

Opportunities to enhance performance and efficiency through nutrient synchrony in concentrate-fed ruminants^{1,2,3}

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ABSTRACT: Synchronization of the ruminal degradation of carbohydrates and CP is projected to increase ruminal microbial protein synthesis and improve N use efficiency. Attempts to synchronize the fermentation of dietary carbohydrates and CP have been met with mixed results, suggesting that ruminal nutrient synchrony is not important or that physiological mechanisms work in concert to synchronize ruminal carbohydrate and N availability. Nitrogen recycling to the rumen is controlled primarily by the concentration of urea in the blood, ammonia in the gut, and the availability of fermentable energy in the gut. We hypothesized that N utilization could be improved by synchronizing the supply of nutrients in one segment of the gut with those in another segment (i.e., synchronize a ruminal N deficiency with a lower gut N excess, etc.) via oscillating the dietary CP between deficient and adequate concentrations. With corn-based diets and oil-seed-based natural protein supplements, N retention has been greater in lambs or steers fed oscillating CP concentrations (at 48-h intervals) than in animals fed a constant CP percentage. Effects of oscillating CP on cattle perfor-

mance have been variable and may depend upon the fermentability of the carbohydrate source (e.g., forage vs. grain, grain processing). Studies with sheep noted that net portal uptake of urea was greater in lambs fed oscillating CP than in lambs fed constant CP concentrations. Nutrient intakes also need to be synchronized with the animals' requirements. One method to adjust nutrient intake with requirements is via phase-feeding. Results of studies with dry-rolled corn-based diets indicate that dietary CP concentrations can be decreased late in the feeding period with no adverse effects on animal performance; however, results of studies using steam-flaked corn-based diets are less consistent, possibly due to differences in the aggressiveness of the implant program used. In conclusion, ruminal nutrient synchrony is theoretically a sound principle; however, it seems that physiological mechanisms such as N recycling may mitigate effects of asynchrony. Methodologies that increase N recycling or increase the utilization of recycled N may benefit animal performance and the environment.

Key words: beef cattle, oscillating, phase-feeding, protein, rumen, synchrony

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INTRODUCTION

The need to improve beef cattle production efficiency while decreasing adverse effects of finishing cattle operations on the environment is becoming increasingly

critical to the cattle feeding industry. The synchronization of the ruminal degradation rate of carbohydrates and CP has been proposed as a method of increasing ruminal microbial protein synthesis, improving N use efficiency, decreasing urinary N excretion, and improving animal performance. A number of studies have used the synchrony index (Sinclair et al., 1993) or other methods in an attempt to synchronize the fermentation rates of dietary OM and CP within the rumen; however, the results have been mixed (Herrera-Saldana et al., 1990; Robinson and McQueen, 1994; Shabi et al., 1998; Dewhurst et al., 2000; Rotger et al., 2006a). Most of these studies have been conducted with moderate- to high-roughage diets.

In contrast to the synchrony theory, it has been demonstrated that cattle fed protein-deficient forages can be supplemented with natural protein sources at 24- to 72-h intervals without adversely affecting animal

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performance (Collins and Pritchard, 1992). These results indicate that either ruminal nutrient synchrony is not important or that N recycling to the rumen and other physiological mechanisms mitigate short-term variations in dietary ruminal N supply. However, the effects of protein supplementation frequency and ruminal degradable N:OM synchrony on ruminants fed high-concentrate finishing diets have not been extensively studied.

The objectives of this review were to generate information concerning ruminal N:OM synchrony in cattle fed high-concentrate finishing diets and to summarize recent protein research in cattle fed finishing diets looking at nutrient synchrony from a larger spatial and temporal scale.

EFFECTS OF CRUDE PROTEIN CONCENTRATION AND SOURCE ON NUTRIENT SYNCHRONY IN FINISHING DIETS

Essentially all the published studies of nutrient synchrony have been conducted with moderate- to high-roughage diets. In one study that used high-concentrate diets, Rotger et al. (2006a) synchronized ruminal OM and N via altering diet composition (corn vs. barley and soybean meal vs. sunflower meal). Rotger et al. (2006a) noted no effect of synchrony on ruminal NH_3 or VFA concentrations, or on diet digestibility. Valkeners et al. (2004, 2006) modified ruminal N:OM synchrony by changing the pattern of feeding diets that were either low or high in degraded intake protein (**DIP**) and noted no effect of dietary synchrony on N retention, ruminal microbial protein synthesis, or ruminal microbial efficiency (g of microbial protein/kg of OM fermented). Richardson et al. (2003) estimated the effects of nutrient synchrony on growth of lambs fed diets containing 30% wheat straw using dietary regimens formulated based on both a calculated ruminal degraded N:OM synchrony index and the time of day each diet was fed. The overall ration fed each day was the same for all lambs; however, the pattern of ingredient presentation (am vs. pm) varied, giving regimens that were synchronous, asynchronous, or intermediate. Dietary synchrony did not affect feed intake, weight gain, N balance, ruminal fluid pH, ruminal VFA concentrations, or ruminal microbial N flow, although it did appear to affect the energy retention and postprandial ruminal and plasma ammonia concentrations of sheep fed a barley based-diet (vs. no effect with a sugar beet pulp-based diet). Thus, the limited data available with moderate- to high-concentrate diets suggest that ruminal synchrony has little, if any, effect on ruminal or whole animal metabolism.

We theorized that studies of CP source and availability, or energy availability (i.e., grain processing, by-products, etc.) are, in a crude way, studies of ruminal synchronization. Therefore, to supplement the meager quantity of data with high-concentrate diets, we devel-

oped 2 data sets from a series of published and unpublished studies to estimate the effects of ruminal N:OM synchrony on performance and ruminal metabolism of beef cattle fed high-concentrate finishing diets.

Data Sets: Brief Description

The first data set consisted of 9 steer performance trials in which dietary concentrate was 85% or greater and in which protein concentrations, protein sources, or energy concentrations were altered. The studies are summarized in Table 1. Two methods were used to reduce trial-to-trial variability in the statistical analysis. First, the ADG of each treatment was predicted using NRC (2000) equations and tabular ingredient energy values. The actual ADG was then divided by the predicted ADG to obtain a relative effect of dietary factors on animal performance. Additionally, ADG, DMI, and G:F for all trials were arithmetically standardized so that the average performance in each trial was equal to the overall mean of the 9 studies. The overall mean of each variable in each trial was divided by the overall mean of the 9 studies to calculate a correction factor. Individual diet values within each trial were then divided by the trial correction factor to obtain the standardized values used in the regression analysis, as described subsequently.

The second data set was composed of 7 published studies in which the site of digestion and ruminal microbial protein synthesis was determined (Table 2). In each trial the dietary roughage concentration was 15% or less, and CP concentrations, supplemental CP sources, or energy concentrations were altered.

Calculation of Dietary Synchrony Index

A synchrony index for each experimental diet was calculated by a modification of the methods of Sinclair et al. (1993). Sinclair et al. (1993) used CP and OM degradabilities of dietary ingredients determined using in situ methods to calculate the N:OM synchrony index. In place of the in situ method, we used the NRC (2000) tabular values for ingredient composition, degradabilities of carbohydrate and CP fractions, and for rates of passage of feed ingredients. The effective extent of degradation of carbohydrates and CP were estimated based on modified equations of Sinclair et al. (1993) for each hour postfeeding. Carbohydrate digestion was determined using the equation

$$\begin{aligned} cP = cA & \\ & + \{[cB1 \times cKdB1]/(cKdB1 + cKpB1)\} \\ & \times [1 - e^{-(cKdB1 + cKpB1)t}] \\ & + \{[cB2 \times cKdB2]/(cKdB2 + cKpB2)\} \\ & \times [1 - e^{-(cKdB2 + cKpB2)t}], \end{aligned}$$

where cP is the effective extent of degradation of carbohydrates; cA is the concentration of the readily soluble

Table 1. Range in unadjusted animal performance and diet characteristics of 9 studies used to develop the animal performance data set

