COMPARATIVE DIGESTION, RUMEN FERMENTATION AND KINETICS OF FORAGE DIETS BY STEERS AND WETHERS

E. C. Prigge, M. J. Baker and G. A. Varga

West Virginia University, Morgantown 26506

Summary

Four rumen fistulated wethers and beef steers were used to evaluate differences in dry matter digestibility (DMD) between cattle and sheep. They were fed either perennial ryegrass or switchgrass hay at an ad libitum or restricted level for four experimental periods. Significant ruminant species x forage and ruminant species x level of intake (P<.05) interactions were observed for digestible dry matter. The steers digested the switchgrass 7 percentage units greater than the wethers while ryegrass was digested equally. Digestibility differences between the steers and wethers were 6 percentage units at the ad libitum level of intake and 1 unit at the restricted level of intake. Crude protein digestibility tended to be greater (P<.10) for sheep with a 7 unit difference for switchgrass and a 3 unit difference for ryegrass. The mean ruminal solids retention time of the digesta was approximately (P<.01) 50% greater (26.0 vs 17.4 h) in cattle, with no difference in ruminal liquid dilution rate (LD) between animal species. Total ruminal volatile fatty acid concentration differed (P<.01) with level of intake; however, no influence due to intake on the molar proportion of acetate (P>.10) or propionate (P>.10) was evident in spite of a difference (P<.01) in LD. Rumen pH (P<.05) and osmolality (P<.01) were affected by both level of intake and forage, with the ryegrass and high level of intake decreasing pH and increasing osmolality. No animal species differences were observed for in situ dry matter disappearance over time as measured using Dacron bags suspended in the rumen, suggesting that differences in DMD between ruminant species was related to solids retention time of digesta rather than differing rates of digestion.

(Key Words: Steers, Wethers, Digestibility, Rumen Turnover, Intake.)

Introduction

Schneider and Flatt (1975) indicated a significant difference existed between cattle and sheep in digestibility coefficients, and that the direction and magnitude of these differences may be associated with the feed and nutrient involved. Cipolloni et al. (1951) compared data on digestion of predominantly temperate forage species from numerous investigations, and concluded that cattle digested these forages approximately 3 percentage units more effectively than sheep. Playne (1978) observed larger differences (15 units) in favor of cattle with tropical forages. Differences in dry matter digestibility (DMD) between cattle and sheep may be greater with poor quality forages. Playne (1978) speculated that a greater recycling of nutrients to the rumen and hence, increased microbial activity, was responsible for the enhanced digestibility by cattle. Poppi et al. (1980) and Rees and Little (1980) indicated that species differences observed with tropical forages were due to differences in rumen retention times.

If retention time of the digesta is responsible for the differences in DMD between cattle and sheep one could expect, based on the data of Mudgal et al. (1982) and Varga and Prigge (1982), that level of intake and forage quality...
could also influence the extent of differences in DMD between these ruminant species.

Objectives of this study were to investigate differences in digestibility between cattle and sheep as affected by forage species and level of intake. In addition, ruminal fermentation, kinetics and in situ digestion were measured in an attempt to relate these variables to differences in digestion between ruminant species.

Experimental Procedure

Four rumen-fistulated crossbred wethers of approximately 9 mo of age and four rumen-fistulated crossbred beef steers of approximately 18 mo of age averaging 46 ± 4 kg and 405 ± 11 kg, respectively, were employed to assess the affects of ruminant species on digestibility and ruminal metabolism of two forages. All animals were fed an orchard grass (Dactylis glomerata L.) hay for 4 wk before the initiation of the study. Forages compared in this experiment were perennial ryegrass (Lolium perenne L.) and switchgrass (Panicum vigatum L.) hay harvested at the early head stage. The hays were ground through a 4-cm screen in a hammer mill and fed ad libitum (high) with a 15% refusal, or a restricted (50 g/kg BW.75·d−1) level of intake (low). Trace mineralized salt and water was offered free choice. Cattle and sheep were confined to metabolism stalls under the same environmental conditions and all feeding and sample collections were conducted simultaneously.

Four experimental periods were utilized, during which animals were fed either the rye-grass or switchgrass hay at either the high or low feeding regimen. The treatments were rotated in a Latin square arrangement within animal species after each period. Experimental periods consisted of a 10-d preliminary period, during which animals were adjusted to diets followed by a 13-d experimental period. Animals were fed once daily at 0800 h.

