Effects of water restriction on feed intake, digestion, and energy utilization by mature female St. Croix sheep

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ARTICLE INFO

Keywords:
Digestion; Feed intake; Sheep; Water

ABSTRACT

Eleven St. Croix ewes (46.9 ± 1.59 kg BW and 3.6 ± 0.67 yr age) were used in a crossover design to evaluate effects of restricted drinking water availability on intake of a 50% concentrate diet, digestion, and energy utilization. After 2 wk to determine ad libitum water consumption, there were two 4-wk periods, with measures in metabolism cages during wk 4. One treatment was water offered at the ad libitum level (CONT) and the other entailed a 25% reduction in wk 1 and 50% thereafter (REST). Although some water was refused in wk 4, with intake of 2556 and 1707 g/day for CONT and REST, respectively (SEM = 170.9), digestibility of gross energy was greater (P = 0.034) for REST than for CONT (66.5 vs. 62.4%; SEM = 1.16); however, because of a numerical difference (P = 0.448) in energy intake (15.79 and 14.66 MJ/day for CONT and REST, respectively; SEM = 1.426 MJ/day), digested energy intake was similar between treatments (P = 0.870). Urinary energy was greater (P = 0.023) for CONT vs. REST (0.62 and 0.52 MJ/day; SEM = 0.038) and methane energy did not differ (P = 0.213) between treatments (0.76 and 0.89 MJ/day; SEM = 0.084), resulting in similar (P = 0.665) ME intake (8.50 and 8.01 MJ/day for CONT and REST, respectively; SEM = 0.30 MJ/day) and recovered energy (-0.10 and -0.30 MJ/day for CONT and REST, respectively; SEM = 0.623) were similar between treatments (P ≥ 0.880). In conclusion, increased digestibility appears an important adaptive response to limited availability of drinking water.

1. Introduction

Ruminant livestock are exposed to many environmental stress factors. Ones associated with climatic conditions are expected to increase in importance with climate change (Devendra, 2012; Naqvi, Kumar, De & Sejian, 2015; Silanikove & Koluman, 2015). Effects of stresses depend on their magnitude, variability over time, and length of exposure. One stress factor associated with climatic conditions is limited availability of drinking water. Climate change is expected to increase areas where supplies of water suitable for consumption by livestock are restrictive and the availability where supplies are already low. However, for this stress factor and others, different species and breeds of ruminant livestock have evolved physiological processes to cope with and minimize adverse effects (Silanikove, 2000).

Tadesse et al. (2019c) conducted a study with hair sheep to determine effects of restricted feed intake on digestibility and energy utilization to help explain effects on variables such as BW observed in a companion study with a relatively large number of hair sheep of different breeds from regions of the USA with varying climatic conditions. Similarly, Hussein et al. (2020) evaluated resilience of the same hair sheep to availability of drinking water limited to 50% of prior ad libitum consumption. A somewhat unexpected result was that in many instances BW was actually slightly greater in the latter segment of the restriction period than earlier when water was available free-choice. Based on some studies in the literature, it was speculated that an increase in digestibility when water availability was limited could have contributed to this finding. Therefore, the objective of this experiment was to determine effects of a moderate to severe restriction of drinking water availability on feed intake, digestion, and energy utilization by mature female St. Croix sheep.

2. Materials and methods

2.1. Animals, experimental design, and treatments

The protocol for the experiment was approved by the Langston...
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Table 1
Ingredient and chemical composition of the diet consumed by mature female St. Croix sheep.

| Item                                                                 | Concentration |
|---------------------------------------------------------------------|---------------|
| Ingredient (% as fed basis)                                         |               |
| Dehydrated alfalfa                                                  | 19.98         |
| Cottonseed hulls                                                    | 29.07         |
| Cottonseed meal                                                     | 8.99          |
| Ground corn                                                         | 19.98         |
| Wheat middlings                                                     | 12.98         |
| Pelletizing agent                                                   | 4.99          |
| Salt                                                                | 1.00          |
| Calcium carbonate                                                   | 0.95          |
| Ammonium chloride                                                   | 1.00          |
| Yeast                                                               | 1.00          |
| Vitamin-mineral mixture                                             | 0.05          |
| Rumensin premix                                                     | 0.01          |
| Chemical composition, DM basis                                      |               |
| Ash (%)                                                             | 8.9 ± 0.07    |
| CP (%)                                                              | 19.4 ± 0.13   |
| NDF (%)                                                             | 33.6 ± 0.26   |
| Gross energy (MJ/kg)                                                | 17.0 ± 0.11   |

