statistical summary of the trials used in the model evaluation^a

Statistic	CP, %	RNB, ^b %	SBW, kg	ADG, kg/d	DMI, kg/d
Mean	11.4	-12.9	266	.8	6
SD	2.7	8	85.5	.4	1.8
Minimum	7.5	-32.9	92	.1	2.1
Maximum	15.4	-.4	376	1.3	8.5

^aData includes 29 treatment groups from Fox and Cook (1977), Boin and Moura (1977), Danner et al. (1980), Lomas et al. (1982), and Abdalla et al. (1988). SD = standard deviation.

^bRNB = ruminal N balance (% of N required to attain zero ruminal N balance).

in the EAllowableBact calculation due to the change in RDCB2 because the submodel calculates microbial growth based on the first-limiting nutrient in the rumen for bacteria growth.

$$\text{Adjusted RDCB}_j = \text{RDCB}_j - \text{FCRed}_j \quad [10]$$

$$\text{Adjusted RECB}_j = \text{RECB}_j + \text{FCRed}_j \quad [11]$$

The percentage of carbohydrate B2 not degraded in the diet as a result of the ruminal N deficiency (**FCRedRatio**, %; Eq. [12]) is predicted by dividing the sum of FC reduction of all feeds by the total RDCB2 estimated from degradation and passage rates (NRC, 1996). This value is used to predict the reduction of DMI due to a reduction in fiber degradation, consequently decreasing fiber passage rate (Van Soest, 1994, chap. 21):

$$\text{FCRedRatio} = \frac{100 \times \text{FCRed}}{\text{RDCB}_2} \quad [12]$$

where FCRed is the sum of FCRed_j and RDCB2 is the sum of RDCB_{2j} for all feeds.

Adjusted Model Evaluation

The model used in this evaluation was CNCPS version 4.0 (Fox et al., 2000), which contains rumen fermentation and animal growth equations similar to the version used in the development of the NRC (1996) model level 2.

Five published studies were used to evaluate this model with the N-limitation adjustment in the rumen submodel. Only published studies that included diets predicted to have a ruminal N deficiency and that gave adequate characterization of animals and feeds needed to obtain inputs for the CNCPS were selected. The CP, DMI, ADG, and body weights of animals in these studies are summarized in Table 2. Reported final shrunk body weight (**FSBW**) and body fat percentage were used to compute FSBW at 25, 27, or 28% body fat composition, using the relationship of 19 kg of empty body weight (**EBW**) for every percentage unit of empty body fat change (Tylutki et al., 1994).

The study of Boin and Moura (1977) used Nellore bulls and had two treatments, ad libitum and restricted

DMI (75 to 80% of ad libitum). The diets contained corn silage (50%), corn grain (30%), and cottonseed meal (20%). Animals in the ad libitum and restricted intake treatments had average shrunk body weight (**SBW**) of 266 and 246 kg, respectively, and the FSBW at 28% body fat were 550 and 600 kg, respectively. Corn silage was characterized as containing 25% corn grain with a 50% intestinal digestibility of carbohydrate B1 fraction (C. Boin, personal communication).

The study of Fox and Cook (1977) used Charolais crossbred steer calves that were fed corn silage or corn silage treated with ammonia-mineral suspension (11.1% CP), aqueous ammonia (12.7% CP), or anhydrous ammonia (10.8% CP). The control diet (corn silage only) was fed alone or supplemented with soybean meal and minerals to a similar CP (11.5%). Average shrunk body weights ranged from 334 to 347 kg, and the FSBW at 28% body fat was 700 kg.

The study of Danner et al. (1980) used Hereford heifer calves averaging 283 kg fed corn silage, corn grain, and soybean meal in varying proportions to provide two energy levels (both having 10.9% CP). All animals received monensin supplement at a level of 33 ppm in the diet DM. The FSBW at 28% body fat were computed to be 376 and 297 kg for low and medium energy level treatments, respectively.

