EFFECT OF CUTICULAR DISRUPTION ON THE NUTRITIVE VALUE OF BLUESTEM PRAIRIE HAY

by

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B.G.S., Kansas University, 1976

A MASTER'S THESIS

submitted in partial fulfillment
of the requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1981

Approved by:

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ACKNOWLEGMENTS

I would like to thank the members of my graduate committee, Dr. Clenton Owensby, Dr. Len Harbers and Dr. Earl Bartley for their advise and assistance in this project. I am especially grateful to Clenton Owensby for getting me started on a line of research I want to pursue.

I would also like to express my appreciation to my parents, Bob and Shirley Jacques, and my grandparents, Leo and Jessie Allison, for their help and support of my extensive higher education. I would also like to assure them that the formal part of my education will soon be over.

Kathryn Ann Jacques
August 16, 1981

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INTRODUCTION

The digestibility and overall nutritive value of a forage to ruminants varies among plant species and changes over the growing season. The lower nutritive value of warm-season perennial grasses relative to cool-season species has been attributed to physiological and anatomical differences. Ecological adaptations like the C_4 photosynthetic pathway, Kranz leaf anatomy and a thick, waxy cuticle give tropical grasses increased photosynthetic efficiency but render nutrients less readily available to microbial degradation (Akin and Burdick 1977).

Structural inhibitors to quality in warm-season grasses intensify as vegetative growth matures (Cogswell and Kamstra 1976). The less digestible fibrous fractions and lignin increase; and a resulting decline in dry matter digestibility is seen. Protein content drops as nitrogen is translocated to storage organs below ground to be held in reserve for spring regrowth. Plant cuticle thickens in response to higher temperatures and low humidity as the season progresses (Skoss 1955; Juniper 1960).

Unfortunately both quality and quantity cannot be maximized at harvest. Cutting date must be selected such that quality and yield are adequate yet plants are allowed sufficient time for regrowth to replenish reserves before winter dormancy. The compromise cutting date for bluestem hay near Manhattan is early-mid July, a time when protein content has dropped to 6-8% and the cuticle and fibrous fractions are well-developed (Owensby and Anderson 1969; Owensby et al. 1970).

Several studies indicate plant cuticle to be the first barrier to rumen microbial digestion. Comprised primarily of cutin and extruded waxes, the cuticle is indigestible; and microbial degradation must begin at cut or

broken surfaces. Monson et al. (1972) were able to increase in vitro dry matter digustibility of a warm-season species by abrading the leaf surface with sandpaper.

Forage nutritive value is often predicted from in vitro data. Advantages of in vitro techniques from the standpoints of cost and time are clear; but adequacy in providing a complete and practical description of nutritive value is in question. Intake is not represented; and it has been suggested that in vitro cellulose digestion beyond 24 hours essentially measures ultimate extent of energy availability (Donefer et al. 1969; Crampton et al. 1960).

Extent of digestibility may not serve best to predict nutritive value, especially where the less digestible forages are concerned. Roughage intake is limited by its physical bulk in the rumen. Lessening the time a given meal spends in the rumen tends to reduce digestion of more resistant fibrous components; but increased nutrient intake more than compensates (Ellis 1978; Blaxter et al. 1961; Balch 1961).

Evaluation of cuticular disruption as a means of increasing the nutritive value of bluestem prairie hay is the object of this study.

MATERIALS AND METHODS

Forage

Forage for this study, both treated and control, came from approximately two acres of loamy upland range site at the Kansas State Research Area five miles northwest of Manhattan in July, 1979. Results of a botanical composition study (Table 1) using the modified step-point technique (Owensby 1973) showed the four warm-season perennial dominants of the tallgrass prairie to be 56% of the total composition. Andropogon gerardi (big bluestem) totaled 32%; Andropogon scoparius (little bluestem), 4.3%; Panicum virgatum

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Table 1. Botanical composition of the study area.

Species present	% Composition by species
Andropogon gerardi	32.1
Andropogon scoparius	4.3
Panicum virgatum	12.2
Sorghastrum nutans	11.1
Sporobolus asper	3.9
Sprobolus heterolepsis	2.3
Bouteloua curtipendula	2.0
Panicum scribnerianum	1.6
Sedges	17.4
Aster species	3.0
Erigeron strigosus	3.6
Asclepias verticillata	1.6
Oxalis stricta	1.6
Panicum wilcoxianum	*
Leptoloma cognatum	*
Poa pratensis	*
Buchloe dactyloides	*
Eragrostis trichodes	*
Ruellia humilis	*
Lespedeza capitata	*
Psoralea species	*
Ambrosia psilostachya	*
Artemisia ludoviciana	*
Sisyrinchium	*
Achillea millefolium	*
Linum	*
Viola pedatifida	*
Schrankia nuttallii	*
Amorpha canescens	*

*Species less than 1% of total composition

(switchgrass), 8.2%; and Sorghastrum nutans (indiangrass), 11.1%. The forb population was dominated by Aster species and Erigeron strigosus. Though sedge species accounted for 17.4% of the composition, their low stature in relation to cutting height meant sedges were not as well represented in baled hay composition.

Disruption of the cuticle was accomplished by running the forage by hand between two sets of wire brushes. One set rotated against a stationary, concave bed of brushes. The specially built machine (see schematic and photo, Figures 1 and 2) was powered by a 3 1/2 horsepower motor. As only small amounts of forage could be treated at a time, forage was cut as needed with a hand-pushed sickle bar mower with a three foot bar. Treated hay was spread on the ground to dry.

Though recommended haying dates for north-central Kansas are early-mid July (Launchbaugh and Owensby 1978), above normal July rainfall delayed harvest date until July 25th. As the treatment process was slow, completion of the desired 25 bales took 12 days. All control forage was cut August 1st using conventional mow, windrow and square baling methods.

Normal precipitation for the area in July averages 11.13 cm; while 14.10 cm fell during July of 1979. Temperatures remained at 34-36°C throughout the harvest period, at no time exceeding 38°C. No rain fell on harvested forage. Bales were protected from weathering by shed storage until used for animal trials.

Drying Time

Three samples each of treated and untreated hay were placed in tin foil pans, weighed and allowed to dry behind a wind shelter. Samples were weighed every 15 minutes for four hours or until reaching a constant weight. Comparisons were made on the basis of the time needed to reach constant weight and the percentage of water lost over time.

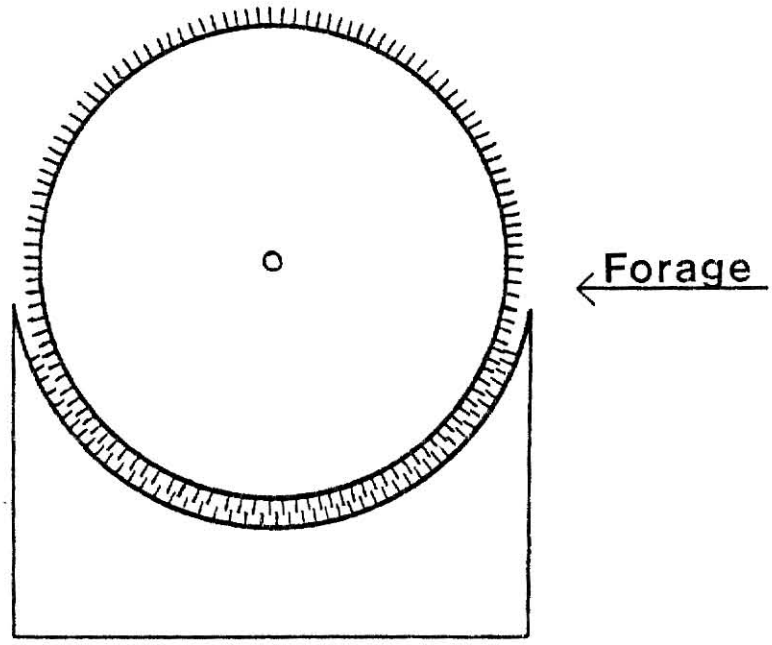

Figure 1. Schematic of the machine used to disrupt plant cuticle.

Figure 2. Photograph of the machine used to disrupt plant cuticle.

Feed/Weight Change Study

Twenty-four suffolk ewe lambs ranging in weight from 61 kg to 75 kg were used for this study. Lambs were blocked by weight, split into two homogenous groups; and each group assigned to either treated or untreated bluestem hay. Groups were divided into three pens of four animals. After a 10-day adjustment period animals were weighed, and intake per pen recorded for 28 days before final weights taken. Lambs were fed only treated or untreated prairie hay twice daily and allowed free access to water and salt. Results of this study were analyzed on the basis of mean weight loss per pen and a ratio established between amount consumed and weight loss per pen using analysis of variance in a completely randomized design.

Digestion Trial

Fourteen western whiteface wethers weighing approximately 50 kg were confined in metabolism crates for a 20-day trial. Seven wethers were randomly assigned to each treatment. A 10-day adjustment period was followed by a five day intake determination and a five day collection period. Bluestem hay was offered without supplementation. Hay was fed long to avoid complicating the effects of cuticular disruption with the results of grinding. Forage, refused hay and fecal samples were collected such that apparent digestion coefficients could be calculated for each wether each day of the trial. Means were used in the analysis of variance for a completely randomized design.

Nutrient Removal Rate Study

Four mature, rumen-fistulated Hereford X Angus steers were used in a 2 X 2 Latin Square with an extra period as described by Lucas (1957)(Figure 3). Two steers were randomly assigned to each treatment. Periods, including a preliminary adjustment were three weeks long with sampling on all animals

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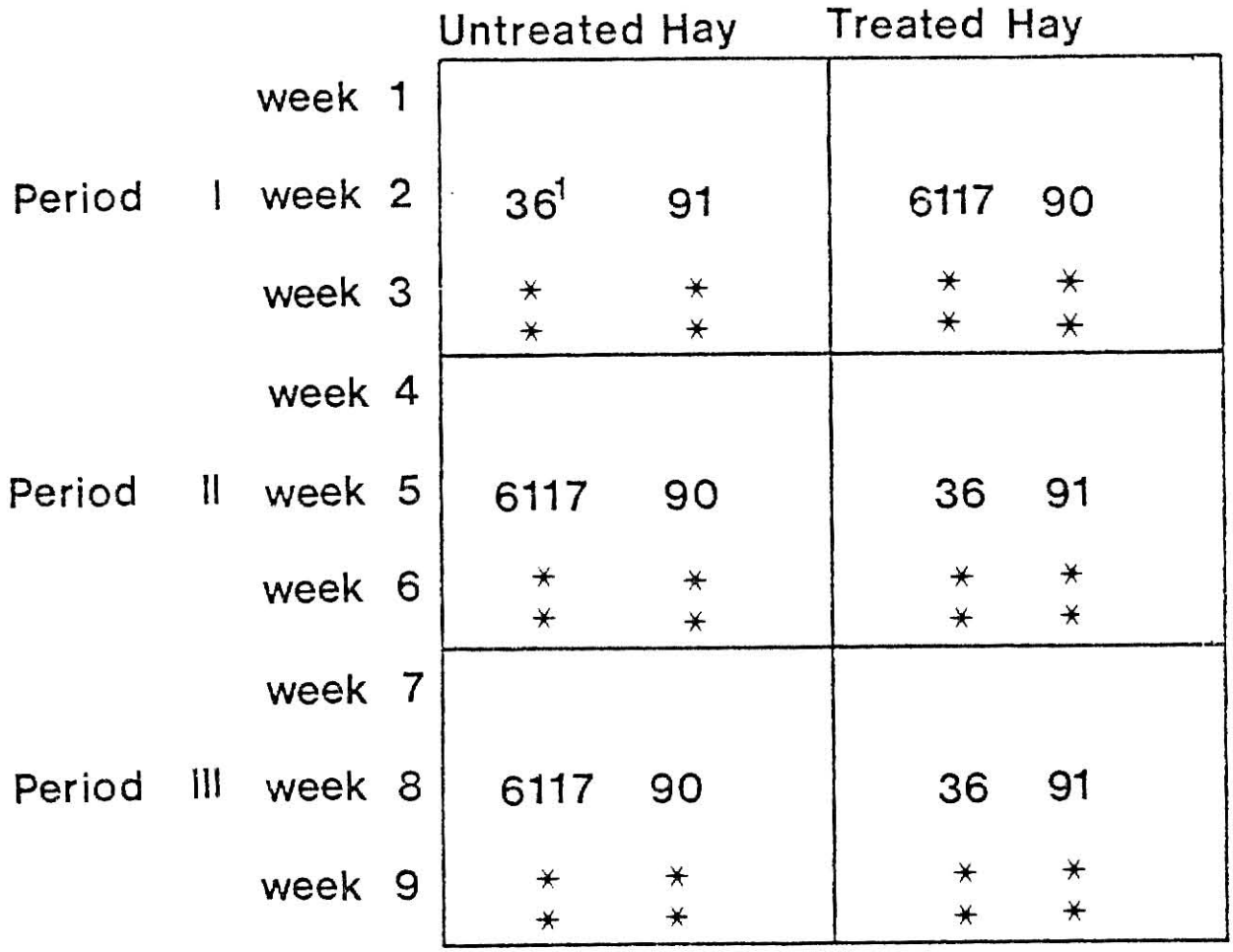
Figure 3. Treatment design for the 2 x 2 Latin square with extra period used in nutrient removal rate study.



