

The influence of high-nitrogen forages on the voluntary feed intake of sheep^{1,2}

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ABSTRACT: The objective of this research was to examine the effect of high concentrations of nonprotein nitrogen (NPN) on the voluntary food intake of sheep fed high-quality grasses. Wether lambs (n = 6 per treatment) were fed dried switchgrass (*Panicum virgatum* L.; Exp. 1) or dried tall fescue (*Festuca arundinacea* Schreb.; Exp. 2). In both experiments, urea was added to the dried forage at 0 (control), 12, or 24 g of N/kg of DM to increase the NPN concentration. Acid detergent fiber concentrations were 305 g/kg of DM in both experiments, although DM digestibility was 663 and 618 g/kg of DM in Exp. 1 and Exp. 2, respectively. Voluntary feed intake of the control forage was 28.2 and 19.1 g/kg of BW in Exp. 1 and Exp. 2, respectively, and decreased for the high-urea treatments to 25.2 and 16.2 g/kg of BW in Exp. 1 ($P = 0.07$) and Exp 2 ($P = 0.03$), respectively. Total feed N concentrations increased

from 29.5 g to 45.7 g of N/kg of DM in Exp. 1 ($P < 0.01$) and from 28.4 to 55.9 g of N/kg of DM in Exp. 2 ($P < 0.01$). Nonprotein N concentrations increased from 28.3 to 53.8% of the total N in switchgrass diets (Exp. 1; $P < 0.01$), and from 26.4 to 64.0% in tall fescue diets (Exp. 2; $P < 0.01$). Plasma urea concentrations of the lambs increased from 3.1 to 6.6 mM (Exp. 1; $P < 0.01$) and from 2.9 to 5.8 mM (Exp. 2; $P < 0.01$) as the amount of urea added to the diets increased. These changes resulted in an increase in plasma osmolality from 298 to 307 mOsm/kg (Exp. 1; $P = 0.04$), and from 299 to 307 mOsm/kg (Exp. 2; $P = 0.06$). Increasing feed N and NPN concentrations through the addition of urea caused a significant decrease in the voluntary feed intake of sheep fed tall fescue and switchgrass. These responses showed no significant cause-and-effect relationship between voluntary feed intake, plasma urea concentrations, and plasma osmolality.

Key Words: Forage, Intake, Nitrogen, Sheep, Urea

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Introduction

The effects of high protein concentrations on voluntary feed intake have not been well investigated. It is generally thought that high protein levels in forage are not a problem because they are often only achieved in legume, which are associated with a high level of voluntary feed intake. Some pasture grasses in temper-

ate regions, however, can have high protein concentrations when fertilized with N (Minson, 1990).

Animals exhibit preferences that reduce food intake in an attempt to balance the nutrients supplied by the diet. This has been shown for protein, for example, as Kyriazakis and Oldham (1993) measured peak voluntary feed intake at between 141 and 172 g/kg of DM CP when feeding lambs with paired choices of diets ranging from 78 to 235 g/kg of DM CP.

Regulation of food intake is a complex process and is under central nervous system control (Provenza, 1995). Blood osmolality may be one metabolic signal of importance linking dietary effects to food intake (Grovmum, 1995). Feedback through decreased rumen motility (Wever et al., 1991; Grovmum and Wever, 1992) and reduced saliva production (Grovmum, 1992) has been observed as plasma osmolality increased.

The objective of these experiments was to examine the role of dietary CP concentrations on food intake of sheep fed two forages: a C4 grass, switchgrass, and a C3 grass, tall fescue. The experiments also tested for a correlation between feed intake and plasma osmolality.

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Materials and Methods

Two experiments were conducted during June 1995 and February 1996. The experimental design was a randomized complete block with three treatments in two blocks with three replications nested in each block. The treatments were untreated hay (control), hay plus 12 g of N/kg of DM as urea (Low Urea), and hay plus 24 g of N/kg of DM as urea (High Urea). The hay used in Exp. 1 was switchgrass (*Panicum virgatum* L. var. Kanlow), and in Exp. 2, tall fescue was used (*Festuca arundinacea* Schreb. var. AU Triumph). In each experiment, 18 4-mo-old castrated lambs (*Ovis aries*) were assigned in three replicates to each of two controlled environment rooms (blocks) in individual metabolism crates. In Exp. 1, Katahdin, Katahdin × Barbado, and Dorset × Barbado lambs were used, and in Exp. 2, Katahdin and Dorset × Barbado lambs were used. In both experiments, lamb breeds were balanced across all treatments but not across both rooms in Exp. 1.

