

DIGESTIBILITY AND RATE OF PASSAGE BY LAMBS OF WATER-STRESSED ALFALFA¹

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ABSTRACT

Two lamb digestion experiments were conducted to evaluate the effect of alfalfa [*Medicago sativa* (L.)] grown under varying levels of water deficiency (stress) on the rate of passage and digestibility of various fibrous components. Experiment 1 consisted of a randomized complete block design in which 12 Suffolk × Hampshire crossbred wethers averaging 40 kg were fed alfalfa hay grown at three (10, 15 or 20 cm water/ha) levels of water per harvest. Experiment 2 consisted of a switchback design in which four Hampshire wethers averaging 45 kg were fed alfalfa hay grown at two (5 or 20 cm/ha) levels of water per harvest. Forage yields ranged from 1,420 (10 cm/ha in Exp. 1) to 4,200 (20 cm/ha in Exp. 2) kg/ha. In both experiments, water stress reduced cell wall constituents (neutral detergent fiber), acid detergent fiber, lignin and cellulose content of the alfalfa hay. Organic matter digestibility was decreased when the percentage of leaves fell below 60% at the highest yield. Digestibility of N and the rate of NDF digestibility were not affected by water stress. The second experiment additionally included nutrient balance and rate of passage measurements. Greater ($P < .10$) amounts of N and P were absorbed from water-stressed than nonstressed hay. Ruminant retention time of particulate markers tended ($P < .10$) to increase with greater water stress. The results of this study are interpreted to indicate that while moderate water stress may have little effect on *in vivo* digestibility of alfalfa, severe stress may reduce digestibility of fibrous fractions and total organic matter.

(Key Words: Digestion, Lambs, Water Stress, Alfalfa, *Medicago sativa*, Forage.)

Introduction

Forage quality at harvest is a result of the genetic potential of the forage as well as environmental factors occurring during plant growth. The decline in quality with increasing maturity has long been known and is well documented (Jensen et al., 1967). Van Soest et al. (1978) reported that, generally, any factor that retards plant development tends to maintain quality. However, there are relatively few measurements available on environmental fac-

tors as they affect plant composition and quality (Reid and Klopfenstein, 1983).

Water stress (moisture limiting) retards plant growth, and has been reported to produce a more highly digestible (*in vitro*) crop of reduced yield (Vough and Marten, 1971; Snaydon, 1972; Miller et al., 1982). Vough and Marten (1971) reported that water stress increased leaf-to-stem ratio of alfalfa (*Medicago sativa*). Because leaves have a higher nutritive value than stems, increasing the percentage of leaves in a forage has been thought to increase the dry matter (DM) intake, DM digestibility and cell wall digestibility (Robles et al., 1981). However, this assumes there is no change in the composition of the leaf and stem fractions due to water stress.

Previous reports agree that chemical analyses indicate that water-stressed forage is higher in nutritive value; however, *in vivo* determinations of the digestibility of various mural and mineral fractions are lacking. Therefore, the objective of this study was to determine the effect of water stress on *in vivo* digestibility and rate of passage of alfalfa by lambs.

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Materials and Methods

Four varieties of alfalfa (Vanguard, Zia, Cody, and Dawson) were grown in research plots (2 to 5 × 9 m/variety) on a Pullman clay loam soil having a pH of 7.2 under a gradient irrigation system (Hanks et al., 1976). Phosphorus was applied to the plots at a rate of 49 kg/ha in the spring; other nutrients were adequate as per soil test. In Exp. 1, alfalfa was harvested when visually estimated to be 10% bloom from plots having three irrigation levels where total water use (irrigation + precipitation - stored soil water) was 20, 15 and 10 cm/ha per harvest in 1984. Eight plots were used for each treatment. Treatments were designated low, medium and high stress, respectively. In Exp. 2, alfalfa was harvested at 10% bloom from the same plots as in 1984. Total water use was 20 and 5 cm/ha per harvest in 1985. Treatments were designated low and high stress, respectively. The low stress was a nonstressed control in each experiment. In both experiments, all four varieties were harvested with a flail chopper from the fourth and fifth harvests of each year and air-dried in a greenhouse. Hay from the different varieties and harvests were combined manually on a concrete floor by stress level to provide sufficient forage for the trial. Previous work (Naylor, 1985) had shown that all varieties had similar increases in leaf:stem ratio with water stress. Subsamples were separated into leaf and stem components to determine leaf:stem ratio.

