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Effect of Increasing Degradable Intake Protein on Intake and Digestion of Low-Quality, Tallgrass-Prairie Forage by Beef Cows¹

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ABSTRACT: Five ruminally and duodenally fistulated Angus × Hereford cows were used in a 5 × 5 Latin square to monitor intake, ruminal fermentation responses, and site and extent of digestion associated with providing increasing amounts of supplemental degradable intake protein (DIP). Cows had ad libitum access to low-quality, tallgrass-prairie forage (1.9% CP, 77% NDF) that was fed twice daily. The supplemental DIP (sodium caseinate; 90% CP) was infused intraruminally at 0630 and 1830 immediately before feeding forage. Levels of DIP were 0, 180, 360, 540, and 720 g/d. Each period consisted of 14 d of adaptation and 6 d of sampling. Forage OM intake increased quadratically ($P < .01$) with increasing supplemental DIP, reaching a peak at the 540 g/d level. True ruminal OM and NDF digestion increased

with the addition of 180 g/d supplemental DIP, but exhibited only moderate and somewhat variable responses when greater amounts of supplemental DIP were infused (cubic, $P \leq .03$). Microbial N flow and efficiency increased linearly ($P < .01$) with increasing supplemental DIP. However, a quadratic effect ($P < .01$) was observed for total duodenal N flow, which was maximized at 540 g/d supplemental DIP. A linear ($P = .02$) treatment effect was observed for ruminal fluid dilution rate. Total ruminal VFA and ammonia concentrations increased ($P < .01$) in response to DIP supplementation. In conclusion, increasing supplemental DIP generally improved forage utilization; intake of digestible OM was maximized when it contained approximately 11% DIP.

Key Words: Beef Cows, Forage, Supplements, Intake, Digestibility, Rumen Fermentation

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Introduction

Low-quality forages are important sources of nutrients used to maintain beef cattle throughout the world. To optimize the utilization of these forages and maintain acceptable animal performance, it is generally desirable to enhance intake and digestion via the provision of supplemental nutrients. Generally, degradable intake protein (**DIP**) is considered to be the dietary component that is “first limiting” to the utilization of low-quality forage. Therefore, providing supplements with adequate amounts of DIP to ruminants fed low-quality forage commonly promotes increased forage intake and flow of nutrients to the

small intestine (Hannah et al., 1991; Lintzenich et al., 1995). Because of the critical role DIP plays in enhancing the use of low-quality forages and because protein supplementation can be costly, it is important to identify the amount of DIP required to maximize digestible OM intake and duodenal protein flow. Furthermore, such information should be used to develop supplementation strategies with the aim of optimizing the utilization of low-quality forages. Therefore, the objective of this study was to determine the amount of DIP needed to maximize digestible OM intake in beef cows consuming low-quality, tallgrass-prairie forage. In addition, associated effects on ruminal fermentation and site and extent of digestion were measured.

Experimental Procedure

Five Angus × Hereford cows (average initial BW 588 kg, average final BW 530 kg, average age 7 yr) with ruminal and duodenal cannulas were used in a 5 × 5 Latin square. Cows had ad libitum access to water and low-quality, tallgrass-prairie forage (Table 1) and

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Table 1. Chemical composition and nitrogen fractions of dormant tallgrass-prairie hay and casein

Component	Prairie hay	Casein
	% of DM	
OM	91.2	96.4
CP	1.94	90.1
NDF	76.6	0
ADF	50.6	0
ADL	6.22	0
AIA	6.17	.03
DIP	1.03	90.1
	% of total N	
N fractions and rates ^a		
A ^b	19.2	.02
B _s ^c	11.5	99.8
B _i ^d	27.7	0
C ^e	41.6	0
k _{ds} ^f	∞	∞
k _{di} ^g	.12	n/a
k _p ^h	.03	.03
DIP ⁱ	53	100

^aProtein degradation rates and fractions determined as described by Krishnamoorthy et al. (1983) and Broderick (1994), respectively.

^bNonprotein N: Buffer-extracted N not precipitated by trichloroacetic acid.

^cBuffer-soluble true protein.

^dBuffer-insoluble, potentially degradable N.

^eUnavailable N fraction: N fraction remaining after 48 h.