In the first trial of Lomas et al. (1982), Charolais crossbred steer calves with an average SBW of 334 to 346 kg were fed corn silage treated at the time of ensiling either with ammonia-mineral suspension (45.29 g/kg DM of corn silage; 11.1% CP), aqueous ammonia (38.11 g/kg DM; 12.7% CP), or anhydrous ammonia (7.55 g/kg DM; 10.8% CP). The reported mean FSBW at 27% body fat was 540 kg. In a second trial, Hereford steer calves and Charolais crossbred steer calves averaging 270 to 335 kg of SBW were fed corn silage only (8% CP) or corn silage treated at the time of ensiling either with anhydrous ammonia at 7.8 g/kg DM (10.3% CP), 10.29 g/kg DM (11.1% CP), or 13.84 g/kg DM (12.3% CP). In a third trial, the cattle were similar to those in trial 2 (SBW of 344 to 381 kg). The diets consisted of corn silage only (7.5% CP), or corn silage treated at the time of ensiling either with anhydrous ammonia at 7.8 g/kg DM (9.5% CP) or 15.6 g/kg DM (12.2% CP). Because no breed effect was observed for Charolais and Hereford animals in trials 2 and 3 (Lomas et al., 1982), a common FSBW at 27% body fat of

488 kg was used. Animals in trials 1 and 2 were implanted initially with Synovex-S and reimplanted after 112 d, whereas those in trial 3 were implanted with Ralgro and reimplanted after 111 d. In trial 3, all diets contained 33 ppm of monensin sodium. The intestinal digestibility of the carbohydrate B1 fraction (mainly starch) was assumed to be 50% because the corn kernels in the silage were whole (appendix table 10, NRC, 1996).

In the study of Abdalla et al. (1988), four treatment groups of Holstein steer calves (averaging 125 to 294 kg) were fed corn silage and minerals (93.3%) or a combination of corn silage (68.7%) and roasted soybeans (25%) to achieve low- (8.3%) and high-protein (15.4%) diets during two consecutive growth periods. In a second trial, the Holstein steer calves fed averaged 92 and 134 kg of SBW in period 1 and from 110 to 188 kg in period 2. Animals were not implanted and the body composition was reported for all treatments.

Statistical Evaluation

Biological models should be compared with observed data to assess robustness, accuracy, and precision (Kohn et al., 1998). Such empirical validations should also include a suitable statistical evaluation (Mitchell and Sheehy, 1997).

The most important characteristic of a model is accuracy. Accuracy can be assessed by computing the average deviations between model prediction and actual observation (Mitchell and Sheehy, 1997). This measure is also called the mean bias (Cochran and Cox, 1957):

$$\text{Mean bias} = \frac{1}{n} \sum_{i=1}^n (\text{predicted}_i - \text{observed}_i)$$

Another measurement of model accuracy is the mean square prediction error (**MSPE**) (Bibby and Toutenburg, 1977):

$$\text{MSPE} = \frac{1}{n} \sum_{i=1}^n (P_i - A_i)^2$$

where n is the number of pairs of model-predicted and observed values being compared and P_i and A_i are the i^{th} model predicted and observed values, respectively.

Comparisons based on the root of MSPE (**RMSPE**) are preferable. The MSPE has been frequently used to address model adequacy, but it has limitations as an indicator of the performance of the model because it removes the negative signs and weights the deviations by their squares, giving more influence to larger deviations (Mitchell and Sheehy, 1997).

The approach we used to evaluate the model performance was the analysis of the regression between observed and model-predicted values, in which observed is the Y-variate and model predicted is the X-variate as described by Mayer and Butler (1993).

Statistical measures of model performance we used were the regression r^2 , mean standard error (**MSE**), slope and intercept confidence intervals (Mitchell, 1997), and the residual plot, which is the residual plotted against regression predicted (Mayer and Butler, 1993). Residual plots were analyzed for outliers and systematic bias (Neter et al., 1996). The slope and intercept confidence interval was used instead of the regression F -test because the test results in ambiguity in plots with much scatter around the line (Mitchell, 1997).

Regression through the origin is a regression in which the intercept is set to be zero and only the slope is parameterized (Neter et al., 1996). The slope of regression when forced through the origin minus 1 has frequently been referred as the model bias. However, regression through the origin was performed only when the intercept of the regular regression did not differ from zero at $P = .05$. When the intercept of the regular regression differed from zero ($P > .05$), the model bias was calculated by dividing the mean of the Y-variate minus the mean of the X-variate by the mean of the X-variate. The use of r^2 as well as other statistics such as the residuals derived from the regression through the origin for comparison purposes is not recommended (Neter et al., 1996).

Another test of model adequacy involved determining the proportion of deviation points (CNCPS model-predicted minus observed) that lie within acceptable limits (Mitchell and Sheehy, 1997). Our limits were established as -0.1 and 0.1 kg/d for ADG and -0.5 and 0.5 kg/d for DMI comparisons.