*Sampling at the beginning and end of each third week on each steer

[1]Numbers of the steers used in the nutrient removal rate study.

at the beginning and end of each third week. Steers were penned individually at the KSU Beef Research Unit and maintained on untreated prairie hay without supplement. All had access to clean water and a salt and mineral block.

The "complete-emptying" sampling procedure described by Yadava and Bartley (1964) was followed. Two animals, one from each treatment, were sampled per day so the procedure could be completed by the normal feeding time. After removal through the fistula rumen contents were weighed, hand-mixed for five minutes and a 600 ml sample taken. Contents were then restored to the rumen. Forage was sampled and a known amount offered. After an hour refused hay was weighed. Twelve hours later the contents were again removed, weighed and sampled. Removal rates were expressed as the percentage of total rumen contents removed in 12 hours.

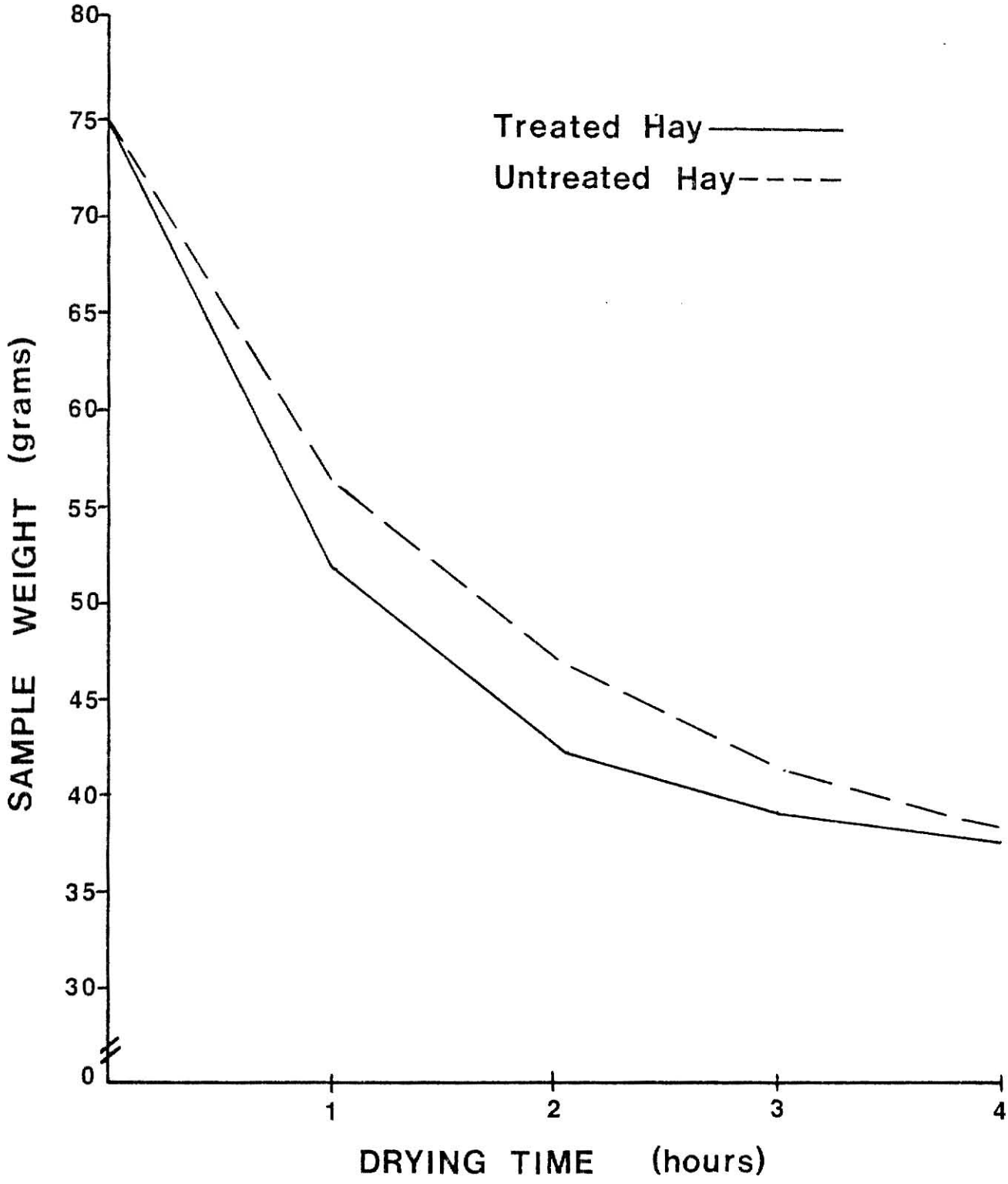
Forage and digesta samples were weighed and dried in a forced-draught oven at 43°C for seven days. Digesta samples were spread in tin foil pans and periodically stirred to prevent crusting. Weights were taken after drying for dry matter determinations on all samples. Samples were ground in a Wiley mill through a 1 mm screen. Analysis included both the proximate and the complete Van Soest analysis. The analysis of variance, described by Lucas (1957)(Table A-1), brought out variation due to steer, period and treatment. Covariance analysis was employed to illustrate relationships between intake and removal rate.

RESULTS AND DISCUSSION

Drying Time

Treated samples lost slightly more water than untreated samples. The difference was only two grams and did not approach statistical significance. The pattern of water loss (Figure 4) differed in that treated samples lost more water in the first two hours thus coming sooner to a more or less constant weight than did untreated forage. While a shorter drying time

Figure 4. Change in weight of treated and untreated bluestem hay samples over time due to water loss.



before baling can reduce the chances of nutrient loss due to leaching, with this type of treatment protection from weathering loss becomes even more desirable.

Forage Quality and the Treatment Process

Analysis of the forage used in the animal trials based on 12 samples each of untreated and treated hay revealed quality differences (Table 2). Cuticular disruption reduced crude fiber relative to untreated samples by 4.16% on a dry matter basis while the percentages of crude protein, ether extract and ash increased slightly. Results of the Van Soest analysis showed larger percentages in treated samples of cell solubles (+1.97% over untreated samples), hemicellulose (+1.27%), ADN (+.01%) and silica (+.97%). Untreated samples were found to contain more cell wall constituents (+1.97% over treated samples), lignin (+1.26%), cellulose (+2.43%) and cutin (+.24%). Alwash and Thomas (1971) found altering physical form of a "dried grass" by grinding and pelleting reduced crude fiber relative to chopped grass samples; but another study by the same authors (1971) showed little effect on forage quality when grass was ground without pelleting.

Differences in amounts of particular forage constituents reflect the action of the machine used for treatment. Though intentions were to merely "scratch" the cuticle allowing more entry points for microbes with minimum damage done the forage; difficulty arose treating a large quanity of forage in the field. Rotating wire brushes on the machine scraped the forage against stationary brushes. Hand-holding the forage as it went through the machine meant tension and results varied along the leaves. Shredding or splitting between vascular bundles occurred when tension was higher, especially toward leaf tips. Shredding probably accounted for the lower amount of cell wall constituents in treated hay. Treatment here resulted in an improvement of forage quality due to removal of some of the more slowly

Table 2. Comparison of forage quality based on 12 samples each of treated and untreated bluestem hay.

Van Soest analysis	Untreated hay (%)	Treated hay (%)	
Cell walls	76.73	74.76	*
Cell solubles	23.27	25.24	*
ADF	45.30	42.06	**
Hemicellulose	31.43	32.70	
Lignin	7.14	5.88	**
Cellulose	33.44	31.01	**
Cutin	2.26	2.02	
ADN	.17	.18	
Silica	3.08	4.05	**
Proximate analysis			
Crude fiber	35.09	30.93	**
Crude protein	4.86	5.49	**
Ether extract	1.87	2.48	**
Ash	6.05	7.19	**

**Significant at alpha=.01 *Significant at alpha=.25

digestible tissues, mainly cellulose and lignin. Despite shredding and loss of ADF constituents the more digestible cell solubles were higher in treated than untreated hay. The percentage of silica was higher in treated hay, suggesting this element bound in tissues besides the epicuticular layer.

Composition of bales and samples differed between treated and untreated hay. Though no composition tests were applied, forbs going through the machine were riddled and little forb leaf tissue became baled.

Feed/Weight Change Study

Mean weight losses for lambs fed treated hay for 28 days was 7.28 kg and 7.58 kg for those on untreated hay (Table 3). Daily intake of treated hay averaged .04 kg higher than untreated hay; and the resulting feed/weight loss ratio was slightly lower for untreated hay. None of these differences approached statistical significance.

Sheep in this feeding trial received bluestem hay as the only nutrient source beside salt and water. While a protein supplement would have been necessary before the diet could have been considered nutritionally complete; associative effects of feed components on ration utilization make it difficult to consider any one component. Eng et al. (1974) showed increasing the roughage component in a corn and bermudagrass hay ration to increase roughage passage rate while the passage rate of corn decreased. Though intake alone has been shown to affect removal rate (Alwash and Thomas 1971; Blaxter et al. 1956), changes in microbial population exert an influence as well. Celluloytic bacteria are less active at the lower rumen pH values associated with cereal grain supplementation thus lowering rate and extent of fiber digestion (Terry et al. 1966). These metabolic changes plus variability in ration formulation have led researchers to conclude information on forage nutritive value to be best obtained when the forage is fed

Table 3. Treatment means for feed/weight change trial using sheep.

	Treated hay	Untreated hay
Intake	.84 kg	.80 kg
Mean weight loss	-7.28 kg	-7.84 kg
Intake/weight loss ratio	-0.1184	-0.1028

alone (Swift 1957).

However, even given that a forage should be considered the total diet when seeking information about nutritive value, evaluation of low quality (low protein, high fiber) forages presents more complicated nutritional problems. If, as Mitchell (1942) says, "... the utilization of any food nutrient for any purpose requires the presence of all other nutrients required for that purpose" then utilization of energy present would be severely limited in poor quality forages by low protein availability. Such a protein-determined threshold to energy utilization may mean a production characteristic like weight change tells relativity little about the nutritive value of low quality forages. Weston (1967), in defining factors that limited wheaton hay intake by sheep, found first protein then residue removal rate limiting.

Digestion Trial

Intake, dry matter digestibility and digestibility of neutral detergent fiber were higher for treated hay while acid detergent fiber digestibility was slightly higher for untreated hay (Table 4 and 5). No treatment differences approached significance.

Precise determinations of intake were difficult in this trial. Lambs were offered 1.0215 kg of hay fed daily in two portions owing to the bulky nature of long prairie hay and small feedbunks. An attempt was made to account for hay lost from bunks by weighing it and charging it equally to all lambs on that treatment. Under these conditions the cuticular disruption process left treated hay easier for confined lambs to handle thus slightly less of it was lost from bunks. Such an error factor would carry over into the analysis of forage fed despite analysis made on all refused forage samples.

Intake means and digestibility coefficients in this trial were low; a reflection of the inadequate protein content (4-5%) in relation to energy

Table 4. Intake means and apparent digestion coefficients for treated and untreated bluestem hay.

	Intake	Dry matter	Cell solubles	NDF	ADF
		% Digestibility			
Treated hay	.793 kg	36.28	30.98	38.70	29.51
Untreated hay	.779 kg	35.42	30.14	37.89	32.64

Table 5. Mean percentages of ADF and NDF in forage and fecal samples collected in digestion trial using sheep.

	Untreated	Treated	Untreated	Treated
	%NDF		%ADF	
Forage	70.34	72.52	41.87	39.42
Fecal	67.47	70.28	44.62	45.26

in the hay. Intake values were .793 kg and .777 kg for lambs on treated and untreated hay, respectively. Dry matter digestibilities were 36.28% and 35.42%; cell solubles digestibilities 30.98% and 30.14%; NDF 38.70% and 37.89%; and ADF digestibilities were 29.51% and 32.64% for treated and untreated hay. Growing lambs should be able to eat 1.0215 kg of hay daily; and digestible dry matter of bluestem hay has been given at 50-55% (Church 1977).