^fDegradation rate of buffer soluble N. We assumed that the rate of degradation of buffer-soluble N was fast enough relative to the rate of passage that none would escape the rumen. Therefore, infinity was used to designate this rate.

^gDegradation rate of buffer-insoluble N.

^hPassage rate (estimated as 50% of fluid dilution rate).

ⁱDIP = $A + B_s(k_{ds}/(k_{ds} + k_p)) + B_i(k_{di}/(k_{di} + k_p))$ (Broderick, 1994).

were housed in an enclosed barn in 1.2 × 1.7 m individual tie stalls with continuous lighting. The average temperature in the barn during the experiment was 21°C. The experimental protocol was approved by Kansas State University's Institutional Animal Care and Use Committee. All surgery was conducted with appropriate anesthesia. One cow died during period 4, but necropsy indicated that death was not related to treatment. Experimental treatments entailed providing increasing amounts of supplemental DIP to the cows: 1) control, 0 g supplemental DIP/d, 2) 180 g supplemental DIP/d, 3) 360 g supplemental DIP/d, 4) 540 g supplemental DIP/d, and 5) 720 g supplemental DIP/d. The supplemental DIP (sodium caseinate) was solubilized in water (7 L/d), divided into two equal portions, and administered intraruminally at 0630 and 1830 immediately before feeding forage. Hay was chopped coarsely and offered at 140% of the previous 5-d average consumption. A trace mineral-salt mixture (composition: 62% NaCl, 17% Ca, 13% P, 7% S, .24% Fe, .08% Zn, .03% Cu, .004% Mg, .007% I) was formulated based on previous research regarding the mineral content of tallgrass-prairie forage in this region (Umoh et al., 1982). Fifty grams of the trace-mineralized salt mixture was

administered intraruminally at 0630 daily to prevent mineral deficiencies.

Sampling. Each experimental period lasted 20 d. Cows were allowed to adapt to diets for the first 14 d of each period. Voluntary intake of forage OM was measured during the following 4 d. Representative feed samples were collected at both feeding times. Ort samples were collected in the morning after orts were weighed. On d 16 through 18, duodenal and fecal grab samples were collected every 6 h. Collection times were advanced 2 h each day to obtain samples that represented every even hour of a 24-h period.

On d 19, treatment effects on ruminal DM and fluid contents were determined by manually removing the contents from each cow's rumen. The total ruminal contents were weighed, mixed, and subsampled in triplicate. Ruminal evacuations were performed just before (0 h) and 4 h after feeding hay and infusing sodium caseinate.

Ruminal fermentation measurements were taken on d 20. Fluid dilution rate was determined by infusing 13 g of Co EDTA (Uden et al., 1980) solubilized in 500 mL of distilled water into various ruminal sites just before the morning feeding (0600). Ruminal fluid samples were collected using a suction strainer (Raun and Burroughs, 1962; 19-mm diameter; 1.5-mm mesh) at 3, 6, 9, 12, and 24 h after dosing. The samples obtained at 0, 3, 6, 9, and 12 h were used for determination of ruminal pH, VFA, and ammonia N concentrations. For ruminal ammonia N analysis, 2 mL of ruminal fluid was added to 8 mL of .1 N HCl. Another 8 mL of ruminal fluid was added to 2 mL of 25% (wt/vol) metaphosphoric acid for VFA analyses. These samples were frozen at -20°C, together with a third sample of ruminal fluid (20 mL) for Co analysis.

Feed and ort samples were dried at 50°C in a forced-air oven for 48 h. Fecal and ruminal evacuation samples were dried at 50°C for 96 h. Duodenal samples for each animal within each period were composited by weight, frozen, and lyophilized. All samples were ground with a Cyclotec sample mill (Tecator, Herndon, VA) to pass a 1-mm screen. Ort and fecal samples were composited for each cow within each period, whereas forage samples were composited into a single sample within each period.