All the statistical analyses were performed using SAS (1991). Regression parameters were estimated by PROC REG. The regression through the origin was obtained using the NOINT option in PROC REG (SAS, 1991). The statistical comparison between observed and predicted values was performed using the two-sample t -test (SAS, 1991).

In order to evaluate the influence of ruminal N deficiency on microbial growth, and consequently DMI depression (Van Soest, 1994, chap. 21), a multiple regression of predicted DMI and FCRedRatio values on observed DMI was evaluated.

Results and Discussion

Evaluation of Model-Predicted ME or MP Allowable Gain

When cattle diets were deficient in N, CNCPS version 4.0 without the adjustment described often overpredicted performance (Table 3). Overall, CNCPS 4.0 overpredicted ADG by 19.2% ($P < .05$), and the N-limitation adjustment reduced this value to 4.7% ($P > .05$). The mean bias value was also low ($.16$ [$P < .05$] vs $.04$ kg/d [$P > .05$], respectively). The N-limitation adjustment also increased the accuracy (lower RMSPE) of ADG prediction ($.14$ vs $.22$, respectively, with and without the adjustment). There were cases in which ME was

Table 3. Comparison between observed ADG and CNCPS-predicted first-limiting metabolizable energy or metabolizable protein allowable ADG and DMI with and without adjustment for negative ruminal N balance^a

Item	Observed	CNCPS-predicted	
		With	Without
ADG, kg/d			
Mean	.829	.868	.988
Mean bias ^b	—	.039	.16
RMSPE or SD ^c	.371	.138	.222
DMI, kg/d			
Mean	6.017	6.018	6.536
Mean bias ^b	—	.001	.519
RMSPE or SD ^c	1.763	.61	1.142

^aCNCPS = Cornell Net Carbohydrate and Protein System.

^bMean bias is the average of predicted minus observed values. Actual DMI was used for the prediction of ADG.

^cRoot mean square prediction error (RMSPE) for predicted and standard deviation (SD) for observed values.

the first-limiting nutrient and N limitation also caused an overprediction of ME allowable gain because the N limitation reduced FC digestibility. However, the most common overprediction was MP allowable gain.

Regressions of observed vs predicted ADG (first limiting of ME or MP allowable gain) without adjustment for rumen N deficiency had an intercept value that was highly significant ($P < .05$), and the mean bias was .16 kg/d (Table 4). When the N-limitation adjustment was added, the intercept was no longer significant ($P > .05$), the r^2 value was higher (.825 vs .875, respectively), and the MSE was lower (.025 vs .018, respectively), as shown in Table 4.

The CNCPS 4.0 model without the ruminal N deficiency adjustment tended to overpredict ADG at low and high observed ADG (Figure 2A). Therefore, the proportion of deviation points lying within $-.1$ and $.1$ kg/d was only 37.9% (Figure 2B). In contrast, the CNCPS model with the ruminal N deficiency adjustment had an even distribution of points along the unity line and, therefore, did not have any systematic prediction error (Figure 3A). Consequently, the proportion of deviation

points lying within $-.1$ and $.1$ kg/d was higher (62.1%; Figure 3B) than without adjustment.

Figure 4 summarizes the relationship between ruminal N balance (A) and FCRedRatio (B) on ADG (g/d). Figure 4A indicates that animal performance (ADG, g/