Rumen contents were sampled from the ventral sac of the rumen on d 1 of the experimental period at 0, .5, 1, 2, 3, 6, 9, 12 and 23 h postfeeding, strained through two layers of cheesecloth in preparation for analysis of pH, volatile fatty acids (VFA) and ammonia-N (NH3-N) as described by Varga and Prigge (1982). Osmolality was determined on the rumen fluid by measuring freezing point depression on centrifuged samples (1,500 × g for 20 min) using an automatic osmometer. Ruminal liquid dilution rates (LD) were determined on d 1 and 2 according to the procedures of Varga and Prigge (1982) by dosing the wethers and steers with 2.5 and 25 g of Co-EDTA (cobalt-ethylenediaminetetraacetic acid), respectively, immediately prior to feeding. Solid retention time (SRT) of the rumen digesta was determined by ruminally dosing the wethers and steers immediately prior to feeding (d 1) with 120 and 1,200 mg of Yb, respectively, applied to portions of the hays at 20 mg/g. Sampling of rumen digesta was as for LD the first 48 h and 12-h intervals until 96 h (d 4). Preparation of the Yb-labelled hays and determination of SRT were as described by Varga and Prigge (1982). For the measurement of digestibility coefficients, forage consumption was accounted for on d 3 through 10 while fecal output was accounted for on d 5 through 12. Samples of the orTs, forage and feces were collected from 0730 to 0830 h. The orTs and fecal samples were composited for each animal and stored at 5°C. Upon completion of each experimental period, samples of the feces, orTs and forage were dried and ground and analyzed for dry matter (DM), acid detergent fiber (ADF), neutral detergent fiber (NDF) and Kjeldahl N according to AOAC (1980) procedures, and digestion coefficients were determined. In addition, acid insoluble lignin content (AOAC, 1980) of the forages was determined.

In situ digestion of the hays was conducted on d 10 through 13 of the experimental period; Dacron bags attached to 150-g weights were suspended in the ventral sac of the rumen at 0800 h of d 10. Dry matter disappearance (DMDS) was determined over time by incubating 5-g dried, ground (1 mm) samples of the hay in Dacron bags (9 x 17 cm) with an average pore size of 50 μm for 4, 10, 24, 48 and 72 h. A total of 10 bags (five of each hay) were incubated in each animal with one bag removed at each time interval, washed three times with warm tap water and twice with deionized distilled water and squeezed lightly after each washing. The bags were then dried at 101°C and in situ DMDS calculated.

The experimental design (SAS, 1982) consisted of two Latin squares, one with wethers and one with steers analyzed as a single experiment with animal within species as the error term for testing animal species effects. Analy-

---

6 Precision Systems, Inc., Sudsbury, MA.
TABLE 1. CHEMICAL COMPOSITION OF PERENNIAL RYEGRASS AND SWITCHGRASS OFFERED TO WETHERS AND STEERS AT TWO LEVELS OF INTAKE

<table>
<thead>
<tr>
<th>Item</th>
<th>Ryegrass (IFN 1-04-064)</th>
<th>Switchgrass (IFN 2-04-794)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry matter, %</td>
<td>88.3</td>
<td>89.8</td>
</tr>
<tr>
<td>Crude protein, %</td>
<td>14.9</td>
<td>9.2</td>
</tr>
<tr>
<td>NDF, %b</td>
<td>59.6</td>
<td>73.1</td>
</tr>
<tr>
<td>ADF, %c</td>
<td>34.1</td>
<td>42.7</td>
</tr>
<tr>
<td>Lignin, %d</td>
<td>3.1</td>
<td>4.9</td>
</tr>
<tr>
<td>Ash, %</td>
<td>10.0</td>
<td>6.9</td>
</tr>
</tbody>
</table>

Dry matter basis.
bNeutral detergent fiber.
cAcid detergent fiber.
dAcid insoluble lignin.

sis of covariance was conducted on LD and SRT, with VFA concentration, acetate to propionate ratios, pH, NH₃-N concentration and osmolality included as covariables to examine possible relationships between these variables and rumen kinetics.

Results

Intake and Digestibility

Chemical composition of the hays is reported in table 1. Lower NDF, ADF and lignin percentages and higher crude protein levels are indicative of the high quality of the ryegrass hay.

The wethers and steers consumed on the average 55% more forage dry matter/kg BW at the ad libitum level of intake compared with the restricted level (table 2). At high intake level consumption of both forages (kg BW) were similar for steers; however, wethers appeared to consume comparatively less switchgrass. Forage offered at the low intake level was fixed at 50 g/kg BW.