Study ¹	DMI, kg/d	ADG, kg	Gain/feed, g/kg	Actual: predicted ADG	Diet CP, % of DM	Diet DIP, % of DM	Synchrony index
Vasconcelos et al., 2007 (1)	7.77 to 8.78	1.29 to 1.55	157 to 178	88 to 94	12.3 to 13.4	5.46 to 8.00	0.38 to 0.51
Vasconcelos et al., 2007 (2)	8.72 to 9.25	1.56 to 1.74	179 to 188	90 to 96	12.8 to 13.9	6.84 to 8.34	0.37 to 0.50
Gleghorn et al., 2004 (3)	8.98 to 9.36	1.61 to 1.76	174 to 190	97 to 105	11.2 to 14.5	6.06 to 9.49	0.08 to 0.40
Cooper et al., 2002a (4)	8.10 to 10.60	1.36 to 1.85	154 to 185	88 to 113	9.1 to 14.9	4.38 to 12.10	0.37 to 0.63
Milton et al., 1997a (5)	9.33 to 10.34	1.24 to 1.46	128 to 145	76 to 85	11.6 to 14.2	6.28 to 8.68	0.50 to 0.59
Scott et al., 2003 (6)	9.30 to 10.60	1.74 to 1.92	180 to 194	98 to 104	14.1 to 14.3	8.56 to 10.48	0.16 to 0.61
Sindt et al., 1993 (7)	9.04 to 9.86	1.52 to 1.58	155 to 176	96 to 100	12.0 to 15.6	7.09 to 8.86	0.57 to 0.69
Barajas and Zinn, 1998 (8)	7.49 to 8.41	1.01 to 1.19	126 to 157	73 to 88	11.8 to 15.6	7.41 to 9.81	0.17 to 0.57
Zinn and Shen, 1998 (9)	6.63 to 7.49	1.41 to 1.69	213 to 234	136 to 152	11.0 to 12.8	6.36 to 11.13	0.20 to 0.43
Overall mean	9.11	1.57	173.2	99.1	12.8	7.92	0.45
SEM	0.18	0.03	3.2	2.2	0.21	0.21	0.02

¹Values in parentheses are trial numbers used in Figures 1 through 4.

fraction; cB1 is the concentration of the starch fraction; cB2 is the concentration of available fiber fraction; cKdB1 and cKdB2 are the digestion constants for starch and available fiber, respectively; cKpB1 and cKpB2 are the ruminal passage rates for starch and fiber, respectively; and t is the time postfeeding in hours.

Crude protein digestion was determined similarly using the following equation:

$$\begin{aligned}
 pP = & pA + \{[pB1 \times pKdB1]/(pKdB1 \\
 & + pKpB1)\} \times [1 - e^{-(pKdB1 + pKpB1) t}] \\
 & + \{[pB2 \times pKdB2]/(pKdB2 + pKpB2)\} \\
 & \times [1 - e^{-(pKdB2 + pKpB2) t}] \\
 & + \{[pB3 \times pKdB3]/(pKdB3 + pKpB3)\} \\
 & \times [1 - e^{-(pKdB3 + pKpB3) t}],
 \end{aligned}$$

where pP is the effective extent of degradation of CP; pA is the concentration of the nonprotein N fraction; pB1 is the concentration of rapidly degraded true protein; pB2 is the concentration of true protein with intermediate degradability; pB3 is slowly degraded true

protein; pKdB1, pKdB2, and pKdB3 are the digestion constants for rapid, intermediate, and slowly degraded true protein, respectively; pKpB1 and pKpB2 are the ruminal passage rates for starch and fiber, respectively; and t is the time postfeeding in hours.

The quantity of N and carbohydrate degraded each hour for each diet was calculated as the difference between that degraded at successive hours. The synchrony index was calculated from the hourly quantity of N and carbohydrate degraded using a modification of the equation of Sinclair et al. (1993, 2000):

$$\begin{aligned}
 SI = & \left\{ [25 / \text{Carb}] \right. \\
 & \left. - \sum_{1-24} \frac{(\sqrt{\{[(25 / \text{Carb}) - \text{hourly N / CHO ratio}]^2\}} / 24)}{(25 / \text{Carb})} \right\}
 \end{aligned}$$

in which SI = the synchrony index, and Carb was the percentage of dietary ruminally available carbohydrate. The value of 25 is based on the study of Czerwaski (1986), which suggested that the optimal ruminal N:fermented OM ratio was 25 g/kg. Because our synchrony index was calculated based on grams of N per kilogram of carbohydrate digested in the rumen,

Table 2. Range in N metabolism characteristics and dietary synchrony index of the 7 trials in the metabolism data set

Study ¹	DMI, kg/d	CP intake, g/d	Duodenal N flow, g/d	Microbial N, g/d	Microbial efficiency, g/kg of OM	Synchrony index
Zinn et al., 1997 (10)	5.59 to 5.62	650 to 1,081	126.3 to 163.4	65.9 to 70.4	22.1 to 28.4	0.32 to 0.44
Milton et al., 1997b (11)	11.10 to 13.70	1,069 to 1,469	264.8 to 322.1	125.9 to 150.8	17.5 to 33.6	0.43 to 0.46
Milton et al., 1997a (12)	6.80 to 7.50	675 to 981	108 to 141	49 to 67	10 to 16	0.18 to 0.51
Zinn et al., 2003 (13)	5.95 to 6.01	631 to 819	119.1 to 126.0	80.3 to 85.8	22.1 to 24.8	0.41 to 0.42
Cooper et al., 2002b (14)	12.50 to 14.50	1,925 to 2,344	234 to 274	138 to 180	23.7 to 25.4	0.44 to 0.50
Barajas and Zinn, 1998 (15)	8.24 to 8.30	875 to 1,169	159 to 202	79 to 97	24.1 to 28.4	0.39 to 0.59
Zinn and Shen, 1998 (16)	6.12 to 6.15	617 to 717	124.7 to 145.7	61.6 to 88.6	21.7 to 26.0	0.40 to 0.51
Overall mean	8.16	1,018	175	92.6	23.3	0.45
SEM	0.55	82	11.8	6.5	0.96	0.01

¹Values in parentheses are trial numbers used in Figures 5 through 8.

we adjusted the value by dividing the value of 25 g/kg by the calculated ruminally available carbohydrate in each diet. Because these synchrony values were calculated differently, they probably do not compare directly with those of Sinclair et al. (1993, 2000). However, the relative comparisons should be valid.

Statistical Analysis

Adjusted animal performance (ADG, DMI, G:F, and ADG:calculated ADG) and N metabolism (duodenal N flow, microbial N flow, microbial efficiency) of each diet were linearly regressed against the synchrony index and quadratically regressed against the synchrony index and synchrony index squared using the REG procedure of SAS (SAS Institute Inc., Cary, NC). Regression equations were calculated for each individual experiment and for the overall data set. In all comparisons, the quadratic regression did not improve the correlation compared with the linear regression; therefore, only the linear relationships are presented.

Results: Performance Data Set

The overall mean unadjusted DMI, ADG, G:F ratio, actual/predicted ADG, dietary CP, and DIP percentage, and calculated synchrony index are presented in Table 1. Daily DIP intake averaged 722.8 ± 22.6 g and undegraded intake protein (UIP) intake averaged 436.1 ± 17.2 g.

Overall, the synchrony index of diets was positively correlated ($P < 0.07$) to adjusted DMI (Figure 1). However, the relative contribution of the synchrony index to adjusted DMI was low ($r^2 = 0.06$). In 6 of the 9 studies, the synchrony index was positively related to DMI, whereas in 2 studies the relationship was negative. Adjusted ADG was not significantly correlated to the synchrony index (Figure 2; $r^2 = 0.005$; $P = 0.97$). The adjusted G:F ratio was negatively correlated ($r^2 = 0.06$; $P < 0.07$) to the dietary synchrony index (Figure 3), but again the contribution of the synchrony index to G:F was low. The relationship was negative in 7 of the 9 studies. The actual ADG:predicted ADG ratio was also negatively correlated ($r^2 = 0.17$; $P < 0.001$) with the dietary synchrony index (Figure 4). Based on these methods, it appears that synchrony index had little, if any, effect on animal performance. In addition, the negative relationships between the synchrony index and G:F and actual:predicted ADG indicate that if N:OM ruminal degradation synchrony had any effect on animal performance, the effect was negative.

Results: Metabolism Data Set

Average bacterial N flow to the duodenum for the 7 studies was 92.6 ± 6.47 g/d, total duodenal N flow averaged 174.9 ± 11.8 g/d and $111.4 \pm 4.5\%$ of N intake, and microbial efficiency averaged $23.3 \text{ g} \pm 0.96 \text{ CP/kg}$ of OM fermented.

Total duodenal N flow, duodenal N flow as a percentage of N intake, and microbial N flow were not significantly correlated with the dietary synchrony index (Figures 5, 6, and 7, respectively). Although microbial N efficiency was significantly correlated ($P < 0.03$) to the dietary synchrony index; the correlation was negative and the relative contribution of the synchrony index to microbial N efficiency was relatively low (Figure 8; $r^2 = 0.17$). The higher microbial N efficiency with lower ruminal N:OM synchrony could be attributable to greater N recycling with asynchronous diets (Holder et al., 1995). The ruminal metabolism results tend to agree with the performance data set and suggest that the synchrony of N and OM degradation in the rumen of cattle fed high-concentrate diets has little, if any, effect on N metabolism.

