Whole Linted Cottonseed as a Forage Substitute: Fiber Effectiveness and Digestion Kinetics^{1,2}

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ABSTRACT

Six ruminally and duodenally cannulated Holstein cows were used in a 6 × 6 Latin square design to 1) evaluate the potential interaction in effectiveness of neutral detergent fiber (NDF) from whole cottonseed (WCS) when it was substituted for forage NDF (FNDF) and fed with ground (G) or steam-flaked (SF) corn and 2) to determine whether the kinetic properties of NDF digestion further clarify the effectiveness of WCS. The six dietary treatments were: forage control with G corn (21% FNDF), 5% WCS with G or SF corn (18% FNDF), 10% WCS with G or SF corn (15% FNDF), and 15% WCS with G corn (12% FNDF). Based on chewing activity, the NDF from WCS was estimated to be 84% (SE = 36%) as effective as alfalfa silage NDF. Decreasing passage and digestion rates of potentially digestible NDF with increasing WCS increased the evacuated pool size of ruminal DM, apparently explaining the similar ruminal mat consistency among treatments. Measures of effectiveness of WCS treatments did not interact with corn source. Fluid dilution rate was estimated based on a two-compartment model describing Co dilution, but no treatment differences were detected. There was a strong linear bias for estimates of ruminal NDF digestibility based on a single compartment model using the digestion rate of potentially digestible NDF and the passage rate of either indigestible NDF or digestible NDF when compared with NDF digestibility calculated using duodenal flows. Although further verification is

needed, these digestion and passage kinetics help explain why WCS are effective at stimulating chewing during eating and rumination.

(Key words: effective fiber, passage rate, rumen, whole cottonseed)

Abbreviation key: CNDF = NDF from cotton products, DNDF = digestible NDF, FCG = forage control with ground corn, FNDF = forage NDF, G = ground corn, HG = high cottonseed with ground corn, INDF = indigestible NDF, k_d = fractional rate of digestion, k_p = fractional rate of passage, LG = low cottonseed with ground corn, LSF = low cottonseed with steam-flaked corn, MG = medium cottonseed with ground corn, MSF = medium cottonseed with steam-flaked corn, SF = steam-flaked corn, WCS = whole cottonseed.

INTRODUCTION

Physically effective fiber is the fraction of the feed that stimulates chewing; chewing stimulates saliva secretion, which buffers acidic end products of fermentation and helps prevent depressions in DMI, ruminal motility, microbial yield, and fiber digestibility (Allen, 1997). Traditionally, physically effective fiber requirements of cattle were met using forages; however, fibrous byproducts may provide an alternate means of increasing the physically effective fiber concentration of the diet. Based on chewing response, whole cottonseed (WCS) appears to be the most effective fiber source from byproduct feeds (Clark and Armentano, 1993; Mooney and Allen, 1997). Additionally, physical effectiveness can be evaluated based on ruminal mat consistency, which alters ruminal retention time of feeds, contributes to differences in effective fiber, and stimulates rumination (Weidner and Grant, 1994a; Mertens, 1997; Allen and Grant, 2000).

Byproduct feeds usually have faster passage rates and slower digestion rates than do forages (Firkins, 1997). Unfortunately, the passage rate of particulate matter in the rumen is hard to estimate, and more progress is needed for use in ruminal models (Firkins et al., 1998). External markers used to evaluate passage

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Figure 1. Why the fractional passage rate (k_p) of potentially digestible (DNDF) and indigestible (INDF) NDF could differ. If three particle fractions (bars) each with 1 g of NDF are assumed to have varying k_p (0.040, 0.045, and 0.030/h) and DNDF and INDF proportions (0.2, 0.5 or 0.8), the average particle k_p would be 0.038/h, but the weighted average k_p would be $[(0.5 \times 0.040) + (0.2 \times 0.045) + (0.8 \times 0.030)] / (0.5 + 0.2 + 0.8) = 0.035/h$ for DNDF and $[(0.5 \times 0.040) + (0.8 \times 0.045) + (0.2 \times 0.030)] / (0.5 + 0.8 + 0.2) = 0.041/h$ for INDF.

rate mark both potentially digestible (**DNDF**) and indigestible (**INDF**) fractions of NDF, whereas ruminal digestibility of only the DNDF (not INDF) fraction is limited by passage rate (k_p). Although both fractions are within a particle and thus have the same k_p , the distribution of particles with different concentrations of DNDF relative to INDF could cause differences in k_p of DNDF and INDF to be aggregated over all ruminal particulate fractions (see Figure 1). Although Firkins et al. (1998) argued that DNDF could pass from the rumen at a rate different than that of INDF, few direct comparisons have been made because duodenal cannulation would be required. Improved estimation of k_p of DNDF from forages and byproducts should help explain differences in digestibility but also in properties affecting rumination activity.

Past research with soybean hulls (Weidner and Grant, 1994a) and wet corn gluten feed (Allen and Grant, 2000) showed that byproducts interacted with forage to increase ruminal mat consistency, decrease the passage rate of the byproduct, increase rumination activity, and increase ruminal extent of digestion. Copcock et al. (1985) speculated that linters entrap WCS in the fibrous ruminal mat so that WCS are chewed during rumination. If decreased clearance of feed DM and reduced feed particle size (WCS replacing forage) alter ruminal volumes of DM or fluid, then this could impact ruminal mat consistency or chewing. Little in-

formation is available to characterize the possible interactions between forage and other byproduct feeds, such as WCS, on ruminal mat consistency and chewing response, which probably explains the increased effectiveness of NDF of WCS as forage particle size decreased (Mooney and Allen, 1997). We postulated that a similar increase in effectiveness of WCS by cows might occur in response to increased starch availability, similar to a response in chewing time with increased concentrate allocation (Robinson and McQueen, 1997). Thus, the objectives of this research were to 1) evaluate the potential interaction between forage and WCS on measures of fiber effectiveness (ruminal mat consistency and chewing) when WCS was substituted for forage and fed with corn differing in ruminal starch degradability, and 2) determine whether kinetic parameters of NDF digestion further clarify the role of effective fiber from WCS.