The percentage of ADF and NDF in the forage consumed was the same regardless of animal species (P>.90) or level of intake (P>.60). However, a tendency (P<.10) for the sheep to consume a greater percentage of dietary protein (.4 percentage units) at the high level of intake was indicated. In addition, the wethers fed switchgrass at the low level consistently had orts representing 3% of the hay offered as opposed to none for the steers. When chemical composition of the feed offered was corrected for orts, no differences were apparent in the composition of the forage consumed.

Results of the digestibility trial (table 2) indicated that although differences were observed in digestible dry matter (DDM) for level of intake (P<.05) and forage (P<.01), ruminant species x forage and ruminant species x level of intake interactions (P<.05) existed. Over both levels of intake the wethers and steers digested the ryegrass to the same extent (69.1 vs 69.5%) while the switchgrass was digested 7 percentage units less by the wethers (51.1 vs 57.7%). At the high level of intake averaging both forages, the wethers digested the hay 6 units less than the steers (57.3 vs 63.2%) while a 1 unit difference (62.9 vs 64.2%) was observed at the low level of intake. The ruminant species x level of intake x forage species interaction was not significant (P>.10). In contrast to DDM, crude protein digestibility averaged over both level of intake and forage species tended to be greater (P<.10) for sheep than cattle (64.4 vs 58.9%). Holter and Reid (1959) and Vona et al. (1982) found sheep digested N to a greater extent than cattle. Level of intake also tended (P<.10) to influence protein digestibility (59.4 vs 63.5% for the high and low level of intake, respectively).

The steers were superior (P<.01) in the digestion of the NDF fraction of the forage fiber while a significant level of intake x forage species interaction was evident. The NDF fraction of the ryegrass was digested to a greater extent at the low intake level. Only differences (P<.01) due to forage species were observed for the ADF digestibility of the forage.
<table>
<thead>
<tr>
<th>Item</th>
<th>Level of intake:</th>
<th>Animal species:</th>
<th>Forage species:</th>
<th>Wethers</th>
<th>Steers</th>
<th>Wethers</th>
<th>Steers</th>
<th>SE^a</th>
<th>Significance^b</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intake, g DM/kg^c</td>
<td>High</td>
<td>Rye-grass</td>
<td>84.1</td>
<td>62.2</td>
<td></td>
<td>87.4</td>
<td>86.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Digestibility of dry matter, %</td>
<td>High</td>
<td>Switch-grass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Digestibility of protein, %</td>
<td>High</td>
<td>Rye-grass</td>
<td>65.3</td>
<td>49.4</td>
<td></td>
<td>68.4</td>
<td>58.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Digestibility of protein, %</td>
<td>High</td>
<td>Switch-grass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Digestibility of NDFc, %</td>
<td>High</td>
<td>Rye-grass</td>
<td>65.6</td>
<td>55.4</td>
<td></td>
<td>66.2</td>
<td>50.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Digestibility of NDFc, %</td>
<td>High</td>
<td>Switch-grass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Digestibility of ADFd, %</td>
<td>High</td>
<td>Rye-grass</td>
<td>66.3</td>
<td>56.2</td>
<td></td>
<td>73.1</td>
<td>63.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Digestibility of ADFd, %</td>
<td>High</td>
<td>Switch-grass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>Rye-grass</td>
<td>51.8</td>
<td>49.1</td>
<td></td>
<td>51.0</td>
<td>53.5</td>
<td>1.55</td>
<td>L*, F**, SxL*, SxF*</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>Switch-grass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>Rye-grass</td>
<td>72.9</td>
<td>52.8</td>
<td></td>
<td>70.6</td>
<td>57.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>Switch-grass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>Rye-grass</td>
<td>73.6</td>
<td>62.9</td>
<td></td>
<td>64.9</td>
<td>53.9</td>
<td>3.17</td>
<td>S†, L†, F**</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>Switch-grass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>Rye-grass</td>
<td>73.7</td>
<td>51.5</td>
<td></td>
<td>74.7</td>
<td>61.7</td>
<td>2.14</td>
<td>S*, F**, LxF**</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>Switch-grass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

^a Standard error of the mean.

^b S = ruminant species, L = level of intake, F = forage species, SxL = ruminant species x level of intake interaction, SxF = ruminant species x forage species interaction, LxF = level of intake x forage species interaction.