Forages

Switchgrass, used in Exp. 1, was obtained from a 20-yr-old stand located at the North Carolina State University Reedy Creek Road Field Laboratory (Raleigh). Forage residue from the previous fall was removed by burning in March 1995. The stand received 80 kg of N/ha as ammonium nitrate on April 5, 1995. On May 5, 1995, the primary growth of approximately 4,000 kg of DM/ha was harvested before heading by direct flailing to a 15-cm stubble, leaving a residual of approximately 1,000 kg of DM/ha. The forage was then placed in a drying barn (Burns et al., 1997) to a depth of 1 m, forced-air dried at 60°C (at inlet) for 36 h, and then returned to an ambient temperature (mean approx. 20°C) for the following 3 d. The resulting hay was baled directly from the drier into conventional square bales of approximately 15 kg and stored indoors until the beginning of the trial on June 5, 1995.

Tall fescue used in Exp. 2 was obtained from a 4-yr-old stand (sown as endophyte free) located at the North Carolina State University Reedy Creek Road Field Laboratory. Forage from the area, pastured the previous 2 yr, was removed (April 17, 1995) when approximately 30% of the culms were headed, leaving a residue of approximately 1,000 kg of DM/ha. The subsequent vegetative regrowth served as the experimental forage and was direct-flail harvested on June 3, 1995, when regrowth accumulated approximately 2,800 kg of DM/ha. The forage was dried as noted for Exp. 1, and bales were stored indoors until the beginning of the trial on January 29, 1996.

Treatments

In both Exp. 1 and 2, the hay was spread uniformly to a depth of approximately 10 cm on a concrete floor in preparation for treatment. The N treatments were

applied to batches of the forage sufficient for 2 to 3 d of feeding at any one time. The urea was applied at a concentration of 173 and 348 g of urea/L for the Low- and High-Urea treatments, respectively, in 150 mL of water/kg of feed, and forage was allowed to air-dry before feeding. The control was sprayed with 150 mL of water/kg of dried grass and air-dried before feeding.

Animals and Feeding

Lambs averaged 28.3 (±2.6) kg in Exp. 1 and 26.1 (±1.5) kg in Exp. 2. Lambs grazing on an all-grass pasture were brought indoors and initially fed the control hay along with a ration of 0.45-kg alfalfa pellets for a 6-d pretrial period. On d 1 of the experiments, lambs were treated for internal parasites with fenbendazole at 10 mL/kg BW (Hoechst Roussel Vet, Warren, NJ) and placed into metabolism crates. An adjustment period of 7 d to the experimental diets was followed by a 7-d intake period. Lambs were then fitted with fecal collection bags and adapted to bags for 5 d before a 6-d digestion period when intake data, feces, and urine were collected.

The lambs in both experiments were fed at 120% of the previous day's intake starting at 1.0 kg/d of dried grass. Feeding occurred at 0900 and 1530 daily with 1/3 and 2/3 of the DM fed at each time, respectively. Orts were removed, weighed, and sampled each morning before feeding. Constant access to water and mineralized salt blocks (consisting of salt and oxides of Zn, Mn, Fe, Cu, carbonates of Fe and Co, calcium periodate, and mineral oil, and containing not less or not more than 970 and 985 g/kg of NaCl and 0.35 and 0.45 g/kg of Ca, and not less than 3.5 g/kg of Zn, 2.8 g/kg of Mn, 1.7 g/kg of Fe, 0.07 g/kg of I, and 0.07 g/kg of Co) was provided to all lambs. During Exp. 1, one Dorset × Barbado lamb was diagnosed as being infected with coccidia on d 9, and consequently, the two other Dorset × Barbado lambs (one per treatment) were given the coccidiostat Corid (9.6% amprolium, Merial Ltd., Duluth, GA) per label recommendations over the following 4 d. No other lambs appeared to be affected. Water delivery to one lamb (High Urea) was faulty on 1 d during Exp. 1 and compromised its intake data. The intake data for that lamb on that day and the following day were removed from analysis. Lambs in Exp. 1 were weighed on d 4, 11, 18, and 23, and lambs in Exp. 2 were weighed on d 4, 10, 21, and 25. Lambs were weighed between 0730 and 0830 just before feeding in both experiments.

