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Effect of ruminal vs postruminal administration of degradable protein on utilization of low-quality forage by beef steers¹

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ABSTRACT: An experiment was designed to determine the effects of ruminal and postruminal infusions of ruminally degradable protein (casein) on intake and digestion of low-quality hay by beef steers. Twelve ruminally fistulated Angus × Hereford steers (initial BW = 563 kg) were blocked by weight and assigned to one of three treatments: control (C; hay only) or hay plus ruminal (R) or postruminal (P) infusion of 400 g/d of sodium caseinate. The trial consisted of five periods: 1) 10-d adaptation to the hay diet; 2) 7-d measurement of hay intake (without infusions); 3) 10-d adaptation to protein infusion treatments (intake measurements continued); 4) 7-d measurement of hay intake and digestibility (infusions continued); and 5) 3-d ruminal sampling period (infusions continued). Steers were given ad libitum access to tallgrass-prairie hay (3.4% CP, 76.6% NDF) throughout the study. Casein was administered once daily before feeding, either directly into the rumen or via anchored infusion lines into the abomasum. Hay intake was increased by supplementation ($P < 0.01$). Ruminal infusion elicited a greater ($P = 0.04$) increase in hay intake than postruminal infusion. Intake tended ($P = 0.11$) to be lower in period 4 than in period 2 for control steers but was greater in period 4

than in period 2 ($P \leq 0.03$) for both R and P steers. The increase in intake between periods 2 and 4 was greater for R than for P steers ($P = 0.03$). Supplementation improved diet OM digestion ($P = 0.04$) but not NDF digestion ($P = 0.18$); however, greater relative error for NDF digestion may have limited the ability to elucidate significant treatment effects. There were no differences in either OM digestion ($P = 0.42$) or NDF digestion ($P = 0.35$) between R and P steers. Plasma urea N at 0 and 3 h after feeding on the last day of the experiment was lower ($P = 0.05$) for C than for R and P steers, but no difference ($P = 0.48$) was evident between R and P steers. Ruminal ammonia N levels also were increased by supplementation ($P < 0.01$), with a much larger increase for R than for P steers ($P < 0.01$). Total VFA concentrations were not affected ($P = 0.21$) by treatment, but R steers exhibited lower proportions of acetate and higher proportions of isobutyrate, valerate, and isovalerate than P steers ($P < 0.01$). In conclusion, ruminal and postruminal infusion of a degradable protein source improved forage utilization, although the response in forage OM intake and total digestible OM intake was greater for ruminal infusion than for postruminal infusion.

Key Words: Beef Cattle, Forage, Protein, Supplementary Feeding

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Introduction

Low-quality roughages are valuable ruminant feed resources worldwide. Considerable research has been directed at supplementation strategies that optimize utilization of these forages and crop residues. Protein

supplementation, in particular, has been shown to stimulate forage intake, digestion, and animal performance (Guthrie and Wagner, 1988; DelCurto et al., 1990; Köster et al., 1996). Inadequate ruminal N supply limits microbial growth, thereby reducing diet fermentation, digesta outflow, and, ultimately, intake (Maeng et al., 1976; Egan, 1980). Supplemental degradable intake protein (DIP) or recycled N (from digested and absorbed undegradable intake protein [UIP], mobilized tissue protein, or digested and absorbed microbial protein) can help meet microbial N requirements. However, there is clearly a cost to the animal from urea production and recycling when the latter serves as a significant source of ruminal N supply (Reynolds, 1992; Lobley et al., 1995; Parker et al., 1995). Knowledge of the relative effects of supplying supplemental protein ruminally vs

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Table 1. Chemical composition (% dry matter) of tallgrass-prairie hay and sodium caseinate

Component	Prairie hay	Casein
Organic matter	91.5	96.6
Crude protein	3.4	89.9
Neutral detergent fiber	76.6	—
Acid detergent fiber	49.5	—
Acid detergent insoluble ash	6.4	—

postruminally would be helpful in designing optimal supplements for cattle consuming low-quality, N-deficient forages. Therefore, a study was designed to compare the effects on forage intake, digestion, and fermentation when casein (a high-quality source of degradable/digestible protein) was supplied directly to the rumen vs the abomasum.