^c Neutral detergent fiber.

^d Acid detergent fiber.

†P<.10.

*P<.05.

**P<.01.
Rumen Kinetics. The LD and SRT data (table 3) are in general agreement with the results of Grovum and Williams (1977), Kennedy and Milligan (1978), Mudgal et al. (1982) and Varga and Prigge (1982) regarding level of intake in that the higher level of forage consumption resulted in an increased dry matter pool, liquid volume (kg BW^-0.75) and LD; however, no influence (P>.40) due to level of intake on SRT was observed. The SRT differed (P<.01) with ruminant species, the cattle retained the digesta approximately 50% longer than the sheep (26.0 vs 17.4 h). In spite of large species differences in SRT, species differences in LD (P>.90) were not evident, therefore a greater proportion of solids than of liquid left the rumen in sheep as compared with cattle.

Rumen Fermentation. Total VFA concentrations (table 4) tended to peak at 12 h regardless of level of intake, animal species or forage. Differences (P>.01) were observed in total concentration due to level of intake (149 for high vs 126 μmol/ml for low); however, no differences in proportions of acetate or propionate were observed as a result of the influence of level of intake on LD. Turnover rate of the liquid and/or solid digesta in the rumen have been related to VFA molar proportion (Hodgson and Thomas, 1975; Thomson et al., 1975); however, the majority of studies have been conducted with high concentrate diets. Rogers et al. (1979) and Varga and Prigge (1982) have not observed a LD effect on acetate to propionate ratios with forage diets.

As for VFA's, rumen pH (figure 1) was not influenced (P>.10) by ruminant species and showed the greatest depression at 12 h post-feeding. Mean rumen pH differed (P<.05) for both level of intake (6.7 for low vs 6.6 for high) and for forage (6.6 for ryegrass vs 6.7 for switchgrass). No species differences (P>.10) in rumen osmolality (figure 2) were observed. Effects due to forage (P<.01), time after feeding (P<.05), forage x time and level of intake x time (P<.01) on rumen osmolality were apparent. Forage fed at the low level of intake resulted in an initial peak (3 h) followed by a decline, while the ad libitum or high feeding regimen resulted in more consistent patterns. It appeared that rumen osmolality reflected the fermentation and general forage consumption patterns from the feeding methods employed (once daily) in this study. Rumen NH₃-N levels are illustrated in figure 3. Differences (P<.01) were observed due to animal species, forage and
time of sampling, but not level of intake. The lack of an intake effect on rumen NH₃-N level has been observed previously (Varga and Prigge, 1982) and ascribed to differences in LD. The NH₃-N levels tended to peak at 1 to 3 h postfeeding, with greater mean values observed for wethers as compared with steers and for ryegrass as compared with switchgrass.

Analysis of covariance conducted on LD and SRT, with total VFA concentrations, acetate to propionate ratio, pH, NH₃-N concentration and osmolality included as covariables indicated that rumen NH₃-N concentration (P<.05) was negatively and osmolality (P<.10) positively related to LD. Similar relationships were ob-

---

**Figure 1.** The influence of forage and level of intake on rumen pH over time postfeeding. EMS = error mean square.

---

**Figure 2.** The influence of forage and level of intake over time postfeeding on rumen osmolality. EMS = error mean square.
Figure 3. The influence of ruminant species and forage on rumen NH$_3$-N levels over time postfeeding. EMS = error mean square.

In Situ Digestion. Results using the Dacron bag technique are illustrated in figure 4. No difference (P>.10) was observed between the microflora of cattle and sheep in their ability to degrade the two forage species, nor was any effect due to level of consumption observed. Significant effects (P<.01) due to time of incubation, forage species and forage species x time of incubation were evident.

The DM disappearance from the nylon bags is indicative of greater rate and extent of degradation for the ryegrass as would be expected and is in agreement with the in vitro dry matter digestions of the same forages incubated over time by Vona et al. (1981).

Discussion

Digestibility in ruminants is a function of the competition between digestion and passage rates (Van Soest, 1982). The results of this investigation indicate that large differences in SRT between steers and wethers exist (table 3) and in the potential rate and extent of in situ digestion of the ryegrass and switchgrass (figure 4). Thus a large portion of the increased digestibility observed for the cattle on switch-
grass could be related to increased retention
time of digesta in the rumen as indicated by
Rees and Little (1980) and Poppi et al. (1980).
The similar in situ digestion of the forages by
the wethers and steers suggests that recycling
of nutrients to the rumen was not a major fac-
tor for rumen species differences in digestibility
observed, contrary to the suggestion by Playne
(1978).