Sampling

The voluntary food intake of each lamb was calculated from the dry weight offered and the dry weight of the orts each day. The average daily DMI over the 7-d intake period was used for analysis. Representative samples of the feed offered and orts for each lamb were collected daily during the intake and digestion periods. The daily samples were pooled, mixed thoroughly, and

then subsamples of both offered feed and orts for each animal from both the intake and digestion periods were oven-dried in paper bags at 50°C for 48 h. All samples were ground in a Wiley mill to pass a 1-mm screen.

Feces were collected daily, weighed, and a subsample of approximately 100 g was weighed and dried for 48 h at 55°C to estimate DM concentration. A composite sample, weighted by daily fecal output, was made from the oven-dried samples for each lamb and was used for N and fiber analysis after grinding.

Urine was sampled between 1000 and 1100 each morning during the 6-d digestion period. The total weight was recorded and a 5% sample taken each day. Samples were bulked together for each lamb and stored at -18°C. Each day, 50 mL of concentrated HCl (37.2%) was placed in each bucket before the next collection. Samples were thoroughly mixed, and a subsample of approximately 20 mL was taken for total N determination.

Blood samples were taken from each lamb on d 14, 17, and 22 of Exp. 1 and on d 15, 20, and 22 of Exp. 2 by venipuncture of the jugular vein in 10-mL tubes treated with sodium heparin. Samples were taken just before the morning feeding and again 2 h after feeding. Some feeding activity was evident, but the disappearance of the offered feed was not measured. Samples were centrifuged in a refrigerated centrifuge at 850 × g for 30 min within 30 min of sampling, and the plasma was frozen at -18°C until tested for plasma urea concentration and osmolality.

Chemical Analysis

Fiber was analyzed with an ANKOM 200 Fiber Analyzer (Ankom Technology Corp., Fairport, NY), sequentially determining the NDF and ADF concentrations according to Van Soest and Robertson (1980).

Total N of offered feed, orts, and feces was assayed by the Kjeldahl procedure (AOAC, 1990). The N components of offered feed were fractionated according to Licitra et al. (1996). The true protein was precipitated using sodium tungstate and analyzed. Nonprotein N was then calculated as the difference between total N and precipitated true protein N. Acid detergent insoluble N was determined by removing and weighing the ADF residue from the synthetic bags following the sequential NDF and ADF analyses and assayed for the remaining N using the Kjeldahl procedure.

Plasma urea concentration was tested by colorimetric assay of ammonia after the urea was hydrolyzed by urease (Procedure 640, Sigma Diagnostics, St. Louis, MO). Plasma osmolality was measured using the freezing point determination method (Osmometre A semi-automatic osmometer, Precision Systems Inc., Mattick, MA).

Statistical Analysis

Data were analyzed using the PROC GLM procedure of SAS (SAS Inst., Inc., Cary, NC). The general form of the model used was:

$$Y_{ijk} = \mu + R_i + Br_j + T_k + e_{ijk} \text{ (Model 1)}$$

For testing, the independent variables of room (R) and breed (Br) were considered random, whereas treatment (T) was considered fixed. Polynomial contrasts were used to test the effects of urea addition. Voluntary feed intake, feed N, and feed fiber results were averaged over both the intake and digestion periods, but digestibility and N balance information was calculated only from the digestion period. Room and breed effects and interactions with treatment were not significant ($P > 0.05$) and are not given any further consideration. The final analysis was conducted using all six lambs per treatment as replicates. A comparison of the pre- and postprandial plasma osmolality in Exp. 1 was obtained using a repeated-measures analysis within PROC GLM of SAS. Loss of original data for pre- and postprandial plasma osmolality from the tall fescue prevented statistical comparison of these data.