1 Original XP™; Diamond V, Cedar Rapids, IA, USA.
2 1.28% Zn, 0.96% Fe, 0.704% Mn, 0.16% Cu, 0.048% I, 0.032% Co, 26,460,000 IU/kg of vitamin A, 6615,000 IU/kg of vitamin D₃, and 11,025 IU/kg of vitamin E (as fed basis).
3 20% monosynel (Elanco, Greenfield, IN, USA).
4 Based on weekly composite samples; SEM follow means.

University Animal Care Committee. Eleven mature female St. Croix sheep (initial BW of 46.9 ± 1.59 [SEM] and age of 3.6 ± 0.67 yr) were used in a study that occurred in the late spring and summer of 2017. An additional animal started the experiment but was removed because of a health issue unrelated to treatments and procedures of the study. Except as indicated below, animals were maintained individually in 0.7 × 1.2 m elevated pens with plastic-coated expanded metal floors. A 50% concentrate (DM basis) pelleted diet (Table 1) was fed twice daily at 08:00 and 15:00 h at up to 71 g/kg BW. A 50% concentrate (DM basis) pelleted diet (Table 1) was fed twice daily at 08:00 and 15:00 h at up to 71 g/kg BW. Approximately 10% of feces and urine excreted was sampled daily to form composites that were stored at −20 °C. Feed and fecal samples were dried in a forced-air oven at 55 °C for 48 h, ground to pass through a 1-mm screen, and analyzed for DM, ash (AOAC, 2006), nitrogen (N; Leco TruMac CN, St. Joseph, MO, USA), gross energy (GE) using a bomb calorimeter (Parr 6300; Parr Instrument Co., Inc., Moline, IL, USA), and NDF following procedures of Van Soest, Robertson and Lewis (1991) and using an ANKOM200 Fiber Analyzer (filter bag technique; ANKOM Technology Corp., Fairport, NY, USA). Urine samples were lyophilized (Stellar Freeze Dryer, Millrock Technology, Kingston, NY, USA) to determine DM and then analyzed for N and GE.

The metabolism cages in the calorimetry room were fitted with a Lexan® (General Electric, New York, NY, USA) head box (41-cm width, 27-cm depth, and 92-cm height) to measure consumption of O₂ and production of CO₂ and CH₄ in an open-circuit respiration calorimetry system (Sable Systems International, North Las Vegas, NV, USA). The boxes included a removable drawer (23-cm height in the front, 15-cm height in the back closest to the animal, 40-cm width, and 28-cm depth) for providing feed and water with a head opening (30.5-cm wide and 55-cm high beginning at the top of the drawer). A ‘sock’ of Cordura® nylon (DuPont, Wilmington, DE, USA) attached to the opening of the head box fitted with a 25-cm long zipper was held snug to the neck with Velcro® (Velcro USA Inc., Manchester, NH, USA) and Elastikon™ ties (Johnson and Johnson, New Brunswick, NJ, USA). Operating procedures of the calorimetry system were similar to those of Puchala et al. (2007, 2009). Oxygen concentration was determined using a fuel cell FC-1B O₂ analyzer and CH₄ and CO₂ concentrations were measured with infrared analyzers (CA-1B and MA-1, respectively; Sable Systems International). Prior to gas exchange measurements, analyzers were calibrated with gases of known concentrations and ethanol burn tests were performed to verify complete recovery of O₂ and CO₂ produced with similar flow rates as during measurements.