Synchrony and DIP Interactions

In many studies of ruminal synchrony the ruminal degradability of OM and CP fractions were altered by changing the dietary ingredients. Thus, in some cases, effects attributed to N:OM synchrony may have been effects of individual ingredients or nutrient fractions. For example, effects of dietary DIP and UIP concentrations may have been of greater importance than actual synchrony. In the 16 studies reviewed, the correlation between dietary DIP (percentage of DM) and the synchrony index ranged from 0.01 to 0.94.

To gauge the relative importance of dietary DIP and ruminal synchrony on steer performance, we reanalyzed the animal performance data of Gleghorn et al. (2004) and N metabolism data of J. T. Vasconcelos, K. W. McBride, A. Gueye, M. L. Galyean, C. R. Richardson (Texas Tech University, Lubbock), N. A. Cole (USDA-ARS, Bushland, TX), and L. W. Greene (Texas Agricultural Experiment Station, Amarillo, unpublished data). In both studies, steers were fed 1 of 9 diets containing 11.5, 13, or 14.5% CP with supplemental CP from urea, cottonseed meal (CSM), or a 50:50 (N basis) blend of urea and CSM (Table 3), and the correlation between dietary DIP and the synchrony index was 0.17 ($P = 0.61$). Because of this low correlation it should be possible to segregate the relative effects of DIP concentration and the synchrony index on animal performance and N metabolism. The UIP concentration of each diet was adequate (NRC, 2000); therefore, the data were analyzed by ANOVA as 9 individual treatments (i.e., dietary DIP percentage) using the GLM procedure of SAS. Least-squares means, determined for each diet using N intake or ME intake as a covariant, were then regressed against dietary DIP or synchrony index using the REG procedure of SAS.

The coefficients of determination for the linear effects of DIP and dietary synchrony index on animal performance when ME intake or N intake were equalized are presented in Table 4. In general, when ME intake or N intake were used as covariants, DIP had a greater correlation with ADG and DMI ($r^2 = 0.39$ to

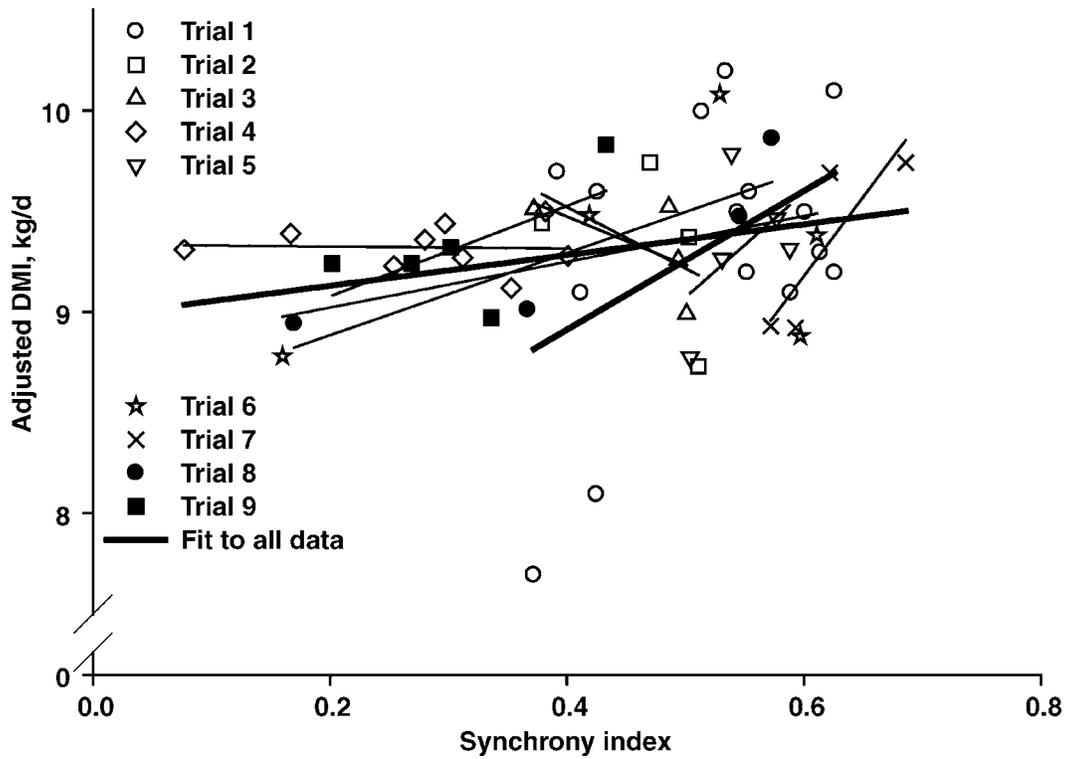


Figure 1. Relationship between dietary synchrony index and adjusted DMI (kg/d) of steers in 9 performance trials. Each symbol is a treatment mean. Regression equation for overall data ("Fit to all data"): $\text{DMI} = 8.976 + (0.763 \times \text{synchrony index})$, $r^2 = 0.06$, $P = 0.07$.

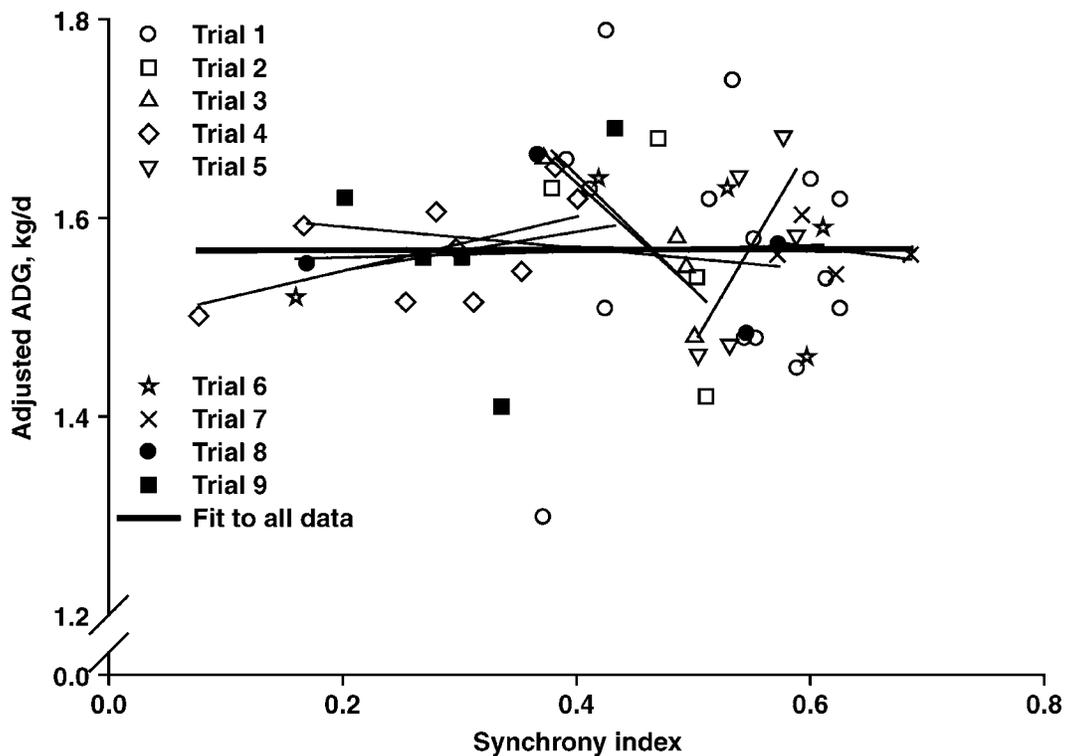


Figure 2. Relationship between dietary synchrony index and ADG (kg/d) of steers in 9 performance trials. Each symbol is a treatment mean. Regression equation for overall data ("Fit to all data"): $\text{ADG} = 1.57 + (0.003 \times \text{synchrony index})$, $r^2 = 0.005$, $P = 0.97$.