MATERIALS AND METHODS

Animals, Treatments, and Experimental Design

Six primiparous Holstein cows (BW = 517 kg) fitted with ruminal and simple T duodenal cannulas were arranged in a 6×6 Latin square design. A description of the cows' feeding and management systems, including the experimental diets and loss of one observation, are described in a companion paper (Harvatine et al., 2002). The forage control diet (**FCG**) with no WCS addition contained the NRC (1989) recommendation of 21% forage NDF (**FNDF**). The WCS diets contained WCS at low (**L**), medium (**M**), or high (**H**) concentrations (5, 10, and 15% of dietary DM, respectively). In diets with ground (**G**) corn, alfalfa silage was replaced with WCS on an NDF basis to achieve diets with 18% FNDF (**LG**), 15% FNDF (**MG**), and 12% FNDF (**HG**). Linted cottonseed hulls were added to the diets in slightly different amounts during each period to balance NDF from forage and cotton products. To evaluate the potential interaction of starch availability and level of forage substitution, the G corn in the LG and MG diet was replaced with steam-flaked (**SF**) corn (**LSF** and **MSF** diets).

Sampling and Laboratory Analysis

Periods consisted of 21 d, with d 1 through 9 serving as an adjustment period and d 10 through 21 as the data collection period. Diets were prepared once daily as TMR and fed twice daily in equal proportions at 0600 and 1800 h for ad libitum intake, and digesta flow was measured using Cr_2O_3 as described previously (Harvatine et al., 2002). Cows were housed in a conventional tie-stall barn, milked at 0530 and 1600 h daily, and allowed access to a concrete lot before milking, except on days when chewing activity was being monitored.

Cows were monitored for chewing activity for a continuous 24-h period on the first day (d 10) of each collection period (Weidner and Grant, 1994b). Every 5 min, cow activity was recorded as standing or lying, and chewing activity was defined as resting, eating, or ruminating. Total time (minutes) spent on each activity was quantified by multiplying the total number of observations for that activity by five. No chewing observations were made while the cows were held in the holding pen or milked in the parlor (average time of 57 min per period). Values for chewing were adjusted proportionally to a 24-h basis [(measured time spent chewing $\times$ 24)/(24 - fraction of an hour in holding pen)].

Ruminal mat consistency was measured at 2 and 6 h after the a.m. feeding on d 11 and at 4 h after the a.m. feeding on d 12 (Weidner and Grant, 1994a). Weights (462 g) were placed into the ventral rumen 2 h before the first measurement. After allowing the ruminal mat to stabilize for 2 h, a counter weight (1.365 kg) was applied outside the rumen, and the distance that the ruminal weight ascended was recorded every 20 s for 9 min. Rate of cumulative ascension at 1, 2, 5, and 9 min was calculated. Data were averaged per cow per period.

Passage rates of WCS and alfalfa silage were determined using $\text{YbCl}_3 \cdot 6\text{H}_2\text{O}$. Whole cottonseed and alfalfa silage were marked separately with Yb using the method described by Bowman et al. (1991). The $\text{YbCl}_3 \cdot 6\text{H}_2\text{O}$ was dissolved in 0.1 N acetic acid and poured over the feed and stirred. The feed was soaked for 24 h and then rinsed three times with 0.1 N acetic acid and then twice with distilled H_2O . Feed was squeezed by hand between rinses to remove as much fluid as possible. The wet Yb-labeled feed was divided into equal doses and frozen. The Yb-labeled alfalfa was thawed and dosed prior to the a.m. feeding (0600 h) on d 13 of each period, and the Yb-labeled cottonseed was dosed before the a.m. feeding (0600 h) on d 18 of each period. After dosing through the ruminal cannula, the ruminal contents were mixed by hand. Ruminal samples were taken at 0 h (for background correction) and at 1, 2, 4, 6, 9, 12, 18, 24, and 36 h postdosing. During sampling, ruminal contents were removed from different parts of the rumen until 600 ml was collected. Contents were mixed, and a subsample was squeezed through two layers of cheesecloth and dried at 55°C. Extra contents were returned to the rumen. Dried samples were ground to pass through a 2-mm screen (Wiley mill, Arthur H. Thomas, Philadelphia, PA). The samples were analyzed for Yb using a procedure described by Ellis et al. (1982). Samples (2 g) were ashed and then dissolved in a solution containing 3 N HCl, 3 N HNO_3 , and 1.91 g/L of KCl. After vortexing at 0 and 6 h, the ash was allowed to settle overnight. The fluid was ana-

lyzed for Yb concentration using atomic absorption spectroscopy with a nitrous oxide flame and standard conditions described by the manufacturer (model SpectrAA 220; Varian Australia, Ltd., Mulgrave, Australia).

To determine liquid passage rates, a 50-ml solution of CoEDTA (Uden et al., 1980) was pulse-dosed through the ruminal cannula at 0600 h, before the a.m. feeding on d 18 of each period. After dosing, ruminal contents were mixed thoroughly by hand. Ruminal contents (1000 ml) were sampled as described previously at 0 h (for background Co correction) and then at 20 and 40 min and 1, 2, 4, 6, 9, 12, 18, 24, and 36 h postdosing. A subsample was squeezed through two layers of cheesecloth, and the fluid portion was frozen. Extra contents and fluids were then returned to the rumen. After thawing, the ruminal fluid was mixed and centrifuged at $27,000 \times g$ at 4°C for 20 min. The supernatant and dose were analyzed for Co concentrations by atomic absorption spectrophotometry (Uden et al., 1980).

Ruminal contents were completely evacuated at 2 h postfeeding and 2 h before feeding on d 20 and 21, respectively, of each period (Dado and Allen, 1995). To aid in proper subsampling, the total contents were squeezed by hand to separate solids and liquids. The liquid portion was strained through a wire mesh screen (5-mm opening) to remove additional solids, which were composited with squeezed solids. A 10% subsample (by weight) of the solids and a 10% subsample of the liquid were taken and reconstituted before freezing. The rest of the ruminal contents was returned to the cow within 30 min of initiating evacuation. After thawing, a 1.5-kg subsample of the reconstituted ruminal digesta sample was dried at 55°C, and moisture loss was used to estimate ruminal fluid volume, assuming a density of ruminal fluid of 1.0 kg/L. Dried digesta samples from both evacuations were composited within cow and period on a weighted DM basis, ground to pass through a 2-mm screen, and analyzed for DM and OM according to AOAC (1990). The concentration of NDF was determined using the method described by Van Soest et al. (1991) using hot ethanol, 8 M urea, and heat stable α -amylase (Sigma A3306; Sigma Chemical Co., St. Louis, MO). The concentration of INDF in the ruminal digesta, feed offered, orts, and duodenal samples was determined by 120-h in vitro fermentation in buffered rumen media without the addition of pepsin (Dado and Allen, 1995).