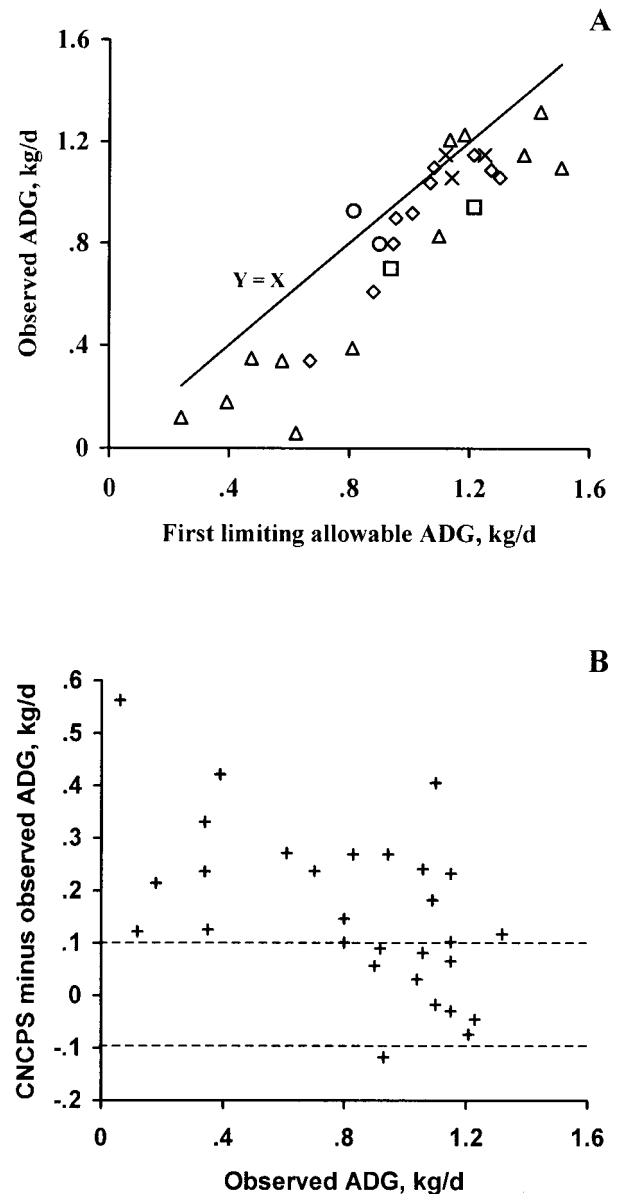


Figure 2. Prediction of ADG (kg/d) by the Cornell Net Carbohydrate and Protein System (CNCPS) without N deficiency adjustment. (A) Relationship between observed (o) ADG and predicted (p) first-limiting metabolizable energy or metabolizable protein allowable ADG (kg/d) not adjusted for a negative ruminal N balance. The data points are Lomas et al. (1982), \diamond ; Boin and Moura (1977), \square ; Abdalla et al. (1988), \triangle ; Fox and Cook (1977), \times ; and Danner et al. (1980), \circ . The regression is $ADG_o = 1.07 \times ADG_p - .2288$, and $r^2 = .83$. (B) Deviation (CNCPS-predicted minus observed ADG) vs observed ADG indicated 37.9% of the points are within the range $-.1$ and $.1$ kg/d.

Table 4. Regression parameters between observed and CNCPS-predicted ADG (kg/d) with and without adjustment for a negative ruminal N balance^a

Adjustment	Intercept	Slope	r^2	MSE
Without	$-.2288 \pm .0982^*$	$1.07 \pm .0948$	82.5%	.025
With	$.035 \pm .0627$	$.9147 \pm .0664$	87.5%	.018
With (origin) ^b	—	$.9487 \pm .0259$	—	.017

^aIntercept was statistically tested whether it differed from 0 and slope whether it differed from 1 using t -test. Values are the mean \pm standard error. CNCPS = Cornell Net Carbohydrate and Protein System.

^bRegression through the origin.

*Statistically different from 0 at $\alpha = .05$.