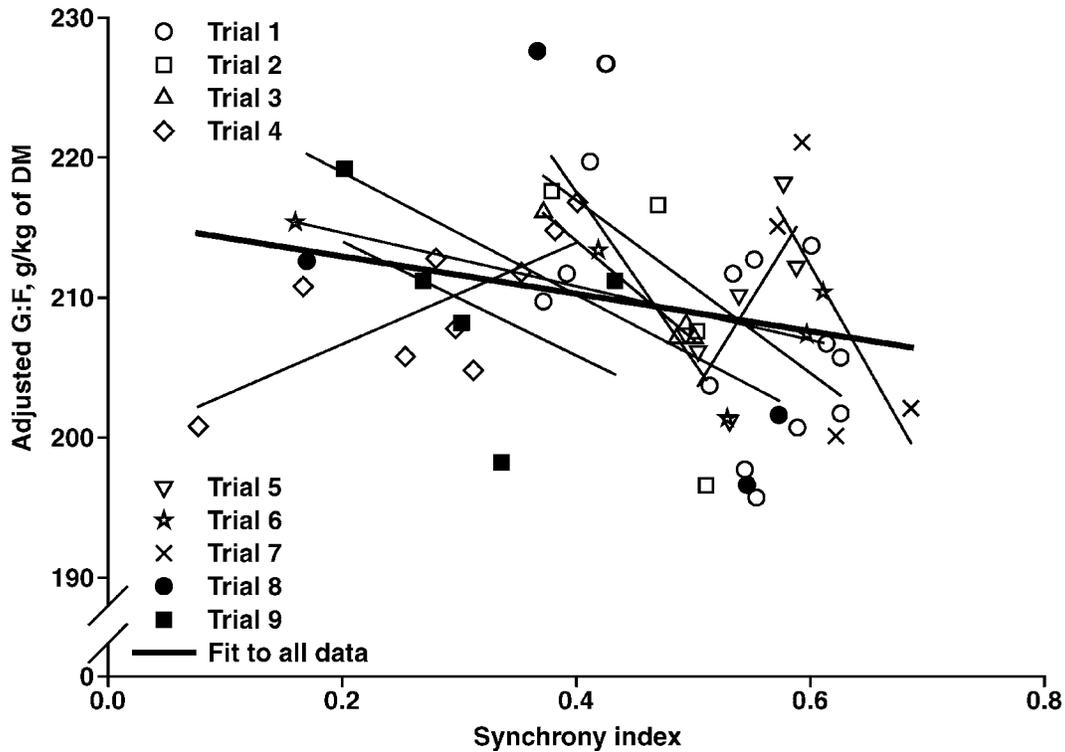


Figure 3. Relationship between dietary synchrony index and adjusted gain:feed (g/kg of DM) of steers in 9 performance trials. Each symbol is a treatment mean. Regression equation for overall data ("Fit to all data"): $G:F = 216 - (13 \times \text{synchrony index})$, $r^2 = 0.06$, $P = 0.07$.

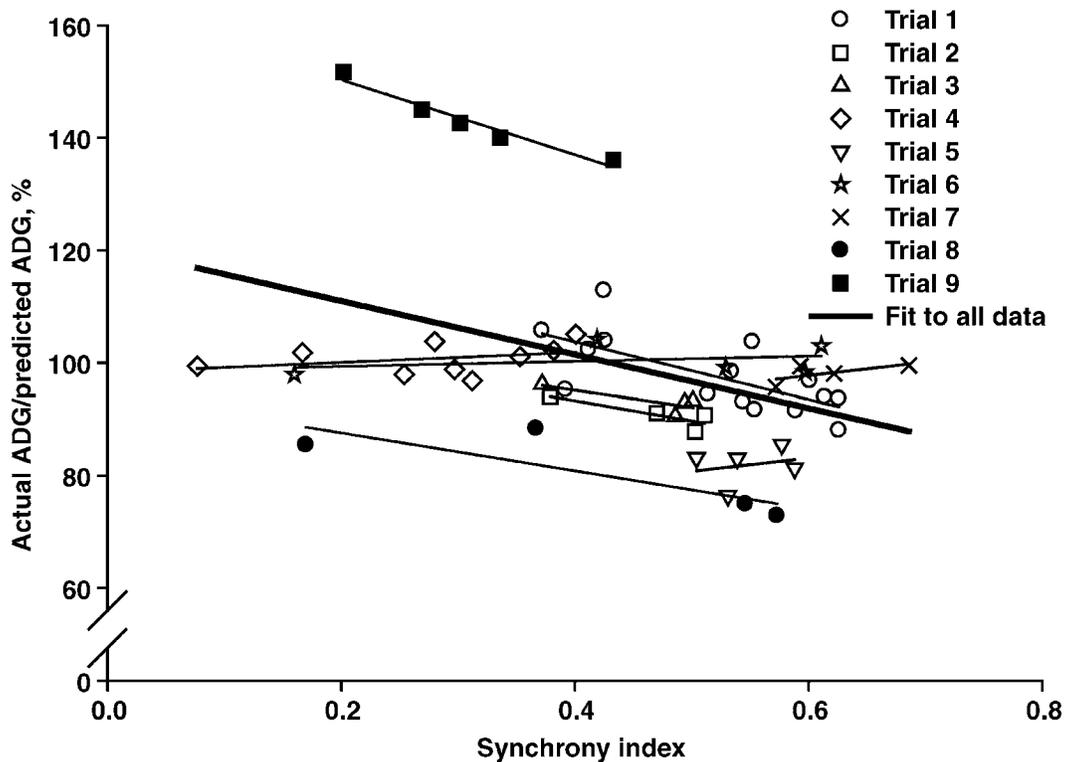


Figure 4. Relationship between dietary synchrony index and actual ADG:predicted ADG (%) of steers in 9 performance trials. Each symbol is a treatment mean. Regression equation for overall data ("Fit to all data"): $\text{Actual/predicted ADG} = 120.5 - (47.6 \times \text{synchrony index})$, $r^2 = 0.17$, $P = 0.001$.

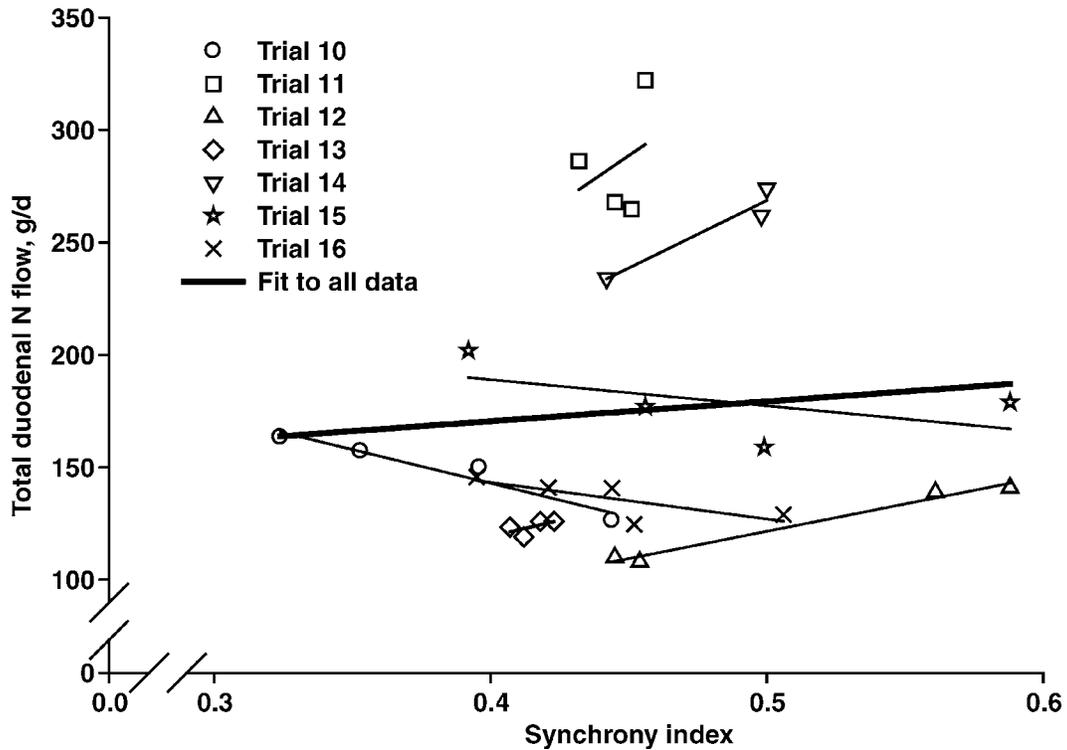


Figure 5. Relationship between dietary synchrony index and total duodenal N flow (g/d) of steers in 7 metabolism trials. Each symbol is a treatment mean. Regression equation for overall data ("Fit to all data"): $N \text{ flow g/d} = 135.4 + (87.9 \times \text{synchrony index})$, $r^2 = 0.008$, $P = 0.66$.