Exp. 1. Twelve Suffolk × Hampshire crossbred wethers averaging 40 kg were blocked by weight and randomly allotted to one of the three alfalfa treatments. All lambs were fed the same alfalfa diet (baled hay from another source) at 1% of body weight for 7 d, and were then fed their experimental diet at 1% of body weight for 10 d. Because the forages were harvested from small research plots, limited amounts of alfalfa were available and feed intakes were limited. Water and feed-grade salt were available continuously. Lambs were housed in individual pens with slatted floors and were equipped with fecal collection bags (Schneider and Flatt, 1975). Feces were collected, weighed and frozen daily for the last 4 d of the experiment.

Feces from each lamb were composited, mixed and subsampled at the end of the collection period. About 500 g of feces were dried at 60 C and ground through a 1-mm screen in a Wiley mill⁶. An additional 500 g were frozen for N analysis. Representative alfalfa samples were collected daily. Alfalfa samples were composited, dried, ground and subsampled at the end of the collection period.

Feed and feces were analyzed for DM by drying at 60 C until no decrease in weight occurred, and for organic matter (OM) by ashing at 450 C for 5 h in a muffle furnace. Nitrogen was determined by micro-Kjeldahl. Acid detergent fiber (ADF), cell wall constituents (neutral detergent fiber, NDF) and cellulose were determined by the procedures of Goering and Van Soest (1970). Cell solubles was calculated as 100 minus NDF. Hemicellulose was calculated as the difference between NDF and ADF. Lignin was determined by both the 72% sulfuric acid procedure (AL) of Van Soest (1963) and by the permanganate procedure (PL) of Van Soest and Wine (1968). Acid detergent fiber ash (ADFIA) was the residual ash (450 C) following the ADF determination.

In vitro rate of NDF digestion was determined by incubating 250 mg of plant material in buffer and ruminal fluid according to the procedure of Tilley and Terry (1963) as modified by Barnes et al. (1971). Fermentations were stopped at 6, 12, 18, 24, 32, 48 and 73 h. Following fermentation, residues were analyzed for NDF. A least-squares regression of the logarithm of digestible fiber remaining vs time was calculated. The slope of this regression line was converted to digestion rate by multiplying by 2.303 (Gill et al., 1969; Smith et al., 1972; Waldo et al., 1972).

Digestibility data were analyzed using the General Linear Models procedure of the Statistical Analysis System (SAS, 1985). Duncan's multiple range test was used to separate differences among means when significant F-values were observed (Steele and Torrie, 1980). Homogeneity of regression rate values was assessed by t-test (Steel and Torrie, 1980).

Exp. 2. Four Hampshire wethers (averaging 45 kg) were used in a crossover design with two 21-d periods. Lambs were on a common diet prior to the study. They were adapted to treatments for 7 d, and were then placed in metabolism stalls for 7 d followed by 7 d of total fecal and urine collection. Two lambs were fed a low-stressed alfalfa and two were

⁶Thomas-Wiley Model 4; Arthur H. Thomas, Philadelphia, PA.

fed a high-stressed alfalfa at 1.25% of body weight in period 1. Treatments were reversed and the procedures repeated in period 2. On d 15 of each period, lambs were dosed orally with 15 g of alfalfa labeled with $\text{YbCl}_3 \cdot \text{XH}_2\text{O}$ (Teeter et al., 1984; Krysl et al., 1985). Rectal grab samples of feces were obtained at 0, 4, 8, 12, 16, 20, 24, 28, 32, 36, 42, 48, 54, 60, 72, 84, 96, 108 and 120 h post-dosing. Total fecal and urine outputs were collected, weighed and subsampled on d 8 to 14 in the metabolism stalls. Water consumption was measured daily.