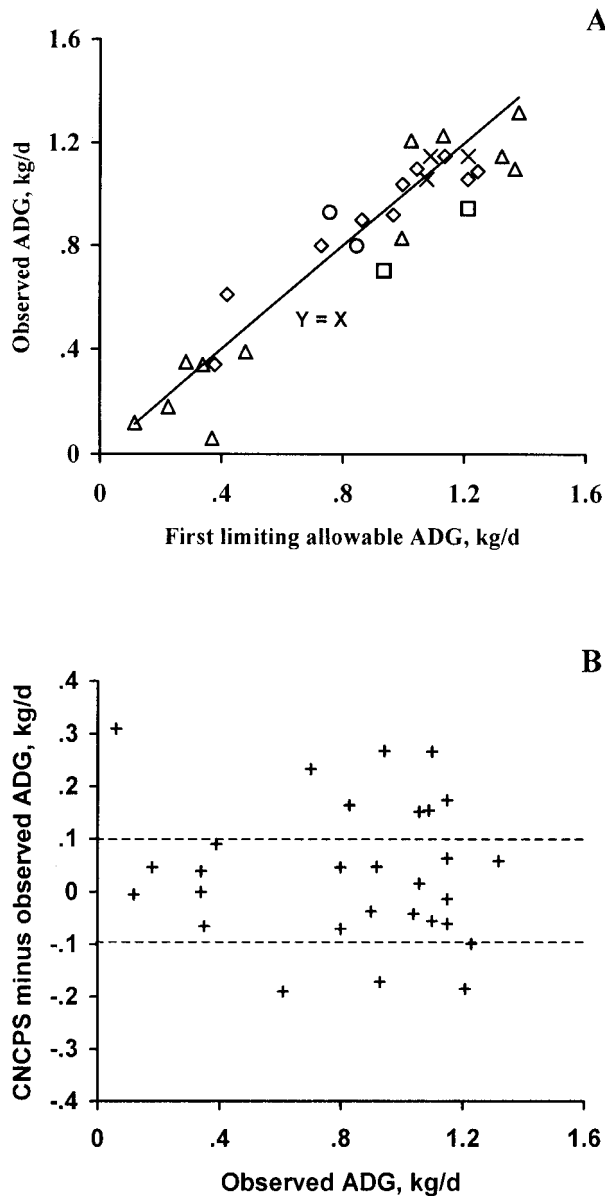


Figure 3. Prediction of ADG (kg/d) by the Cornell Net Carbohydrate and Protein System (CNCPS) with N deficiency adjustment. (A) Relationship between observed (o) ADG and predicted (p) first-limiting of metabolizable energy or metabolizable protein allowable gain (kg/d) adjusted for a negative ruminal N balance. The data points are Lomas et al. (1982), \diamond ; Boin and Moura (1977), \square ; Abdalla et al. (1988), \triangle ; Fox and Cook (1977), \times ; and Danner et al. (1980), \circ . The regression is $ADG_o = .9147 \times ADG_p + .035$, and $r^2 = .88$. The regression through the origin is $ADG_o = .9487 \times ADG_p$. (B) Deviation (CNCPS-predicted minus observed gain) vs observed ADG indicated 62.1% of the points are within the range $-.1$ and $.1$ kg/d.

d) was improved with increasing levels of urea in the diet until the ruminal N balance was close to zero (Y_{max} occurred at $.6\%$ of required ruminal N). The pattern of the regression suggests that a further increase in

A ruminal N would not increase animal performance. This lack of animal response is likely to occur due to the lack of available ruminally degraded carbohydrate to support microbial growth in forage-based diets, not dietary N (Van Soest, 1994, chap. 18). This is supported by results observed by Shain et al. (1998), who found that adding urea (DM basis) at $.88$, 1.34 , and 1.95% did not improve ADG. Milton et al. (1997b) also did not

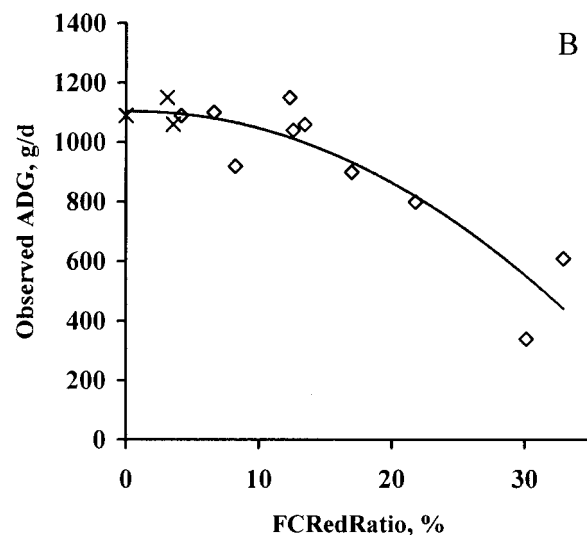
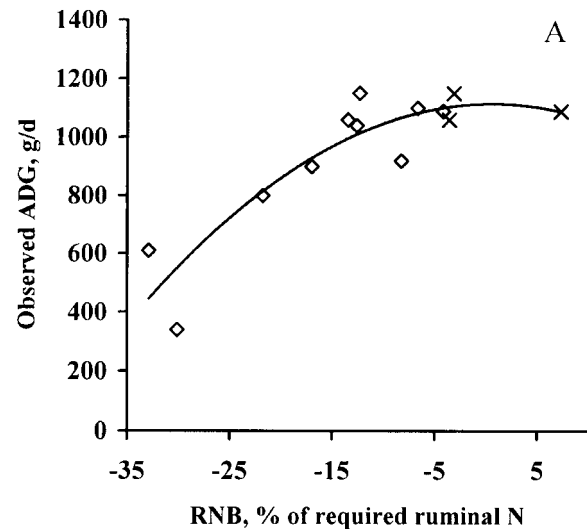


Figure 4. Relationship of observed (o) ADG (g/d) and (A) predicted (p) ruminal N balance (RNB, % of required ruminal N to attain balance of zero) and (B) reduction in fiber digestibility (%) by the Cornell Net Carbohydrate and Protein System (CNCPS) for animals fed corn silage diets only. (A) The equation is $Y = 1114 + .79X - .595X^2$ with an R^2 of $.82$. (B) The equation is $Y = 1102 + .83X - .636X^2$ with an R^2 of $.82$. The data points are from Lomas et al. (1982), \diamond and Fox and Cook (1977), \times . FCRedRatio = fiber carbohydrate reduction ratio (%).