Heat energy (HE) was based on the Brouwer (1965) equation without considering urinary N. Methane energy was estimated assuming 39.5388 kJ/l (Brouwer, 1965). Recovered energy (RE) was the difference between ME intake and HE. Heart rate (HR) was monitored as described by Puchala, Tovar-Luna, Sahlul, Freely and Goetsch (2009). Animals were fitted with 10 × 10 cm electrodes prepared from stretch conductive fabric (Less EMF, Albany, NY, USA), glued to ECG electrodes (VermedPerformancePlus, Bellows Falls, VT, USA), and attached to the chest slightly below the left elbow and behind the shoulder blade on the right side of the body. Electrodes were connected by ECG snap leads (Biocomnect, Sandiego, CA, USA) to T61 coded transmitters (Polar, Lake Success, NY, USA). Human S610 HR (Polar) monitors with wireless connection to the transmitters were used to collect HR data at 1-min intervals, and HR data were analyzed using Polar Precision Performance SW software.

2.3. Statistical analyses

For the baseline period with ad libitum intake of water by all animals, means, SEM, and minimum and maximum values are presented in Table 2. Although these animals had been used in a number of trials with similar conditions since the fall of 2015, feed and water intakes were lower when in metabolism cages in wk 4 than earlier. Hence, an analysis to compare intakes in wk 3 and 4 was conducted with a mixed effects model (Littell, Henry & Ammerman, 1998; SAS, 2013). Fixed effects were treatment, period, week, and treatment × week, with period × week as the repeated measure and animal as random and the subject. A similar analysis also was conducted with inclusion of all interactions involving period in the model. The model for data collected in wk 4 included treatment and period as fixed effects, with animal intake (CONT) and the other
random and the subject for the repeated measure of period. Intake of DM in g/day in wk 3 was analyzed with the same model as well. Different covariance structures were compared via Akaike’s Information Criterion, but values were lower for variance components or differences were not marked. Means were separated by least significant difference with a protected F test.

3. Results and discussion

3.1. Diet composition

The chemical composition of the diet (Table 1) was fairly similar to that of the same diet used by Hussein et al. (2020) and Tadesse et al., (2019a, Tadesse et al., 2019b, Tadesse et al., 2019c) in studies of the same project, but the CP concentration was slightly greater (19.4 vs. 17.3–18.2%). The NDF concentration of 33.6% was similar to that noted by Tadesse et al. (2019b); 34.2%) though lower than reported in other experiments (36.9, 37.7, and 42.4% in Hussein et al. (2020), Tadesse et al. (2019a), and Tadesse et al. (2019b), respectively).

3.2. Preliminary period data

There was appreciable variation in some measures of the 2-wk preliminary period (Table 2), an example being initial BW that ranged from 39.7 to 55.8 kg. A possible reason for relatively high variability is that the animals were derived from four areas of the USA with different climatic conditions. As described by Hussein et al. (2020), regions were the Midwest (portions of Iowa, Minnesota, Wisconsin, and Illinois), Northwest (primarily Oregon with one farm in southern Washington), Southeast (Florida), and central/eastern Texas.

3.3. Water and feed intake in wk 3 and 4

As noted earlier, the animals had been previously used in trials conducted in the same building under similar conditions; however, they had not been situated in metabolism cages. Though values in Table 3 differ from 39.7 to 55.8 kg. A possible reason for relatively high variability is that the animals were derived from four areas of the USA with different climatic conditions. As described by Hussein et al. (2020), regions were the Midwest (portions of Iowa, Minnesota, Wisconsin, and Illinois), Northwest (primarily Oregon with one farm in southern Washington), Southeast (Florida), and central/eastern Texas.

Table 2

| Item | Mean | SEM | Minimum | Maximum |
|------|------|-----|---------|---------|
| BW (kg) | 46.9 | 1.59 | 39.7 | 55.8 |
| After 1 wk | 48.8 | 1.78 | 40.8 | 59.6 |
| Final | 48.4 | 1.63 | 40.2 | 58.2 |
| Water intake | 3784 | 196.3 | 2488 | 4672 |
| % BW | 7.88 | 0.325 | 5.91 | 9.39 |
| DM intake | 3.43 | 0.140 | 2.48 | 4.02 |

Table 3

| Item | Ad libitum water intake | Restricted water intake | SEM | Week | SEM |
|------|-------------------------|-------------------------|-----|------|-----|
| Water intake | 3472 | 2565b | 2255b | 1699b | 179.3 |
| DM intake | 1116b | 853b | 47.0 |

\(^{a,b,c}\)Means within grouping without a common superscript letter differ (P < 0.05).