Feed and fecal samples were analyzed for DM, OM, ash, NDF, ADF and N as previously described. Urine was analyzed for N by micro-Kjeldahl. Feed and feces for Yb analysis were extracted by the procedure of Hart and Polan (1984) and analyzed for Yb by atomic absorption spectroscopy. Fecal Yb excretion curves were evaluated using the two-compartment model of Grovum and Williams (1973). Passage rate and digestibility data were compared using a paired t-test (SAS, 1985). Linear relationships between leaf:stem ratio and forage yield were examined using the General Linear Model procedure (SAS, 1985).

Results and Discussion

Forage Composition. The fiber and nutrient composition of the alfalfa forage harvested at three levels of water stress in Exp. 1 and two levels in Exp. 2 are presented in table 1. Both NDF and ADF content declined with increasing water stress, while AL was not affected. Hemicellulose declined with increasing water stress in Exp. 1 but not in Exp. 2. Permanganate lignin decreased 3.4 percentage units with increasing water stress in Exp. 1. Permanganate lignin averaged 4 to 6 percentage units higher than AL. Thus, a fraction equal to 4 to 6% of the OM that was insoluble in the ADF solution was removed by the 72% sulfuric acid, but not the permanganate solution. This fraction is probably composed of phenolic or polyphenolic constituents because the 72% acid procedure is known to remove lignin/phenolic compounds (Van Soest, 1982). The cellulose content of the alfalfa forage, by either procedure, declined 5 to 6 percentage units in Exp. 1 and 3 percentage units in Exp. 2 with increasing water stress. Nitrogen content of alfalfa was lower in Exp. 2 than Exp. 1 and was not affected by the levels of water stress imposed in either experiment. Although forage analyses were conducted on

single composite samples, changes in composition were very similar to changes noted in previous intensive agronomic studies (Naylor, 1985).

In Vivo Digestibility. Dry matter digestibility of high-stress alfalfa was lower ($P < .05$) than DM digestibility of low- and medium-stress alfalfa in Exp. 1 but was similar to DM digestibility of low-stress alfalfa in Exp. 2 (table 2). In Exp. 1 OM digestibility was similar for all treatments; however, in Exp. 2 OM digestibility of high-stress alfalfa was higher ($P < .05$) than digestibility of low-stress alfalfa.

Results from Exp. 1, where DM digestibility declined with water stress while the OM digestibility remained constant, are due to the higher ash content of the high-water-stress alfalfa forage. Most of the difference in ash content was caused by differences in ADFIA. The high-water-stress alfalfa contained 9.2% ADFIA; the moderate and low levels contained 4.1 and 4.5%, respectively. The elevated ADFIA is thought to have been caused by soil contamination and is likely to have had little effect on digestibility other than a dilution effect (Van Soest and Jones, 1968).

When the results of the two studies were combined, a linear ($r = .93$; $P < .05$) relationship was obtained between leaf:stem and forage yield (figure 1A). In contrast, OM digestibility

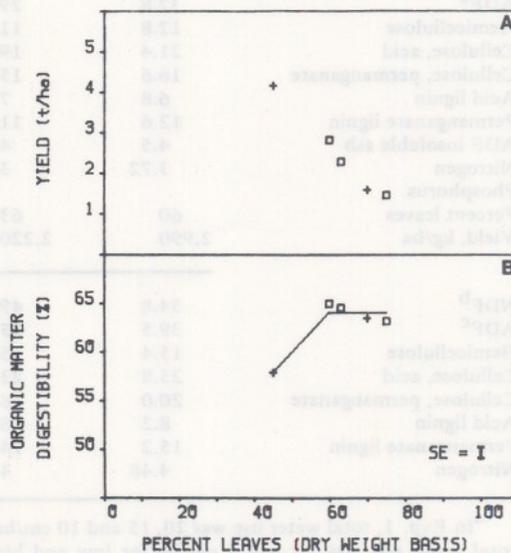


Figure 1. Relationship of alfalfa yield (A) and organic matter digestibility (B) to leaf percentage in Exp. 1 (□) and Exp. 2 (+).