Materials and Methods

Twelve ruminally fistulated Angus \times Hereford steers (average initial BW 563 kg; average final BW 498 kg) were housed in an enclosed barn (average temperature 26°C) in 1.2- \times 1.7-m individual tie stalls. Animals had continuous access to water and commercial trace mineral/salt blocks (salt, \geq 96%; Zn, 0.40%; Fe, 0.16%; Mn, 0.32%; Cu, 0.037%; I, 0.01%; and Co, 0.004%; American Stockman, Overland Park, KS). The basal diet consisted of a low-quality, tallgrass-prairie forage (Table 1) coarsely chopped to approximately 13 mm in length and offered daily at 130% of the previous 5-d average consumption. The experimental protocol was approved by Kansas State University's Institutional Animal Care and Use Committee and included the use of anesthesia when surgery was performed. Steers were blocked by weight (four weight blocks) and then randomly assigned within block to one of three treatments: control (**C**; hay only) or hay plus ruminal (**R**) or postruminal (**P**) infusion of 400 g/d of casein. Casein (sodium caseinate, New Zealand Milk Products, Santa Rosa, CA) was selected as a protein source that would be readily degraded in the rumen and(or) digestible in the small intestine. The dosage level was selected to provide sufficient supplemental DIP to significantly improve forage intake and digestion when administered ruminally (Köster et al., 1996) but small enough to avoid complications from administering a pulse-dose abomasally. Casein was administered once daily either directly into the rumen (for the R treatment) or directly into the abomasum via an infusion line passed through the reticulo-omasal orifice and anchored in the abomasum (for the P treatment). Ruminal degradability of casein placed directly into the rumen was assumed to be essentially complete under the dietary conditions of our study.

The experiment consisted of five time periods: 1) 10-d adaptation to the hay diet; 2) 7-d measurement of voluntary intake (no infusions); 3) 10-d adaptation to protein infusion treatments (intake measurements con-

tinued); 4) 7-d measurement of hay intake and digestibility (infusions continued); and 5) 3-d ruminal sampling period (infusions continued).

Orts were removed and weighed daily. Beginning with period 2, 5% of each ort sample was retained daily and dried at 50°C in a forced-air oven for 48 h. A representative sample of forage also was collected daily, composited, and dried as described above. Casein samples were retained from each 20-kg package of product, composited, and retained for subsequent analyses. During period 4, fecal grab samples were collected from each steer at the same time each morning and dried at 50°C in a forced-air oven for 96 h.

On d 35, ruminal evacuations were performed just before (0 h) and 4 h after feeding hay and administering casein. Ruminal contents of each steer were removed manually, weighed, mixed by hand, subsampled in triplicate, and then returned to the rumen. These subsamples were dried at 50°C in a forced-air oven for 96 h.

Prior to feeding on d 37, each steer received a 500-mL pulse dose of Cr-EDTA solution (Binnerts et al., 1968) that was administered into several ruminal sites. Ruminal fluid samples were collected just before dosing (0 h) and at 3, 6, 9, 12, and 24 h after dosing. The pH of each sample was recorded immediately with a combination electrode (Orion Research, Boston, MA), and subsamples of ruminal fluid were prepared and frozen (-20°C) for later determination of ruminal VFA, ammonia, and Cr concentrations. At 0 and 3 h after feeding on d 37, blood samples were collected from each steer in 15-mL heparinized tubes, cooled, and centrifuged for 12 min at 1,000 \times g before storage at -20°C.

Fecal and Orts samples were composited for each animal within period. All dried samples were ground with a Wiley mill (Model-4, Thomas Scientific, Swedesboro, NJ) to pass a 1-mm screen. Feed, Orts, and fecal samples were analyzed in duplicate for DM, ash, and Kjeldahl N (AOAC, 1990). Neutral detergent fiber and ADF concentrations were determined as described by Robertson and Van Soest (1981), with the exclusion of sodium sulfite and decalin from the procedure. Acid detergent insoluble ash (**ADIA**) in forage, supplement, Orts, ruminal digesta, and fecal samples was analyzed by the method of Van Soest et al. (1991) and used as an internal marker to estimate digestibility and passage rate. Digestibilities were calculated as described by Cochran and Galyean (1994). Passage rate was calculated by dividing average intake of ADIA by ruminal mass of ADIA.