Calculations

The methods of Dado and Allen (1995), based on INDF rumen pool size, were used to estimate NDF digestion kinetics. In this procedure, a steady-state and a single compartment model are assumed. Ruminal pool

size of INDF was calculated as the average rumen DM pool size multiplied by the INDF concentration of ruminal digesta samples. Intake and duodenal flow of INDF were calculated similarly. The technique of Dado and Allen (1995) assumes that the intake of INDF (feed offered corrected fororts) should equal duodenal flow of INDF. To test this assumption, the k_p of INDF was calculated using the following two equations:

$$\text{INDF } k_p \text{ (h}^{-1}\text{)} = (\text{INDF intake/ruminal INDF pool size})/24 \quad [1]$$

$$\text{INDF } k_p \text{ (h}^{-1}\text{)} = (\text{duodenal INDF flow/ruminal INDF pool size})/24 \quad [2]$$

The duodenal flow was calculated with chromic oxide (Harvatine et al., 2002). The concentration of DNDF was calculated as total NDF – INDF. Passage rate of DNDF can be calculated as below (Firkins et al., 1998):

$$\text{DNDF } k_p \text{ (h}^{-1}\text{)} = (\text{duodenal DNDF flow/ruminal DNDF pool size})/24 \quad [3]$$

After k_p of DNDF has been determined, the digestion rate (k_d) of DNDF can be calculated as intake rate of DNDF minus the k_p of DNDF (Firkins et al., 1998):

$$\text{DNDF } k_d \text{ (h}^{-1}\text{)} = [(\text{DNDF intake}/24)/\text{ruminal DNDF pool size}] - k_p \text{ of DNDF} \quad [4]$$

The k_p of DNDF [3] must be calculated using duodenal flow measurement; that is, no relationship for INDF as in equations [1] and [2] exists for DNDF because considerable but varying amounts of DNDF get degraded in the rumen. To avoid the duodenal flow measurements, some researchers have assumed that the k_p of DNDF from equation [3] can be approximated using the k_p of INDF from equation [1]. If the k_p of DNDF is calculated (or assumed equivalent to the k_p of INDF), k_d can be solved using equation [4], and then ruminal NDF digestibility can be calculated:

$$\text{Apparent ruminal NDF digestibility (\%)} = (\text{DNDF intake/NDF intake}) \times [k_d/(k_d + k_p)] \times 100 \quad [5]$$

If the k_p of INDF and the k_p of DNDF are not equivalent, then the substitution of the k_p of INDF for the k_p of DNDF in equation [5] would affect the accuracy of the NDF digestibility estimation. Moreover, the estimate of k_d of DNDF from equation [4], which is needed in equation [5], is also affected by this assumption of equality of k_p of INDF and DNDF, further compounding error.

Figure 2. Plot of the residuals of NDF digestibility (%) calculated based on flow of total NDF at the duodenum using Cr_2O_3 as a digesta marker and flux of potentially digestible NDF (DNDF). The passage rate of DNDF (equation [3]) was approximated by the passage rate of indigestible NDF (INDF) from equation [1], and the passage rate of INDF was substituted directly for the passage rate of DNDF in equations [4] and [5]. $y = 1.07x$ (SE = 0.17) – 37.2 (SE = 6.6). Symbols represent the following treatments: forage control with ground corn (+), low cottonseed with ground corn (○), medium cottonseed with ground corn (Δ), high cottonseed with ground corn (□), low cottonseed with steam-flaked corn (●), and medium cottonseed with steam-flaked corn (▲).

Therefore, the NDF digestibilities estimated using equation [5], determined with or without the assumption of equality of k_p of INDF and DNDF, were compared to NDF digestibilities calculated using duodenal flow measurements $[(\text{NDF intake} - \text{NDF flow})/\text{NDF intake}]$. The residuals of NDF digestibilities calculated using duodenal flow (Harvatine et al., 2002) minus those obtained with the flux procedure (equation [5]) were graphed against the NDF digestibility based on duodenal flow with the assumption that the k_p of INDF could be substituted for the k_p of DNDF (Figure 2) or using the actual k_p of DNDF (Figure 3). The regression lines were fit using simple linear regression using least squares analysis.

Ruminal fluid Co concentrations were corrected for 0-h background effect. The Co concentration at time t (Co_t) was fit to the biexponential equation $\text{Co}_t = \text{Ae}^{-\alpha t} + \text{Be}^{-\beta t}$ or to a single exponential model using SAAM II (1997). A monoexponential model ($n = 5$) was estimated

Figure 3. Plot of the residuals of NDF digestibility (%) calculated based on flow of total NDF at the duodenum using Cr_2O_3 as a digesta marker and flux of potentially digestible NDF (DNDF). The passage rate of DNDF was estimated using equation [3], and the passage rate of DNDF was used in equations [4] and [5]. $y = 0.62x$ ($\text{SE} = 0.13$) - 24.4 ($\text{SE} = 5.1$). Symbols represent the following treatments: forage control with ground corn (+), low cottonseed with ground corn (○), medium cottonseed with ground corn (△), high cottonseed with ground corn (□), low cottonseed with steam-flaked corn (●), and medium cottonseed with steam-flaked corn (▲).

when the algorithm failed to converge with the biexponential model. Data for one cow during period 1 were removed because the data could not be fit to a monoexponential or biexponential model. The lack of fit was most likely due to incomplete mixing of the Co dose or nonrepresentative ruminal samples because of that cow's thick ruminal mat. Passage rate of Yb was done as for Co except that all Yb concentrations (corrected for background and calculated per g of sample DM) followed a monoexponential model.

For the data that fit the monoexponential model, the first-order rate α corresponds to the rate of passage of Co from the rumen, which is assumed to represent ruminal fluid dilution rate in a one-compartment model. For the remaining data that fit biexponential dilution, a two-compartment model was derived (Figure 4). The volume of compartment 1 (v_1) was solved as the dose of Co divided by the sum of A plus B. Then the fractional transfer rates among compartments were calculated.

Figure 4. A schematic representation depicting fractional rates of transfer (k) of CoEDTA to and from two compartments of ruminal fluid.

$$k_{10} = \text{dose}/(v_1 \cdot (A/\alpha + B/\beta)) \quad [6]$$

$$k_{21} = \alpha \cdot \beta/k_{10} \quad [7]$$

$$k_{12} = \alpha + \beta - k_{10} - k_{21} \quad [8]$$

The k_{10} is interpreted to approximate fluid dilution rate from the rumen (Figure 4).