Variability between animals and in individual observations was high for all digestion coefficients and intake. Expansion of the analysis of variance to include variation in observations of a single lamb found it significanat at $P < .10$. The low intake and digestibility coefficients in these data again illustrate a problem inherent in a nutritive value study of a poor quality forage. Though associative effects of forages and concentrates are problematic, without additional protein prairie hay intake and digestibility drop below a realistic and useful range.

12-Hour Nutrient Removal Rate Study

Though no significant differences between treatments appeared in the analysis of variance, treated hay removal rates means were consistently higher for dry matter, cell solubles, cell wall constituents, acid detergent fiber, cellulose and hemicellulose (Table 6). The Duncan Multiple Range Test (Table 6) found dry matter and cell wall removal rates significantly higher (alpha = .05) for steers on treated hay.

Removal rate variation between steers and in individual observations of any one steer was high in this study; a finding observed in all passage and removal rate studies reviewed. In the analysis of variance animal variation was highly significant for every variable but cell wall removal rate. Whether this variation is an inherent animal characteristic or related to the sampling process, or both, is still to be determined. Shellenberger and

Table 6. Summary of the analysis of variance for the effect of cuticular disruption on 12-hour rumen removal rates. (1) Untreated bluestem hay (2) Treated bluestem hay

	Treatment mean		St. error of mean	F value	PR F
Dry matter intake	(1) 2.14 kg *		.2435	3.53	.0774
	(2) 2.88 kg		.2024		
Dry matter removal rate	(1) 28.94 %	*	2.2830	0.96	0.3399
	(2) 34.90 %		2.2680		
Cell solubles removal rate	(1) 29.07 %		2.5120	0.16	0.6909
	(2) 32.49 %		2.0825		
Cell wall removal rate	(1) 28.62 %	*	2.6475	1.48	0.2410
	(2) 38.00 %		3.4613		
Acid detergent fiber removal rate	(1) 28.01 %		2.1468	.22	0.6426
	(2) 32.55 %		2.8277		
Cellulose removal rate	(1) 33.09 %		2.7262	0.00	0.9457
	(2) 36.67 %		2.6211		
Hemicellulose removal rate	(1) 33.86 %		2.7151	.27	0.6106
	(2) 40.58 %		3.6025		

*Means significantly different using Duncan's Multiple Range Test (alpha=.05)

Kessler (1966) showed dairy cows at higher lactation levels had faster passage rates; but variation existed between animals at similar production levels as well. McCullough (1969) noted that part of animal variation could be attributed to body size, but primarily responsible were inherent differences not yet understood. Yadava and Bartley (1964) found the complete-emptying technique to depress intake when repeated on a second or third consecutive day. Variation still existed, however, when data was taken on the same animal two weeks later. The authors suggested sampling methods which can pick up small differences between animals are needed.

Composition of rumen contents (Tables 7A and 7B) remained fairly constant as reported by Burroughs et al. (1946) and Yadava and Bartley (1964). If contents were 72% cell walls before feeding, they tended to be about 72% 12 hours later. Rumen contents ranged from 69-73% cell walls, 27-30% cell solubles, 45% ADF, 25-29% hemicellulose, 10-11% liqnin and 25-29% cellulose on a dry matter basis. At morning sampling rumen contents were about 12% dry matter in all animals. Twelve hours later 1-2% less dry matter was present after being held off feed during the day while digestion and removal took place.

Removal rate means were remarkably similar between nutrients. Dry matter, cell solubles, cell walls and acid detergent fiber removal rates all were near 30%. Yadava and Bartley (1964) found that removal rates of the more soluble constituents of alfalfa (crude protein and ether extract) were higher than more resistant crude fiber rates. This was reflected in the fact that percentages of the fibrous components were higher in rumen contents then feed; while percentages of protein and ether extract were higher in the forage. In the present study rumen percentages of cell walls tended to be essentially the same or higher in the rumen than in forage. Acid detergent fiber data were more consistent with Yadava and Bartley's

Table 7A. Composition of rumen contents of steers fed treated bluestem hay at 0 hour (before feeding) and at 12 hours (after feeding).

	#90*		#90		#36		#36		#36		#36	
	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr
%DM	14.93	11.01	12.09	11.89	13.33	10.25	11.06	11.01	12.72	10.26	13.50	10.54
%CW	76.75	72.79	70.04	71.50	71.65	68.50	68.81	72.45	75.15	69.18	72.20	71.40
%CS	23.55	27.21	29.26	28.50	28.35	31.50	31.19	27.55	24.85	30.82	27.80	28.60
%ADF	49.35	48.51	46.30	44.15	44.66	44.88	39.38	45.03	49.72	48.54	46.52	44.07
%HEM	27.29	24.28	23.74	27.35	26.99	24.02	29.43	27.42	25.43	20.64	25.69	27.33
%LIG	09.90	06.10	12.09	09.27	10.54	11.81	08.61	11.06	10.66	06.75	11.48	04.07
%CELL	34.01	33.21	26.97	26.72	28.45	25.02	24.10	27.66	33.32	35.60	32.16	32.10
	#91		#91		#6117		#6117		#6117		#6117	
	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr
%DM	14.32	13.54	13.26	11.33	11.38	09.30	11.23	09.85	10.67	10.00	11.73	11.01
%CW	73.99	72.97	68.47	72.91	69.09	68.09	72.76	72.31	70.69	68.00	73.33	77.97
%CS	26.01	27.03	31.53	27.09	30.41	31.91	27.24	27.69	29.31	32.00	26.67	22.03
%ADF	49.41	50.19	47.66	45.24	46.11	43.95	45.26	45.92	46.25	48.90	44.51	50.23
%HEM	24.59	22.78	20.81	27.67	22.99	24.14	27.50	26.39	24.44	19.10	28.82	27.73
%LIG	10.03	12.78	08.87	07.84	11.62	11.75	11.14	10.76	09.61	10.25	10.84	11.66
%CELL	30.78	29.30	33.57	27.47	28.08	24.85	27.85	28.88	28.54	41.94	26.32	33.62

*Steer identification number

Table 7B. Composition of rumen contents of steers fed untreated bluestem hay at 0 hour (befor feeding) and at 12 hours (after feeding).

	#36		#36		#90		#90		#90		#90	
	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr
%DM	12.20	13.70	12.50	11.59	10.35	10.66	12.50	09.67	12.23	11.05	12.66	11.18
%CW	78.93	78.06	70.39	75.49	68.58	71.43	74.90	72.91	73.12	70.16	70.49	71.75
%CS	21.07	21.94	29.61	24.51	31.42	28.57	25.10	27.28	26.88	29.84	24.51	28.25
%ADF	49.06	49.89	44.02	47.17	22.94	46.52	47.92	47.22	48.61	47.29	44.05	43.80
%HEM	29.81	28.17	26.37	28.32	29.58	24.91	26.98	25.49	24.51	22.86	26.44	27.95
%LIG	12.10	12.37	09.37	10.33	05.11	09.46	11.80	08.06	11.26	11.85	05.77	09.84
%CELL	31.86	30.58	33.43	30.08	29.58	28.35	28.68	29.65	29.32	28.76	29.42	26.75
	#6117		#6117		#91		#91		#91		#91	
	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr	0 hr	12 hr
%DM	12.09	10.00	11.23	09.32	12.35	10.59	12.28	11.07	11.90	10.47	12.53	12.13
%CW	75.87	71.47	70.00	70.61	67.61	75.97	69.31	72.21	69.23	70.93	69.63	72.41
%CS	24.13	28.53	30.00	29.39	32.39	25.03	30.69	27.79	30.77	29.07	30.37	27.59
%ADF	47.39	49.05	47.20	45.55	48.31	47.86	43.39	45.29	43.54	46.33	45.17	46.54
%HEM	28.48	22.41	22.81	25.06	19.30	27.11	25.92	26.93	25.69	24.60	24.45	25.88
%LIG	11.42	13.02	11.12	08.12	09.28	11.53	10.70	11.90	09.76	11.90	10.15	08.09
%CELL	30.93	28.08	29.45	27.08	27.98	29.10	25.60	26.11	28.15	27.85	26.50	26.36

*Steer identification numbers

data in that rumen percentages were always higher than forage ADF.

The explanation proposed here for the similarity between cell wall, ADF and cell soluble removal rates is nutritional inadequacy of the bluestem hay as the total diet. Crude protein levels were 4.98% in untreated hay and 5.49% in treated hay. Total cell wall constituents were 76.73% and 74.76% in untreated and treated hay, respectively. ADF percentages were 45.3% and 42.06%. Without adequate available protein for rumen microbes, the amount and rate at which energy can be digested drops. When digestibility rate declines, intake and removal rate follow (Church 1976).

Steers on treated hay consumed on the average .66 kg ($P < .10$) more than when on untreated hay. Two interrelated factors, initial quality and condition, explain this result. The cuticular disruption process left a slightly higher percentage of cell solubles and slightly less cell walls than untreated forage. Because treated forage was offered only on sampling days, the main reason attributed to higher intake was increased physical acceptability after treatment. The wire brushes, along with scratching cuticular material, reduced the course nature of culms and forb stems. Baled treated hay fed was well-mixed, less coarse and animals were not as tempted to pull hay out of the feed bunk. Although research reviewed has shown intake and removal rate interdependent, this study speaks only to the influence of intake on removal rate. To look directly at the effect of removal rate on intake it would be necessary to maintain animals on treated hay.

Covariance analysis of dry matter intake on rates of removal for dry matter, cell walls, cell solubles, acid detergent fiber, hemicellulose and cellulose are presented in Figures 5 through 10. Variability in th necessitated the use of a covariate of intake to show the relevant relationships between intake and removal rates. For all six variables removal

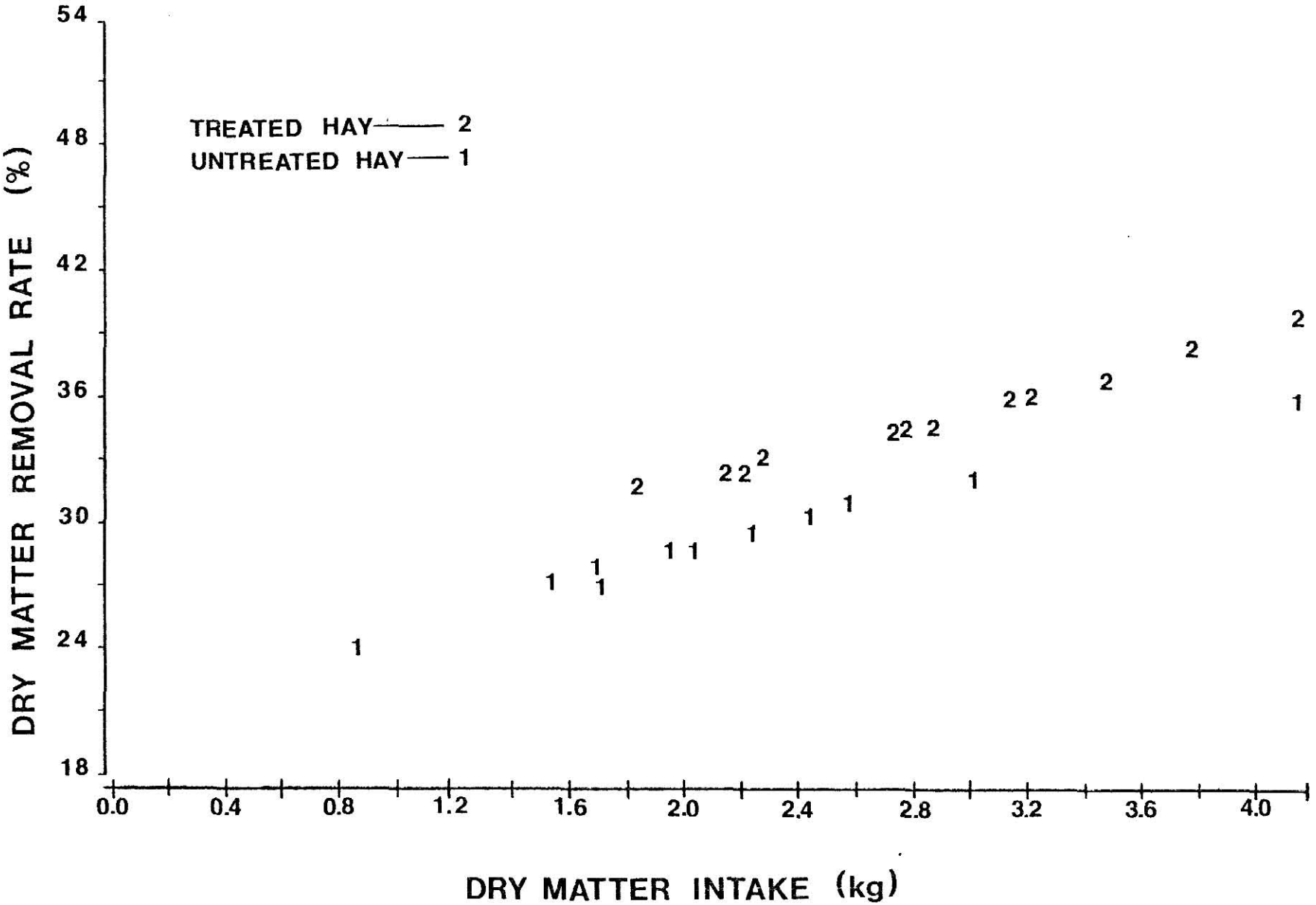


Figure 5. Regression of predicted 12-hour rumen dry matter removal rates on dry matter intake for steers fed treated or untreated bluestem hay.

