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Salivary Secretion Volume Related Ruminal Distension and Suppression of Dry Forage Intake in Large-type Goats

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ABSTRACT : Two experiments under sham feeding conditions were conducted to determine whether or not ruminal distension brought about by feed boluses entering the rumen is a factor in the marked suppression of feed intake after 40 min of feeding. In experiment 1, a comparison was made between the intraruminal insertion of a water filled balloon (RIB) treatment and normal control (non-insertion of a balloon, NIB). In experiment 2, saliva lost due to sham feeding conditions was replenished via an intraruminal infusion of iso-osmotic artificial saliva. A comparison of dry forage intake was then conducted between the intraruminal replenishment of iso-osmotic artificial saliva and insertion of a balloon (RRIAS-RIB) treatment, and the intraruminal replenishment of iso-osmotic artificial saliva and non-insertion of a balloon (RRIAS-NIB) control. In experiment 1, eating rates in the RIB treatment 30 min after the commencement of feeding tended to be lower than those in the NIB control. In comparison with the NIB control, cumulative dry forage intake in the RIB treatment was 29.7% less ($p<0.05$) upon conclusion of the 2 h feeding period. The secreted saliva weight in the NIB control and the RIB treatment during the 2 h feeding period was 53.2% and 60.9% total weight of the boluses, respectively. In experiment 2, eating rates in the RRIAS-RIB treatment 30 min after the commencement of feeding was significantly lower ($p<0.05$) than those in the RRIAS-NIB control. Cumulative dry forage intake in the RRIAS-RIB treatment was a significant 45.5% less ($p<0.05$) compared with that in the RRIAS-NIB control upon conclusion of the 2 h feeding period. The secreted saliva weight in the RRIAS-NIB control and the RRIAS-RIB treatment during the 2 h feeding period was 54.1% and 64.2% total weight of the boluses, respectively. The level of decrease in dry forage intake in the RRIAS-RIB treatment of experiment 2 was larger than that in the RIB treatment of experiment 1. In the present experiments, due to the sham feeding conditions, the increases in osmolality of ruminal fluid and plasma, and a decrease in ruminal fluid pH which are normally associated with feeding were not observed. The results indicate that the marked decrease in feed intake observed in the second hour of the 2 h feeding period is related to ruminal distension caused by the feed consumed and the copious amount of saliva secreted during dry forage feeding. (**Key Words :** Salivary Secretion Volume, Ruminal Distension, Dry Forage Intake Suppression, Large-type Goats)

INTRODUCTION

Ruminants consume an enormous amount of hay (lower energy content) in short time. Saliva in large-type goats is secreted in large volumes during the first hour after the commencement of dry forage feeding (Sunagawa et al., 2007). Saliva acts as a lubricant in the mouth and esophagus and assists in the mastication and swallowing of dry forage. Saliva also acts as an alkali and serves to buffer the decrease in the pH of rumen fluid due to the volatile fatty acid production of microbial fermentation in the rumen. In this way, saliva plays an important role in eating and homeostatic regulation of acid-base balance in rumen fluid. On the other hand, Thang et al. (2010) has found that in esophageal-fistulated large-type goats fed dry forage twice daily, the amount of salivary secretion was larger than dry forage intake. Therefore, it is thought that salivary secretion volume during dry forage feeding may work in conjunction with consumed feed to form the ruminal load responsible for ruminal distension.

Campling and Balch (1961) reported that feed intake was decreased when a balloon was inserted into the rumen and inflated with water in cows fed on hay and silage. On the other hand, Grovum (1995) reported that the increase in ruminal fluid osmolality by intraruminal infusion of the same dose of hyperosmotic NaCl, polyethylene glycol-400 (PEG), sodium acetate or sodium propionate resulted in the same-sized decreases in alfalfa pellet intake by sheep. However, Anil et al. (1993) reported that in cows, if a balloon inserted into the rumen was not filled with enough

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water or if the increase in ruminal fluid osmolality was insufficient, the amount of dry forage or silage intake was not decreased. In experiments (Campling and Balch, 1961; Anil et al., 1993) in which a balloon was inserted into the rumen and filled with water, it is unclear as to how the volume of water is determined and whether the level of ruminal distension is within the physiological range. Consequently, it is not clear whether the ruminal distension produced by feed boluses entering the rumen during dry forage feeding was a physiological suppressing factor on dry forage intake in ruminants.