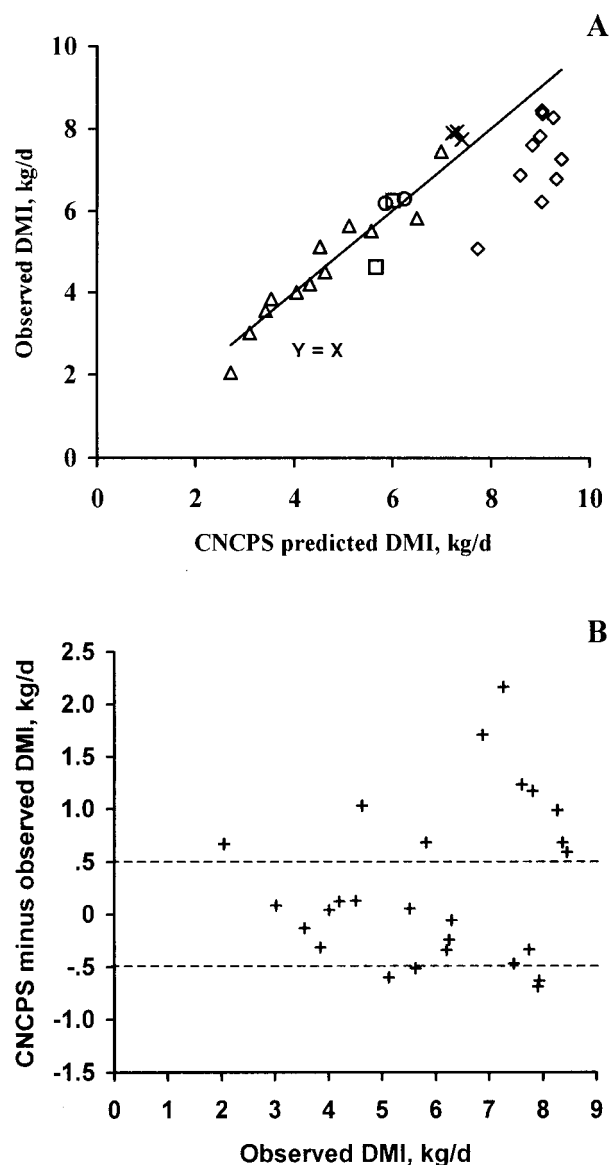


Figure 5. Prediction of DMI by the Cornell Net Carbohydrate and Protein System (CNCPS) without N deficiency adjustment. (A) Relationship between observed (o) DMI and CNCPS-predicted (p) DMI (kg/d) not adjusted for the reduction of fiber carbohydrate degradation. Data were taken from Lomas et al. (1982), \diamond ; Boin and Moura (1977), \square ; Abdalla et al. (1988), \triangle ; Fox and Cook (1977), \times ; and Danner et al. (1980), \circ . The regression is $DMI_o = .7192 \times DMI_p + 1.3166$, and $r^2 = .77$. (B) Deviation (CNCPS-predicted minus observed DMI) vs observed DMI indicated 41.4% of the points are within the range $-.5$ and $.5$ kg/d.

observe a response to a dietary urea level higher than .5%. Additionally, Thomas et al. (1984) reported no animal performance improvement when urea level was higher than .7%.

In a similar way, Figure 4B results were obtained regressing ADG (g/d) on the reduction in fiber digestibil-

ity (Eq. [12]). This figure indicated that increasing the amount of fiber not degraded (decreasing fiber digestibility) had a negative impact on animal performance (ADG, g/d), which is expected once less energy is being obtained from fiber degradation (Van Soest, 1994, chap. 18). In a study of beef steers consuming tallgrass prairie