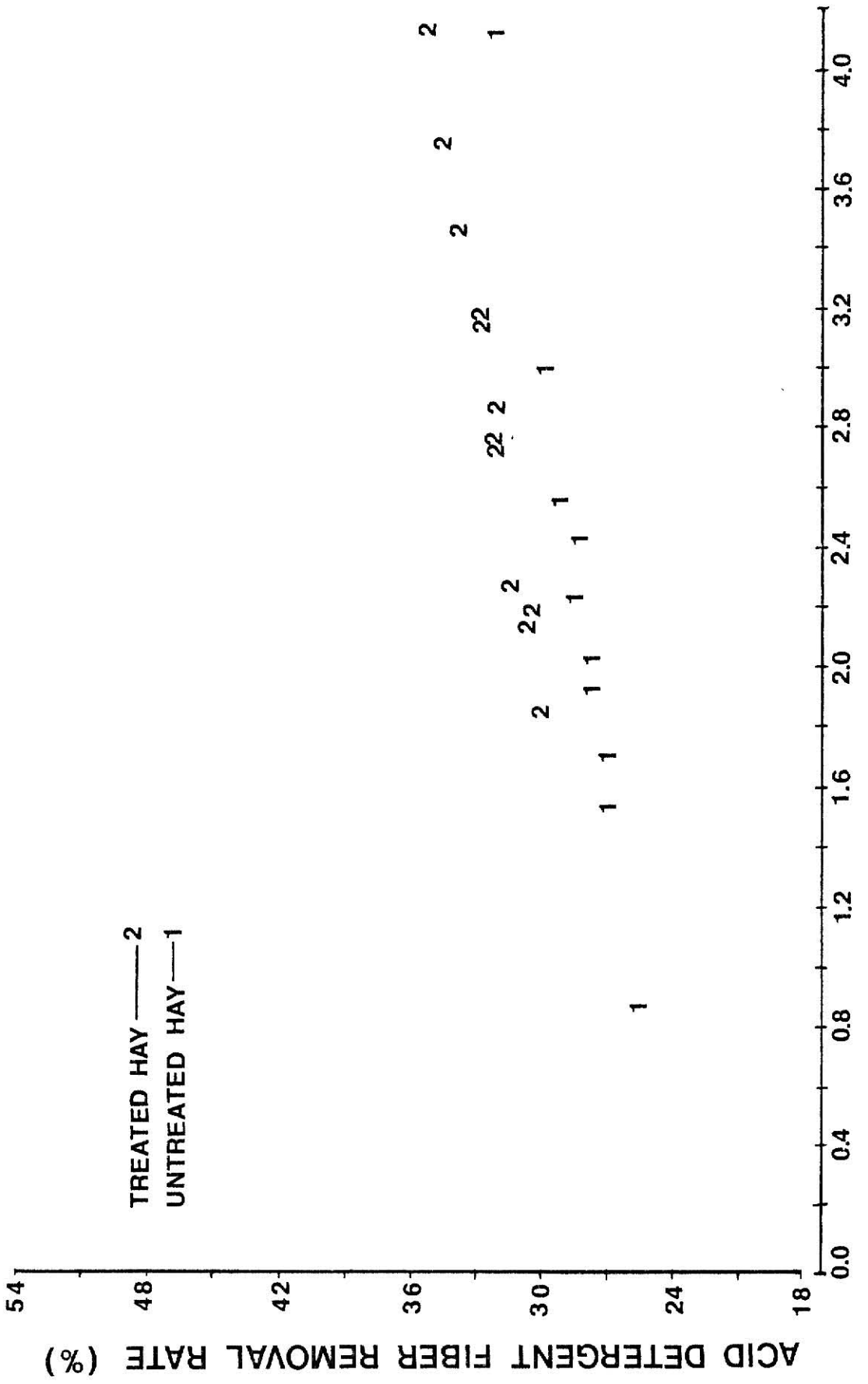


Figure 6. Regression of predicted 12-hour rumen ADF removal rates on dry matter intake for steers fed treated or untreated bluestem hay.

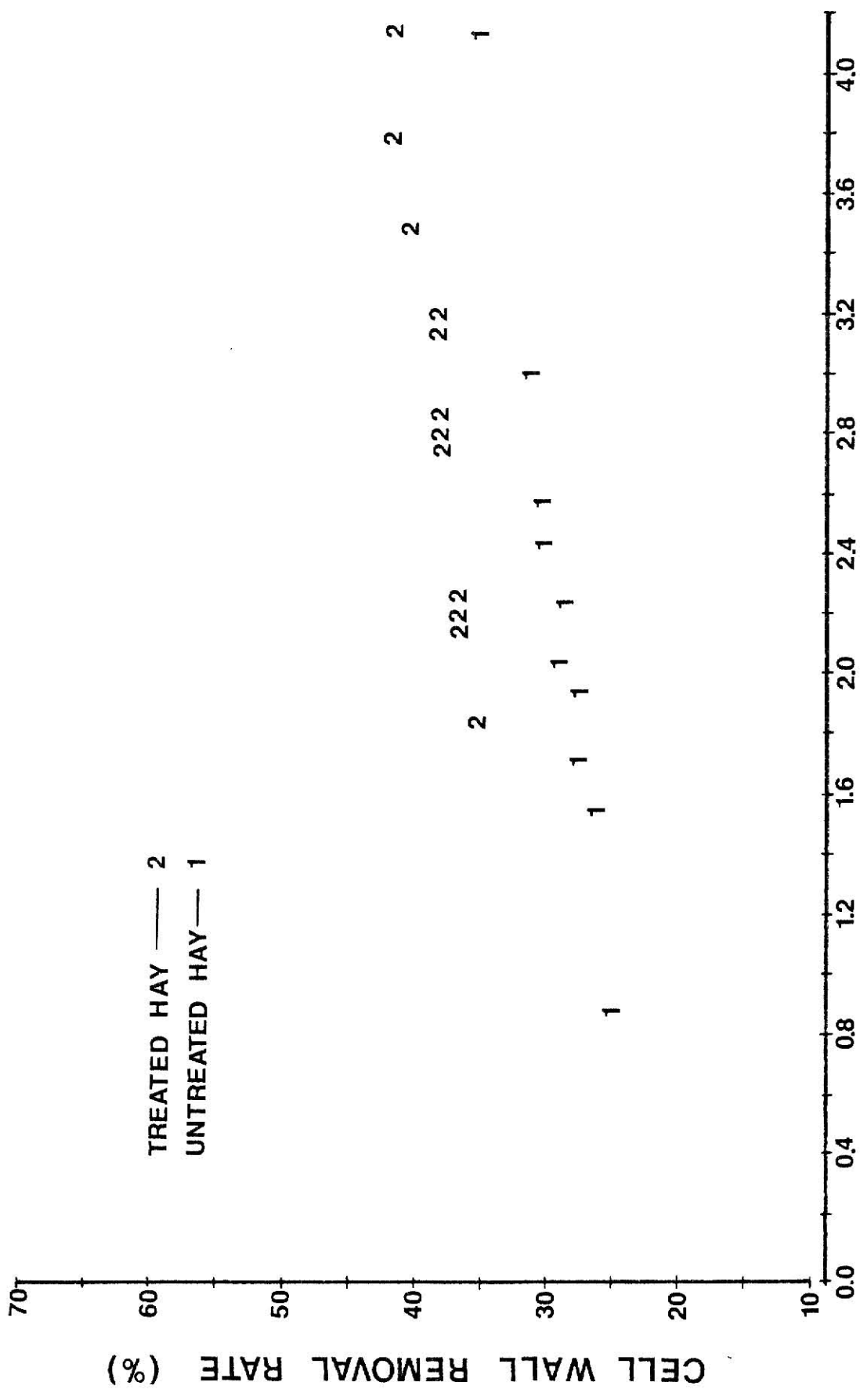


Figure 7. Regression of predicted 12-hour rumen cell wall removal rates on dry matter intake for steer fed treated or untreated bluestem hay.

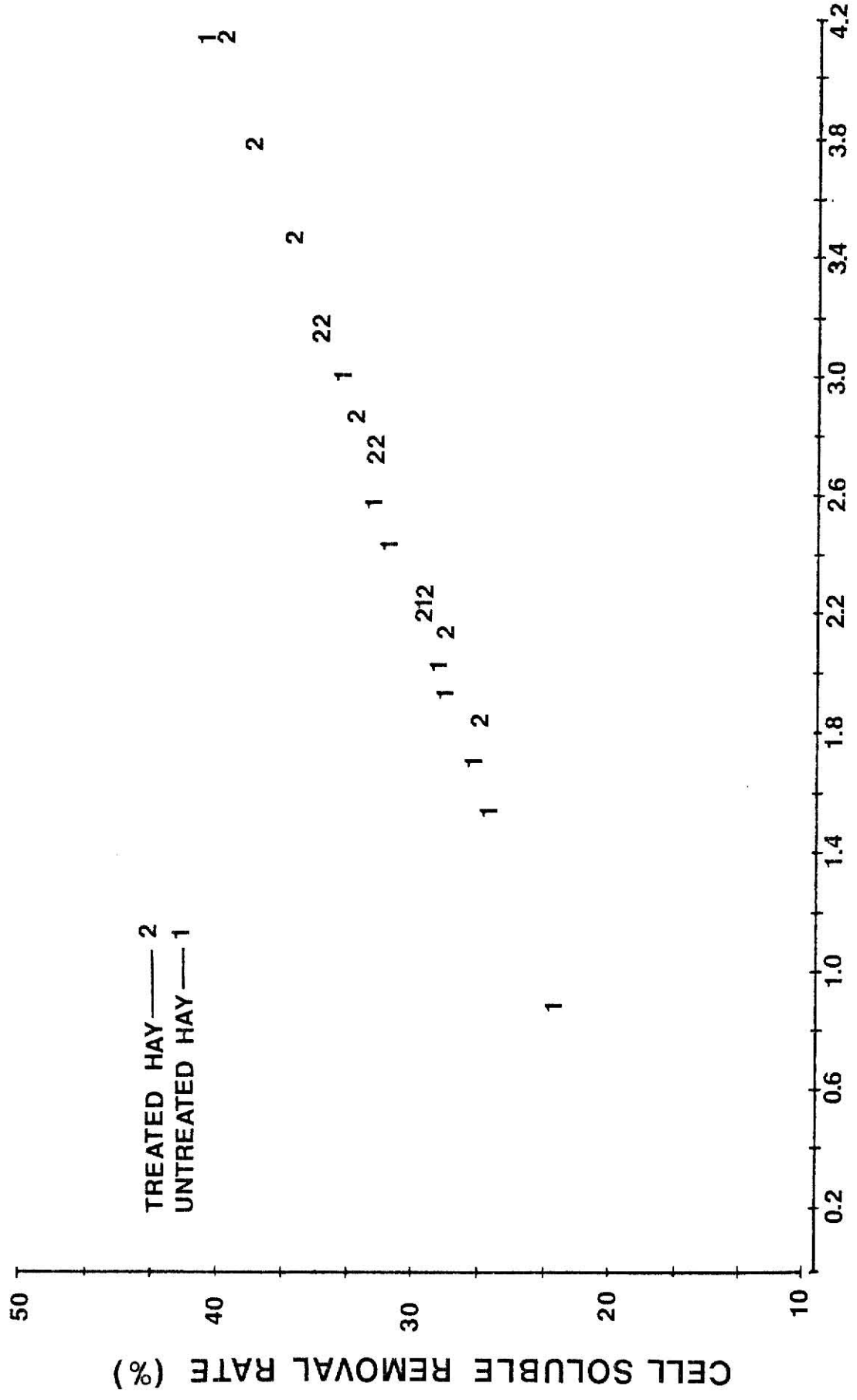


Figure 8. Regression of predicted 12-hour rumen cell soluble removal rates on dry matter intake for steers fed treated or untreated bluestem hay.