Laboratory analyses. Feed, ort, and fecal samples were dried at 100°C in a convection oven to determine DM. Organic matter concentrations were determined by ashing samples in a muffle furnace at 500°C for 8 h. Kjeldahl N was determined by the procedure described by AOAC (1990), and NDF was measured as described by Van Soest et al. (1991). Acid-insoluble ash (Van Keulen and Young, 1977; .2 N HCl procedure) concentration was determined in feed, ort, fecal, and duodenal samples and used as the digestibility marker. Ruminal bacteria were isolated from ruminal contents collected during the ruminal evacuation conducted 4 h after feeding. Saline solution (9 g/L; 500 mL/kg ruminal contents) was added to

approximately 2 kg of ruminal contents and blended, and the mixture was strained through two layers of cheesecloth. Feed particles in ruminal samples were removed via centrifugation at $1,000 \times g$ for 10 min. Bacteria were separated from the supernatant by centrifuging at $20,000 \times g$ for 20 min, washing with saline solution (9 g/L), and then centrifuging a second time at $20,000 \times g$ for 20 min. Isolated bacteria were frozen and lyophilized before being analyzed for ash and N. Bacteria and duodenal samples were analyzed for purine concentration (Zinn and Owens, 1986) in order to determine the microbial N flow to the duodenum and microbial efficiency. True ruminal OM digestion was calculated by correcting the amount of apparent ruminal OM digested for bacterial OM flow to the small intestine. Duodenal samples also were reconstituted to 3% DM in .1 N HCl, mixed, and centrifuged at $20,000 \times g$ for 20 min (Hannah et al., 1991). The supernatant then was analyzed for ammonia N according to the procedure described by Broderick and Kang (1980).

At each time period, pH of all ruminal fluid samples was measured immediately after collection using a portable pH meter with a combination electrode (Orion Research, Boston, MA). After thawing at room temperature, ruminal fluid samples for ammonia N, VFA, and Co analyses were centrifuged at $20,000 \times g$ for 20 min. The supernatant was analyzed for ammonia N by the same phenol hypochlorite procedure described for duodenal ammonia N. The VFA concentrations in the supernatant were measured by gas chromatography (Vanzant and Cochran, 1994). Cobalt concentration was determined in the supernatant with an atomic absorption spectrophotometer with an air-acetylene flame. The natural logarithm of Co concentration was regressed against sampling time to calculate fluid dilution rate (Warner and Stacy, 1968). Ruminal fluid and DM contents were determined from manual evacuation of ruminal contents.

Prairie hay and casein samples were incubated with *Streptomyces griseus* protease to determine their rate of protein degradation (Krishnamoorthy et al., 1983). Briefly, a .5-g sample was incubated in 40 mL of borate-phosphate buffer for 1 h, followed by the addition of 10 mL of protease solution (.33 units/mL protease type XIV from *S. griseus*; Sigma Chemical, St. Louis, MO). Samples were collected at 0 h (buffer soluble) and after exposure to protease for .25, .5, 1, 2, 4, 6, 8, 12, 18, 24, 36, and 48 h at 39°C. Forage protein fractionation using *S. griseus* and calculation of protein degradability were as described by Broderick (1994). Passage rate used in degradability calculations was estimated as 50% of the average fluid dilution rate (Owens and Goetsch, 1986) observed in this study (Table 3) over all five treatment groups.

Statistical Analysis. Intake, digestibility, and flow data were analyzed as a 5×5 Latin square using the GLM procedure of SAS (1988), and treatment means

were calculated using the LSMEANS option. Effects in the model were cow, period, and treatment. Treatment sums of squares were partitioned into linear, quadratic, and cubic effects of DIP level with orthogonal polynomials. Because digestible OM intake (DOMI) represents an integrated assessment of treatment effects on forage intake and digestion, we felt that estimates of DIP "requirement" were expressed best in relation to the amount required to maximize DOMI. Therefore, the first derivative of the quadratic regression of DOMI on DIP intake was determined. This equation was set equal to zero and solved. This resulting value was the DIP intake needed to maximize DOMI. This value was inserted in the original quadratic regression equation and the equation solved for the corresponding DOMI value. The DIP intake was expressed as a percentage of this calculated DOMI value (i.e., the DOMI at the plateau). In addition, DIP requirement was estimated using a single slope, broken-line model (Robbins, 1986) with the NLIN procedure of SAS (1988). Ruminal liquid and solid contents, as well as fermentation measurements (pH, VFA, and ammonia N), were analyzed as a Latin square, split-plot design using the MIXED procedure of SAS (1992). Whole-plot sources of variation were animal, period, and treatment, and the subplot sources included time and the treatment \times time interaction. Animal \times period \times treatment was used to test the whole-plot effects, and residual error was used to test the subplot effects. Linear, quadratic, and cubic contrasts were used to partition the treatment sums of squares.