Ruminal fluid subsamples destined for VFA analysis were combined with 25% (wt/vol) metaphosphoric acid (8 mL ruminal fluid to 2 mL acid) prior to freezing. Similarly, as preparation for ammonia N analysis, 2 mL of ruminal fluid was added to 8 mL of 0.1 N HCl before freezing. Ruminal fluid samples (10 mL) collected for Cr analysis were frozen without addition of chemical agents. After thawing, all ruminal fluid samples were centrifuged at 20,000 \times g for 20 min. Ruminal VFA concentrations were determined by gas chroma-

tography (Vanzant and Cochran, 1994). Chromium concentration was determined using an atomic absorption spectrometer with an air-acetylene flame. Fluid dilution rate was calculated by regressing the natural logarithm of Cr concentrations against sampling times (Warner and Stacy, 1968). Ruminal DM and liquid contents were determined directly from manual evacuation of ruminal contents. Rumen ammonia N and plasma urea N (PUN) concentrations were determined using an autoanalyzer (Technicon Analyzer II, Technicon Industrial Systems, Buffalo Grove, IL).

The MIXED procedure of SAS (SAS Inst. Inc., Cary, NC) was used to evaluate intake data within periods 2 and 4, the difference in mean forage intakes between periods 2 and 4, time in days between initiation of infusion and positive intake response, the slope of the change in intake from the point of a positive response to the end of the adaptation period, and OM and NDF digestion. Classes were treatment and block, where block (i.e., weight) was specified as a random effect. Contrast statements were constructed to compare supplemented with unsupplemented treatments and to compare P and R treatments. Liquid dilution rates were analyzed similarly. Total VFA concentration, molar proportions of individual VFA, pH, ruminal NH_3 concentration, PUN concentration, and particulate (ADIA) passage rates and fill data also were analyzed with the MIXED procedure of SAS (SAS Inst. Inc.). In this analysis, treatment, time, and the treatment \times time interactions were considered fixed effects, whereas block and treatment \times block were treated as random effects. The same contrast statements were used to compare supplemented and unsupplemented treatments and R and P treatments.

Results

Before infusion treatments began (period 2), no significant differences were observed in intakes among treatment groups (Table 2). However, in period 4 (after adaptation to infusion treatments) both P and R groups exhibited increased hay OMI, total OMI, and total digestible OMI (TDOMI) relative to controls ($P < 0.01$). Ruminal casein supplementation was associated with greater increases in hay and total OMI ($P \leq 0.06$), as well as in digestible OMI ($P = 0.09$), compared with postruminal supplementation. Compared with the OMI of the control group during period 4, P and R steers consumed about 28% and 62% more forage, respectively. The net change in mean OMI from period 2 to 4 (OMI change, Table 2) was negative for the control animals, possibly in response to a continued depletion of protein status. This decline contrasted markedly ($P < 0.01$) with the increased intake of forage by supplemented animals. Again, R steers showed a greater increase in forage intake across periods than P steers ($P = 0.03$). Also, the pattern of intake change varied between these treatments; the intake response was delayed more ($P = 0.02$) for P than for R steers. Whereas ruminal

casein infusion resulted in an immediate positive intake response, P steers actually seemed to follow the declining slope of the C group for several days before increasing their OMI (Figure 1). In fact, it took 4 d for the P group to display an increase in forage intake. However, after the P group began to respond positively to infusion, the rate of increase, until response dampened, was similar ($P = 0.32$) to that for the R group. Supplementation also increased OMD ($P = 0.04$), regardless of infusion site ($P = 0.42$). There were no significant treatment effects on NDFD.

Treatment did not significantly affect ruminal pH or total VFA concentrations, but there were significant treatment differences in molar proportions of individual VFA (except propionate and butyrate) and in ammonia N concentrations (Table 3). Treatment \times time interactions were significant for molar proportions of acetate, isobutyrate, valerate, and isovalerate, as well as for ammonia N concentration ($P \leq 0.01$); however, these interactions were largely due to differences in magnitude of response (for example, for the control vs supplemented animals) at specific time points. Therefore, to facilitate interpretation of treatment effects, treatment means over time are presented. Ruminal DIP supplementation shifted VFA proportions away from acetate and increased molar percentages of isobutyrate, valerate, and isovalerate ($P < 0.01$) compared with postruminal supplementation. Proportions of these VFA for the two supplemented groups were found to differ ($P \leq 0.07$) from those for the control; however, this seemed to be largely due to responses to ruminal infusion.