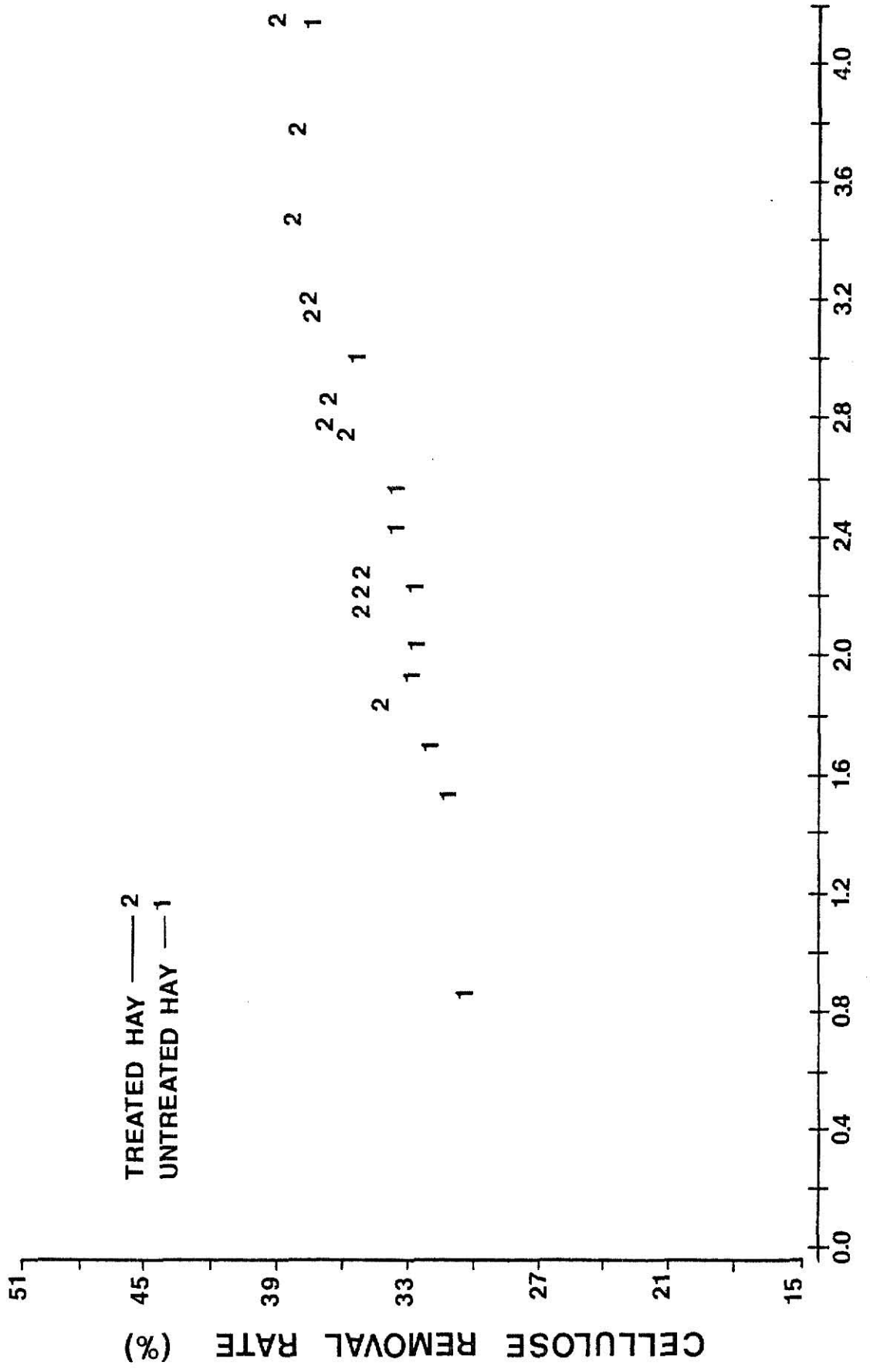


Figure 9. Regression of predicted 12-hour rumen cellulose removal rates on dry matter intake for steers fed treated or untreated bluestem hay.

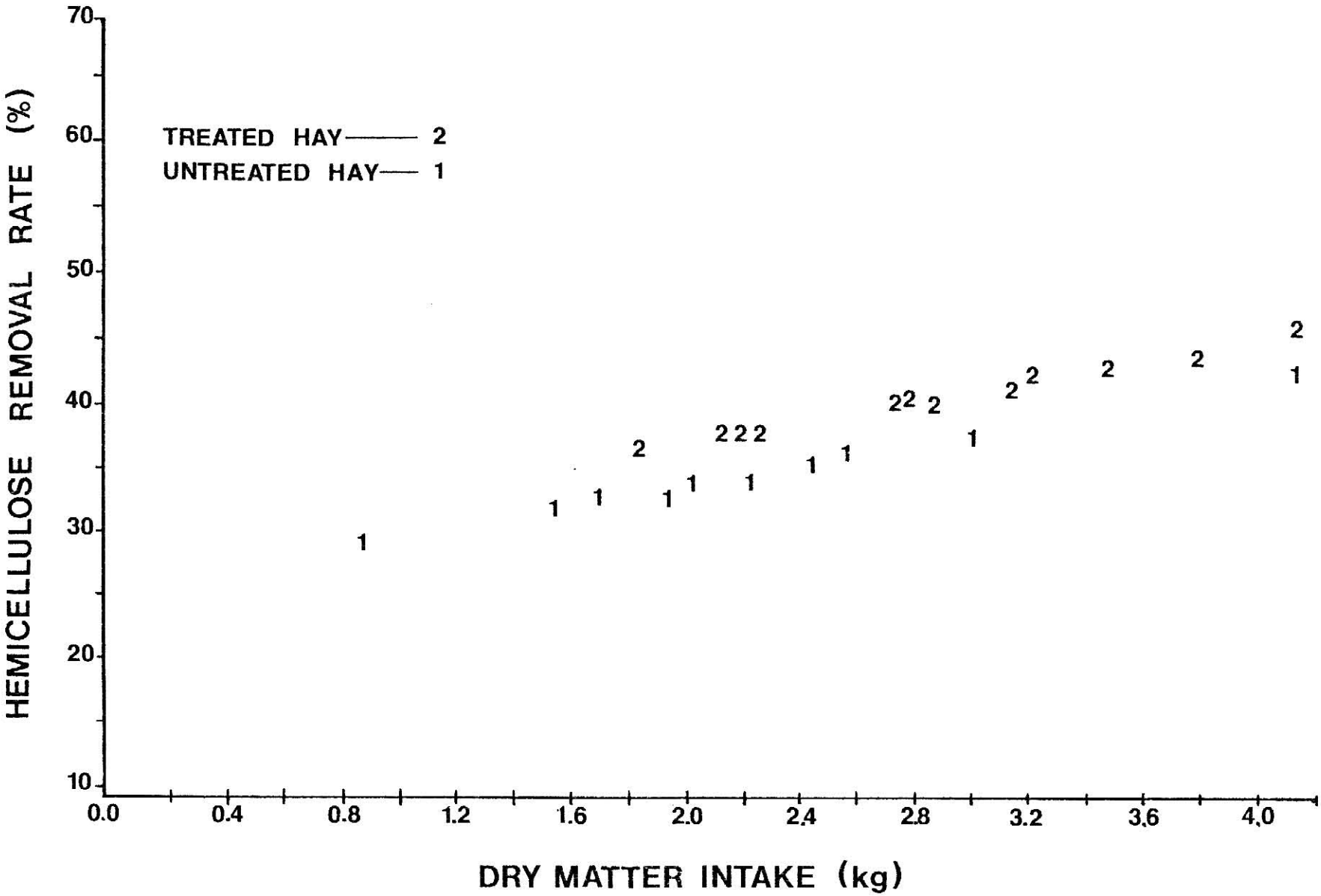


Figure 10. Regression of predicted 12-hour rumen hemicellulose removal rates on dry matter intake for steers fed treated or untreated bluestem hay.

rate increased with intake. Slopes of regression lines are essentially the same; indicating similar rates of increasing nutrient availability with increasing intake from both treated and untreated prairie hay. Y-intercepts differ, however, in that at a given intake level removal rate of a nutrient is higher for treated than untreated bluestem hay. That relationship holds for dry matter, cell walls, ADF, hemicellulose and cellulose. Regression lines were the same between treatments for cell solubles.

At a given intake level the difference between treatment regression lines is most pronounced for cell wall and dry matter removal rates. To the extent that "gut fill" limits intake of low quality forages, removal of cell walls and overall dry matter is most important in terms of bulk in the rumen. Though the positive relationship between intake and removal rates were shown in this study, low intake levels indicate nutritional level, not "gut fill" here limited intake.

Conclusions

With respect to nutritive value, increasing intake and nutrient removal rate indicate cuticular disruption to have had an upgrading effect; but the data fails to explain the effect completely. In addition to scratching the cuticle the machine also reduced the bulky nature of the forage. It is difficult to tell if increased removal rates are a result of cuticular disruption, a decrease in particle size or both.

In vivo digestion and the feeding trial using sheep showed no differences between treated and untreated hay. Low digestibility and intake values indicated nutritional level might be inadequate both for animal needs and

to point out treatment differences in this type of study. In addition, measuring a gross production characteristic like weight change appears inappropriate when seeking nutritive value information using a poor quality forage. Similar removal rates of the more highly digestible cell solubles and the slowly available cell wall constituents indicate low nutrition effects at work in the steer removal rate study as well. Despite the troubling associative effects of forages and concentrates in the rumen, realistic and useful intake levels of bluestem hay cannot be maintained without additional protein.

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APPENDIX

Part I

A REVIEW OF THE LITERATURE ON THE PHYSICAL AND PHYSIOLOGICAL FACTORS AFFECTING NUTRITIVE VALUE OF C_4 PLANTS AND THE FACTORS INFLUENCING INTAKE AND FEED RESIDUE MOVEMENT THROUGH THE RUMINANT GASTRO-INTESTINAL TRACT

Warm-season grass species, which use the C_4 or β-carboxylation photosynthetic pathway, simultaneously possess the best and worst characteristics sought in a forage for ruminants. Under optinum conditions C_4 species will exceed production of C_3 plants two and three times and can better withstand high extremes of light intensity, temperature and dryness, but are lower in digestibility and overall nutritive value. Research on the disparaties in digestibility has revealed the microanatomical structures associated with high productivity and efficiency in C_4 plants to be the same characteristics rendering nutrients less available to rumen microbes. The following is a review of the literature on the physical and physiological factors affecting nutritive value of C_4 plants and the factors influencing intake and feed residue movement through the ruminant gastro-intestinal tract.

C_4 PLANTS: PHOTOSYNTHETIC PATHWAY AND MICROANATOMY

The C_4 photosynthetic pathway, first described by Kortschak and coworkers in 1965, begins fixation with the incorporation of CO_2 into 4-carbon compounds, either aspartate or malate. After synthesis the 4-carbon compound is decarboxylated to provide CO_2 for the Calvin cycle (C_3) reactions. Thus tropical plants use two interconnected metabolic systems while temperate species use only the C_3 or reductive pentose pathway (Downton 1971; Zelitch 1971; Hatch and Slack 1966).

Plants using C_4 metabolism typically have low CO_2 compensation points, insignificant photorespiration and are unaffected by changes in oxygen concentration (El-Sharkawy and Hesketh 1964; Forrester et al. 1966). Photosynthetic rate and optimal light and temperature conditions are high; efficient use is made of water and nitrogen (Brown 1978; Black et al. 1969). These characteristics can be related to the specialized Kranz-type leaf anatomy of C_4 plants (Downton and Tregunna 1968; Downton 1971; Waller and Lewis 1979). Leaf tissues are arranged such that vascular bundles are surrounded by two tightly-packed chlorophyllous layers. Next to the vascular tissue is the thick-walled parenchymal bundle sheath which is in turn surrounded by a thinner-walled mesophyll layer (Downton 1971; Metcalfe 1960).

This type of anatomy serves to compartmentalize biochemical events. Synthesis of the C_4 acid occurs in the mesophyll cells with a carboxylase linking phosophoenolpyruvate (PEP) and CO_2. After formation the 4-carbon compound is transported to the bundle sheath cells wherein take place the Calvin reactions. There it is decarboxylated to provide CO_2 for the reductive pentose Calvin cycle. Photosynthates are translocated in the disaccharide sucrose form via the nearby vascular system or temporarily deposited in bundle sheath plastids (Downton 1971; Zelitch 1971; Esau 1965).

In contrast, C_3 plants lack the tightly-compacted leaf anatomy. Similar chloroplasts are distributed throughout the leaf mesophyll; and the Calvin cycle operates in each cell. Thus, unlike C_4 plants, nutrient-rich starch granuals are throughout the leaf (Downton 1971).