Statistical Analyses

Data were analyzed as a Latin square with cow as a random effect using the MIXED procedure of SAS (1999) as described previously (Harvatine et al., 2002). Significant differences were declared at $P < 0.05$ unless otherwise stated. When the MIXED procedure failed to converge [eating, ruminating, and total chewing time (all minutes per day) and ruminating time (minutes per kilogram of FNDF)], data were analyzed using Proc GLM (SAS, 1999), with cow assumed to be a fixed effect. Ruminal mat consistency data were analyzed over time using a repeated measures model using the MIXED procedure of SAS. First-order autoregressive [AR(1)] was used as the covariance structure residuals within

cow $\times$ period. When interactions of treatment $\times$ time were not deemed to be significant ($P \geq 0.10$), averages over all times were analyzed for treatment effects.

The equations developed by Mooney and Allen (1997) to calculate coefficients for physical effectiveness of fiber were modified to calculate an effectiveness value for cotton NDF (CNDF; linted WCS plus linted cottonseed hulls). Individual cow observations for all treatments ($n = 35$) were used. Total chewing times were adjusted by subtracting the assumed basal chewing time [355 min/d; calculated by Mooney and Allen (1997)] from the observed total chewing time (ruminating plus eating) because the model would not solve when our individual observations were used to estimate basal chewing time. The MIXED procedure of SAS (1999) was used to analyze factors relating to effective fiber for CNDF and alfalfa silage NDF using the following model:

$$Y_{ijk} = \text{Cow}_i + \text{Per}_j + \beta_1 \text{FNDF} + \beta_2 \text{CNDF} + e_{ijk} \quad [9]$$

where Y_{ijk} = corrected chewing time, Cow_i = random effect of i th cow, Per_j = random effect of j th period, β_1 = regression coefficient for chewing time (minutes per kilogram) of alfalfa silage NDF, FNDF = alfalfa silage NDF intake (kilograms per day), β_2 = regression coefficient for chewing time (minutes per kilogram) of CNDF intake, CNDF = CNDF intake (kilograms per day), and e_{ijk} = random error $\sim N(0, \sigma_e^2)$. The SE of the ratio of β_2/β_1 was estimated using the following formula (Kendall and Stuart, 1969):

$$V(y_2/y_1) = (\mu_2^2 \sigma_1^2 + \mu_1^2 \sigma_2^2 - 2\mu_1 \mu_2 \sigma_{12})/\mu_1^4 \quad [10]$$

where $V(y_2/y_1)$ = variance of β_2/β_1 ; μ_2 = mean of β_2 ; σ_1^2 = variance of β_1 ; μ_1 = mean of β_1 ; σ_2^2 = variance of β_2 ; and σ_{12} = covariance of β_1 and β_2 . There was a correlation of -0.3057 between β_1 and β_2 . The means, variances, covariance and correlation estimates were obtained using Proc MIXED (SAS, 1999).

RESULTS AND DISCUSSION

Chewing Activity

Eating, ruminating, and total chewing activity, expressed as minutes per day, did not differ across diets (Table 1). Eating time increased as WCS replaced forage when expressed per unit of FNDF but not per unit of FNDF + CNDF. Although ruminating time tended ($P < 0.10$) to have quadratic effects when expressed per DM or NDF intake, total chewing time tended to decrease linearly ($P < 0.11$) when expressed per unit of DM or NDF intake. Quadratic responses to level of WCS for ruminating and total chewing times per unit

of FNDF intake remained significant ($P = 0.04$ for both). These data, combined with the lack of effect in total chewing time per unit of FNDF + CNDF intake, indicate that the CNDF appears to be nearly as effective as NDF from alfalfa silage in maintaining chewing activity in low forage diets. In prior studies, the replacement of FNDF with NDF from WCS promoted more chewing than NDF from short-cut alfalfa silage but resulted in less chewing than long-cut alfalfa silage (Mooney and Allen, 1997); NDF from WCS maintained chewing activity similar to that of a 21% FNDF control in another study (Slater et al., 2000).

The substitution of SF for G corn did not interact with WCS substitution for FNDF or have any significant effect on chewing activity. Although true ruminal digestibility of both nonstructural carbohydrates and OM were increased, ruminal pH was not affected by the substitution of SF for G corn in L and M WCS diets, although DMI was reduced (Harvatine et al., 2002). This suggests that CNDF stimulates sufficient chewing activity to produce enough salivary buffers to compensate for the increased acid production associated with ruminal degradation of SF corn.

Chewing coefficients were calculated for FNDF and CNDF using multiple regression of various factors regressed against total chewing time corrected for basal chewing time using equation [9]. Cottonseed hulls were added to the diets in slightly different amounts during each period to balance NDF and enable the replacement of alfalfa silage NDF with CNDF on a one-to-one basis as alfalfa silage NDF varied during periods. The ratio of WCS to cottonseed hulls was, on average, 10 parts WCS to one part cottonseed hulls. As a result, it was not possible to isolate the individual effects of WCS and cottonseed hulls on chewing. Because previous researchers (Clark and Armentano, 1993; Mooney and Allen, 1997) have shown a significant contribution for the effective fiber from WCS based on total chewing response, both FNDF and CNDF were included in the multiple regression using procedures described by Firkins et al. (2001). The effect of treatment and the quadratic term (CNDF $\times$ CNDF) were not significant ($P > 0.10$) and were removed. When the quadratic term (FNDF $\times$ FNDF) was used in the model with CNDF and FNDF, the effect of CNDF became nonsignificant ($P > 0.10$). The quadratic term (FNDF $\times$ FNDF) was excluded rather than the effect of CNDF based on our preplanned objectives to quantify the effectiveness of CNDF. The final model included the random effects of cow and period and the fixed effects of FNDF and CNDF intakes, all of which were significant ($P < 0.05$). Chewing coefficients were calculated based on FNDF and CNDF intakes (kilograms per day) rather than percentages of the diets (Mooney and Allen, 1997) because

Table 1. Least squares means for chewing responses by cows fed diets in which whole cottonseed replaced alfalfa silage and was fed with ground or steam-flaked corn.