was similar in alfalfa containing 60 to 75% leaves but was lower ($P < .05$) in alfalfa containing 45% leaves (figure 1B). Robles et al. (1981) noted that alfalfa diets containing either 50 or 100% leaves had similar digestible energy values, while diets containing 0% leaves had significantly lower digestibilities. This would suggest that a relationship between leaf content and digestibility exists only when the leaf content falls below 50 to 60%. The similar digestibility of diets containing 60 to 75% leaves may reflect differences in either physical or chemical characteristics of the forage. Although these possible relationships are based on comparisons over years, the linear relationship between yield and leaf:stem over years

suggests that these relationships are valid. In addition, if the digestible energy values of Robles et al. (1981) are adjusted by adding 7%, the relationship between digestibility and leaf:stem is similar in both studies.

The greater yield of the low-stress alfalfa in Exp. 2 compared with low-stress alfalfa in Exp. 1 indicates that, despite similar water use, conditions for growth were better in 1985 than in 1984. Yields of high-stress alfalfa in Exp. 2 were similar to yields of high-stress alfalfa in Exp. 1 despite lower water use (5 vs 10 cm/ha). Other environmental factors, therefore, appear to play a major role in determining both the quantity and quality of forage harvested at a similar stage of maturity.

TABLE 1. FIBER AND NUTRIENT COMPOSITION OF ALFALFA GROWN AT DIFFERENT LEVELS OF WATER STRESS

| Item | Level of water stress ^a | | | | |
|-------------------------|------------------------------------|--------|-------|--------|-------|
| | Exp. 1 | | | Exp. 2 | |
| | Low | Medium | High | Low | High |
| | % Dry matter basis | | | | |
| Dry matter | 89.2 | 89.5 | 89.4 | 91.8 | 92.9 |
| Organic matter | 83.0 | 83.5 | 76.6 | 84.7 | 84.4 |
| Ash | 17.0 | 16.5 | 23.4 | 15.3 | 15.6 |
| Cell solubles | 54.5 | 58.6 | 62.2 | 54.2 | 56.7 |
| NDF ^b | 45.5 | 41.4 | 37.8 | 45.8 | 43.3 |
| ADF ^c | 32.8 | 29.7 | 30.3 | 39.4 | 35.4 |
| Hemicellulose | 12.8 | 11.3 | 7.4 | 6.4 | 7.9 |
| Cellulose, acid | 21.4 | 19.5 | 15.2 | 25.6 | 23.7 |
| Cellulose, permanganate | 16.6 | 15.0 | 11.5 | 23.0 | 20.0 |
| Acid lignin | 6.8 | 7.0 | 6.3 | 6.6 | 6.0 |
| Permanganate lignin | 12.6 | 11.7 | 9.2 | 13.2 | 12.4 |
| ADF insoluble ash | 4.5 | 4.1 | 9.2 | 4.2 | 4.4 |
| Nitrogen | 3.72 | 3.96 | 3.80 | 3.38 | 3.53 |
| Phosphorus | | | | .36 | .38 |
| Percent leaves | 60 | 63 | 75 | 45 | 70 |
| Yield, kg/ha | 2,990 | 2,220 | 1,420 | 4,200 | 1,620 |
| | % Organic matter basis | | | | |
| NDF ^b | 54.8 | 49.6 | 49.3 | 54.1 | 51.3 |
| ADF ^c | 39.5 | 35.6 | 39.6 | 46.5 | 41.9 |
| Hemicellulose | 15.4 | 13.5 | 9.7 | 7.6 | 9.4 |
| Cellulose, acid | 25.8 | 23.4 | 19.8 | 30.2 | 28.1 |
| Cellulose, permanganate | 20.0 | 18.0 | 15.0 | 27.2 | 23.7 |
| Acid lignin | 8.2 | 8.4 | 8.2 | 7.8 | 7.1 |
| Permanganate lignin | 15.2 | 14.0 | 12.0 | 15.6 | 14.7 |
| Nitrogen | 4.48 | 4.74 | 4.96 | 3.99 | 4.18 |

^aIn Exp. 1, total water use was 20, 15 and 10 cm/ha for low, medium and high stress, respectively. In Exp. 2, total water use was 20 and 5 cm/ha for low and high stress, respectively. Water was not a limiting factor in low-stressed treatments.