The unique Kranz-type anatomy lends itself to efficient CO_2 utilization. CO_2 compensation point (the point at which photosynthetic CO_2 uptake equals respiratory CO_2 evolution in a closed chamber) is only in the 0-10 ppm range, indicating insignificant photorespiration (Downton and Tregunna 1968). Though respired CO_2 is a normal by product of the Calvin cycle reactions,

Bowes and Ogren (1972) suggest that mesophyll cells tightly-packed around the bundle sheath refix photorespiratory CO_2 preventing its release into the atmosphere. Since low compensation point means negligible CO_2 release during photosynthesis, for C_4 plants gross photosynthesis is essentially the same as net photosynthesis. C_3 plants, which have considerably higher compensation points, have lower net photosynthesis (Downton and Tregunna 1968).

Concentration of CO_2 in the insulated environment of the bundle sheath cells of C_4 plants allows CO_2 assimilation to be unaffected by outside changes in O_2/CO_2 ratios (Downton and Tregunna 1968; Chollet 1976). The advantage of this efficient use of CO_2 when atmospheric concentrations are low is further increased when light and temperature conditions are high. Data from several sources have shown that CO_2 fixation rates in C_4 plants increases under high light and temperature while fixation in C_3 plants drops drastically (Waller and Lewis 1979; Black et al. 1969; Downes and Hesketh 1968).

STRUCTURAL FACTORS IN TISSUE DEGRADATION

Introduction

Though productive efficiency and competitive ability of C_4 plants makes them high yielding forage crops and hardy native grassland components, feeding value of these species is relatively low. Knowledge about the relationship between various tissue types and microbial digestion can provide a basis for understanding animal utilization of a forage and for suggesting techniques by which it could be improved. The following discussion emphasizes the structural components of C_4 leaf tissue in relation to microbial degradation.

Cuticle

The plant cuticle is a non-cellular continuous membrane overlying and merging into leaf epidermal cells. In thinner form cuticle extends into and lines stomatal cavities. Chief components of this layer are cutin, which provides a structural framework, and waxes embedded in the membrane and extruded onto the surface. The cuticle is somewhat multilayered in that cellulose and pectin occur admixed with cutin in the region nearing epidermal cell walls (Martin and Juniper 1970).

Much work has been done on the relationship between climatic conditions and cuticular development. Conditions of low atmospheric humidity and high light intensity promote increased cuticular and wax thickness (Skoss 1955; Juniper 1960). Water relations play a part as well. Skoss (1955) found that Nicotiana glauca plants undergoing water stress produced nearly twice as much cuticle as those regularly watered. These findings are in agreement with the importance of the cuticle in water conservation (Martin and Juniper 1970).

That plant cuticle is indigestible to rumen microbes has been shown several times (Hanna et al. 1973; Akin and Burdick 1975). Using sections of fresh leaf material incubated in rumen fluid Monson et al. (1972) found digestion began at cut or broken surfaces in the cuticle. No digestion occured when cuticle edges were sealed in wax. In a related study Monson and Burton (1972) discovered that abrading the cuticle of fresh leaf sections increased 48 hour in vitro dry matter disappearance (IVDMD) of Pennisetum typhoides (pearl millet), Pennisetum purpureum (napiergrass) and Cynodon dactylon (bermudagrass) from an average of 17% (for intact 2 cm leaf sections) to 54%. The abrasion treatment produced more of an increase in dry matter disappearance than did reducing the length of cut from 2.5 cm to .3 cm or first chewing by the animal. Reducing cut length increased IVDMD from 17%

to 42.8%. Samples collected as they entered the rumen of a fistulated steer showed only a 50% increase in IVDMD.

Silica

Silica, another substance present in the epicuticular layer, is present in great quantities in many soils. Silica is taken up by roots and transported to transpiring areas where it is deposited. Metabolic forms include an opaline deposition in cell walls and phytoliths embedded in cuticular material. Deinum (1974) classified silica as a structural inhibitor thinking it prevented microbial penetration of leaf tissue. Van Soest and Jones (1968) found a 3% average decline in digestibility of dry matter per unit of silica in cell wall constituents in several grasses studied, including both warm- and cool-season species. They suggested the effect of silica upon digestibility was limited to cell walls and it therefore reduced availability of organic constituents to rumen microbes.

Both shape of silica phytoliths and patterns of deposition differ among species. Andropogon geradi (big bluestem) and Andropogon scoparius (little bluestem) phytoliths are in the Panicoid group (Twiss et al. 1969; Metcalfe 1960). These dumbell-shaped phytoliths are found banded in rows above vascular tissue in the cuticular layer of both abaxial and adaxial surfaces (Brazle et al. 1979). X-ray dispersion of Festuca arundinacea (tall fescue) and Bromus inermis (smooth brome) showed silicon in every abaxial epidermal cell. Silica was also banded in epidermal cells over vascular bundles, but not between the ridges (Harbers et al. 1981). Scanning electron microsope observations of the bluestems after 24 hours fermentation in rumen fluid revealed microbes selectively attacked the adaxial surface avoiding cells near rows of phytoliths. Epidermal cells near silica bodies appeared to resist collapse even after removal of mesophyll below. However, while microbes were prevented from attacking through silica-embedded epidermal

tissue, silica did not deter degradation of below-lying mesophyll and phloem once microbes were exposed to these tissues.

Similar results relating silica to microbial digestion were observed for tall fescue and smooth brome. Using scanning electron microscopy to observe effects of rumen incubation, the authors saw that adaxial cells between vascular ridges had been destroyed; but abaxial cells where silica was deposited throughout remained intact (Harbers et al. 1981). In observing wind damage to epidermal layers of tall fescue, Thompsen (1974) similarly noted less damage to the abaxial surface. Though he attributed the reason to a protective abaxial curling of leaves, Harbers et al. (1981) suggest silica may play a part.

The observation that silica acts as a structural inhibitor detering microbial penetration without impeding degradation of underlying tissues suggests that location of the inhibitor is as important as its quantity. If it were present largely in cuticular material it could explain why little or no effect due to silica was exerted on organic matter digestibility of Southwest grasses observed by Smith et al. (1971) (Harbers et al. 1981).

Ease and Extent of Tissue Degradation

Once microbes gain access to leaf tissues through cut or broken surfaces (provided by mastication and rumination) the pattern of tissue degradation is essentially the same for both tropical and temperate species. Leaf mesophyll is the first component digested, followed by phloem tissue. Epidermal and parenchymal bundle sheath cells are more slowly broken down; and schlerenchyma, lignified vascular tissue and cuticular material generally remain undigested (Hanna et al. 1973; Akin et al. 1973; Akin and Burdick 1975).

While the sequence is essentially the same, rate and extent of degradation of particular tissue types vary between warm- and cool-season types and

among species and cultivars due to differences in leaf microanatomy. Hanna et al. (1973) compared digestion patterns of 2 cm fresh leaf sections of Arena sativa L., Secale cereal L., Lolium multiflorum Lam., Poa pratensis L., Dactylis glomerata, Festuca elatior L. (cool-season species), pearl millets and coastal bermudagrass. The authors found 24, 48 and 96 hours were required for microbes to cause observable digestion of entire 2 cm sections of the cool-season grasses, pearl millets and bermudagrasses, respectively. Differences were attributed to leaf microanatomy. Leaf mesophyll in the cool-season species had wide intercellular spaces which allowed microbes contact with greater surface area in a given time. The bermudagrasses had the more compact cellular arrangement around vascular bundles characteristic of C_4 grasses. Similar results came from a comparison of leaf anatomy and digestion rate between coastal bermudagrass and the cool-season 'Ky-31' tall fescue. Temperate leaf lamina succombed more quickly to microbial action; and scanning electron microsopy revealed that epidermal and bundle sheath cells were more slowly degraded in both species (Akin et al. 1973).

Differences in the ease of degradation of various tissue types led Akin and Burdick (1975) to suggest that relative amounts of the slowly and non-digestible tissues could affect the general rate of forage degradation in the rumen and thus forage quality. Four tropical species, coastal and 'coast-cross-1' bermudagrass, Paspalum notatum (Pensacola bahiagrass), Paspalum dilatatum (dallisgrass), and six temperate species, smooth brome, Dactylis glomerata (orchardgrass), 'Ky-31', Poa pratenses (Kentucky bluegrass), Phleum pratense (timothy) and 'Kenhy' tall fescue were investigated with respect to both the amounts and relative ease of tissue type degradation. The bermudagrasses had more total vascular tissue (36%) than the other tropical grasses, 27% of which was the slowly digestible parenchymal bundle

sheath cells. Sheath cells comprised more than 50% of the vascular tissue in the tropical grasses, but less than 50% in the temperature species studied. Correspondingly, mesophyll percentages in warm-season species ranged from 35% to 52.4% but were 52.8% to 65.7% of the temperate leaf blades. Observation under the scanning electron microscope after six hours incubation in rumen fluid revealed mesophyll and phloem tissues of tropical species degraded or in process. Epidermal cells were degraded more slowly. Phloem, mesophyll and epidermis of temperate species were degraded or in the initial stages except for epidermal tissue of Ky-31 fescue. After 12 hours incubation, an important time interval when considering actual rumen turnover or removal rate, tropical species had portions of potentially digestible tissues remaining. Temperate species generally had only lignified vascular tissue, schlerenchyma and cuticle left. This difference was attributed to the comparatively greater structural integrity of tropical bundle sheath cells.

Akin and Burdick (1977), using transmission electron microscopy, showed starch granuals in the sheath cell chloroplasts of bermudagrass, but none in the mesophyll. Starch was not available to microbes until this "sheath barrier" was degraded. The authors concluded anatomical arrangement may be a factor in the lower nutritive value of warm-season grasses to the ruminant.

Another aspect of the differing rates of digestibility of tissue types is the mode of bacterial degradation. The thin walls of mesophyll and phloem cells were degraded apparently by extracellular enzymes without bacterial attachment. Bundle sheath and epidermal cells required attachment and in some cases an extracellular substance before the hydrolytic fraction of the enzyme could degrade cell walls (Akin et al. 1974; Akin and Amos 1975).

Lignin

A 1973 study by Akin and Burdick on microanatomy and digestion of warm-season grasses and Ky-31 fescue (cool-season) showed differing amounts of lignification. Coastal bermudagrasses showed lignified cell walls present throughout the first order inner bundle sheath, in schlerenchyma and in a thick band of cells separating xylem and phloem and in xylem tissue. Ky-31 fescue had less-developed, thinner-walled bundles sheathes; and lignin was limited to the area bisecting xylem and phloem.

Though lignification was a factor in the slowly-degradable nature of sheath cell walls, indications were that the effect was one of location rather than amount. Both warm- and cool-season grasses in the study had similar amounts of lignin; and other studies have pointed out that alfalfa has both more lignin yet is more digestible than coastal bermudagrass (Van Soest 1968). Harbers et al. (1981), in looking at degradation of smooth brome and tall fescue, observed that lignin delayed hydrolysis of epidermal cells, schlerenchyma and vascular tissues, but had not effect on mesophyll digestion. Furthermore, the linkage between plant polysaccharides and lignin has been found to vary. Harkins (1973) found three distinct types of lignin in a single timothy plant. Barton and Akin (1977) showed that although lignin doess depress rate and extent of digestibility, delignified cell walls were still degraded at different rates indicating inherent differences in cell wall constituents. The authors concluded association with cell wall polysaccharides, lignin type and site of lignification should be considered along with amount in determining the influence of lignin on digestibility.

Summary

The microanatomical structures of C_4 plants allow high photosynthetic efficiency but render nutrients less quickly available to rumen microbes. The thick cuticle of C_4 plants, embedded silica bodies and lignin structurally inhibit microbial attack. Research on lignin and silica has revealed that location of an inhibitor is as important as amount when considering impact on forage digestion.

Scanning electron microscopy of C_3 and C_4 plants at different phases of incubation in rumen fluid has shown mesophyll and phloem to be degraded first, followed by epidemal and parenchymal tissue. The compacted cellular arrangement and thick-walled bundle sheath tissues of C_4 plants make them more slowly and less completely digested than C_3 leaf tissues.

FACTORS AFFECTING VOLUNTARY INTAKE AND RATE OF MOVEMENT OF DIGESTA THROUGH THE GASTRO-INTESTINAL TRACT

Introduction

In order to characterize the overall feeding value of a given diet a number of interrelated factors must be considered. Balch (1961) listed four factors: 1) Rate of movement of the food residue through the gut, 2) amount consumed, 3) rate of digestion at any given point in the gut, and 4) nature of the digestion end products. Though all four exert considerable influence on the value of a particular diet to the animal, indications from the work of Balch and his associates, along with more recent studies, are that rate of food residue movement through the gut may be the most important single factor, largely through its influence on intake.