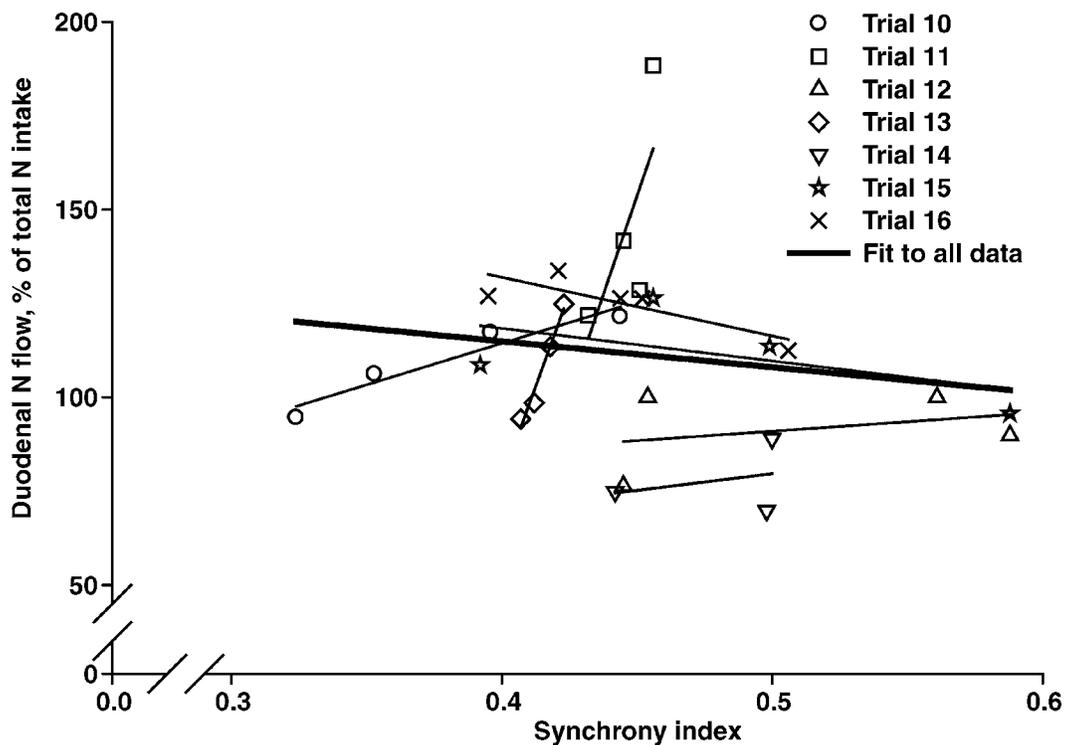


Figure 6. Relationship between dietary synchrony index and duodenal N flow as a percentage of total N intake of steers in 7 metabolism trials. Each symbol is a treatment mean. Regression equation for overall data ("Fit to all data"): $N \text{ flow } \% = 142.5 - (69.1 \times \text{synchrony index})$, $r^2 = 0.03$, $P = 0.37$.

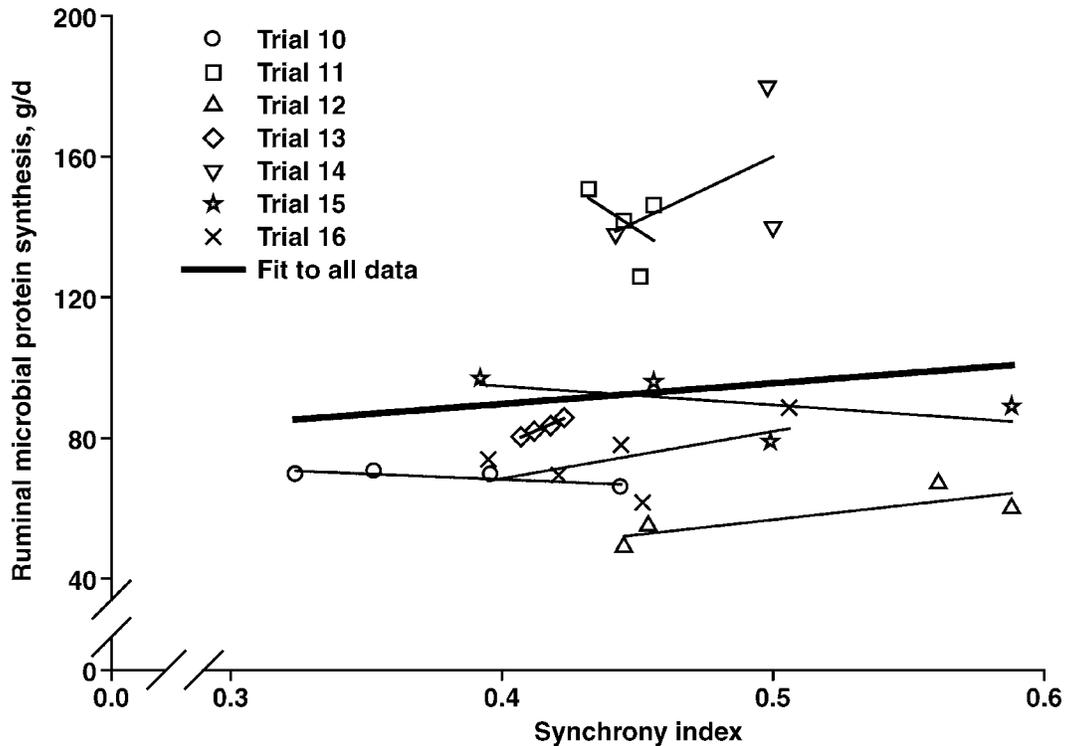


Figure 7. Relationship between dietary synchrony index and ruminal microbial protein synthesis (g/d) of steers in 7 metabolism trials. Each symbol is a treatment mean. Regression equation for overall data ("Fit to all data"): Microbial protein = $66.2 + (58.6 \times \text{synchrony index})$, $r^2 = 0.01$, $P = 0.60$.

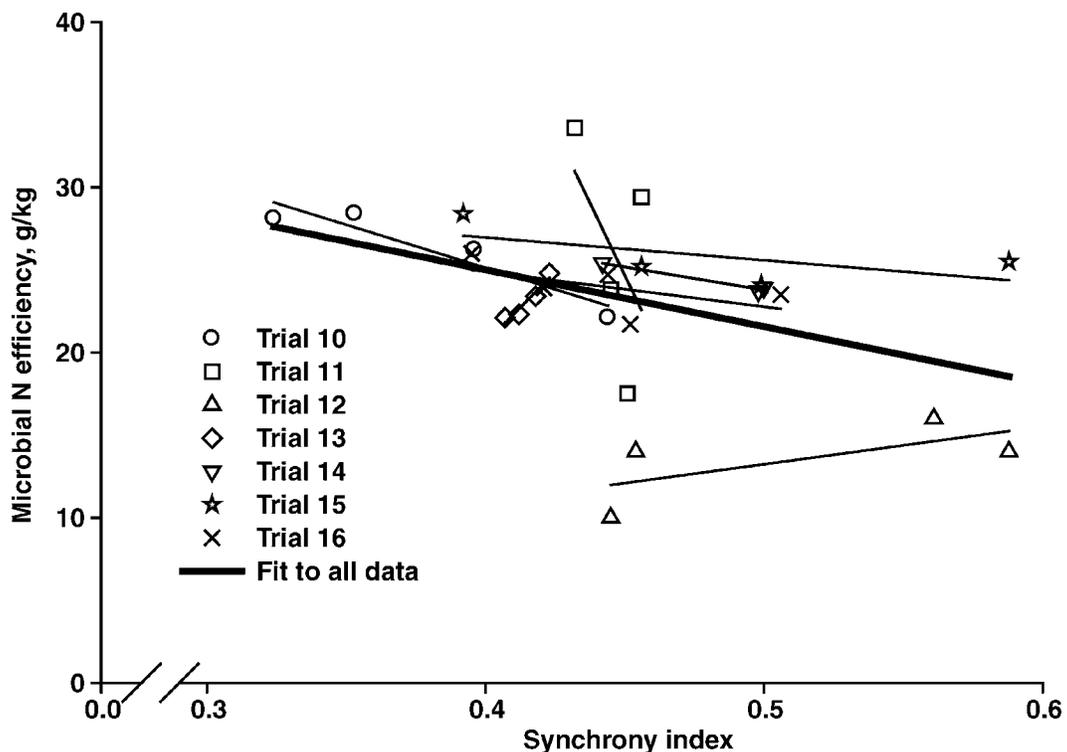


Figure 8. Relationship between dietary synchrony index and microbial N efficiency (g of microbial CP/kg of OM fermented) of steers in 7 metabolism trials. Each symbol is a treatment mean. Regression equation for overall data ("Fit to all data"): Microbial efficiency = $38.7 - (34.4 \times \text{synchrony index})$, $r^2 = 0.17$, $P = 0.03$.

Table 3. Diets used in studies of Gleghorn et al. (2004) and Vasconcelos et al. (2008)

Diet symbol ¹	CP, %	U/C ratio (N basis)	DIP, % of DM	Synchrony index	ADG, kg	G:F, g/kg
11.5-C	11.5	0/100	6.15	0.25	1.62	179
11.5-B	11.5	50/50	6.46	0.31	1.62	178
11.5-U	11.5	100/0	6.74	0.35	1.65	185
13.0-C	13.0	0/100	7.03	0.17	1.70	184
13.0-B	13.0	50/50	7.70	0.30	1.68	181
13.0-U	13.0	100/0	8.22	0.38	1.76	188
14.5-C	14.5	0/100	7.92	0.08	1.61	174
14.5-B	14.5	50/50	8.91	0.28	1.71	186
14.5-U	14.5	100/0	9.74	0.40	1.73	190
Mean	—	—	7.52	0.28	1.676	182.8
SEM	—	—	0.39	0.03	0.017	1.72

¹11.5, 13.0, and 14.5 = % dietary CP (DM basis); C = protein supplement was cottonseed meal, B = protein supplement was a 50:50 (N-basis) blend of cottonseed meal and urea, and U = protein supplement was urea.