Ammonia N concentration was quite low for C steers (range of 0.5 to 0.6 over time) but increased ($P < 0.01$) with supplementation. Additionally, average concentrations were about threefold higher ($P < 0.01$) for R than for P steers (ranges over time of 2.0 to 5.9 and 1.1 to 1.6, respectively). In contrast, PUN concentrations were not different ($P = 0.48$) between the R and P groups. Both infusion treatments exhibited PUN concentrations that were more than double that of the controls ($P = 0.05$).

Treatment did not significantly affect ruminal DM contents (Table 4), although supplemented animals tended ($P = 0.08$) to have more liquid contents than control animals. In addition, P steers tended ($P = 0.12$) to have more liquid contents than R steers, as well as larger ($P = 0.05$) amounts of ADIA. Liquid dilution rate was not significantly changed by treatment, but ADIA passage was increased ($P < 0.01$) by casein infusion. Passage rate of ADIA was also notably faster ($P < 0.01$) in R than in P steers.

Discussion

Increased intake of low-quality forage in response to protein supplementation in our study is consistent with numerous published reports (Hunter and Siebert, 1973; Lee et al., 1985; Beaty et al., 1994). The magnitudes of increases seen in our research (28% and 62% more hay

Table 2. Effect of ruminal or postruminal casein infusion on voluntary intake and digestibility in steers fed low-quality, tallgrass-prairie hay

Item ^a	Treatment ^b				Contrast ^d	
	C	P	R	SEM ^c	S vs Non	P vs R
Period 2 OMI, g/kg BW ^{0.75}	54.6	54.3	56.2	3.1	0.88	0.69
Period 4 hay OMI, g/kg BW ^{0.75}	47.8	61.0	77.4	4.9	0.01	0.05
Period 4 total OMI, g/kg BW ^{0.75}	47.8	64.4	80.7	4.9	<0.01	0.06
Period 4 TDOMI, g/kg BW ^{0.75}	18.9	30.1	36.0	1.94	<0.01	0.09
OMI change, g/kg BW ^{0.75}	-6.8	10.1	24.6	1.97	<0.01	0.03
Days to positive OMI change	NA ^e	4.3	1.0	0.53	NA	0.02
Slope of OMI increase	NA	2.3	2.7	0.24	NA	0.32
OMD, %	39.5	47.1	44.7	2.10	0.04	0.42
NDFD, %	39.8	44.9	42.1	3.69	0.18	0.35

^aOMI = OM intake; TDOMI = total digestible OMI; Period 2 = hay only; Period 4 = hay plus infusion treatments; OMI change = difference in hay intake between periods 2 and 4; days to positive change = number of days after infusion treatments began until intake began to increase; slope of increase = daily increase (kg/d) in hay OMI after initiation of increase; OMD = OM digestion; NDFD = NDF digestion.

^bC = Control, P = postruminal infusion, R = ruminal infusion.

^cSEM = standard error of the mean (n = 4).

^dS vs Non = supplemented vs nonsupplemented, P vs R = postruminal vs ruminal infusion.

^eNA = not applicable.

OMI with P and R, respectively) also fall within the range reported by Minson (1990), who summarized numerous literature reports regarding the effect of protein supplementation on low-quality forage intake.

Improvements in intakes by the P and R groups in our study seemed to be a function of supplying key dietary constituents to the ruminal ecosystem and the changes associated therewith. Chief among these limiting dietary components is a source of ruminally available N. Inadequate N supply to the rumen limits microbial growth and, as a result, negatively affects diet fermentation and digesta outflow (Maeng et al., 1976; Egan, 1980). Clearly, provision of a N source to the rumen in the case of the P group would depend on recycling of postruminally infused DIP to the rumen as

urea. The increased ammonia N concentration observed in this group suggests that this did occur. In addition, it has also been proposed that increasing metabolizable protein supply to the host, via increased microbial protein and/or dietary UIP flow to the small intestine, has a direct stimulatory effect on intake (Egan, 1977). The delayed intake response in the P group after infusions began suggests that although this may be important, a lag in response may occur until metabolic status has changed sufficiently to prompt increased intake. This concurs with the observations of Lee et al. (1985), who reported that when cows maintained on a protein-deficient diet were given a high-UIP supplement, their intake response was delayed several days, as was the case with our P steers; Lee et al. (1985) attributed this delay to lag time required to increase rumen fill. However, this contrasts with a report by Egan (1977), who noted that postruminal infusion of casein in sheep elicited an immediate, rapid increase in intake. It is possible this discrepancy might be explained by differences in nutrient status of the animals in these different trials. If dietary nutrient supply was substantially deficient, as in our experiment, initial increases in postruminally available protein might be utilized preferentially by the gut and liver for energy and/or protein synthesis. Until these immediate deficiencies are addressed, the gastrointestinal tract may essentially serve as a protein sink. If so, increases in PUN and N recycling would not occur until the gut and liver were replenished. Clarification of the nature of the intake response to postruminal infusion via additional research may shed light on the relative contributions of ruminal (e.g., increased digestion and/or passage) and extraruminal (e.g., central nervous system response to changing metabolic status) mechanisms to the response to supplementation.