Results

Because of the slow rate of ruminal passage for this type of diet (Del Curto et al., 1990; Hannah et al., 1991; Lintzenich et al., 1995), the low protein concentration of the forage, and the ready digestibility of casein, we assumed that all of the buffer-soluble protein was degraded in the rumen (Table 1). As a result, casein degradability (percentage of total N) was estimated to be 100% (approximately 90% on a DM basis). In contrast, ruminal degradability of the forage protein was approximately 53% of the total N (1% of the DM).

Forage OM, total OM, digestible OM (including both digestible forage and casein OM), and total N intake increased in a quadratic ($P < .01$) manner with increasing additions of supplemental DIP (Table 2). The largest incremental response was observed with the first addition of supplemental DIP (180 g DIP/d). Thereafter, intake generally increased, but at a decreasing rate. The two exceptions to this general pattern were forage and total OM intake, both of which peaked at 540 g supplemental DIP/d. By taking the first derivative of the quadratic regression equation for total DOMI, the DIP required to maximize

Table 2. Effect of increasing amount of degradable intake protein (DIP) on OM and N intakes; OM, NDF, and N digestibilities, total N, bacterial N, ammonia N, and nonammonia-nonmicrobial N flows to the duodenum; and fecal N loss in cows fed dormant tallgrass-prairie forage

Item	DIP level (g/d)					SEM ^b	Contrasts ^a		
	0	180	360	540	720		L	Q	C
OM intake, g/kg BW ^{.75}									
Forage	29.3	48.1	57.3	64.7	61.6	2.72	<.01	<.01	.91
Casein	0	1.62	3.24	4.86	6.48				
Total	29.3	49.7	60.5	69.6	68.1	2.73	<.01	<.01	.91
Digestible OM intake	12.9	26.8	33.1	35.5	37.4	1.77	<.01	<.01	.26
Total N intake, g/d	13.4	48.6	80.5	110.9	137.8	1.23	<.01	<.01	.94
Ruminal digestibility, % of intake									
Apparent OM	43.3	47.3	47.4	45.3	47.4	1.36	.22	.28	.12
True OM	46.1	52.4	54.4	53.1	58.1	1.29	<.01	.30	.03
NDF	47.2	55.6	56.7	53.2	54.6	1.15	.01	<.01	.01
Apparent N	-139.5	-34.9	-15.0	2.0	23.2	16.20	<.01	.03	.14
Duodenal flow, g/d									
Total N	30.7	65.6	92.4	111.7	109.3	5.83	<.01	<.01	.51
Microbial N	19.3	46.3	67.0	80.0	90.4	6.06	<.01	.12	.86
Ammonia N	.31	.77	1.94	4.20	4.77	.35	<.01	.36	.07
NANMN ^c	11.1	18.5	23.5	27.5	14.1	2.87	.17	<.01	.16
Microbial efficiency, g N/kg OM truly digested	12.2	15.2	17.0	19.1	20.0	1.21	<.01	.43	.98
Total tract digestibility, %									
OM	44.6	54.3	54.2	51.3	53.8	2.27	.09	.09	.08
NDF	50.3	58.7	57.9	54.6	55.6	1.85	.34	.04	.06
N	-39.8	39.0	51.1	60.5	70.4	6.96	<.01	<.01	.02
Fecal N loss, g/d	18.0	29.7	39.5	47.1	45.2	2.24	<.01	<.01	.34

^aL = linear, Q = quadratic, C = cubic.

^bStandard error of the mean (n = 5).

^cNonammonia-nonmicrobial N.

DOMI was calculated to be 15.8% of the DOM (5.83 g/kg BW^{.75}; Figure 1). In contrast, when using a broken-line model (Figure 2), we estimated that approximately 11% of the DOM (4 g total DIP/kg BW^{.75}) would be required to maximize DOMI of low-quality prairie hay by mature, nonpregnant beef cows.

Apparent ruminal OM digestibility was not greatly affected ($P \geq .12$) by increasing amounts of supplemental DIP. When ruminal digestibility was corrected for bacterial OM flow to the small intestine, however, the resulting estimates of true ruminal OM digestibility generally increased in response to increasing supplemental DIP, although the response was somewhat variable (cubic, $P = .03$). Ruminal NDF digestibility responded in a similar fashion (cubic; $P = .01$). Apparent ruminal N digestibility exhibited a quadratic ($P = .03$) response; the largest incremental response was to the initial provision of supplemental DIP.