Item	Diets ¹						SE ²		P ³				
	FCG	LG	MG	HG	LSF	MSF	n = 5	n = 6	L	Q	C	Corn	Intx
Eating													
min/d	271	294	300	284	252	266	28	25	NS	NS	NS	0.16	NS
min/kg of DMI	15.4	14.9	14.9	14.0	13.4	14.3	1.5	1.4	NS	NS	NS	NS	NS
min/kg of NDF intake	49.6	46.9	47.0	43.9	42.6	45.4	5.0	4.5	NS	NS	NS	NS	NS
min/kg of FNDF intake ⁴	71.7	81.8	96.9	114.1	73.6	92.9	9.8	8.9	<0.01	NS	NS	NS	NS
min/kg of FNDF + CNDF intake ⁵	71.7	70.3	70.9	67.4	63.3	68.1	7.3	6.6	NS	NS	NS	NS	NS
Ruminating													
min/d	514	505	434	520	461	455	44	39	NS	NS	NS	NS	NS
min/kg of DMI	29.4	25.3	22.1	25.8	24.0	24.5	2.4	2.2	0.17	0.10	NS	NS	NS
min/kg of NDF intake	94.6	79.9	69.2	81.3	76.9	77.7	8.1	7.2	0.14	0.09	NS	NS	NS
min/kg of FNDF intake	137	143	143	210	132	159	15	13	<0.01	0.04	NS	NS	NS
min/kg of FNDF + CNDF intake	137	120	105	124	114	117	11	10	NS	0.10	NS	NS	NS
Total chewing													
min/d	785	799	734	805	713	722	53	46	NS	NS	NS	NS	NS
min/kg of DMI	44.8	40.7	37.0	39.8	37.4	38.8	3.1	2.8	0.11	0.20	NS	NS	NS
min/kg of NDF intake	144	128	116	125	120	123	11	10	0.10	0.18	NS	NS	NS
min/kg of FNDF intake	209	223	240	324	206	252	18	17	<0.01	0.04	NS	NS	NS
min/kg of FNDF + CNDF intake	209	192	176	192	177	185	15	13	NS	NS	NS	NS	NS

¹FCG = Forage control with ground corn; LG = low cottonseed with ground corn; MG = medium cottonseed with ground corn; HG = high cottonseed with ground corn; LSF = low cottonseed with steam-flaked corn, and MSF = medium cottonseed with steam-flaked corn.

²For the LG treatment n = 5; for all other treatments n = 6.

³Probability of a treatment response; NS = not significant ($P > 0.20$). Contrasts compared the linear (L), quadratic (Q), and cubic (C) effects of increasing level of whole cottonseed in the diet when ground corn was used as the corn source (FCG, LG, MG, and HG). Contrast Corn compared the effect of corn source (ground vs. steam-flaked) when low or medium levels of cottonseed were fed (LG and MG vs. LSF and MSF). Contrast Intx evaluated the interaction of corn source (ground or steam-flaked) and level of cottonseed (low or medium) in LG, MG, LSF, and MSF treatments.

⁴FNDF = NDF from forage.

⁵CNDF = NDF from cotton products (whole linted cottonseed and linted cottonseed hulls).

there was a treatment effect for both DMI and NDF intake (Harvatine et al., 2002).

With the model specified by equation [9], the regression coefficients were estimated to be 97.1 min/kg of FNDF (SE = 13.5) and 82.0 min/kg CNDF (SE = 30.2). The physical effectiveness factor for CNDF relative to FNDF would be (β_2/β_1) or 0.84 (asymptotic SE = 0.36). Thus, the NDF from CNDF was estimated to be 84% as effective as NDF from alfalfa silage in stimulating chewing activity. Because of its high asymptotic SE, which resulted from compounding variation from both slope estimates, the physical effectiveness factor of WCS is not different ($P > 0.05$) from 1.0, explaining the similar chewing activity (minutes per day) across diets. Mooney and Allen (1997) calculated a physical effectiveness factor of NDF from WCS to be 0.50 and 1.27 when long- or short-cut alfalfa silages, respectively, were used as the standards; these had mean NDF particle sizes of 11.4 and 5.8 mm, respectively. The alfalfa silage used in this study had a mean DM particle size of 5.6 mm, as determined by wet sieving (Harvatine et al., 2002).

Grant (1997) noted that rumination per unit of FNDF intake often increased when the dietary NDF concentration was reduced; these observations, including the current quadratic responses of ruminating and total chewing time per unit of FNDF (Table 1), suggest that cows may possess an adaptive mechanism whereby they ruminate more efficiently under conditions of limited amounts of effective fiber. However, by design, there was a linear decrease in FNDF and a linear increase in CNDF as CNDF replaced FNDF in the current study, so it is not possible to determine whether the cows responded to low FNDF diets by chewing more efficiently independent from CNDF effects.

Because the basal chewing time used in the model was not determined with values from this study, the effect of varying basal chewing time was considered. Reducing the basal chewing time from 355 to 250 min/d increased the regression coefficients to 123 min/kg of FNDF and 102 min/kg of CNDF, whereas increasing the basal chewing time from 355 to 450 min/d reduced the regression coefficients to 74 and 64 min/kg of FNDF

Table 2. Least squares means for ruminal mat consistency for cows fed diets in which whole cottonseed replaced alfalfa silage and was fed with ground or steam-flaked corn.

Item	Diets ¹						SE ^{2,3}	
	FCG	LG	MG	HG	LSF	MSF	n = 5	n = 6
Total distance traveled, cm								
1 min	15.0	14.6	12.7	16.5	12.4	11.9	3.5	3.2
2 min	20.5	21.3	18.2	23.9	17.7	18.7	4.3	4.0
5 min	31.9	33.0	28.1	36.3	27.7	30.0	4.8	4.4
9 min	40.9	42.2	36.2	45.1	40.0	38.6	4.8	4.4
Cumulative ascension rate, cm/s								
First min	0.25	0.24	0.21	0.27	0.21	0.20	0.06	0.05
First 2 min	0.17	0.18	0.15	0.20	0.15	0.16	0.04	0.03
First 5 min	0.11	0.11	0.09	0.12	0.09	0.10	0.02	0.01
First 9 min	0.076	0.078	0.067	0.083	0.074	0.072	0.009	0.008

¹FCG = Forage control with ground corn; LG = low cottonseed with ground corn; MG = medium cottonseed with ground corn; HG = high cottonseed with ground corn; LSF = low cottonseed with steam-flaked corn, and MSF = medium cottonseed with steam-flaked corn.