Rate of movement of digesta through the gastro-intestinal tract (GIT) is expressed in several ways and evaluated using a wide range of approaches. The term "rumen turnover" is used to express the average length of time

digesta remains in the rumen and is calculated for a particular feed component by dividing the amount present in the rumen before a meal by the feeding rate (amount/time). Rate of passage is the rate at which undigested residues from a given meal pass a point in the gut or appear in the feces (Church 1976). Rate of passage is often incorrectly referred to as "retention time", most often in studies using the stained hay technique. Retention time is similar to turnover, and is the length of time a component remains in the rumen. Rate of removal is defined as the rate at which a component disappears from the rumen due to digestion, absorption or passage of undigested residues to the lower GIT. Removal rate can be expressed as the percentage of each nutrient removed from the rumen based on either 1) amount present in the rumen after feeding, or 2) amount fed (Yadava and Bartley 1964).

Studies on passage of digesta through the GIT employ cannulas or markers of a variety of types. Natural feed components such as lignin, chromogens, iron and silica have been used to chart concentration changes of nutrients or water during digestion on the presumption they are not absorbed to any great extent (Church 1976). External markers such as chromic oxide, a Cr-EDTA complex, cerium or cesium, stained food particles, plastic particles of various sizes and polyethylene glycol have all been employed. The plastics and dyed particles have been used primarily to determine passage rate. Chromic oxide and the metals have been used for this purpose and to detect concentration changes through the gut. Estimations of rumen fluid content can be determined using polyethylene glycol. Values derived using these markers vary; and assumptions underlying their use are not always valid. Different markers pass through the GIT at different rates; and the usefulness of these markers is limited to the study of feed components with very similar characteristics (Church 1976).

Two other methods are available which make alteration of the feedstuff or use of a marker unnecessary. The "complete empty" method using rumen-fistulated animals is probably the simplest and most direct. Removing all digesta for weighing and sampling allows feed constituents to be calculated on both a dry matter basis and as a percentage of total rumen contents. Also, hand-mixing of digesta before sampling and returning to the rumen allows a more representative sample to be obtained (Bailey 1965).

Photosynthetic incorporation of $^{14}CO_2$ into growing alfalfa plants allows breakdown and metabolism to be charted on the basis of total activity of rumen volatile fatty acids (VFA) (Yadava et al. 1964; Yadava and Bartley 1964; Alexander et al. 1969). Though selective marking is not possible, any ^{14}C activity in rumen VFA can only result from metabolism of labeled hay.

The following is a discussion of the factors influencing and affected by the rate of feed residue movement through the GIT.

Intake and "Gutfill"

Conrad et al. (1964) observed that for rations in the lower ranges of digestibility voluntary intake was most closely correlated with animal body weight and digestibility of the ration. He believed this to be related to the animal's ability to process undigested residues, and proposed that "gutfill" controlled intake for less digestible feeds. Therefore voluntary intake would increase with increasing ration digestibility until the point where combined intake and digestibility provided nutritive energy equal to utilization capacity (net energy requirement). Beyond that point increasing digestibility would only result in enough dry matter intake to provide energy equal to that needed to metabolize it. The point after which metabolic factors control dry matter intake was found to differ with production level. Intake increased with organic matter digestibility until

approximately 70% digestible organic matter was reached for cows producing 27 kg of milk daily, but only to 65% for those at 13 kg of milk per day. Baumgardt (1970) reasoned that the factors influencing fill, indigestibility of the ration, digestion rate and retention time, would be different on long forage and pelleted rations. He found that with a mixed rations, ground and pelleted, intake was not limited when digestibility was as low as 56%. He proposed that density of the ration, in addition to digestible dry matter (DDM), could better predict intake and describe nutritive value than DDM alone. This was done on the assumption that at a given level of digestibility a feed with higher density (e.g. ground and pelleted versus long hay, grain versus roughage) would be more rapidly digested, have a faster passage rate and occupy less space in the rumen. Using digestible energy (DE) because of its high correlation with DDM, Baumgardt found that as ration digestible energy increased both dry matter intake and DE intake increased to a certain level of DE. After that point DE intake leveled off, but dry matter intake decreased (diagram Figure A-1)

Generally, higher intake levels are associated with more digestible forages; but this relationship is not always consistent. Two forages having similar digestibilities can differ considerably with respect to intake (Minson 1964; Crampton et al. 1960). It appears physical factors controlling intake level involve characteristics of both the animal and the plant (Ellis 1978). Study by a number of authors on intake as it relates to digestibility and passage of digesta through the GIT indicate a more useful concept of digestibility would be to consider the fraction digested as determined by the rate of digestion and the rate of passage of undigested residues through the gut (Ellis 1978; Campling et al. 1961; Freer and Campling 1963).

The effect of "gutfill" on intake was demonstrated by Campling and Balch (1961) using rumen-fistulated cattle on roughage diets. Removing or adding digesta through the cannula increased and decreased intake, respectively. Placing a large water-filled bladder in the rumen to simulate fill and created distension also decreased intake; but merely adding the same amount of water produced no change. The latter was expected in view of the ruminant's ability to utilize large quanities of succulent forage.

Intake and Rate of Passage

Campling et al. (1961) sought to determine whether rumen capacity or an equilibrium with rate of dissappearance of digesta controlled intake. That rumen capacity and animal size would in some way affect intake had seemed sufficiently obvious to cause researchers to express intake in terms of body weight. Conrad et al. (1964) reasoned that if volume of the GIT was proportional to body weight, then intake would be proportional to body size when eating capacity is restricted by fill and undigested residues.

Crampton (1960) and Blaxter et al. (1961) concluded that intake in sheep varied with metabolic size ($W^{.734}$). In the Campling et al. (1961) study cows were fed either ryegrass hay or oatstraw ad libitum and at 10 lb and 15 lb intake levels. They found amounts of digesta present before and after feeding were less for animals fed straw, indicating less fill and distension. Despite hay intake twice that of straw, percentages of dry matter in the rumen were much the same before the next feeding. The authors concluded that an equilibrium with residue movement through the gut influenced intake more than did capacity of a particular animal.

In this same study, passage rate was determined using the stained hay technique. Though considerable variation in passage rate existed between animals, in all cases stained straw particles passed through the animal

more slowly. Mean passage rate of stained hay was 73 hours, while straw particles required 100 hours.

Campling et al. (1961) attributed lower intake of straw to a) the lower digestibility of straw in the rumen, and b) the longer time straw particles are retained in the rumen. They suggested the slower breakdown of straw into particles of optimum size for passage through the reticulo-omasal orifice to be the reason for slower passage.

Intake Level

While these studies have shown that faster passage rates are reflected in higher intake levels, intake level itself can in turn affect passage rate. Blaxter et al. (1956) found that at three intake levels fine and medium-ground pelleted stained hay were excreted faster than long hay; but in all three forms passage rate increased with intake level. Similar results were reported by Campling et al. (1961), Freer and Campling (1963), Shellenberger and Kessler (1961) and Balch and Campling (1965).

Alwash and Thomas (1974) fed Suffolk x Masham wethers "dried grass hay" (species unreported) at intake levels 1.1 and 2.4 times the energy maintainance requirement and ground to four different particle sizes. Retention time, measured with stained hay, was longer at the lower intake level while apparent digestibility of organic matter and crude fiber were higher. At both intake levels digestibility decreased with particle size. The authors suggested changes in digestibility of forage constituents were related to intake level and particle size due to associated changes in rumen retention time. A similar study in 1971 by the same authors using chopped, ground and pelleted "dried grass" attributed lower digestibility at higher intake levels to shorter retention time.

Cox et al. (1956) and McCullough (1956), among others, have correlated

intake level to production level in dairy cows; but point out that animal variability makes such correlations hard to demonstrate. McCullough (1969) attributed a part of this variation to animal size, but primarily to inherent differences in animals of similar size and production. Though these differences are not clearly understood, often they are large enough to prevent measurable differences in intake due to other factors from being apparent.

Particle Size

The forage breakdown process involves chewing, rumination and microbial digestion, which are important both in reduction to a particle size that will pass the reticulo-omasal orifice and in providing greater surface area for microbial attack. The rate at which this process proceeds is heavily influenced by the physical characteristics of the digesta (Evans et al. 1973).

Gill et al. (1966) found particle size in swallowed boluses to be larger when dairy cows were fed freshly-cut herbage (ryegrass) than when fed the same species as mature hay. They also found significant differences between animals in swallowed particle size. Bailey (1961) observed higher rates of swallowing associated with higher feed moisture and higher rates of salivation.

Hungate (1966) regarded the comminution of fibrous material in the rumen as transfer from a large-particle, rumination pool to a small-particle pool which is discharged into the abomasum. When newly eaten material reaches the rumen, contractions of the reticulum, reticuloruminal fold and cranial sac move coarse, fibrous digesta into the dorsal area. This low-density material is the upper most strata (rumination pool). Further contractions move the digesta (especially the fluid portion) in a somewhat circular movement, bathing upper strata periodically with rumen fluid. Digesta in the ventral sac, which is more fluid with finer particles, is

either recirculated or removed through the reticulo-omasal orifice (Evans et al. 1973; Church 1976).

A study done by Welch and Smith (1978) on the range of particle sizes which would pass the reticulo-omasal orifice of steers used polypropylene ribbon to avoid size changes due to rumination and microbial decomposition. They found the .5 cm size passed significantly more than larger sizes; but recovery in feces for all sizes was low. The authors also noted that a large proportion of rumen dry matter was smaller than 1mm; and attributed their low recovery to entrapment in the digesta mass preventing escape to an area nearer the reticulo-omasal orifice.

Schalk and Amadon (1928) thought specific gravity kept a coarse-size mass on top of other rumen contents. They reasoned that as specific gravity increased through particle size reduction, saturation and partial decompositon; the particles would sink toward the ventral sac thus increasing chances of passage. Balch and Kelley (1950) found no significant differences in specific gravity of dorsal and ventral digesta; but noted specific gravity of contents was between 1.022 and 1.055.

Pearce and Moir (1964) found that feeding Merino wethers a high roughage ration (chaffed oaten hay and lucerne chaff) but preventing rumination nearly tripled retention time of stained hay particles. They also attributed considerable comminution ability to rumen microbes. Despite restriction from rumination the sheep were able to consume about 500 grams of the high roughage ration a day though ability to adapt to the regimen varied. When animals were allowed to ruminate, counts of bacterial concentration were twice as high on the long hay ration than when the same ration was ground.

Surface area available for microbial attack in relation to particle size varies with forage type. Hanna et al. (1973) attributed faster digestion rate of 2 cm sections of six cool-season species (rye, oats, annual ryegrass,

Kentucky bluegrass, orchardgrass and tall fescue) compared to warm-season species (pearl millet, and bermudagrass) to leaf microanatomy. Cool-season species had wide intercellular spaces providing microbes contact with more surface area at a given time. Akin and Burdick (1975) reported that warm-season species studied (coastal bermudagrass, Pensacola bahiagrass and dallisgrass) had a higher proportion of slowly and non-digestible tissue types than did temperate species studied (smooth brome, orchardgrass, Kentucky bluegrass, timothy and tall fescue).

The effects of grinding and pelleting roughages on digestion end products, intake and passage rate have been studied many times. While grinding and pelleting usually increase voluntary intake and passage rate, extent of this effect depends on the type of roughage and fineness of grind. (Campling and Freer 1966; Thomas et al. 1967).

O'Dell et al. (1963) fed stained coastal bermudagrass hay to dairy heifers in baled, pelleted and ground forms. An estimate of passage rate was determined by the recovery of stained particles in each section of the GIT after slaughter. Though pellet-fed heifers had essentially the same amount of rumen dry matter as those fed baled hay, and 31% more than heifers on ground hay, only 13.6% of the stained pellets were recovered in the GIT while 61.5% and 31.0% of the stained baled and ground hays respectively were found. While faster removal from the rumen of pelleted hay was reflected in its higher daily intake (2.38 lbs per 100 lbs live weight compared to 2.00 lbs), the relationship did not appear to hold for ground hay. Passage rate of ground hay exceeded that of baled hay, but intake levels were lower (1.63 lbs vs 1.71 lbs).

Thomas et al. (1967) fed dairy cows very finely ground (.9% retained on a Size 16 Syler sieve), medium (39.8% retained) and coarsely ground (66.9% retained) alfalfa to study the effect of particle size on milk fat

levels. They had considerable difficulty switching cows to the finely ground diet. Intake dropped; and the cows craved fibrous material. Rumen motility decreased, as did milk fat content and the percentage of acetic acid produced relative to propionic.