^bNeutral detergent fiber.

^cAcid detergent fiber.

TABLE 2. APPARENT DIGESTIBILITY OF ALFALFA FRACTIONS AT THREE (EXPERIMENT 1) OR TWO (EXPERIMENT 2) LEVELS OF WATER STRESS DETERMINED BY TOTAL FECAL COLLECTION

| Item | Level of water stress ^a | | | | | | SE ^b |
|---------------------------------------|------------------------------------|--------------------|-------------------|--------|-------------------|-------------------|-----------------|
| | Exp. 1 | | | Exp. 2 | | | |
| | Low | Medium | High | Low | High | High | |
| Dry matter intake, g/d | 357 | 358 | 357 | 413 | 418 | 418 | .94 |
| Apparent digestibility, % | | | | | | | |
| Dry matter | 60.9 ^c | 61.0 ^c | 56.7 ^d | .88 | 54.0 | 54.0 | .58 |
| Organic matter | 65.0 | 64.6 | 63.2 | .94 | 63.5 ^d | 63.5 ^d | 1.14 |
| Ash | 40.3 ^c | 43.2 ^d | 35.3 ^c | .84 | 30.4 ^c | 2.7 ^d | 5.90 |
| NDF ^f | 50.0 ^c | 45.9 ^c | 32.1 ^d | 1.57 | 43.7 | 39.2 | 1.51 |
| ADF ^g | 35.5 ^c | 32.7 ^c | 21.9 ^d | 1.94 | 33.4 | 33.4 | 2.47 |
| Hemicellulose | 87.7 ^c | 81.4 ^d | 74.5 ^c | 1.86 | 54.4 | 65.4 | 6.51 |
| Cellulose, acid | 57.5 ^c | 55.1 ^{cd} | 50.6 ^d | 2.00 | 63.5 ^d | 70.0 ^c | 1.26 |
| Cellulose, permanganate | 50.9 ^c | 46.2 ^{cd} | 40.2 ^d | 2.56 | 64.2 | 69.2 | 1.52 |
| Acid lignin | -6.4 | -4.0 | -12.3 | 3.38 | -19.2 | -10.1 | 3.35 |
| Permanganate lignin | 29.7 ^c | 24.7 ^c | 8.0 ^d | 2.22 | 25.3 | 27.1 | 2.12 |
| Nitrogen | 81.3 | 82.5 | 81.8 | .69 | 76.1 | 79.5 | .93 |
| Phosphorus | | | | | 24.2 | 47.0 | 9.38 |
| Rate of dry matter digestibility, %/h | 11.0 | 10.4 | 11.0 | | | | |
| r ² | 76 | 69 | 88 | | | | |

^aIn Exp. 1, total water use was 20, 15 and 10 cm/ha for low, medium and high stress, respectively. In Exp. 2, total water use was 20 and 5 cm/ha for low and high stress, respectively. Water was not a limiting factor in low-stressed treatments.

^bStandard error of treatment mean, n = 4.

^{c,d,e}Means in the same row for each experiment without a common letter in their superscript differ (P < .05).

^fNeutral detergent fiber.

^gAcid detergent fiber.

In Exp. 1, not only did the content of the fibrous constituents decrease, but digestibility of every fibrous component declined ($P < .05$) with increasing water stress, with the decline being significant between medium- and high-stress treatments (table 2). The declines in digestibility of NDF, ADF and hemicellulose were 17.9, 14.6 and 13.2 percentage units, respectively. Cellulose digestibility decreased 6.9 and 10.7 percentage units when determined by the acid and permanganate procedures, respectively.

Nitrogen, P and water metabolism (table 3) were not affected ($P > .10$) by diet in Exp. 2. However, lambs fed high-stressed alfalfa tended ($P < .10$) to have greater total N absorption, P absorption and P balance.