All total-tract digestibility values measured (OM, NDF, N) were higher when any amount of DIP was fed but were somewhat variable with increasing amounts of DIP (cubic, $P \leq .08$). Digestion coefficients for OM and NDF increased at the lower DIP levels but tended to decline with the addition of 540 to 720 g DIP/d. Total tract N digestibility was lowest and

negative for the control, exhibited the greatest incremental increase at 180 g DIP/d, and had smaller incremental increases when more supplemental DIP was provided.

Increased provision of supplemental DIP increased total N flow to the duodenum in a quadratic ($P < .01$) fashion, with N flow peaking at 540 g supplemental DIP/d. Total N flow was greater than N intake for the 0, 180, and 360 g/d treatments, was similar for the 540 g/d treatment, and was less than N intake for the 720 g DIP/d level. Microbial N and ammonia N flow to the duodenum increased linearly ($P < .01$) as supplemental DIP increased. Flow of nonammonia-nonmicrobial N to the duodenum increased in a quadratic fashion ($P < .01$), showing maximum response at 540 g supplemental DIP/d. Efficiency of microbial growth increased linearly ($P < .01$) as supplemental DIP increased. Amount of N appearing in the feces increased in response to increasing DIP, but at a decreasing rate (quadratic; $P < .01$). The peak in fecal N loss was observed at the 540 g DIP/d infusion level.

Time of ruminal evacuation did not interact ($P > .10$) with supplementation level for ruminal DM and liquid contents (Table 3). Ruminal DM contents tended ($P = .09$) to decrease linearly with increasing DIP infusion level. In contrast, ruminal liquid contents decreased somewhat with the 180 g DIP/d level,

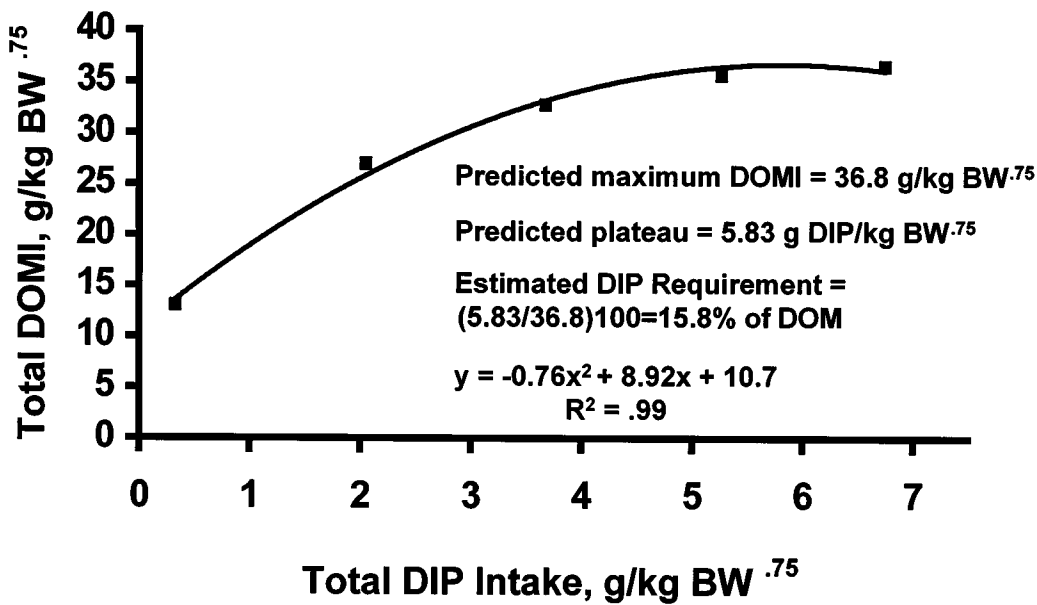


Figure 1. Degradable intake protein (DIP) required to maximize digestible OM intake (DOMI). Estimated by determining first derivative of quadratic regression equation. Standard error of the estimate = 1.13. Coefficient of determination (R^2) was calculated as described by Kvålseth (1985): $1 - \frac{\sum(Y_{\text{observed}} - Y_{\text{predicted}})^2}{\sum(Y_{\text{observed}} - Y_{\text{mean}})^2}$.

but increased somewhat thereafter (cubic, $P < .01$). Fluid dilution rate increased linearly ($P = .02$) with the addition of increasing supplemental DIP.