Regression analysis was used to determine the effect of plasma osmolality on intake using PROC GLM with the model $Y_{ijk} = b_0 + R_i + Br_{j(i)} + b_1 O_{ijk} + e_{ijk}$ (Model 2). Intake (Y) was predicted and the model included the effects of room (R), breed (Br) and osmolality (O).

Results

Feed Nitrogen and Fiber Fractions

The N concentration of the control switchgrass in Exp. 1 was relatively high (Table 1). Nonprotein N accounted for 28.3% and ADIN accounted for 4.3% of the total N. Spraying urea on the control forage resulted in a linear increase in total and nonprotein N concentrations ($P < 0.01$, Table 1). True protein and ADIN were unaffected. The nonprotein N fraction accounted for 41.7 and 53.8% of the total N for the Low- and High-Urea treatments, respectively.

Similarly, the N concentration of the control tall fescue in Exp. 2 was relatively high (Table 1). Nonprotein N accounted for 26.4% of the total N and ADIN made up 3.0% of the total N (Table 1). As in Exp. 1, adding urea elicited a linear increase in the total and nonprotein N concentrations ($P < 0.01$, Table 1). The true protein concentrations of the treatments receiving urea were lower than the control. Nitrogen recovery, expressed as the percentage of the N added as urea present on the forage analyzed, averaged only 67% in Exp. 1, but averaged 106% in Exp. 2. All added N that was recovered was in the nonprotein N fraction (Table 1).

The average NDF and ADF concentrations of the untreated switchgrass were 674 g/kg of DM and 305 g/kg of DM, respectively (Table 1). The fiber profile was not affected by the addition of urea to switchgrass (Table 1). The NDF and ADF concentrations of the control tall fescue were 635 g/kg of DM and 305 g/kg of DM, respectively, while treatment with urea caused a linear decline in both NDF and ADF concentrations ($P < 0.01$, Table 1).

Table 1. Nitrogen and fiber fractions in switchgrass and tall fescue forage and after treatment with urea at 12 or 24 g of N/kg of DM

Item	Treatments			Probability for contrasts		SE ^c
	Control	Low urea ^a	High urea ^b	Linear	Quadratic	
Exp. 1: Switchgrass						
N fractions, g/kg of DM						
Total N	29.5 ^d	37.4	45.8	<0.01	0.79	0.76
True protein N	21.1	21.7	21.1	0.93	0.14	0.30
Nonprotein N	8.4	15.7	24.7	<0.01	0.38	0.76
ADIN	1.3	1.3	1.4	0.17	0.50	0.06
Total N recovery, %		66	68			
Fiber fractions, g/kg of DM						
NDF	674	672	667	0.22	0.79	4.99
ADF	305	305	300	0.11	0.47	2.28
Exp. 2: Tall fescue						
N fractions, g/kg of DM						
Total N	28.4 ^d	40.2	55.9	<0.01	0.04	0.70
True protein N	20.9	20.6	20.0	<0.01	0.52	0.16
Nonprotein N	7.5	19.6	35.9	<0.01	0.02	0.63
ADIN	0.9	0.8	0.8	0.09	0.61	0.03
Total N recovery, %		98	114			
Fiber fractions, g/kg of DM						
NDF	635	621	598	<0.01	0.27	3.09
ADF	305	301	290	0.01	0.06	1.49

^aUrea applied at 12 g N/kg DM.

^bUrea applied at 24 g N/kg DM.

^cSE = $\sqrt{[\text{mean square error (Model 1)/6}]}$.

^dEach value is the mean of six observations (feed offered each animal).

Intake, Apparent Digestibility, and Nitrogen Balance

Lamb BW did not change throughout Exp. 1 or Exp. 2 and was similar for each treatment (Table 2). Adding urea to the control forage did not alter voluntary food intake in Exp. 1 ($P = 0.07$), but did cause a linear decrease in voluntary food intake in Exp. 2 ($P = 0.03$). Nitrogen intake (g/kg BW) increased in Exp. 1 with switchgrass ($P = 0.04$) and in Exp. 2 with tall fescue ($P < 0.01$, Table 2). The apparent digestibility of DM, NDF, and ADF was unaffected by adding urea to the control forage in both experiments, although it was higher in Exp 1 than in Exp. 2 (Table 2). The apparent N digestibility increased linearly with the addition of urea in both Exp. 1 and Exp. 2 ($P < 0.01$, Table 2).