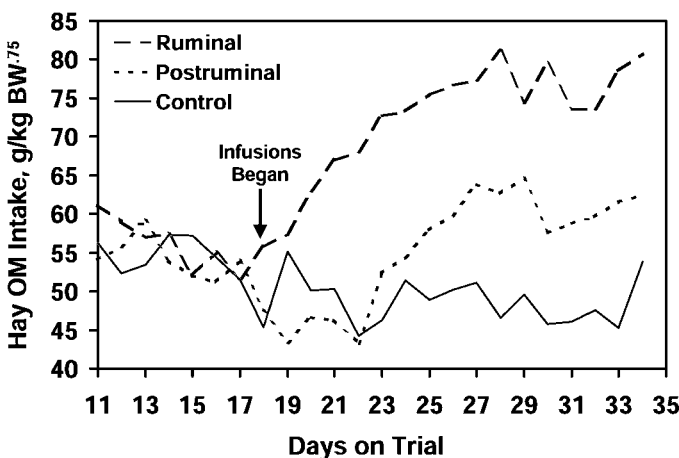


Figure 1. Hay intake over time in beef steers receiving low-quality tallgrass-prairie forage; treatment groups were infused ruminally or postruminally with 400 g/d casein beginning on d 18.

Table 3. Effect of ruminal or postruminal casein infusion on ruminal pH, ammonia nitrogen concentration, total VFA concentration, VFA proportions, and plasma urea nitrogen concentration in steers fed low-quality tallgrass-prairie hay

Item	Treatment ^a			SEM ^b	Contrast ^c	
	C	P	R		S vs Non	P vs R
pH	6.67	6.60	6.50	0.13	0.42	0.54
Ammonia N, mM	0.55	1.35	4.16	0.32	<0.01	<0.01
Total VFA, mM	69.9	77.6	81.5	6.7	0.21	0.64
Plasma urea N, mM	0.83	2.59	2.05	0.49	0.05	0.48
	mol/100 mol					
Acetate	78.7	78.9	76.1	0.23	<0.01	<0.01
Propionate	13.0	13.5	14.8	0.42	0.11	0.16
Butyrate	7.1	6.6	6.7	0.37	0.34	0.85
Isobutyrate	0.47	0.37	0.83	0.05	0.07	<0.01
Valerate	0.26	0.30	0.88	0.04	<0.01	<0.01
Isovalerate	0.43	0.37	1.12	0.07	<0.01	<0.01

^aC = control, P = postruminal infusion, R = ruminal infusion.

^bSEM = standard error of the mean (n = 4).

^cS vs Non = supplemented vs nonsupplemented, P vs R = postruminal vs ruminal infusion.

The fact that ruminal DIP administration elicited approximately double the increase in forage intake observed with postruminal administration has significant implications in formulating supplements for cattle fed low-quality, N-deficient forages. In this case it seems that addressing the ruminal protein (N) deficiency should be the first priority. Then, in those cases in which the metabolizable protein requirement exceeds that provided by microbial protein plus UIP, consideration should be given to the potential benefits of additional UIP supplementation.

Increased intake in the R vs P group must be related to increased outflow of ingested material (via digestion and/or escape) or increased willingness to accommodate particulate matter in the rumen. Reports exist in the literature of protein-stimulated increases in intake that are accompanied by increases in ruminal fill, but without large or consistent increases in digestibility or passage rate (Egan and Doyle, 1985; Ndlovu and Buchanan-Smith, 1987; Hannah et al., 1991). In our study, the amount of ADIA in the rumen of the R steers was less than in the P steers. Thus, increased outflow

of ingested material apparently was responsible for the increased intake observed for the R steers. Clearly, both digestion (e.g., increased particle degradation) and passage could contribute to such efflux. However, quantitatively assessing the importance of digestive differences per se is difficult because treatments were confounded with changes in intake and passage.