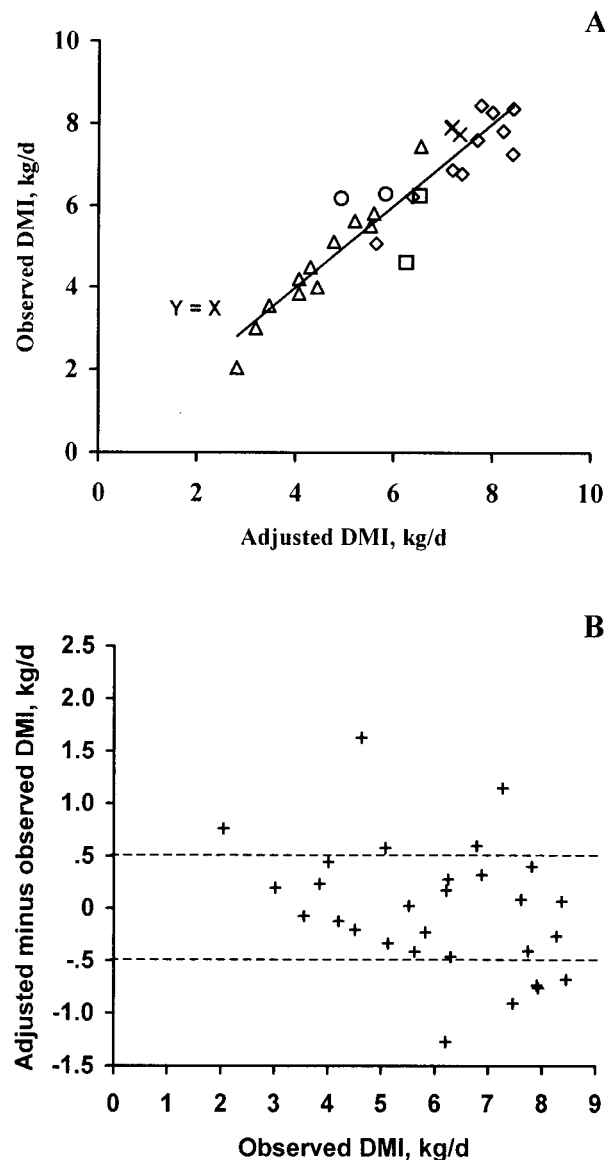


Figure 6. Prediction of DMI by the Cornell Net Carbohydrate and Protein System (CNCPS) with N deficiency adjustment. (A) Relationship between observed (o) DMI and CNCPS-predicted (p) DMI (kg/d) adjusted for the reduction of fiber carbohydrate degradation. Data were taken from Lomas et al. (1982), \diamond ; Boin and Moura (1977), \square ; Abdalla et al. (1988), \triangle ; Fox and Cook (1977), \times ; and Danner et al. (1980), \circ . The regression is $DMI_o = .7138 \times DMI_p - .0708 \times FCRedRatio + 2.2672$, and $r^2 = .88$. (B) Deviation (adjusted DMI minus observed DMI) vs observed DMI indicated 65.5% of the points are within the range $-.5$ and $.5$ kg/d. $FCRedRatio$ = fiber carbohydrate reduction ratio (%).

hay (4.9% CP), Olson et al. (1999) observed a linear increase in total tract digestion of NDF from 55.7% to 67.9% with the addition of degradable intake protein (DIP).

Evaluation of DMI Depression

The CNCPS 4.0 predicts DMI for growing animals using the NRC (1996) equation:

$$\text{DMI} = (\text{SBW}^{0.75} \times (0.2435 \times \text{NE}_m - 0.0466 \times \text{NE}_m^2 - a)/\text{NE}_m) \times \text{Factors}$$

where NE_m is net energy value of the diet for maintenance (Mcal/kg), a is either .1128 for growing calves (< 1 yr old) or .0869 for growing yearlings, and Factors are animal, environment, and management adjustment factors (NRC, 1996). The NRC (1996) DMI equation development (regression of observed vs predicted, 185 data points) had an r^2 of .73 and bias (observed as the X-variate) of -1.86% (NRC, 1996).

The reduction in DMI is associated with low-N diets, usually in diets below 7% of CP. This CP concentration is typically below the N requirement of ruminal bacteria, resulting in digestibility depression. This depression decreases fiber passage rate with a consequent increase in the ruminal retention time of the fiber (Van Soest, 1994, chap. 21). This is supported by Olson et al. (1999), who found a linear effect of DIP supplementation on passage rate (from 1.83 to 2.78%/h of acid detergent-insoluble ash) in degradable-protein-deficient, high-NDF diets.