²For the LG treatment n = 5; for all other treatments n = 6.

³None of the contrasts were significant ($P > 0.20$).

and CNDF. However, the physical effectiveness factor did not change considerably when basal chewing time was changed (0.83 and 0.87). This demonstration documents the relatively high confidence in the accuracy of the physical effectiveness of a test feed (i.e., β_2/β_1 in equation [9]) rather than the absolute regression coefficients (i.e., β_1 or β_2) but illustrates the importance of documentation and standardization of the test forages when comparing physical effectiveness values among studies.

Ruminal Mat Consistency

Ruminal mat consistency did not differ across treatments (Table 2). Ruminal mat consistency decreased when FNDF was replaced with NDF from nonforage fiber sources without coarsely chopped hay (Weidner and Grant, 1994a; Allen and Grant, 2000). Reduced ruminal mat consistency probably decreased total chewing time when wet corn gluten feed was used as a forage replacer (Allen and Grant, 2000). These results (Table 2) also support the adaptive response of WCS fiber in maintenance of ruminating and chewing activities (min/d; Table 1) across treatments and the greater response for WCS than other byproducts.

Passage Kinetics of NDF

The DM and NDF percentages of the ruminal digesta increased linearly with increasing level of WCS substitution for forage (Table 3). Ruminal mass of wet digesta did not differ across treatments; however, the mass of rumen DM, OM, NDF, INDF, and DNDF increased linearly with increasing level of WCS addition. There was a quadratic response in DMI: 17.8, 19.8, 20.5, and

20.3 kg/d for FCG, LG, MG, and HG, respectively (Harvatine et al., 2002). The differences in rumen pool sizes of DM and fiber probably explain the lack of differences in ruminal mat consistency (Table 2). Replacement of FNDF with NDF from nonforage fiber sources other than WCS has reduced ascension time (i.e., reduced ruminal mat consistency) in past studies (Weidner and Grant, 1994a; Allen and Grant, 2000). Therefore, increased ruminal DM mass seemed to have provided resistance to ascension of the ruminal weight that counteracted the decrease in mat consistency resulting from decreased forage. Increased ruminal mass appeared to have stimulated tension receptors (Allen, 2000) or provided enough tactile stimulation to maintain similar chewing time as CNDF replaced FNDF (Table 1).

The k_p of INDF (Table 3) was calculated based on the flux technique (see footnote 5) presented by Dado and Allen (1995) or based on duodenal flow of INDF (see footnote 6). The similarity in intake and duodenal flow of INDF within treatments supports the use of INDF intake to calculate k_p of INDF and explains why both calculation methods yielded similar values for k_p of INDF.

A key assumption for using the flux technique to alleviate duodenal sampling is that the k_p of INDF should approximate the k_p of DNDF, assuming that both fractions are found in the same physical particle. However, DNDF and INDF are determined from a conglomerated mix of particles with varying DNDF and INDF concentrations. Assuming that the k_p of the particle might not be linearly related with the percentage of total NDF that is comprised by DNDF, this assumption of equivalent k_p of DNDF and INDF might not be valid (see Figure 1).

Table 3. Least squares means for ruminal pool sizes and ruminal digestion kinetics for cows fed diets in which whole cottonseed replaced alfalfa silage and was fed with ground or steam-flaked corn.

Item ⁴	Diets ¹						SE ²		P ³				
	FCG	LG	MG	HG	LSF	MSF	n = 5	n = 6	L	Q	C	Corn	Intx
Rumen digesta													
DM, %	12.7	13.6	14.8	16.0	14.7	14.5	0.5	0.5	<0.01	NS	NS	0.05	<0.01
NDF, % of DM	54.2	54.2	56.8	58.3	56.4	58.2	1.2	1.2	<0.01	NS	NS	0.04	NS
Rumen mass, kg													
Wet digesta	65.9	65.3	63.6	64.6	66.4	67.2	5.7	5.6	NS	NS	NS	NS	NS
DM	8.24	8.83	9.38	10.26	9.80	9.61	0.73	0.71	<0.01	NS	NS	0.09	NS
OM	7.40	7.96	8.53	9.41	8.90	8.81	0.65	0.63	<0.01	NS	NS	0.05	NS
NDF	4.48	4.79	5.32	5.97	5.50	5.60	0.42	0.41	<0.01	NS	NS	<0.01	0.17
INDF	3.48	3.72	4.04	4.27	4.10	4.08	0.34	0.33	<0.01	NS	NS	0.17	NS
DNDF	1.00	1.07	1.27	1.70	1.39	1.52	0.14	0.13	<0.01	0.06	NS	<0.01	NS
Intake, kg/d													
INDF	2.73	2.95	2.97	2.95	3.13	3.06	0.21	0.19	NS	NS	NS	NS	NS
DNDF	2.81	3.25	3.55	3.51	2.89	2.89	0.22	0.20	<0.01	NS	NS	0.01	NS
Duodenal flow, kg/d													
INDF	2.71	2.97	3.19	3.19	3.16	3.03	0.21	0.19	0.02	NS	NS	NS	NS
DNDF	0.635	0.845	0.896	0.767	0.618	0.723	0.188	0.173	NS	NS	NS	0.18	NS
Rate of passage, /h													
INDF ⁵	0.035	0.033	0.031	0.030	0.033	0.032	0.003	0.003	0.11	NS	NS	NS	NS
INDF ⁶	0.035	0.033	0.034	0.032	0.032	0.032	0.003	0.003	NS	NS	NS	NS	NS
DNDF ⁷	0.051	0.037	0.030	0.018	0.019	0.021	0.016	0.015	0.09	NS	NS	NS	NS
Alfalfa silage ⁸	0.063	0.078	0.065	0.048	0.063	0.060	0.007	0.007	0.02	<0.01	NS	0.07	NS
Rate of digestion, /h													
DNDF ⁹	0.130	0.100	0.088	0.059	0.057	0.050	0.029	0.026	0.05	NS	NS	0.12	NS
DNDF ¹⁰	0.114	0.097	0.090	0.071	0.071	0.062	0.015	0.014	0.02	NS	NS	0.04	NS
Ruminal fluid volume, L ¹¹	57.3	56.1	53.8	53.8	56.1	57.2	5.0	4.9	0.10	NS	NS	NS	NS
Fluid rate of passage, /h ¹²	0.199	0.164	0.177	0.162	0.196	0.173	0.017	0.015	0.14	NS	NS	NS	0.19

¹FCG = Forage control with ground corn; LG = low cottonseed with ground corn; MG = medium cottonseed with ground corn; HG = high cottonseed with ground corn; LSF = low cottonseed with steam-flaked corn, and MSF = medium cottonseed with steam-flaked corn.