Rate of Digestion and Passage. Although total NDF digestibility was reduced by water deficiency, water stress did not affect the *in vitro* rate of NDF digestion of alfalfa forage in Exp. 1 (table 2). This would tend to suggest a change in fiber composition, the accumulation of a stress metabolite that was affecting fiber digestion, or a change in the rate of passage

with water stress.

Metabolites such as coumestrans and flavonoids, which possess antifungal activity, have been shown to accumulate in alfalfa in response to stress induced by disease (Wood, 1979). Further, Jung and Fahey (1983) have reported that phenolic compounds derived from the lignin biosynthetic pathway may inhibit microbial growth and enzymatic digestion of forages. A decrease in the amount of PL with increasing water stress may indicate the presence of more phenolic monomers in the water-stressed plants (metabolites produced but not synthesized into lignin). Additionally, a reduction in PL but not AL, as well as differing digestibilities of PL (table 2) with water stress, may indicate a change in the composition of the lignin fraction with water stress. Either of these two mechanisms could result in phenolic monomers that might affect fiber digestion.

Lambs fed high-stressed alfalfa tended ($P < .10$) to have slower ruminal rate of passage (k_1) and longer ruminal particulate retention times than lambs fed the low-stressed alfalfa (table 4). The longer ruminal retention times of

TABLE 3. NITROGEN, PHOSPHORUS AND WATER METABOLISM OF LAMBS FED LOW- OR HIGH-STRESSED ALFALFA IN EXPERIMENT 2

| Item | Low stress ^a | High stress | SE ^b |
|---------------------------------|-------------------------|-------------------|-----------------|
| | g/d | | |
| Nitrogen | | | |
| Intake | 13.9 | 14.7 | .15 |
| Fecal N | 3.3 | 3.0 | .11 |
| Urine N | 11.2 | 11.1 | .26 |
| N absorbed | 10.6 | 11.7 ^c | .23 |
| N balance | -.57 | .57 | .36 |
| Phosphorus | | | |
| Intake | 1.50 | 1.57 | .02 |
| Fecal P | 1.14 | .84 | .14 |
| Urine P | .43 | .37 | .17 |
| P absorbed | .36 | .75 ^c | .15 |
| P balance | -.06 | .38 ^c | .12 |
| Water | | | |
| Total intake | 2,598 | 2,217 | 397 |
| Fecal water | 120 | 94 | 7.6 |
| Urine water | 1,912 | 1,606 | 357 |
| Evaporative losses ^d | 565 | 516 | 74.6 |

^aIn Exp. 1, total water use was 20, 15 and 10 cm/ha for low, medium and high stress, respectively. In Exp. 2, total water use was 20 and 5 cm/ha for low and high stress, respectively. Water was not a limiting factor in low-stressed treatments.

^bStandard error of the mean, $n = 4$.

^cDiffers from mean of low-stress alfalfa ($P < .10$).

^dEstimated as total water intake - (fecal + urine water).

TABLE 4. PARTICULATE EXCRETION PATTERNS IN LAMBS FED LOW- OR HIGH-STRESSED ALFALFA IN EXPERIMENT 2

| Item | Low stress ^a | High stress | SE ^b |
|---------------------------|-------------------------|-------------------|-----------------|
| $k_1 \times 100^d$ | 2.32 | 2.10 ^c | .19 |
| $k_2 \times 100^e$ | 8.73 | 7.83 | .62 |
| Ruminal retention time, h | 45.5 | 50.3 ^c | 4.68 |
| Mean retention time, h | 78.0 | 82.8 | 6.39 |
| Transit time, h | 20.6 | 19.4 | 1.38 |

^aIn Exp. 1, total water use was 20, 15 and 10 cm/ha for low, medium and high stress, respectively. In Exp. 2, total water use was 20 and 5 cm/ha for low and high stress, respectively. Water was not a limiting factor in low-stressed treatments.

^bStandard error of the mean, n = 4.

^cMean of high-stress alfalfa differ from mean of low-stress alfalfa ($P < .10$).

^d k_1 = rate of passage through rumen.