The increase in N intake (g/d) was significant in both experiments ($P < 0.04$, Table 2). Increasing N intake resulted in a linear increase in urinary N excretion in both experiments ($P < 0.01$, Table 2). Consequently, N retention was significantly altered in Exp. 1 ($P = 0.02$) but not in Exp. 2 ($P = 0.83$).

Plasma Urea Nitrogen and Plasma Osmolality

The data were averaged over time and day of sampling before analysis. Average plasma urea concentrations in both the switchgrass and tall fescue experiments increased linearly ($P < 0.01$, Table 3) with the addition of urea to the control forage. Average blood plasma osmolality also increased linearly ($P < 0.04$ Exp. 1; $P < 0.06$ Exp. 2; Table 3) in sheep fed switchgrass

and tall fescue treated with urea. There was no significant ($P = 0.61$, Table 3) difference between pre- and postprandial plasma osmolality when measured during the switchgrass experiment. The relationship between plasma osmolality and DMI was not significant (Exp. 1, $P = 0.62$; Exp. 2, $P = 0.21$).

Discussion

Urea additions were successful in changing feed N concentrations from 29.5 g of N/kg of DM in the switchgrass control forage to 45.7 g of N/kg of DM in the High-Urea treatment. The N concentrations of the forage in the tall fescue experiment ranged from 28.4 g of N/kg of DM in the control to 55.9 g of N/kg of DM in the High-Urea treatment. Within this framework, the nonprotein N levels ranged from 26 to 64% of the total N pool, providing a good platform to test the hypothesis that high levels of rapidly available N may cause a decline in voluntary food intake. The use of urea in the switchgrass experiment gave a smaller range of both total N and nonprotein N than in the tall fescue experiment because of the lower recovery of the applied N, although both experiments had a wide range. Lower recovery in the switchgrass experiment may have been due to hot and humid conditions, which slowed drying of the hay after urea treatment. This could have resulted in some volatilization of the applied urea during the drying process. Minson (1990) summarized a large number of data sets from the literature to show that

Table 2. Daily voluntary feed intake and nitrogen intake, and the apparent digestibility of dry matter, nitrogen, and fiber fractions of switchgrass and tall fescue altered by additions of urea

Item	Treatments			Probability for contrasts		SE ^c
	Control	Low urea ^a	High urea ^b	Linear	Quadratic	
Exp. 1: Switchgrass						
Sheep BW, kg	30.8 ^d	26.2	28.0	0.44	0.20	1.94
Feed intake, g/kg of BW	28.2	28.5	25.2	0.07	0.29	1.64
N intake, g/kg of BW	0.88	1.11	1.18	0.04	0.50	0.09
Diet digestibility, g/kg of DM						
DM	667	667	655	0.62	0.78	16.2
NDF	686	688	680	0.86	0.81	15.4
ADF	669	668	654	0.73	0.67	16.5
N	740	789	823	<0.01	0.75	13.2
N balance, g/d						
N intake	26.4	28.6	33.2	0.04	0.69	2.55
N in feces	6.9	6.5	5.9	0.14	0.90	0.53
N in urine	9.7	14.1	22.9	<0.01	0.25	1.46
N retention	9.8	8.0	4.4	0.02	0.73	1.86
Exp. 2: Tall fescue						
Sheep BW, kg	26.2 ^d	27.5	24.7	0.33	0.14	1.09
Feed intake, g/kg of BW	19.1	18.6	16.2	0.03	0.46	1.05
N intake, g/kg of BW	0.61	0.76	1.00	<0.01	0.58	0.07
Diet digestibility, g/kg of DM						
DM	619	616	618	0.96	0.86	9.5
NDF	622	633	603	0.25	0.14	10.1
ADF	620	617	621	0.21	0.06	10.5
N	677	734	813	<0.01	0.21	6.9
N balance, g/d						
N intake	15.8 ^d	20.7	24.6	<0.01	0.82	1.72
N in feces	5.1	5.4	4.6	0.39	0.24	0.41
N in urine	8.0	14.7	17.0	<0.01	0.05	0.84
N retention	2.7	0.6	3.0	0.83	0.12	1.15