Ruminal pH generally decreased with increasing infusion of supplemental DIP (Table 4), although the largest incremental change occurred for the initial infusion level (cubic, $P < .01$). Ammonia N and most VFA were characterized by treatment \times time ($P < .01$)

interactions. However, the interactions were largely due to variation in magnitude of differences within each time period. Therefore, data were averaged across time. Ammonia N increased linearly ($P < .01$) as DIP supplementation was increased. Total VFA concentration increased rapidly at the initial infusion level and continued to increase slightly with increasing DIP infusion (cubic, $P = .07$). Acetate proportion

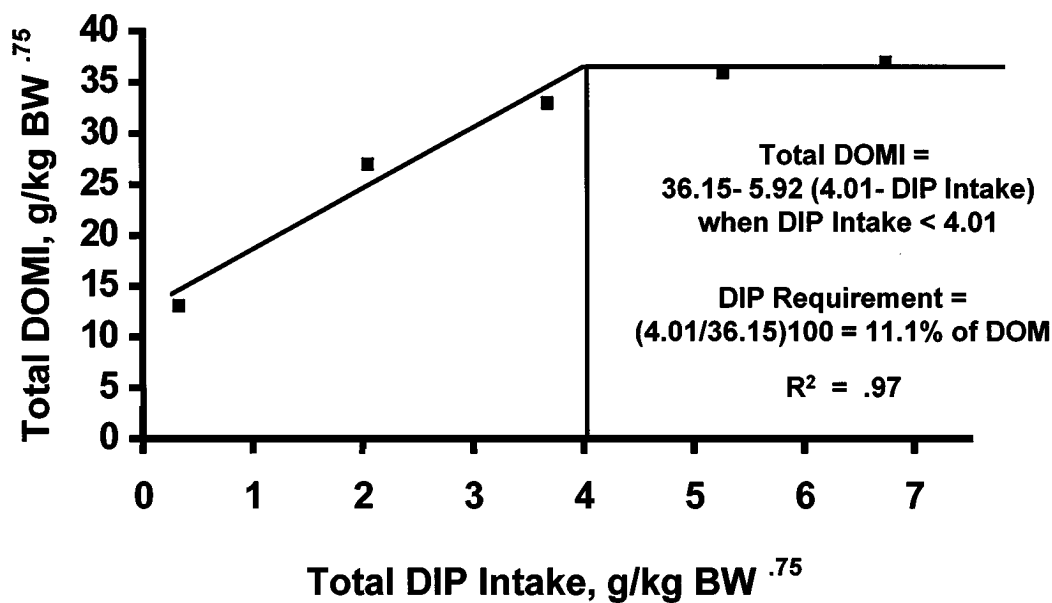


Figure 2. Degradable intake protein (DIP) required to maximize digestible OM intake (DOMI). Estimated using a single slope, broken-line model. Standard error of the estimate = 1.84. Coefficient of determination (R^2) was calculated as described by Kvålseth (1985): $1 - \frac{\sum(Y_{\text{observed}} - Y_{\text{predicted}})^2}{\sum(Y_{\text{observed}} - Y_{\text{mean}})^2}$.

Table 3. Effect of increasing amount of degradable intake protein (DIP) on ruminal dry matter and fluid contents, and fluid dilution rate in cows fed dormant tallgrass-prairie forage

Item	DIP level (g/d)					SEM ^b	Contrasts ^a		
	0	180	360	540	720		L	Q	C
Ruminal DM contents, g/kg BW	15.3	14.7	15.9	12.3	12.4	.40	.09	.95	.22
Ruminal fluid contents, g/kg BW	101.9	96.0	104.3	109.4	105.1	2.50	.03	.99	<.01
Fluid dilution rate, %/h	4.74	5.47	6.29	7.07	6.39	.48	.02	.16	.37

^aL = linear, Q = quadratic, C = cubic.