^e k_2 = rate of passage through lower gut.

high-stressed alfalfa could account for the higher ($P < .05$) OM digestibility of the high-stressed alfalfa compared with low-stressed alfalfa in Exp. 2. Although not significantly different, in Exp. 2 high-stressed alfalfa tended to have lower NDF and ADF digestibility than low-stressed alfalfa, despite a longer ruminal retention time. This tends to support the conclusion that differences in digestibility were the result of chemical factors in the forage rather than differences in the rate of passage or rate of digestibility. Ruminal retention time of particulate matter tended to be longer than values reported by Faichney and Griffiths (1978) and Uden et al. (1982), probably due to the low feed intakes used in the present study (Mudgal et al., 1982). Rate constants for particulate passage through the lower gut (k_2) were lower than values obtained by Dhanoa et al. (1985), but were greater than those determined by Uden et al. (1980, 1982).

Results of this study are interpreted to indicate that water stress increases the leaf percentage of alfalfa, lowers the concentration of most fibrous components and can have a significant effect on forage digestibility. However, the reduction in digestibility is not linear with changes in leaf percentage and is positively related to PL content. Fiber digestibility of high-stressed alfalfa was reduced despite a slightly longer ruminal retention time, suggesting that chemical factors in the forage, possibly produced as a result of water deficiency, were a primary factor causing reduced digestibility.

Literature Cited

- Barnes, R. F., L. D. Muller, L. F. Bauman and V. F. Collenbrander. 1971. In vitro dry matter disappearance of brown midrib mutants of maize (*Zea mays* L.). *J. Anim. Sci.* 33:881.
- Dhanoa, M. S., R. C. Siddons, J. France and D. L. Gale. 1985. A multicompartamental model to describe marker excretion patterns in ruminant feces. *Brit. J. Nutr.* 53:663.
- Faichney, G. J. and D. A. Griffiths. 1978. Behaviour of solute and particle markers in the stomach of sheep given a concentrate diet. *Brit. J. Nutr.* 40:71.
- Gill, S. R., H. R. Conrad and J. W. Hibbs. 1969. Relative rate of in vitro cellulose disappearance as a possible indicator of digestible dry matter intake. *J. Dairy Sci.* 52:1687.
- Goering, H. P. and P. J. Van Soest. 1970. Forage fiber analysis. USDA, ARS Agr. Handbook No. 379.
- Grovum, W. L. and V. J. Williams. 1973. Rate of passage of digesta in sheep. 4. Passage of marker through the alimentary tract and the biological relevance of rate-constants derived from the changes in concentration of marker in feces. *Brit. J. Nutr.* 30:313.
- Hanks, R. J., J. Keller, V. P. Rasmussen and G. D. Wilson. 1976. Line source sprinkler for continuous variable irrigation-crop production studies. *Soil Sci. Soc. Amer. J.* 40:426.
- Hart, S. P. and C. E. Polan. 1984. Simultaneous extraction and determination of ytterbium and cobalt ethylenediaminetetraacetate complex in feces. *J. Dairy Sci.* 67:888.
- Jensen, E. H., M. A. Massengale and D. O. Chilcote. 1967. Environmental effects on growth and quality of alfalfa. Nevada Agr. Exp. Sta. Western Reg. Res. Pub. 1-9.
- Jung, H. G. and G. C. Fahey, Jr. 1983. Nutritional implications of phenolic monomers and lignin: A review. *J. Anim. Sci.* 57:206.
- Krysl, L. J., F. T. McCollum and M. L. Galyean. 1985.