²For the LG treatment n = 5; for all other treatments n = 6.

³Probability of a treatment response; NS = not significant ($P > 0.20$). Contrasts compared the linear (L), quadratic (Q), and cubic (C) effects of increasing level of whole cottonseed in the diet when ground corn was used as the corn source (FCG, LG, MG, and HG). Contrast Corn compared the effect of corn source (ground vs. steam-flaked) when low or medium levels of cottonseed were fed (LG and MG vs. LSF and MSF). Contrast Intx evaluated the interaction of corn source (ground or steam-flaked) and level of cottonseed (low or medium) in LG, MG, LSF, and MSF treatments.

⁴INDF = Indigestible NDF determined by 120-h in vitro fermentation, and DNDF = potentially digestible NDF (NDF – INDF).

⁵Fractional passage rate of INDF based on intake of INDF. See equation [1].

⁶Fractional passage rate of INDF based on duodenal flow of INDF. See equation [2].

⁷Fractional passage rate of DNDF based on duodenal flow of DNDF. See equation [3].

⁸Fractional passage rate of alfalfa silage from the rumen using Yb as a marker.

⁹Fractional digestion rate of DNDF calculated using equation [4] but assuming that passage rate of INDF (from equation [1]) equals the passage rate of DNDF (Dado and Allen, 1995) (substituted for the result from equation [3]).

¹⁰Fractional digestion rate of DNDF calculated using equation [4] and using the actual fractional passage rate of DNDF from equation [3].

¹¹Ruminal fluid = wet digesta mass – (55°C DM * wet digesta mass).

¹²Determined using Co-EDTA to mark the fluid portion of ruminal contents.

When k_p of INDF and DNDF were calculated using duodenal flows (see footnotes 6 and 7 of Table 3), the k_p of INDF was not affected, but the k_p of DNDF tended to decrease linearly from 0.051 to 0.018/h as CNDF replaced alfalfa silage NDF. Because DNDF contributes to particle buoyancy and retention in the rumen, Firkins et al. (1998) suggested that k_p of INDF should be faster than the k_p of DNDF, but the current results refute this assumption or narrow it to comparisons among forage sources.

Our results support the suggestion that WCS are retained in the ruminal mat through entanglement of WCS linters with longer forage particles, which would slow the passage rate of WCS (Coppock et al., 1985). Bhatti and Firkins (1995) reported that the functional specific gravity of ground cottonseed hulls remained relatively unchanged over 27 h of in vitro incubation, but they had a fast rate of hydration, implying little buoyancy delay of the ground cottonseed hulls. However, little information related to passage kinetics of

WCS is available. The passage rate of alfalfa silage (determined by Yb) decreased linearly with increasing level of WCS inclusion (Table 3). In previous studies with soybean hulls (Weidner and Grant, 1994a) and wet corn gluten feed (Allen and Grant, 2000), forages and nonforage fiber sources interacted to decrease the k_p of the nonforage fiber sources; however, it is not clear whether the k_p of forage was also affected in these studies. Wattiaux et al. (1992) reported that alfalfa silage reached a functional specific gravity conducive for passage faster than did alfalfa hay because the former was prehydrated, and WCS could thereby help to slow the passage of alfalfa silage particles through entanglement (rather than vice versa). The increasing DM percentage with increasing WCS (Table 3) also supports our contention that particle entanglement of WCS helped slow passage. An alternative explanation is that the decreasing k_p of Yb-marked alfalfa silage could be a result of Yb migration to slower passing WCS particles. Alfalfa NDF decreased from 70 to 39% of total NDF with increasing WCS (data not shown). Firkins et al. (1998) noted that typical markers, such as Yb, often overestimate ruminal passage rate through migration, although procedures similar to those used in this experiment can reduce migration (Bernard and Doreau, 2000).

The dilution of Yb concentration after dosing of Yb-labeled WCS was extremely variable. None of the models tested for any of the 35 datasets could be estimated (lack of convergence of the optimization algorithm). The linters apparently prevented the WCS dose from being mixed or diluted well, providing observational corroboration to the significant entanglement and retention of WCS.

When the k_d of DNDF was calculated using the k_p of INDF (footnote 9) or the k_p of DNDF (footnote 10), the SE almost doubled for the INDF assumption (Table 3). However, there was a numerically larger linear effect of increasing WCS addition when the k_p of INDF was substituted for the k_p of DNDF. Bhatti and Firkins (1995) reported that ground alfalfa had a higher rate of digestion (0.0547 compared with 0.0208 h^{-1}) and shorter lag time in vitro than ground cottonseed hulls. Palmquist (1995) noted that cotton linters were not degraded in the first 12 to 16 h of incubation in situ or in vitro; degradation increased linearly thereafter to achieve 90% digestibility after 96 to 120 h of incubation. The flux technique assumes no lag time, so a longer lag time would decrease the k_d of DNDF using the current procedure.

Despite a 1.2 kg/d lower DMI (Harvatine et al., 2002), the mass of OM, NDF, and DNDF increased when SF corn replaced G corn (Table 3). Because digestibility of OM was increased and that of NDF was unchanged

by SF addition (Harvatine et al., 2002), these results appear to be related to the larger volume taken by SF than G corn or to trends for slower k_p of alfalfa and slower k_d of DNDF for SF versus G corn.

Ruminal NDF digestibility based on NDF flux (equation [5]) compared with NDF digestibility based on duodenal flow of NDF resulted in a positive linear bias that was stronger (higher slope and more negative intercept) when the k_p of INDF was substituted for the k_p of DNDF (Figure 2) than when the actual k_p of DNDF was used directly (Figure 3). The average ruminal NDF digestibility was numerically similar for estimates based on duodenal flow of NDF using Cr_2O_3 [(38.3%; see (Harvatine et al., 2002)] and estimates based on k_p of DNDF (39.4%; data from Figure 3) than based on the k_p of INDF (35.8%; data from Figure 2). The bias between NDF digestibilities (Figures 2 and 3) could be a result of errors in duodenal flow estimation using Cr_2O_3 or to the assumptions used (Firkins et al., 1998). However, duodenal flow of NDF is the net result of all kinetic events, whereas the flux techniques used in our study are based on a single compartment model (i.e., only one pool of DNDF) with no delay (lag) terms affecting either digestion or passage. If more than one compartment or delay term exist, they are aggregated into the simple model assumed by the flux technique.