^bStandard error of the mean (n = 5).

declined linearly ($P < .01$), whereas propionate and the acetate:propionate ratio responded in a quadratic ($P \leq .03$) manner. The highest propionate proportion and lowest acetate:propionate ratio existed for the 540 g/d treatment. Isobutyrate, valerate, and isovalerate proportions increased with increasing amount of supplemental DIP but exhibited the largest incremental increases at infusion levels of 180 and 720 g supplemental DIP/d (cubic, $P \leq .09$).

Discussion

The results obtained in this study confirm that DIP supplementation can elicit a dramatic increase in the intake of low-quality forage by beef cows. This corroborates earlier findings in which forage intake increased in response to providing increasing quantities of "protein" supplements to ruminants fed low-quality forages (Guthrie and Wagner, 1988; Stokes et al., 1988; Scott and Hibberd, 1990). The diminishing responses of forage OM intake to higher levels of DIP highlight the fact that the potential to stimulate

intake via DIP supplementation is limited. The limits probably are set by both inherent fermentability of the forage and the protein requirements of the animal. Scott and Hibberd (1990) also demonstrated diminishing responses in forage OM intake when incremental levels of DIP were fed to similar cattle (mature beef cows weighing 500 to 600 kg) eating a similar forage.

Owens et al. (1991) reviewed research regarding protein supplementation and suggested that improved performance resulting from protein supplementation was likely due to either increased DOMI and/or improved efficiency of ME use. Although the latter may be important, they reported that most research indicates that increased DOMI can explain the majority of the performance response to protein supplementation. Therefore, we felt that achieving maximal DOMI would be an appropriate response criterion for evaluating the "requirement" for supplemental DIP in forage-based diets. Furthermore, expressing the desired DIP as a percentage of the DOMI underscores the fact that the DIP required to maximize DOMI will vary with the inherent digestibility of the forage. The mathematical approaches

Table 4. Effect of increasing amount of degradable intake protein (DIP) on pH, ammonia N, and total VFA concentrations and VFA proportions in cows fed dormant tallgrass-prairie forage

Item	DIP level, g/d					SEM ^b	Contrasts ^a		
	0	180	360	540	720		L	Q	C
pH	6.92	6.62	6.63	6.58	6.52	.03	<.01	<.01	<.01
Ammonia N, mM	.24	1.36	3.47	5.17	6.87	.56	<.01	.74	.61
Total VFA, mM	43.3	65.9	71.7	74.4	76.4	2.58	<.01	<.01	.07
	mol/100 mol								
Acetate ^c	78.0	75.4	74.7	73.6	72.4	.56	<.01	.27	.29
Propionate	15.2	16.1	16.3	16.5	15.8	.35	.25	.02	.78
Butyrate	6.11	6.18	5.98	6.19	6.33	.13	.36	.30	.66
Isobutyrate ^c	.43	.78	.93	1.11	1.70	.10	<.01	.17	.06
Valerate ^c	0	.68	.93	1.17	1.60	.09	<.01	.14	.04
Isovalerate ^c	.17	.84	1.18	1.40	2.22	.16	<.01	.78	.09
Acetate:propionate	5.14	4.70	4.59	4.48	4.66	.14	.02	.03	.92

^aL = linear, Q = quadratic, C = cubic.

^bStandard error of the mean (n = 5).

^cTrt × time ($P < .01$).

used to estimate the DIP "requirement" yielded substantially different results. The single slope, broken-line model yielded a lower estimate than the polynomial regression procedure (11.1% vs 15.8% of DOM respectively). In general, the quadratic regression procedure yields higher values (Baker, 1986) because it predicts requirements where maximum response is obtained. Therefore, considering the cost of DIP supplementation and the decreased magnitude of improvement for DOMI as maximum response is approached, the broken-line model is likely the preferable approach (Baker, 1986; Robbins, 1986). The DIP required to maximize intake in the study conducted by Scott and Hibberd (1990; estimated with single slope, broken-line model) was approximately 2% less than that calculated from our study. However, when total CP requirements were compared, Scott and Hibberd (1990) observed that approximately 2% more total CP was required to maximize DOMI. The differences observed may be due to the fact that supplements in the Scott and Hibberd study were common feedstuffs that also provided some undegradable intake protein (UIP). This additional UIP and concomitant increases in total N flow to the small intestine may have contributed positively to the intake response (Egan, 1965; Egan and Doyle, 1985; Garza et al., 1991). Alternatively, recycling of UIP N to the rumen as urea may have contributed to the ruminally degradable N fraction. This, in turn, could have reduced the apparent DIP requirement, because part of the DIP need would have been met via an indirect route.