Figure 5B schematizes the relationship between observed and predicted DMI for CNCPS 4.0. The intercept was different from zero ($P < .05$) and the proportion of deviation points lying within -.5 and .5 kg/d was 41.4%. Evaluations indicated that CNCPS 4.0 overpredicted DMI by 8.6% (Table 3) with a mean bias of .52 kg/d. The r^2 (.77; Table 5) and the bias (8.5%, using observed as the X-variate; not shown) were higher than ones reported by NRC (1996).

Equation [13] was obtained when both DMI and FCRecRatio (Eq. [12]) predicted by the CNCPS model were regressed on observed DMI:

$$\text{DMI}_{\text{ad}} = 2.267 + .714 \times \text{DMI}_{\text{p}} - .071 \times \text{FCRedRatio} \quad [13]$$

where DMI_{ad} is the DMI adjusted (kg/d), DMI_{p} is the DMI predicted by CNCPS (kg/d), and FCRedRatio is the fiber reduction (%) estimated by Eq. [12].

The use of the FCRedRatio variable and the DMI predicted by the CNCPS increased the r^2 from .77 to .88, the MSE decreased from .733 to .416, and RMSPE improved from 1.14 to .61 (Table 5). Also, the proportion of deviation points lying within -.5 and .5 kg/d was increased from 41.4% to 65.5% (Figure 6B). These results indicated the FCRedRatio estimate accounted for much the variation between predicted DMI by CNCPS and observed DMI when nitrogen was limiting in the rumen. Equation [13] also implies that DMI decreases 7.1% as less fiber carbohydrate is degraded in the rumen due to a ruminal N deficiency.

The response of DMI to levels of nonprotein N supplementation has been variable, including no correlation (Shain et al., 1998), negative correlation (Thomas et al., 1984; Milton et al., 1997b), and positive correlation (Zinn, 1995; Olson et al., 1999). These inconsistencies are likely due to the level of fiber in the diet and the levels of ruminally degraded N fed relative to FC fermenting bacterial N requirements (Zinn, 1995). Olson et al. (1999) observed an increase in DMI (70.2 to 106.5 g/SBW^{.75}) with increasing levels of DIP in high-NDF diets deficient in ruminally degraded N.

Overall, the N-limitation adjustment reduced the overprediction of the animal ADG and DMI by the CNCPS 4.0, but the bias was not completely eliminated. The present ruminal N deficiency adjustment assumed that all other required nutrients for microbial growth were adequate, and this assumption may not always be valid (Gorosito et al., 1985). Ruminal cellulolytic bacteria require branched-chain acids (isovaleric, isobutyric, and 2-methylbutyric) as well as N, and these acids are derived from the fermentation of branched-chain AA (Leu, Val, and Ile) (Allison, 1969). Microbial growth might be initially reduced by branched-chain AA instead of N, when BCAA is below the adequate level.

Branched-chain acid production can be predicted from the fermentation of amino acids in the CNCPS, but at least some NFC bacteria can utilize branched-chain acids (Allison et al., 1984). However, in this case the question is what fraction of the ruminally available branched-chain acids can be utilized by FC bacteria.

Table 5. Regression between observed (o) and CNCPS-predicted (p) DMI with and without fiber carbohydrate reduction (FCRedRatio, %)^a

DMI _o , kg/d	Intercept	Slope		R ²	MSE
		DMI _p , kg/d	FCRedRatio, %		
-FCRedRatio	1.317 ± .516*	.719 ± .0751#	—	.77	.733
+FCRedRatio	2.267 ± .439*	.714 ± .0566*	-.071 ± .0152*	.88	.416

^aIntercept was statistically tested whether it differed from 0, and slope whether it differed from 1, using the *t*-test. Values are the mean ± standard error. CNCPS = Cornell Net Carbohydrate and Protein System.

*Statistically different from 0 at $\alpha = .05$.

#Statistically different from 1 at $\alpha = .05$.

Implications

When the Cornell Net Carbohydrate and Protein System rumen model was modified to include equations to account for a ruminal N deficiency, the ability to predict dry matter intake and average daily gain in growing/finishing steers was significantly improved. Accounting for this effect is very important in improving forage utilization and the performance of cattle fed high-forage diets. A modeling approach is needed to design appropriate experiments to further test this revision to the model. Included are having treatments predicted by the model to range from deficient to adequate concentration of N and animals that are predicted to increase average daily gain or milk production with additions of nonprotein N to the diet. Only a few published experiments that had a deficiency in ruminal N and animal responses to the addition of dietary N along with adequate inputs needed for evaluation with the model provided data adequate for testing it.

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