^aUrea applied at 12 g of N/kg of DM.^bUrea applied at 24 g of N/kg of DM.^cSE = $\sqrt{[\text{mean square error (Model 1)/6}]}$.^dEach value is the mean of six animals.

the average CP concentration was 21 g of N/kg of DM in temperate grasses, and 16 g of N/kg of DM in tropical grasses. A significant number of reports ranged up to 40 g of N/kg of DM for both temperate and tropical grasses, whereas some studies measured up to 48 g of

N/kg of DM. The results obtained in this study covered the upper range of CP levels found in forages. The decline in intake was evident in both experiments though greater in lambs fed tall fescue. This reflects the trend measured by Kyriazakis and Oldham (1993), who also

Table 3. Plasma urea concentrations and plasma osmolality in sheep fed switchgrass or tall fescue altered by additions of urea

Item	Treatments			Probability for contrasts		SE ^c
	Control	Low urea ^a	High urea ^b	Linear	Quadratic	
Exp. 1: Switchgrass						
Plasma urea, mM	3.13 ^d	5.58	6.64	0.01	0.23	0.37
Plasma osmolality, mOsm/kg	298	302	307	0.04	0.81	1.8
Preprandial	298	303	308	0.01	0.93	0.93
2 h postprandial	299	304	307	0.01	0.54	1.03
Exp. 2: Tall fescue						
Plasma urea, mM	2.91 ^d	4.41	5.81	0.01	0.90	0.32
Plasma osmolality, mOsm/kg	299	303	307	0.06	0.96	2.0

^aUrea applied at 12 g of N/kg of DM.^bUrea applied at 24 g of N/kg of DM.^cSE = $\sqrt{[\text{mean square error (Model 2)/6}]}$.^dEach value is the mean of six animals.

found lower intakes at high feed N concentrations. This was not the case when Kyriazakis and Oldham (1993) added urea to increase N concentrations, although concentrations were only increased to approximately 38 g/kg of DM. The difference between the two diets may be related to the acceptance of the diet, or to variations in palatability caused by the addition of the urea.

Nitrogen retention by the lambs was relatively high in both the switchgrass and tall fescue experiments. The N intake required for a 30-kg lamb at maintenance is approximately 14 g of N/d, and 30 g of N/d when growing at 225 g/d (NRC, 1985). The total N intake of the lambs in the switchgrass experiment was between 26 and 33 g/d, sufficient to support a growth rate of 200 to 250 g/d. However, the NE intake, calculated from the digestibility data using NRC (1985) guidelines, ranged between 1,050 and 1,320 kcal/d, and should support gains of between 60 and 90 g/d (NRC, 1985). A gain of this size would suggest a N retention requirement of approximately 3 g/d, whereas N retention was between 4.4 and 9.8 g/d. Lambs fed the control diet in the tall fescue experiment had an N intake of 15.8 g/d and a NE intake of 770 kcal/d. Lambs fed the High-Urea diet had an N intake of 24.6 g/d and a NE intake of 620 kcal/d. Thus, the control diet had enough N for maintenance and an energy intake to support growth at 20 g/d. Lambs on the High-Urea diet had sufficient N to support growth at approximately 150 g/d, but only consumed enough energy for maintenance. The N retention values measured in the tall fescue experiment were relatively high compared with the slow calculated growth rate of the lambs.

Nitrogen retention decreased with increasing feed N concentration in the switchgrass experiment, when intake was not significantly affected, but was not significantly affected in the tall fescue experiment when intake declined. This presents an anomaly as the reverse was expected. These N retention values may be an artifact of the calculation of N retention by difference, with any lost N during the measurement process being allocated to this pool, and may not be an accurate record of true N retention.