0.60) than did the synchrony index ($r^2 = 0.15$ to 0.28). However, when ME intake was equalized, the synchrony index tended to have a greater correlation to G:F than DIP concentration ($P = 0.09$). When N intake was equalized, DIP was significantly correlated with DMI, and G:F; however, the synchrony index was not correlated.

When ME intake was held constant, the dietary synchrony index was not significantly correlated with any N metabolism variable measured, whereas dietary DIP concentration was correlated ($P < 0.05$) with urine N excretion, urinary urea-N, apparent N digestion, and blood urea-N (Table 5). When N intake was held constant, the dietary synchrony index was correlated ($P < 0.05$) with apparent N digestion, but was not correlated with any other N metabolism variable measured (Table 5). In contrast, when N intake was the covariant, dietary DIP concentration was correlated ($P < 0.05$) with urinary N excretion, urinary urea-N, N retention, and blood urea-N. These statistical results again indicate that dietary synchrony index has little effect on N metabolism or animal performance in cattle fed high-concentrate diets and that in some trials, ef-

Table 4. Linear coefficients of determination (r^2) for least squares means of steer performance (Gleghorn et al., 2004) regressed against dietary degraded intake protein (DIP, % of DM) or dietary synchrony index when ME intake or N intake are used as a covariate

Item	DIP	Synchrony index
ME intake as a covariate		
ADG	0.46*	0.15
DMI	0.60**	0.15
G:F	0.17	0.40†
N intake as a covariate		
ADG	0.39†	0.28
DMI	0.59*	0.14
G:F	0.66**	0.07

†Correlation greater than 0, $P < 0.10$.

*Correlation greater than 0, $P < 0.05$.

**Correlation greater than 0, $P < 0.01$.

fects attributed to synchrony index could actually be confounded with other dietary factors, such as DIP concentration.

PHYSIOLOGICAL SYSTEMS THAT MAY BUFFER RUMINAL N:OM SYNCHRONY

The contrasting results with ruminal synchrony studies indicate that either ruminal nutrient synchrony is not important or that other physiological factors work in concert to synchronize ruminal OM and N availability. Calculations of ruminal N:OM syn-

Table 5. Linear coefficients of determination (r^2) for least squares means of steer N metabolism¹ regressed against dietary degraded intake protein (DIP, % of DM) or dietary synchrony index when ME intake or N intake are used as a covariant

Item	DIP	Synchrony index
ME intake as a covariant		
Urine N excretion, g/d	0.69**	0.005
Urinary urea-N, % of urine N	0.77**	0.007
Urine N, % N intake	0.41	0.04
N retention, g/d	0.005	0.03
N retention, % of N intake	0.17	0.006
N retention, % of N absorbed	0.19	0.01
Apparent N digestion, %	0.74**	0.21
Blood urea-N, mg/dL	0.67**	0.03
N intake as a covariant		
Urine N excretion, g/d	0.70**	0.003
Urinary urea-N, % of urine N	0.76**	0.002
Urine N, % N intake	0.70**	0.009
N retention, g/d	0.63**	0.007
N retention, % of N intake	0.64**	0.007
N retention, % of N absorbed	0.66**	0.005
Apparent N digestion, %	0.09	0.51*
Blood urea-N, mg/dL	0.66**	0.03

¹J. T. Vasconcelos, K. W. McBride, A. Gueye, M. L. Galyean, C. R. Richardson (Texas Tech University, Lubbock), N. A. Cole (USDA-ARS, Bushland, TX), and L. W. Greene (Texas Agricultural Experiment Station, Amarillo, unpublished data).

*Correlation greater than 0, $P < 0.05$.

**Correlation greater than 0, $P < 0.01$.

chrony generally assume N metabolism, N recycling, and other N utilization mechanisms are relatively constant. However, cattle or ruminal microbes, or both, may rapidly adapt to dietary regimens via altering metabolic processes, urea recycling, or other mechanisms.

Feeding patterns and meal frequency can potentially affect the rate of digestion, rate of passage, and site of digestion; all of which could affect the ruminally degradable N:OM ratio. The N:OM synchrony premise tends to assume that animals consume only 1 or 2 meals daily. Although finishing cattle are routinely fed 2 or 3 times per day, in reality, cattle fed high-concentrate diets normally consume an average of 6 to 12 meals daily (Schwartzkopf-Genswein et al., 2003, 2004). With more frequent meals, it is possible that degradation of protein or carbohydrate, or both, from one meal may be synchronized with degradation of that from another meal. Thus an apparently unsynchronized diet could be synchronized via feeding pattern. Sinclair et al. (2000), Kyriazakis and Oldham (1997), and Rotger et al. (2006b) noted that feeding behavior differed among ruminants fed synchronous and asynchronous diets. Unfortunately, feeding patterns were not recorded in the studies used to develop our performance and N metabolism data sets. Differences in feeding pattern could contribute to the low correlations noted previously between the calculated synchrony index and performance and N metabolism variables.

Ammonia-urea recycling to the gut may potentially buffer ruminal NH_3 extremes. Holder et al. (1995) reported that N recycling was greater with asynchronous diets than synchronous diets. However, the capture of recycled N is also critical (Huntington and Archibeque, 1999; Sunny et al., 2007). The potential importance of N recycling to ruminal synchrony has been reviewed (Reynolds and Kristensen, 2008).

Although ruminal NH_3 concentrations may be adequate for microbial activity in the rumen, for maximal growth, amylolytic bacteria appear to require free amino acids and peptides (Russell et al., 1992; Atasoglu et al., 1999; Demeyer and Fievez, 2004). However, the relative contribution of NH_3 vs. preformed amino acids to ruminal microbial protein synthesis is not fixed and varies with the available N source, with the contribution of NH_3 ranging from 18 to 100% (Cotta and Russell, 1982; Atasoglu et al., 1999). Because the ratio varies between diets and throughout the day on any single diet, the proportion of microbial protein formed from NH_3 and alpha-amino N sources can also vary widely. Although ruminal microorganisms appear to readily adapt to use the N sources available, it is less clear if feeding asynchronous diets will decrease ruminal microbial activity as a result of an alpha-amino N deficiency.

In steers fed by intragastric infusion, Orskov et al. (1986) noted that endogenous flow of protein-N was equal to 195 mg/kg of metabolic BW. Based on these

values, which probably represent minimal values, the daily ruminal endogenous protein N supply for a 500-kg steer would be equivalent to 20.6 g of N daily, or close to 10% of daily N intake. Ludden and Cecava (1995) noted that free alpha-amino N (amino acids + hydrolyzable peptides) concentrations in the rumen and flows of free amino acids to the duodenum were similar in steers fed urea- and soybean meal (SBM)-supplemented diets. Based on the results of Orskov et al. (1986) and Ludden and Cecava (1995), it is probable that alpha-amino N provided by the grain and forage ingredients in the diet, and scavenged from the breakdown of ruminal microbes and endogenous proteins, provide adequate concentrations of peptides and amino acids for optimal ruminal microbial growth in spite of asynchronous dietary N:OM. It is also possible that movement of alpha-amino N sources from the portal system to the ruminal contents can provide additional alpha-amino N if there is a deficiency within the rumen (Remond et al., 2000).

Microbial activity within the rumen may naturally modify to buffer ruminal imbalances of degradable N and OM. Shifts in ruminal protozoal concentrations can affect the rate of ruminal starch digestion (Mendoza et al., 1993) and microbial CP flow (Koenig et al., 2000). Thus, shifts in protozoa numbers in the rumen may help to synchronize N and OM release (Bach et al., 2005). In addition, during periods of N deficiency, protozoa and bacteria can synthesize and store polysaccharides that can be used later when the N supply is adequate (Dewhurst et al., 2000).

SYNCHRONIZED OSCILLATIONS: OSCILLATING DIETARY CP

In contrast to the synchrony theory, it has been demonstrated that cattle fed protein-deficient forages can be supplemented with natural protein sources at 24- to 72-h intervals without adversely affecting animal performance (Collins and Pritchard, 1992). Although, the frequency of protein supplementation may not have adverse effects on the performance of cattle gaining appreciably below their genetic potential, until recently, the effects of protein supplementation frequency on ruminants fed high-concentrate finishing diets had not been extensively studied.