Passage Kinetics of Ruminal Fluid

When ruminal fluid volume was measured using rumen evacuation, ruminal fluid volume tended ($P = 0.10$) to decrease linearly with increasing WCS (Table 3). However, there were no differences in fluid rate of passage (Table 3).

The single rate of Co dilution (α) from data that fit best a monoexponential model (Co concentration at time $t = Ae^{-\alpha t}$) ranged from 0.131 to 0.178/h and averaged 0.148/h ($n = 5$). The k_{10} data from the two-compartment model (Figure 4) ranged from 0.129 to 0.296 and averaged 0.186/h ($n = 29$). Because the effect of passage rate model (one or two compartments) was $P > 0.10$ when added as a fixed effect into the statistical model (data not shown), a data file with combined α and k_{10} (and no effect of model choice) was evaluated statistically to compare effects of treatment on ruminal fluid dilution rate (Table 3). These mean dilution rates for treatments are higher than data typically reported because most researchers ignore the potential contribution of a first exponential term. However, in two previous studies (Younker et al., 1998; Oldick et al., 2000), similar high values for weighted dilution rates were reported when data were fit to biexponential models. Using k_{10} to estimate ruminal fluid dilution rate probably is more theoretically appropriate than using a single

weighted average of α and β as done by the previous authors because it integrates differential equations describing transfer to and from compartments.

For the five observations using a one-compartment model, ruminal fluid volume (dose of Co/A) averaged 59% higher than the volumes estimated using rumen evacuation. Overestimation of total fluid volume compared with evacuation could be partially explained by tactile stimulation of passage of fluid during evacuation or by incomplete rumen evacuation. However, it seems unlikely that these errors could accumulate to 59%, thereby decreasing the likelihood that a one-compartment model adequately describes ruminal fluid kinetics.

Because the compartments were not sampled separately, elimination of Co using the two-compartment model was constrained to compartment 1, all samples were assumed to have been all from this pool, and v_1 was estimated as the Co dose/(A + B). Assuming instantaneous mixing of Co and steady-state conditions, the volume of compartment 2 (v_2) could be solved as $v_1 \times k_{12}/k_{21}$. When the v_1 and v_2 were summed per animal (data not shown; $n = 34$), the combined total volume averaged 90.9 L, which is 64% higher than the total ruminal fluid volume determined by evacuation (55.5 L). However, when four extreme data were removed ($n = 30$), then the total volume of v_1 plus v_2 averaged 66.6 L (data not shown), which still overestimated evacuation data by 20%.

Overestimation of total fluid volume (v_1 plus v_2), particularly for the four observations, compared with evacuation could be partially explained by underestimated evacuation volumes. However, a more likely explanation is related to sampling error at early times after dosing. Delayed distribution of CoEDTA throughout both compartments after dosing would have a larger impact on the accuracy and precision of the measurements used to derive the first exponential term because much of the flux of Co between compartments 1 and 2 would be occurring in a relatively short time after dosing. In fact, 15 and 8 samples (out of 34) taken at 20 and 40 min postdosing, respectively, were outliers that needed to be deleted. Assuming the evacuation data to be correct and the second exponential term to have much less sampling error (data were spread over a longer time after dosing), the A term was apparently underestimated, leading to overestimation of v_1 . Because v_2 was solved using an algebraic equation in which v_2 is directly proportional to v_1 , it follows that the v_2 would also be overestimated proportionally, further compounding the error when Co-derived ruminal fluid volume (v_1 plus v_2) was compared to the manually determined fluid volume. Although further verification of a two-compartment model is needed, it seems more

appropriate than using a single compartment model. The significant fit of Co data to biexponential models for 29 of 34 observations supports this contention. From these 29 solutions, the β rates averaged 0.056/h (data not shown), which would be an unreasonably low estimate for fluid dilution rate but would be increased if data were aggregated into a single exponential model. The rate of elimination of Co from the rumen (k_{10} in Figure 4) is calculated using Equation [6]. If v_1 is calculated as dose/(A + B), and the latter is substituted into equation [6], then

$$k_{10} = (A + B)/(A/\alpha + B/\beta) \quad [11]$$

Thus, the errors related to data fitting would tend to cancel (A is on the numerator and denominator [11], although A and α are potentially correlated positively) rather than amplify as when used to estimate ruminal fluid volume. Thus, we conclude that a two-compartment model should be evaluated for potential use to more accurately estimate fluid dilution rate from the rumen. In future experiments, improved distribution of dose (better manual mixing), more time points, and improved sampling procedures could be used to improve the accuracy of determination of true fluid dilution rate from the rumen.

The biological meaning of these two compartments should be interpreted with caution until both compartments can be sampled simultaneously (the current procedure assumed sampling from compartment 1 only). However, we suggest that compartment 1 is fluid that is immediately capable of exiting the rumen, but compartment 2 is fluid that is associated within or immediately surrounding particles that are retained in the rumen until hydration and digestion are completed to allow the particles (and associated fluid) to have a functional specific gravity that promotes passage (Firkins et al., 1998).

CONCLUSIONS

Based on total chewing activity, CNDF appeared to be approximately 84% as effective in stimulating chewing as the alfalfa silage NDF used in this experiment. Thus, there is potential to use WCS at up to 15% of DM to maintain chewing activity in low FNDF diets. Passage and digestion properties of WCS and apparent interactions among WCS and alfalfa silage for passage from the rumen appeared to help maintain ruminal mat consistency and chewing activity as WCS replaced alfalfa silage. Lack of an interaction between WCS and starch source for measures of effectiveness suggests that the effective fiber response of WCS was independent of ruminal starch availability.

Ruminal NDF digestion kinetics showed a bias for the flux technique determined without collection of duodenal digesta compared against the traditional duodenal flow technique, so more work is needed to compare estimations of ruminal NDF digestibility using the k_p of INDF before this procedure adequately replaces traditional duodenal flow methods. In addition, more work is needed to validate the assumption of a single compartment model to assess ruminal fluid dilution rate; our work supports the development of a two-compartment model, especially to evaluate ruminal fluid volume using markers.

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