The plasma osmolalities of control sheep measured in these two studies averaged 298 and 299 mOsm/kg. These were within the range of 280 to 300 mOsm/kg found in many other studies (e.g., Warner and Stacy, 1965; Froetschel et al., 1987). The average increase in plasma osmolality measured in this study was approximately 8 to 9 mOsm/kg, with increasing N intake as urea. This increase was similar in both experiments while plasma urea increased by 3.5 and 2.9 mM in Exp. 1 and 2, respectively. A direct link between plasma urea and osmolality seems unlikely, but the increase in dietary urea concentration may have also influenced plasma osmolality by increasing rumen osmolality and pH (Owens and Zinn, 1988), resulting in an increase in water flux from the blood to the rumen, thus increasing plasma osmolality.

Pre- and postprandial results from the switchgrass experiment showed no change by 2 h after feeding. Stevens (1997) recorded plasma osmolality before morning feeding and at 2.5 and 5 h after feeding. Plasma osmolality before feeding and 2.5 h after feeding fresh switchgrass was similar and then increased 7 mOsm/kg by 5 h after feeding. It is possible that the timing of the sampling did not coincide with a major feeding event, or that the changes in plasma osmolality did not occur in the measured time frame. The continual access to forage may have meant that the rumen was relatively full from an early-morning feeding before presentation of new feed at 0900, and so a significant feeding event may not have occurred during the 2 h after the first measurement.

An increase in plasma osmolality of approximately 3 mOsm/kg was reported by Grovum (1995) in food-deprived sheep when offered alfalfa pellets. He measured a significant reduction in intake when this plasma osmolality change was associated with infusions to the rumen but none when associated with infusions to the abomasum. Inhibition of both salivation and rumination by increasing plasma osmolality by up to 30 mOsm/kg has been reported (Wever et al., 1991; Grovum, 1992; Grovum and Wever, 1992). The current study reported plasma osmolality changes of 8 to 9 mOsm/kg induced by diet in both experiments but with no direct effect on intake apparent. This suggests that osmolality may not be directly involved in intake control.

Plasma urea levels ranged from approximately 2.50 to 7.49 mM in individual sheep fed switchgrass, and from approximately 2.00 to 5.49 mM in sheep fed tall fescue. In both experiments, the increases in plasma urea were related to increases in the N intake of the lambs rather than the N concentration of the feed. An increase in plasma urea has long been associated with an increase in N intake (Torrell et al., 1974) and with the ratio of N and energy intakes (Huntington, 1980). The range of values generated in these experiments was greater than that observed in normal production systems, which are between 1.67 and 4.16 mM in sheep (Mukhoty et al., 1969; Torrell et al., 1974), dairy cows (Morbeck et al., 1991; Hayes et al., 1996), and beef cattle (Huntington, 1980; Yambayamba et al., 1996).

The models for effects of oversupply of nutrients outlined by Forbes (1995) and Illius and Jessop (1996) describe a peak intake followed by a plateau of lower intake before toxic effects lead to a decline in intake. It would seem that the plateau, while broad for dietary N, is related to the digestibility of the diet with animals fed high digestibility diets more tolerant of high nonprotein N concentrations. Preference studies, which have shown the choice of moderate-N diets, often fail to report or measure the total daily food intake, so conclusions are less clear about effects on overall intake. Sinclair et al. (1993) fed diets of rapidly or slowly available N and carbohydrate in several combinations and monitored the effect on voluntary food intake. Voluntary

food intake did not vary with diet, and they concluded that the impact of urea recycling and continual carbohydrate and protein digestion in a diet eaten ad libitum negated the effects of meal-by-meal imbalances. The high-N diets fed in these studies had a depressing effect on DMI only in the tall fescue study, and the evidence suggests that N concentration of the diet has a minor role in regulating voluntary feed intake.

Implications

These experiments created a range of dietary N concentrations and blood plasma osmolalities occurring at the high end of that found in normal foraging situations and animal physiological states. These levels of nonprotein nitrogen are not common in forage, so other factors, such as rate of digestion, water-soluble carbohydrates, and hedonistic properties of forages, should be the focus of future research to explain variation in forage intake. Forage managers will still need to consider factors such as nitrate poisoning, and the metabolic cost of excreting surplus N when determining the effects of forage N concentrations. Changes in plasma osmolality seem unlikely to be a signal that controls voluntary food intake under normal physiological conditions.

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