Cole (1999) hypothesized that if sufficient fermentable carbohydrate is available within the ruminal contents, N utilization could be improved via increased or optimized N recycling to the rumen. He theorized that by oscillating dietary CP at a rate similar to the rate of digesta passage, the overall quantity of CP fed could be decreased without adversely affecting animal performance. The objective was to synchronize the supply of nutrients in the upper digestive tract with nutrients in the lower digestive tract in order to optimize N recycling, that is, he attempted to synchronize a ruminal N deficiency with a N excess in the lower gut, and similarly, to synchronize any ruminal N ex-

Table 6. Summary of oscillating CP trials in which the diets were high-concentrate; values are oscillating treatment as a % of the static CP treatment

Item ¹	Reference or treatment comparison ²								
	Cole (1999)				Cole et al. (2003)		Archibeque et al. (2007a,b,c)		
	1a	1b	1c	1d	2a	2b	2007a	2007b	2007c
N digested, %	101.9	100.5	98.3	99.4	—	100.9	105.3*	98.3	—
N retained, g/d	121.8	140.6*	88.7	102.8	—	111.9	110.4†	167.5*	—
N retained, % of absorbed	119.4	139.4*	88.9	102.9	—	108.2	103.2	149.0*	—
PUN, mg/dL	94.4	98.4	107.8	110.8	—	86/98	—	—	98.2
Urine N, g/d	97.8	90.4	102.3	98.6	—	102.1	102.3	86.8	—
ADG, kg	—	—	—	—	105.5	116.5†	—	—	98.6
DMI, kg	—	—	—	—	100.9	102.9	—	—	100.8
Gain/feed, g/kg	—	—	—	—	104.2	113.3*	—	—	98.2
Hepatic net alpha-amino N flux, mmol/h	—	—	—	—	—	—	—	177.1*	—
Urea-N net flux – PDV, mmol/h	—	—	—	—	—	—	—	165.6†	—
Heat production, Mcal/d	—	—	—	—	—	—	96.2	—	—

¹PUN = plasma urea-N; PDV = portal drained viscera.

²Dietary treatments compared with static CP treatment: 1a = 24-h oscillating CP, cottonseed meal (CSM) supplement; 1b = 48-h oscillating CP, CSM supplement; 1c = 24-h oscillating CP, urea + CSM supplement; 1d = 48-h oscillating CP, urea + CSM supplement; 2a = 48-h oscillating CP in pen feeding study; and 2b = 48-h oscillating CP in individual steer feeding study.

†Oscillating CP effect, $P < 0.10$.

*Oscillating CP effect, $P < 0.05$.

cess with a N deficiency in the lower gut by oscillating the dietary CP percentages between deficient and adequate or excessive concentrations.

High-Concentrate Diets

The results of published oscillating CP studies are presented in Tables 6 and 7. In initial studies, Cole (1999) oscillated dietary CP concentrations (10 and 15%) of sheep at 24- or 48-h intervals. Oscillating dietary CP at 24-h intervals (Table 6, comparison 1a) did not affect N retention; however, oscillating at 48-h intervals (comparison 1b), a value closer to the estimated rate of passage, increased N retention by 38%, compared with a static 12.5% CP diet when the protein supplement was CSM. When the supplement was a 50:50 blend (N basis) of CSM and urea, N retention was not affected (comparisons 1c and 1d).

In a subsequent study with steers, Cole et al. (2003) oscillated 10 and 14% CP, steam-flaked corn (SFC)-based diets at 48-h intervals and noted no significant effect of CP oscillation (compared with static 12% CP) on apparent N digestion or N retention (Table 6; comparison 2b). With DRC-based diets, Archibeque et al. (2007a) noted greater apparent N digestion in steers on an oscillating CP regimen (9.1 and 13.9% CP vs. static 11.8%) but no effect of oscillating CP (9.9 and 14.2% vs. static 12.5% CP) on apparent N digestion in sheep (Archibeque et al., 2007b). Nitrogen retention was numerically increased in the steer study (Archibeque et al., 2007a) and increased ($P < 0.05$) in the sheep study (Archibeque et al., 2007b).

In one study, Cole et al. (2003) noted that ADG and G:F of steers tended to be increased ($P < 0.10$) by an oscillating CP regimen (Table 6: Comparison 2b). Average daily gain and G:F of steers fed a static 12% CP

diet (1.64 kg and 151 g/kg, respectively) were lower ($P < 0.05$) than steers fed a static 14% CP diet (1.95 kg and 170 g/kg, respectively); however, performance of steers fed the oscillating CP regimen (mean 12% CP:

Table 7. Summary of oscillating CP trials in which diets were 65% bromegrass hay; values are oscillating treatment as a percentage of the static CP treatment

Item ¹	High-roughage study		
	Ludden et al., 2002a	Ludden et al., 2002b	Ludden et al., 2003
N digested, %	93.8†	99.4	—
N retained, g/d	58.1	—	—
N retained, % of absorbed	62.0	—	—
PUN, mg/dL	—	—	86.4†
Urine N, g/d	96.6†	—	—
ADG, kg	84.6	—	103.6
DMI, kg	101.9	—	99.6
Gain/feed, g/kg	84.8	—	104.0
GIT weight, kg	109*	—	—
Ruminal starch digestion, %	—	108.5	—
Total starch digestion, %	—	99.1	—
Ruminal NDF digestion, %	—	95.5	—
Total NDF digestion, %	—	100.6	—
Particulate passage rate, %/h	—	111.4	—
Liquid passage rate, %/h	—	124.0**	—
Rumen NH ₃ , mg/dL	—	90.8†	—
Rumen VFA, mM	—	106.0*	—
Microbial N, g/d	—	96.9	—
Microbial efficiency, g of N/kg of OM fermented	—	107.9	—
Total N flow, g/d	—	101.1	—

¹PUN = plasma urea-N; GIT = gastrointestinal tract.

†Oscillating CP effect, $P < 0.10$.

*Oscillating CP effect, $P < 0.05$.

**Oscillating CP effect, $P < 0.01$.

1.82 kg and 164 g/kg, respectively) was not significantly different from steers fed the static 14% CP diet. In contrast, with DRC-based diets, Archibeque et al. (2007c) noted no effect of oscillating dietary CP on cattle performance (Table 6). However, in the study of Archibeque et al. (2007c) steers fed an oscillating CP regimen and steers fed a static 11.8% CP diet had performance similar to cattle fed a static 14.9% CP diet, suggesting the 11.8% CP diet was adequate in protein.

In agreement with the theory of Cole (1999), Archibeque et al. (2007b) noted that oscillating dietary CP (9.9 and 14.2% vs. static 12.5% CP) tended ($P < 0.06$) to increase uptake of urea by the portal drained viscera (i.e., N recycling; Table 6). Nitrogen recycling was similar in lambs fed the oscillating CP regimen and lambs fed a static protein-deficient (9.9% CP) diet. Net hepatic flux of alpha-amino N was also greater ($P < 0.05$) in lambs on the oscillating CP regimen (Table 6; Archibeque et al., 2007b).

High-Forage Diets

Results of studies of oscillating CP with high-forage diets have been less promising in improving N retention than studies with high-concentrate diets (Table 7). Although Collins and Pritchard (1992) reported increased N retention and decreased urinary N excretion in steers supplemented at 48-h intervals, studies in Wyoming (Ludden et al., 2002a,b; 2003) and Virginia (Simpson et al., 2001) did not note consistent improvements in N retention, nutrient digestion, or animal performance when dietary CP concentrations were oscillated at 48-h intervals.

Oscillating dietary CP increased ($P < 0.05$) ruminal liquid passage rate and tended to decrease ruminal ammonia (Ludden et al., 2002b) and plasma urea-N (Ludden et al., 2003) concentrations of lambs. Although increased ruminal turnover rate is normally associated with increased ruminal microbial protein synthesis (Meng et al., 1999), Ludden et al. (2002b) noted that microbial protein synthesis and microbial efficiency were similar for oscillating- and static-CP lambs, despite the difference in liquid turnover rate.

Possible Reasons for the Variable Results with Oscillating CP

The disparity in results of oscillating CP feeding studies could be caused by several factors including protein requirements of the animals used in the study, timing of CP oscillations, dietary CP and DIP concentrations, and dietary energy and OM fermentability. As previously noted, Archibeque et al. (2007b) noted that oscillating dietary CP might increase urea recycling to the rumen. Cole (1999) theorized that for an oscillating CP regimen to increase N recycling to the rumen, compared with a static CP concentration, one of the oscillated diets would need to be deficient in

DIP, and the average CP or DIP concentration would have to be near, or below, animal requirements. In some oscillating CP studies the low CP diet was adequate in DIP, consequently limiting or preventing an increase in N recycling. Another factor possibly affecting the results of an oscillating-CP regimen is the quantity of recycled N captured as microbial protein (Sunny et al., 2007). Capture of recycled N should be greater with more fermentable, higher-concentrate diets than with higher-forage diets.