The ruminant species x forage interaction
\((P<.05)\) for DMD (table 2) is most likely a
function of both the rate of digestion of the
forages and the rumen retention time. The
shorter SRT for the sheep would be expected
to have a lesser influence on ruminal digestion
of the more rapidly digesting ryegrass as op-
posed to the slower digesting switchgrass. The
in situ technique, however, estimates only the
ability of the rumen microflora to degrade the
forages and does not account for differences in
rumination, mastications and other physical
factors that would influence in vivo degradation
rates.

The reduced DMD for high levels of intake
has been reported by Van Soest (1982) and
others. However the 6-unit difference in DMD in
favor of the steers at the high level of intake
vs a 1 unit difference at low intake cannot be
fully explained by the variables measured.
Mudgal et al. (1982) and Varga and Prigge
(1982) indicated that rumen retention time
tended to be influenced by level of intake.
However, neither level of consumption \((P<.40)\)
or level of intake x forage interactions
\((P<.10)\) influenced SRT, possibly due to the
relatively large standard error of the mean
\((2.53)\) associated with SRT.

Differences in NDF digestibility between
ruminant species could be related to SRT, how-
ever, the level of intake x forage \((P<.05)\)
interactions likely are not because intake did
not affect SRT. Only forage effects \((P<.01)\)
were evident for ADF digestibility suggesting
effects on NDF digestibility were due to
differences in digestion of the hemicellulose
\((\text{NDF-ADF})\) content. While Van Soest (1982)
indicated that the intake related depressions in
digestibility should have the largest influence
upon the slower digesting cell wall fractions, it
appeared in this study that the more highly
digestible component of the forage cell walls
\((\text{hemicellulose})\) seemed to have the greatest
influence on digestibility.

The trend toward increased protein diges-
tibility for the wethers was not unexpected, how-
ever, it would be difficult to conclude that the
differences observed were due to actual degra-
dation of the forage protein. Sheep at the high
level of intake consumed a diet higher in crude
protein and presumably protein availability,
which may account for part of the response;
however, the species difference in protein di-
gestibility appeared to be greater at the low
intake level. Based on similar rumen LD and pH
for the steers and wethers and greater \(\text{NH}_3\)-N
levels for the sheep, less incorporation of
\(\text{NH}_3\)-N into microbial protein in the sheep
could result in less microbial trapping of N and
greater urinary N output as opposed to fecal N,
resulting in greater apparent CP digestibility
for the wethers. Urinary N, however, was not
measured.

Because both level of intake and forage
species influenced LD whereas SRT was only
influenced by ruminant species, it appears that
LD is independent of SRT. Liquid dilution rate
was related to rumen \(\text{NH}_3\)-N level and osmol-
ality. The association with rumen \(\text{NH}_3\)-N is possi-
bly due to dilution of \(\text{NH}_3\) due to liquid turn-
over (Varga and Prigge, 1982). Osmolality may
directly influence LD (Harrison et al., 1976;
Rogers et al., 1979). Increased levels of feed
intake have also been found to influence osmolality (Balch and Campling, 1965; Nichol-
son and Sutton, 1969; Hogan and Weston,
1971) as in this study.

From the results of this investigation and
those of Poppi et al. (1980) and Rees and Little
(1980) it is probable that a portion of the dif-
terence in apparent digestibility observed be-
tween cattle and sheep could be accounted for
by retention time of digesta in the rumen. The
degree of this difference appears to be influ-
enced by rate of degradation of the forage and
possibly the contribution of endogenous com-
ponents to the determination of apparent
digestibility.

Literature Cited

Association of Official Analytical Chemists,
Washington, DC.

Balch, C. C. and R. C. Campling. 1965. Rate of pas-
sage of digesta through the ruminant digestive
tract. In: R. W. Dougherty (Ed.) Physiology of
Digestion in the Ruminant. Butterworths, WA.

Cipolloni, M. A., B. H. Schneider, H. L. Lucas and
H. M. Pavlech. 1951. Significance of the differ-
cences in digestibility of feeds by cattle and sheep.

Grovum, W. L. and V. J. Williams. 1977. Rate of pas-
sage of digesta in sheep. 6. Effects of level of feed
intake on mathematical predictions of the kine-