The observed increases in diet digestibility with protein supplementation were consistent with other reports (Fleck et al., 1988; Del Curto et al., 1990; Lintzenich et al., 1995) and presumably were due to improved protein (N) availability for the ruminal microbes (Petersen, 1987). Responses in fiber digestion to protein supplementation have been less consistent, with some authors reporting improvements (Fleck et al., 1988; Beaty et al., 1994; Köster et al., 1996) and others not (Hannah et al., 1991; Freeman et al., 1992; Lintzenich et al., 1995). We saw no treatment differences in NDF digestibility, which may have been due to the counteracting forces of digestion and passage rate (Hoover, 1986). However, greater relative error for NDF digest-

Table 4. Effect of ruminal or postruminal casein infusion on ruminal DM, acid detergent insoluble ash (ADIA), and liquid contents, as well as liquid and ADIA passage rates in steers fed low-quality tallgrass-prairie hay

Item	Treatment ^a			SEM ^b	Contrast ^c	
	C	P	R		S vs Non	P vs R
DM contents, g/kg BW ^{0.75}	115	127	115	6.82	0.46	0.22
Liquid contents, g/kg BW ^{0.75}	712	859	762	40.3	0.08	0.12
ADIA contents, g/kg BW ^{0.75}	6.8	8.1	6.9	0.38	0.19	0.05
Liquid dilution rate, %/h	4.61	4.79	5.34	0.71	0.62	0.60
ADIA passage, %/h	2.06	2.26	3.36	0.13	<0.01	<0.01

^aC = control, P = postruminal infusion, R = ruminal infusion.

^bSEM = standard error of the mean (n = 4).

^cS vs Non = supplemented vs nonsupplemented, P vs R = postruminal vs ruminal infusion.

ibility than for OM digestibility also may have limited our ability to elucidate significant treatment effects.

The low ruminal ammonia concentrations of the C steers in our trial are similar to published values for cattle consuming unsupplemented, low-quality forage (Pritchard and Males, 1982; Hannah et al., 1991; Lintzenich et al., 1995) and fall well below reported optimal levels for microbial efficiency (Satter and Slyter, 1974; Hoover, 1986). Both P and R treatments increased ruminal availability of ammonia, presumably meeting at least part of the microbial N requirement and thereby improving fermentation, passage rate, and intake. Although Hoover (1986) cited a wide range of "optimal" NH₃ N concentrations reported in the literature, the value of 3.6 mM (Satter and Slyter, 1974) frequently is cited as a reference guideline. However, these authors also reported that limitations on microbial growth were removed when the NH₃ N concentration was about 1.4 mM or higher. The fact that OM digestibility was increased similarly by the R and P infusions seems to agree with their observation (note that the NH₃ N concentration of the P group approached 1.4 mM).

Supplementation did not change ruminal concentration of total VFA, which averaged 76 mM. Other authors reporting similar mean levels also failed to detect treatment differences in total VFA (McCullum and Galyean, 1985; Lee et al., 1987; Caton et al., 1988). In contrast, protein supplementation has been reported to increase total VFA concentration relative to those of control animals, which had VFA levels in the range of 43 to 57 mM (Del Curto et al., 1990; Hannah et al., 1991; Köster et al., 1996). However, it is also important to note that ruminal liquid pool size tended to be larger for the supplemented steers in our study, which could have affected relative VFA concentrations. Ruminal DIP infusion did alter the molar proportion of VFA present in the rumen. Ruminally infused steers had relatively less acetate and more propionate, isobutyrate, valerate, and isovalerate. The fact that isobutyrate, valerate, and isovalerate increased in response to ruminal but not abomasal protein infusion suggests that little, if any, backflow of the protein infusate from the abomasum to the rumen occurred. Significantly higher ruminal ammonia concentrations in the ruminally infused group also seem to support this conclusion.

Implications

Efficient supplementation strategies specifically address diet inadequacies that limit utilization of the basal forage. Until protein (nitrogen) needs of the ruminal microflora are met and the host animal is maintained at some basal nitrogen status, degradable intake protein supplements will more effectively increase voluntary intake of low-quality, protein-deficient forages than undegradable intake protein sources.

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