Potential Adverse Consequences of Oscillating CP

Oscillating dietary CP also has several potentially adverse metabolic consequences. Increased N absorption from the rumen or N recycling, or both, may lead to an increase in hepatic ureagenesis, which is energetically expensive (Krehbiel et al., 1998; Huntington and Archibeque, 1999). Thus, increased ureagenesis may potentially increase maintenance energy requirements in animals on an oscillating CP regimen. However, Archibeque et al. (2007b) noted no effect of oscillating CP on either hepatic urea synthesis or oxygen consumption in lambs (data not shown).

Similarly, the gut and liver each can account for 25% or more of body energy expenditures (Huntington and Reynolds, 1987). Ludden et al. (2002a) noted that the empty weight of the gastrointestinal tract was greater ($P < 0.03$) in lambs fed an oscillating CP regimen than in lambs fed a static CP diet (Table 7). Such an increase in gut mass could potentially result in increased maintenance energy requirements. However, it has been reported that heat production of steers (Table 6; Archibeque et al., 2007a) and splanchnic oxygen consumption of sheep (Archibeque et al., 2007b) were not affected by oscillating dietary protein concentrations.

Feeding excess quantities of ruminally available N can result in increased urinary N losses due to rapid absorption and subsequent excretion of excess N. However, Cole (1999) theorized that oscillating dietary CP would prevent such an increase in urinary N excretion by increasing N recycling to the lower gut. Archibeque et al. (2007b) and Collins and Pritchard (1992) reported decreased urinary N excretion in ruminants fed oscillating CP regimens, although other studies (Cole, 1999; Ludden et al., 2002a; Cole et al., 2003; Valkeners et al., 2004; and Archibeque et al., 2007a) have noted no effect of CP oscillation on urinary N excretion.

Ruminants appear to adapt rapidly to some changes in diet. Liu et al. (1995) noted that when lambs were switched from an adequate-CP to deficient-CP diet, total protein flux, protein synthesis, and protein degradation all decreased immediately and urinary N excretion decreased by 20% on d 1. Similarly, Collins and Pritchard (1992) noted a 30% decrease in urinary N excretion within 24 h of a decrease in dietary CP concentration. These rapid adaptations to dietary changes

Table 8. Effects of phase feeding of dietary CP on calculated cumulative N metabolism assuming a 180-d feeding period (kg/steer; n = 6 pens/treatment)

Item	Dietary treatment regimen ¹				SEM	P-value ²
	11.5	13.0	13 to 11	13 to 11 at 28 d		
ADG, kg						
Last 56 d	1.30	1.29	1.18 ^{ab}	1.12 ^{ab}	0.02	0.03
Overall	1.42	1.46	1.42	1.36 ^a	0.01	0.04
Gain:feed, g/kg						
Last 56 d	159	155	151	148 ^{ab}	3.0	0.04
Overall	186	184	186	181	1.71	0.02
N intake, kg/head	24.22 ^a	29.79	27.32 ^{ab}	27.14 ^{ab}	0.48	0.01
Total N excretion, kg/head	18.01 ^a	24.93	21.51 ^{ab}	22.96 ^b	0.62	0.04

^aMean differs from continuous 13.0% CP diet ($P < 0.05$).

^bMean differs from continuous 11.5% CP diet ($P < 0.05$).

¹11.5 = continuous 11.5% CP; 13.0 = continuous 13.0% CP; 13 to 11 = fed 13.0% CP and switched to 11.5% CP with 56 d left on feed; and 13 to 11 at 28 d = fed 13% CP and switched to 11.5% CP with 28 d left on feed.

²Treatment P-value from analysis of variance.

may be in part due to labile protein and N reserves (Biddle et al., 1975). With high-forage diets, Atkinson et al. (2006) suggested that alpha-amino N may serve as a temporary means of hepatic storage of excess N between supplementation events. Thus, changes in whole body protein metabolism may occur rapidly to conserve N when dietary protein concentrations are altered.

Cattle fed high-concentrate diets may endure a significant acid load caused by the rapid synthesis of VFA and lactic acid in the rumen. Blood ammonia may serve as a systemic buffer in cattle fed high-concentrate diets (Heitmann and Bergman, 1978; Trenkle, 1979). Based on this premise, feeding lower CP (or DIP) diets or oscillating between a relatively high- and low-CP (or DIP) diet could potentially cause an increased risk of acidosis. However, working with small numbers of steers, Cole et al. (2003) noted no adverse effect of oscillating CP on arterial concentrations of important acid-base constituents.

Aside from the many, still unanswered questions about oscillating dietary CP, use of oscillating dietary CP regimens may not be practical under most current situations because of the logistics of feeding multiple diets in feedyards. Although additional research is needed, in the future, oscillating CP may provide an option for producers who are compelled to reduce N inputs or ammonia emissions, or both, from feedlot operations without sacrificing performance (Archibeque et al., 2007a).

SYNCHRONIZING PROTEIN INTAKE AND REQUIREMENTS: PHASE-FEEDING

Nutrient synchrony also needs to be considered on a larger temporal scale, that is, the nutrients available to the animal need to be synchronized with the animals' requirements. Although common in the swine and poultry industries, phase-feeding has rarely been used in US cattle feeding, in part due to logistics (labor,

feedmill, and feed truck management, etc.) and the low cost of urea. Studies with DRC-based diets (Erickson et al., 1999; Cooper et al., 2000; Trenkle, 2002) demonstrated that dietary CP concentrations can be substantially decreased late in the feeding period with little or no effect on cattle performance. Although Vasconcelos et al. (2006) reported similar results in cattle fed SFC-based diets, in a larger study with SFC-based diets the phase-feeding of protein appeared less promising (Cole et al., 2006; Table 8). Cole et al. (2006) noted that ADG, DMI, and G:F during the last 56 d on feed were similar in steers continuously fed an 11.5% CP diet and steers continuously fed a 13.0% CP diet. However, steers changed from the 13.0% CP diet to the 11.5% CP diet with 56 d left on feed had lower ($P < 0.05$) ADG and DMI than those continuously fed the 13% CP diet, indicating an adjustment period may be required when changing diets late in the feeding period. Differences in results of phase-feeding between studies using DRC- and SFC-based diets are likely attributable to differences in DIP requirements (Cooper et al., 2002a,b; Gleghorn et al., 2004). Differences in the results of the studies of Vasconcelos et al. (2006) and Cole et al. (2006), when SFC-based diets were fed, may be the result of differences in the aggressiveness of the implanting strategies used.

Although Cole et al. (2006) noted depressed performance (ADG and G:F) in phase-fed cattle during the last 56 d on feed, they also noted that phase-feeding decreased N intake by 1.4 to 3.8 kg/steer, decreased N excretion by 0.1 to 2.9 kg/steer, and decreased estimated N volatilization by approximately 4.4 kg/steer, or 22% compared with continuous feeding of the 13.0% CP diet. Similar decreases in N excretion (Cooper et al., 2000; J. T. Vasconcelos, K. W. McBride, A. Gueye, M. L. Galyean, C. R. Richardson (Texas Tech University, Lubbock), N. A. Cole (USDA-ARS, Bushland, TX), and L. W. Greene (Texas Agricultural Experiment Station, Amarillo, unpublished data) and estimated N volatilization losses (Erickson et al., 1999; Cole et al.,

2005; Todd et al., 2006) have been reported in beef cattle when dietary protein concentrations are decreased near the end of the feeding period.

Several beta-agonists are now cleared for feeding during the last 20 to 45 d on feed. These feed additives significantly increase N retention in the carcass; however, their effects on protein requirements are not clear (Reeds and Mersmann, 1991) because the increase in N required for N retention may be countered by improvements in protein utilization (Walker et al., 2006). If a beta-agonist is fed during the last 20 to 45 d on feed, it would be relatively easy to decrease dietary CP concentrations at the same time. However, it is not known if beta-agonists would limit the use of phase-feeding of protein late in the feeding period. In addition, Cole et al. (2006) noted that decreasing dietary CP during the last 28 d on feed (vs. last 56 d) significantly decreased animal performance (Table 8). Thus, additional research is obviously needed to clarify how phase-feeding of CP can be used with beta-agonists.

SUMMARY AND CONCLUSIONS

In conclusion, although ruminal nutrient synchrony is theoretically a sound principle, it appears that N recycling and other physiological adaptations can rapidly buffer ruminal nitrogen-carbohydrate synchrony. Methodologies that increase N recycling or increase the capture of recycled nitrogen may benefit animal performance and the environment. Although the use of oscillating crude protein regimens is an unlikely scenario in our current feeding system, with increased knowledge, it might provide a potential tool that cattle feeders can use to more closely manage nutrient losses in the future. Phase feeding of protein may improve nitrogen use efficiency; however, it appears any benefits are modulated by factors such as the implant program and grain processing method. Research is needed to determine the possible benefits or liabilities of using phase feeding in combination with dietary beta-agonists.

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