1 P of < 0.001, 0.841, <0.001, and 0.017 for treatment, period, week, and treatment × week, respectively.

2 P of 0.473, 0.303, < 0.001, and 0.924 for treatment, period, week, and treatment × week, respectively.

Table 4

| Item | Treatment | SEM | P value |
|------|-----------|-----|---------|
| BW (kg) | 50.5 | 49.1 | 2.05 | 0.001 |
| Water intake | 2556 | 1707 | 0.001 |
| % BW | 5.05 | 3.48 | 0.272 | <0.001 |
| OM | 3.10 | 2.25 | 0.218 | <0.001 |
| DM Intake | 1112 | 853a | 47.0 |

\(^1\) Heat energy:heart rate.
with the difference in water intake between wk 3 and 4 greater in period 1 than in period 2 (916 vs. 543 g/day). Nonetheless, in addition to the substantial difference between treatments in water intake in wk 4, presumably there also was carryover impact of the greater magnitude of difference in wk 2 and 3.

3.4. BW

In one sense, greater BW for CONT than for REST does not seem surprising because of less water intake by REST, but the magnitude of difference was not substantial (i.e., 1.4 kg, SED of 0.29). However, Hussein et al. (2020) noted greater BW in the fifth week of an experiment when drinking water availability was limited to 50% of earlier ad libitum intake of St. Croix from each of the four regions (differences of 1.7–2.1 kg), Dorper from two of the regions (differences of 2.2 and 2.5 kg), and Katahdin from one region (difference of 2.8 kg). Factors proposed as contributing to the differences include greater digestibility, greater digesta mass in the gastrointestinal tract, and a considerable ability to minimize water loss when availability was limited. These differences occurred despite lower DM intake for restricted than ad libitum water intake (average difference of 219, 258, and 101 g/day for Dorper, Katahdin, and St. Croix, respectively).

3.5. Intake

Water intake in g/day for REST averaged 33% less than for CONT in wk 4 (Table 4). There were no treatment effects on intake of DM or any of its constituents (P ≥ 0.443). Conversely, there have been many studies with small ruminants in which DM intake was decreased by drinking water restriction. Limiting water availability to Aardi does at 75 and 50% of ad libitum intake for 6 days decreased DM intake by 14 and 22%, respectively (Alamer, 2009). Mengistu et al. (2016) reported reductions in DM intake of 31 and 44% by Katahdin sheep, 22 and 34% by Boer goats, and 19 and 35% by Spanish goats when intake of water was decreased gradually by 10% from 100% to 50% and 40% of ad libitum intake, respectively. Offering water to Lacanu ewes at 80 or 60% of ad libitum intake for 4 wk decreased DM intake by 16 and 36%, respectively (Casamassima et al., 2016). Restricting access of Baluchi lambs to water low or high in total dissolved solids at 50% of ad libitum intake for 6 wk decreased DM intake by 40 and 42%, respectively (Vosooghi-Postindoz et al., 2018). But, there are other studies in which water restriction did not influence feed intake or impact was not marked. When Comisana ewes were offered water ad libitum versus at 80 or 60%, DM intake did not differ (Casamassima et al., 2008). Similarly, DM intake by crossbred German Fawn does was not altered by restricting water availability to 87 or 73% of ad libitum intake but declined by 13% when the level was 56% of ad libitum intake (Kaliber, Koluman & Silanikove, 2016). 3.6. Digestion

Digestibilities of DM (P = 0.037), OM (P = 0.038), energy (P = 0.034), and NDF (P = 0.021) were greater for REST vs. CONT, and there was a tendency for a difference in CP digestibility (P = 0.078; Table 4). Magnitudes of difference were 3.9 (6.1%), 3.9 (6.0%), 4.1 (6.6%), 3.0 (4.4%), and 8.2 (22.3%) percentage units for DM, OM, GE, CP, and NDF, respectively. However, because levels of intake of all constituents were numerically greater for CONT than for REST, there were no differences in intake of digested DM, OM, energy, CP, or NDF (P ≥ 0.493).