Ellis (1978) and McCollum and Galyean (1985) suggested that improvements in voluntary intake of low-quality forages as a result of N supplementation frequently are associated with increases in the rate of passage and forage digestion, as seems to have occurred in the present experiment. Similarly, our results concur with those of previous studies that reported increased digestibility when N was supplemented to beef cattle consuming low-quality forages (Del Curto et al., 1990; Scott and Hibberd, 1990; Hannah et al. 1991). The ammonia N concentrations (Table 3) were quite low in our study when no DIP was supplemented and probably limited ruminal microbial growth (Satter and Slyter, 1974) and fiber digestion. Therefore, it seems likely that the increases in OM and NDF digestibility observed with the initial increment of supplemental DIP were due to provision of N as well as other nutrients (e.g., branched-chain VFA) to the fiber-digesting microbes. Because increased intake and passage rate result in a shorter retention time of OM in the rumen (Staples et al., 1984), less time is available for cellulolytic microorganisms to digest fiber. Hence, the slight decline observed in NDF digestibility when higher levels of DIP were supplemented was probably the result of the competing effects of passage and diges-

tion. The negative ruminal N digestibilities observed at the lower infusion levels were reported in previous research with unsupplemented low-quality diets (Church and Santos, 1981; Hannah et al., 1991) and were largely the result of N recycling (Bunting et al., 1989).

The estimates for microbial efficiency in our study are low compared with those in studies that used better quality forage (Merchen and Bourquin, 1994). However, the efficiencies in our study were similar to those from studies in which N was supplemented to cattle consuming low-quality forages (Kropp et al., 1977; Redman et al., 1980; Lintzenich et al., 1995). Low microbial efficiencies observed in cattle fed low-quality forages (i.e., diets with limited ruminally available protein and slow carbohydrate fermentation rates) probably are due to slow microbial growth rates and fluid dilution rates (Owens and Goetsch, 1988). Slow fluid dilution rates may result in a high proportion of available energy being used for the maintenance of bacterial cells (Owens and Goetsch, 1986). The fact that microbial efficiency increased with the provision of supplemental DIP is consistent with these observations.

The decline in ruminal pH with increasing DIP levels reflects an increase in ruminal fermentation; however, all values were well within acceptable levels for cellulolytic bacteria. Enhanced ruminal ammonia N concentrations observed in our study with increasing DIP supplementation agree with other research (McCollum and Galyean, 1985; Lee et al., 1987; Stokes et al., 1988) and reflect the provision of a readily available N source. Ammonia N levels without supplementation were low and apparently limited forage fermentation, as shown by the substantial increase in total VFA when DIP was supplemented. In addition, the increase in total diet intake also would contribute to a higher total VFA concentration when greater amounts of DIP were supplemented. The reduced acetate and increased propionate proportions observed in this study with the addition of DIP supplement are in agreement with previous research (McCollum and Galyean, 1985; Hannah et al., 1991). The slight increase in propionate and substantial increase in the minor VFA may have been responsible for the decline in molar percent of acetate. Increased propionate concentrations have been reported in response to dietary conditions that increase digestion and fluid dilution rate (Van Soest, 1982). Branched-chain amino acids serve as precursors to the branched-chain VFA. Therefore, the large increase in branched-chain VFA in the supplemented cows seems directly linked to the provision of readily available precursors in the DIP. In addition, the disproportionately large increase in branched-chain VFA proportion at the 720 g DIP/d level suggests that a threshold for branched-chain VFA use in this diet may have been exceeded.

Implications

Providing protein sources with a high concentration of degradable intake protein can address intake and digestibility limitations frequently observed with low-quality forages. To maximize the total digestible organic matter intake of mature, nonpregnant cows fed low-quality, tallgrass-prairie forage required that the digestible organic matter contain 11% degradable intake protein (4 g/kg BW^{0.75}). Whether the resulting metabolizable protein reaching the small intestine would be adequate to support maximal performance within the energy constraints of the diet would depend on the protein requirements of the animal.

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