- Estimation of fecal output and particulate passage rate with a pulse dose of ytterbium-labeled forage. *J. Range Manage.* 38:180.
- Miller, D. D., D. W. Kellogg, M. L. Wilson and B. A. Melton. 1982. Effect of limited water application on in vitro organic matter disappearance and crude protein of alfalfa of varying genetic origins. *New Mexico Agr. Exp. Sta. Res. Rep.* 468.
- Mudgal, V. D., R. M. Dixon, P. M. Kennedy and L. P. Milligan. 1982. Effect of two intake levels on retention times of liquid, particle and microbial markers in the rumen of sheep. *J. Anim. Sci.* 54:1051.
- Naylor, C. H. 1985. Compositional analysis of four alfalfa varieties under water-stressed conditions. M. S. Thesis. West Texas State Univ., Canyon.
- Reid, R. L. and T. J. Klopfenstein. 1983. Forage and crop residues: Quality evaluation and systems of utilization. *J. Anim. Sci.* 57(Suppl. 2):534.
- Robles, A. Y., R. L. Belyea and F. A. Martz. 1981. Intake, digestibility, ruminal characteristics and rate of passage of alfalfa diets fed to sheep. *J. Anim. Sci.* 53:774.
- SAS. 1985. SAS User's Guide: Statistics. Statistical Analysis System Institute Inc., Cary, NC.
- Schneider, B. H. and W. P. Flatt. 1975. The Evaluation of Feeds Through Digestibility Experiments. Univ. of Georgia Press, Athens.
- Smith, L. W., H. K. Goering and C. H. Gordon. 1972. Relationships of forage compositions with rates of cell wall digestion and indigestibility of cell walls. *J. Dairy Sci.* 55:1140.
- Snaydon, R. W. 1972. The effect of total water supply, and of frequency of application upon lucerne. II. Chemical composition. *Australian J. Agr. Res.* 23:253.
- Steel, R.G.D. and J. H. Torrie. 1980. Principles and Procedures of Statistics. McGraw-Hill Book Co., New York.
- Teeter, R. G., F. N. Owens and T. L. Mader. 1984. Ytterbium chloride as a marker for particulate matter in the rumen. *J. Anim. Sci.* 58:465.
- Tilley, J.M.A. and R. A. Terry. 1963. A two-stage technique for the in vitro digestion of forage crops. *J. Brit. Grassl. Soc.* 18:104.
- Uden, P., P. E. Colucci and P. J. Van Soest. 1980. Investigation of chromium, cerium and cobalt as markers in digesta. Rate of passage studies. *J. Sci. Food Agr.* 31:625.
- Uden, P., R. R. Rounsaville, G. R. Wiggins and P. J. Van Soest. 1982. The measurement of liquid and solid digesta retention in ruminants, equines and rabbits given timothy (*Phleum pratense*) hay. *Brit. J. Nutr.* 48:329.
- Van Soest, P. J. 1963. Use of detergents in the analysis of fibrous feeds. II. A report on methods for the determination of fiber and lignin. *J. Assoc. Official Agr. Chem.* 46:829.
- Van Soest, P. J. 1982. Refractory and inhibitory substances. In: P. J. Van Soest (Ed.) *Nutritional Ecology of the Ruminant*. pp 118-138. O & B Books, Corvallis, OR.
- Van Soest, P. J. and L.H.P. Jones. 1968. Effects of silica in forages upon digestibility. *J. Dairy Sci.* 51:1644.
- Van Soest, P. J., D. R. Mertens and B. Deinum. 1978. Pre-harvest factors influencing quality of conserved forage. *J. Anim. Sci.* 47:712.
- Van Soest, P. J. and R. H. Wine. 1968. Determination of lignin and cellulose in acid detergent fiber with permanganate. *J. Assoc. Official Anal. Chem.* 51:780.
- Vough, L. R. and G. C. Marten. 1971. Influence of soil moisture and ambient temperature on yield and quality of alfalfa forage. *Agron. J.* 63:40.
- Waldo, D. R., L. M. Smith and E. L. Coy. 1972. Model of cellulose disappearance from the rumen. *J. Dairy Sci.* 55:125.
- Wood, G. E. 1979. Stress metabolites in plants—A growing concern. *J. Food Prot.* 42:496.
- Results of this study are interpreted to indicate that water stress increases the percentage of silica, lowers the concentration of most fibrous components and can have a significant effect on forage digestibility. However, the reduction in digestibility is not linear with changes in test percentage and is positively related to PL content. Fiber digestibility of high-moisture alfalfa was reduced despite a slightly longer ruminal retention time, suggesting that chemical factors in the forage, possibly produced as a result of water deficiency, were a primary factor causing reduced digestibility.