Greater digestibilities for REST than for CONT was most likely the result of a slower rate of digesta passage and longer retention time of digesta in the gastrointestinal tract (Chedid et al., 2014; Ghassemi Nejad et al., 2014; Silanikove, 2000). With similar DM intake between treatments in the present experiment, a slower passage rate may have been directly influenced by the quantity of water consumed (Kaske & Groth, 1997). The passage rate of fluid through the gastrointestinal tract decreases as an adaptation mechanism when water availability is restricted for use of the rumen as a water reservoir and to increase retention in the body (Silanikove, 1994). Similar to findings of the present experiment, Silanikove (1985) reported that restricting water availability to desert and non-desert goats from ad libitum access each day to every 3 days decreased intake of alfalfa hay DM by 12 and 40 g/kg BW0.75 and increased DM digestibility from 71.6 to 74.1% and 66.8 to 71.2%, respectively. Vosooghi-Postindoz et al. (2018) also found that a 50% restriction level decreased intake of a 40% alfalfa hay diet by Baluchi lambs and increased digestibilities of OM, NDF, acid detergent fiber (ADF), and CP. In contrast, Freudenberger & Hume (1993) showed that digestibilities of DM and ADF did not increase when mature goats having free access to alfalfa hay had water availability restricted to 57% of ad libitum consumption. Similar to findings of the present experiment, Tadesse et al. (2019c) noted a much greater effect of restricted feed intake on digestibility of NDF than other DM constituents in Katahdin wethers. A number of studies were cited to explain this finding, most importantly no or low NDF in endogenous fecal DM and greater depressions in digestibility with diets containing concentrate compared with ones primarily of forage and diets small vs. large in particle size (ARC, 1990; Doreau et al., 2003; Freity et al., 1995; Grimaud et al., 1998, 1999; Leite et al., 2015; SCA, 1990). Urinary N tended (P = 0.066) to be lower for REST than for CONT (2 g/day and 13.7%, and urinary energy was less for REST (P = 0.023; 0.10 MJ/day and 16.1%; Table 4). Although, again, because of numerically greater N intake for CONT, N balance did not differ between treatments (P = 0.793). But, N balance values suggest an under-estimation of excretion. For example, with assumed protein concentrations in accreted tissue of 10, 15, and 20%, average predicted ADG values are unreasonably high, 256, 171, and 128 g, respectively. This may reflect some volatilization of ammonia from urine, since digestibilities of CP were not greatly different than expected based on true protein digestibility and metabolic fecal CP estimated by Moore et al. (2004) for goats (i.e., 88% and 2.67% of DM intake, respectively; 74.2% CP) and summarized by Preston (2011) for sheep (i.e., 90% and 3%, respectively; 74.5%). Methane energy was numerically greater for REST than for CONT in MJ/day (0.13 MJ/day, P = 0.213) and as a percentage of gross energy intake (1.03 percentage units, P = 0.151; Table 4). These findings are in line with greater NDF digestibility for REST, which may have been accompanied by an increased acetate to propionate ratio. Even though the magnitude of difference between treatments in ME intake as a percentage of gross energy intake (3.5 percentage units and 6.6%; Table 4) was similar to that for energy digestibility, the difference was not significant (P = 0.170) because of increased variability associated with the additional considerations of urinary and methane energy. Likewise, there were no treatment differences in ME intake in MJ/day or kJ/kg BW0.75 or as a percentage of intake of digested energy (P ≥ 0.665).

3.8. HE, RE, and hr

Heat energy in MJ/day and kJ/kg BW0.75 was similar between treatments (P ≥ 0.580), as was also true for RE and HR (P = 0.824 and 0.706, respectively; Table 4). Likewise, the ratio of HE to HR, often measured so that HR in free-moving settings can be used as an indirect estimate of HE (Goetsch et al., 2017; Keli et al., 2017; Silva, Puchala, Gipson & Sahlu & Goetsch, 2018), was similar between treatments (P = 0.906).
Acknowledgements

This project was supported by the USDA National Institute of Food and Agriculture (NIFA), 1890 Institution Capacity Building Grant Program Project OKLUGOETSCH2013 (Accession Number 1000926) and the USDA NIFA Evans-Allen Project OKLUSAHLU2017 (Accession Number 1012650).

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