Blaxter et al. (1956) fed sheep long hay and pellets made from the same roughage with either fine or medium-size particles. Stained particles of the finely-ground pellets were excreted faster than medium-size pellets which in turn appeared before stained long hay. Campling and Freer (1966) found similar results when equal and restricted amounts of ground or long dried ryegrass were fed; but found differences in passage rate and intake disappeared when animals ate all libitum. They also noted that grinding and pelleting the highly digestible dried grass did not increase average intake; but preparing oat straw, a low digestibility roughage, in this manner resulted in 26% more of it eaten.

Alwash and Thomas (1974) ground "dried grass" with a hammer mill through 12.7 mm, 4.75 mm, 2.06 mm and 1.00 mm screens and fed the forage at two intake levels. At both intake levels digestion coefficients and stained hay retention decreased with particle size.

Digestibility

When intake and removal passage rate of a roughage increased, digestibility (the fraction digested) is lowered (Ellis 1978; Campling et al. 1961). This drop in efficiency is related to the shorter amount of time rumen microbes spend attacking the particles; thus the more resistant fibrous components are most affected. However, indications are that higher producing animals have faster rates of removal/passage despite the inefficiency (Shellenberger and Kessler 1961). The increase in intake and nutrient removal rate must more than compensate for the slight reduction in digestibility (Church 1976).

King et al. (1963) fed coastal bermudagrass hay to heifers in baled, ground and pelleted (pellets had smallest particle size) form. Intake was essentially the same; but digestibility coefficients tended to go down with particle size. Decreases in apparent digestibility were significant for pelleted hay compared to either baled or ground hay for dry matter, crude protein, energy and TDN. The decreased crude fiber digestibility in pelleted hay relative to baled hay was significant.

Pearce and Moir (1964) found that grinding the roughage component of the ration lowered retention time, apparent digestibility of crude fiber, dry matter and organic matter. When retention time was increased by restricting rumination with a muzzle, crude fiber digestibility increased nearly 13.6%. This reflected longer time microbes were able to attack particles. Alwash and Thomas (1971, 1974) reported similar results.

Yadava and Bartley (1964) found little differences in digestibility either among or between twin pairs, but large variations in nutrient removal rate. This variation in passage and removal rate was noted by all authors reviewed, but did not result in inconsistent findings. Despite these differences, in all animals the nutrient with greatest digestibility was removed fastest from the rumen. Nitrogen-free extract and crude protein had both greater digestibilities and removal rates than did crude fiber.

Removal Rates of Various Forage Constituents

Using ^{14}C-labeled alfalfa and comprehensive scheme for defining chemical fractions of the forage, Alexander et al. (1969) were able to chart metabolism in the rumen on the basis of total activity of rumen VFA. Most active metabolism of labeled hay occurred 4-8 hours after feeding. Cellulose metabolism was highest during the first 12 hours with very little remaining after 36 hours. Rates of removal were calculated on the basis of percent

^{14}C activity remaining at sampling time. In pre-bud, bloom and seed stages of alfalfa soluble sugars were most rapidly metabolized, followed by the dry matter, pectin, protein and lipid fractions. Hemicellulose was metabolized slower than both cellulose and chlorite-extractable lignin. Acid-insoluble lignin was slowest to be metabolized. These data agree with Bailey's work (1965) with unlabeled red clovers. Using the complete-empty techniques he found 80% of the soluble sugars gone two hours after feeding. Scarcely any of the hemicellulose or cellulose, and only 10% of the pectin was gone after three hours. This suggested to Bailey a lag time before breakdown to a particle size allowing microbial digestion. In contrast, Alexander et al. (1969) found 30-50% of the alfalfa cellulose fraction removed from the rumen three hours after feeding. This indicated to the authors little lag time or microbial selectivity.

Summary

In summary, it is possible to visualize interaction of various factors affecting rate of digesta movement at almost every point in the digestion process. Voluntary intake of a roughage is largely determined by the rate at which residues can be removed from the rumen. This rate is governed by physical and physiological characteristics of both the animal and the forage. Studies reviewed report wide variability between animals in passage/removal rate due to either inherent individual characteristics, sampling method or both. Size and production level also contribute to animal variability in utilization and intake of a given forage.

Roughages vary in several characteristics which affect the speed with which they can be removed from the rumen. Microanatomical structure in C_4 plants, the thick walled parenchymal bundle sheaths and the tightly packed cells surrounding them, render nutrients less quickly available to

microbes than the more loosly structured C_3 plants. Relative amounts of the more slowly and non-digestible tissues vary. Location and amount of structural inhibitors to microbial attack such as lignin and silica can also affect the rate of forage breakdown in and removal from the rumen.

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APPENDIX

PART II

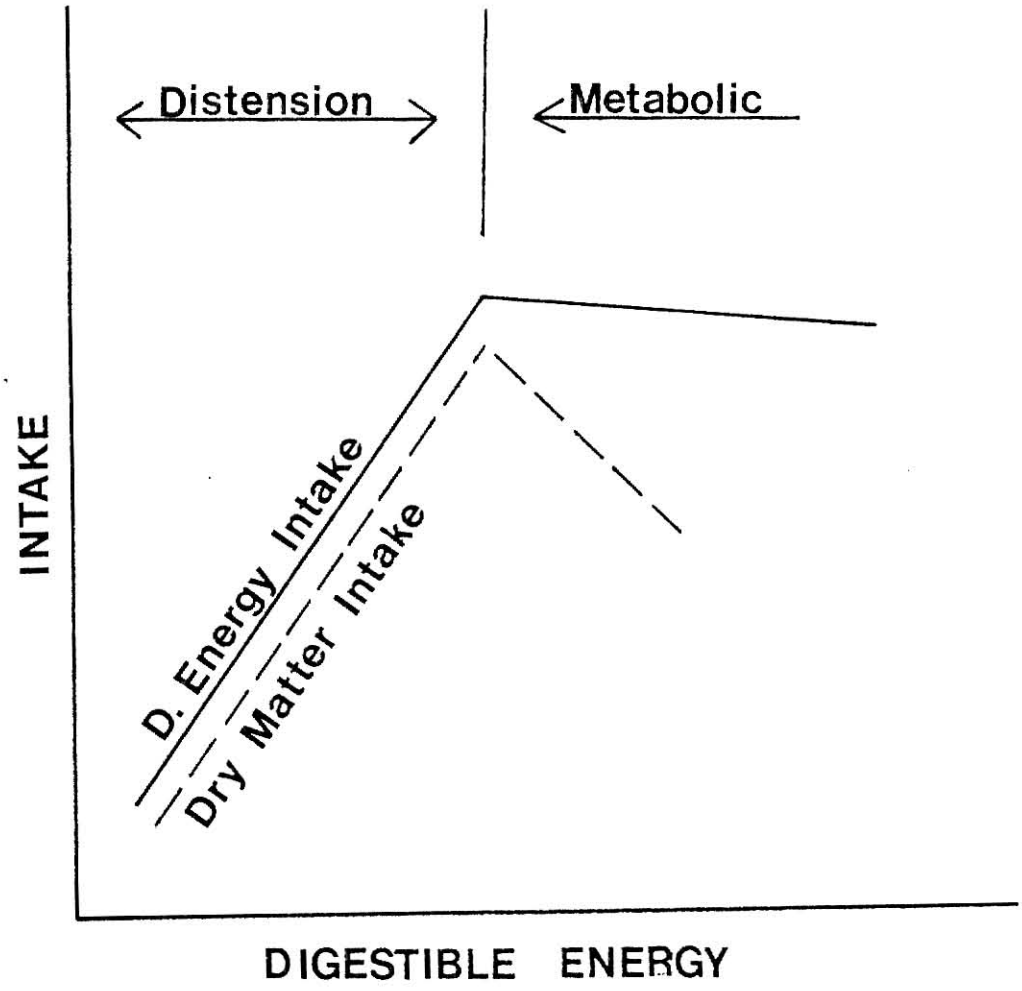

Figure A-1. Diagram of the relationships discussed in Baumgardt's work (1970).

Table A-1 Analysis of variance for intake in the 2 x 2 Latin square with extra period (Lucas 1957).

Source	DOF	Sum of Squares	Mean Square	F value	PR F
Model	6	7.5107	1.2518		
Period	2	2.0114		1.90	0.1797
Animal	3	3.6318		2.29	0.1150
Treatment	1	1.8676		3.53	0.0774
Error	17	8.9877	0.5287		
Total	23	16.4984			

Table A-2 Analysis of variance for weight change by treatment in feed/weight change trial using sheep.

Source of variation	DOF	Sum of squares	Mean square	F
Treatment	1	2.3437	2.3437	.4639
Observations/treatment	4	20.2083	5.0521	
Total	5	22.5521		

Table A-3. Analysis of variance for the ratio established between feed and weight change.

Source of variation	DOF	Sum of squares	Mean square	F
Treatment	1	.0005	.0005	1.111
Observations/treatment	4	.0018	.00045	
Total	5	.0023		

Table A-4. Dry matter data collected in 12-hour nutrient removal rate study on steers fed treated and untreated bluestem hay.

Steer	Intake	AM Rumen Dry Matter (%)	DM Removal Rate
		Untreated hay	
36	4.133 kg	12.20 %	31.46 %
36	2.577	12.50	44.59
6117	2.448	12.10	41.19
6117	2.041	11.20	30.74
90	1.710	10.30	24.90
90	.868	12.50	20.45
90	1.940	12.20	32.97
90	1.530	12.70	21.44
91	2.220	12.40	20.00
91	1.684	12.30	26.54
91	3.011	11.90	30.05
91	1.531	12.50	22.97
		Treated hay	
36	2.143	13.30 %	38.98 %
36	2.730	11,10	29.74
36	2.871	12.70	51.77
36	3.470	13.50	46.71
6117	3.138	11.40	38.20
6117	2.858	11.20	33.22
6117	1.837	10.70	29.65
6117	3.776	11.70	34.69
90	3.215	14.90	32.51
90	2.194	12.10	29.06
91	4.134	14.30	29.05
91	2.271	13.30	25.07

Table A-5. Y-Intercept values from the covariance analysis for the variables illustrated in Figures 5-10.

Variable	Treatment	Y-Intercept value
Dry Matter Removal Rate	(1)	24.4898
	(2)	21.2023
Cell Wall Removal Rate	(1)	29.4696
	(2)	22.275
Cell Soluble Removal Rate	(1)	17.0090
	(2)	17.5489
Acid Detergent Fiber Removal Rate	(1)	26.5330
	(2)	23.5308
Hemicellulose Removal Rate	(1)	28.9253
	(2)	25.1917
Cellulose Removal Rate	(1)	30.6506
	(2)	28.6150

EFFECT OF CUTICULAR DISRUPTION ON THE NUTRITIVE VALUE OF BLUESTEM PRAIRIE HAY

by

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B.G.S., Kansas University, 1976

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment

of the requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1981

ABSTRACT

The effects of cuticular disruption on the nutritive value of bluestem hay were studied. Plant cuticle was disrupted by means of a machine which rotated a set of wire brushes against a stationary, concave bed of brushes such that abaxial and adaxial leaf surfaces could be treated. Forage was allowed to dry on the ground before baling with conventional square baling methods.

Three experiments were conducted to evaluate treated hay. In the first study 24 Suffolk ewe lambs were divided into two groups and fed either treated or untreated hay for 28 days before final weights taken. Comparisons were made on the basis of mean weight change and a ratio established between intake and weight change. A second experiment consisted of a standard digestion trial using 14 western whiteface wethers. Apparent digestion coefficients were determined for NDF, ADF, cell solubles and dry matter. A third trial employed the "complete-emptying" technique to compare 12-hour rumen removal rates of treated and untreated hay. Rumen contents were weighed and sampled before feeding the steer a known amount of forage with sampling repeated 12 hours later. All feed and rumen samples were analyzed with the Van Soest scheme. Removal rates for individual forage constituents were calculated on the basis of total rumen contents. Animals in all three trials received bluestem hay as the total diet.

No statistically significant differences between treatments were observed in either the feed/weight change or digestion trials. Intake of treated hay tended to be higher; but weight losses on the first trial and low digestion coefficients indicated low protein level in the diet may be a problem when seeking nutritive value information about poor quality forages with these in vivo methods.

Steers in the removal rate study consumed significantly greater amounts of treated hay than untreated hay. Removal rates for treated hay were consistently higher than untreated hay, but only dry matter and cell wall removal rates approached significance in analysis of variance. Considerable variability in removal rate existed between animals and in indivdual observations. Covariance analysis showed increasing removal rates with increasing intake for both treated and untreated hay; but at a given intake level removal rates were higher for treated hay than untreated hay.