In large-type goats fed on dry forage for 2 h twice daily, eating rates rapidly decreased in the first 30 or 40 min of feeding and were subsequently reduced to very low rates for the remainder of the 2 h feeding period (Sunagawa et al., 2002, 2003, 2007). Sunagawa et al. (2002, 2007) reported that ruminal infusion of parotid saliva and the intravenous infusion of artificial saliva reduced dry forage intake suppression caused by a reduction in circulating plasma volume which is a result of increased salivary secretion during the initial stages of dry forage feeding. However, the mechanism responsible for the suppression of dry forage intake after 40 min of feeding is unclear. Under these normal feeding conditions, ruminal distension, ruminal fluid osmolality, and thirst level all increased at the same time during dry forge feeding (Thang et al., 2010). Because of this, it is difficult to clarify which factors are mainly involved in the suppression of dry forage intake after 40 min of feeding in experiments conducted under normal feeding conditions (Campling and Balch, 1961; Anil et al., 1993; Grovum, 1995).

The utilization of the esophageal-fistulated goats enables the isolation of factors that are presumed to control dry forage intake. Based on the weight of bolus output, it also allows the volume of water infused into the balloon to be within the physiological range.

In this study, two experiments under sham feeding conditions were conducted to determine whether or not ruminal distension brought about by feed boluses (a mixture of secreted saliva and consumed feed) entering the rumen is a factor in the marked suppression of feed intake after 40 min of feeding.

MATERIALS AND METHODS

Animals

Five large-type male esophageal- and ruminal-fistulated goats (crossbred Japanese Saanen/Nubian, aged 3 to 5 years, weighing 65.5±3.76 kg) were used in this study. The goats were maintained in individual metabolism cages (length 2 m×width 1 m×height 2 m) that allowed for the separate collection of urine and feces. The laboratory room was maintained under thermoneutral conditions (room temperature 25.6±0.42°C; relative humidity 86.6±1.25%).

The animals were fed twice daily at 10:00 h and 16:00 h for 2 h each time. During the morning feeding period (10:00 to 12:00 h), the animals were fed 1.5 to 2.5 kg of roughly crushed alfalfa hay cubes. At 16:00 h each day, the animals were fed 300 g of hay and 200 g of concentrated beef cattle feed and half a spoon of multivitamins. The animals were given 5 kg of water at each meal.

The alfalfa hay cubes (84.3% dry matter) contained, on a dry matter basis, 18.7% crude protein, 2.4% crude fat, 29.7% crude fiber, 39.7% nitrogen free extract (NFE), 45.9% neutral detergent fiber (NDF), and 36.6% acid detergent fiber (ADF). The concentrated beef cattle feed (86.9% dry matter) contained, on a dry matter basis, 13.4% crude protein, 3.6% crude fat, 3.7% crude fiber, 71.0% nitrogen free extract (NFE), 14.6% neutral detergent fiber (NDF), and 5.4% acid detergent fiber (ADF). Alfalfa hay cubes were ground with a Wiley mill (type 40-525P, Ikemoto, Rika Kougyou, Tokyo). The diameter of the holes of the mill grid was 1 mm. The chemical components of the feeds were quantified using the procedures described by the Official Methods of Analysis (AOAC, 1990).

Experimental design

Experiment 1 : *The effect of intraruminal insertion of a balloon on dry forage intake in large-type goats during sham feeding* : The 5 esophageal- and ruminal-fistulated goats were divided into two groups of three and two animals each. Each group received the intraruminal non-insertion of a balloon (NIB) control and the intraruminal insertion of a balloon (RIB) treatment during sham feeding conditions, respectively, according to a cross-over design.

In the NIB control, a balloon was not intraruminally inserted. But in the RIB treatment, a balloon was intraruminally inserted before the commencement of feeding and 7.2±0.73 L of water was infused into the balloon upon the commencement of feeding using a bath tub pump. The volume of water that was infused into the balloon was similar to the weight of feed boluses removed via an esophageal fistula during the 2 h feeding period.

Experiment 2 : *The effect of intraruminal replenishment of iso-osmotic artificial saliva and insertion of a balloon on dry forage intake in large-type goats during sham feeding* : Similar to in the experiment 1, the animals were split into two groups. Each group received the intraruminal replenishment of iso-osmotic artificial saliva and non-insertion of a balloon (RRIAS-NIB) control and the intraruminal replenishment of iso-osmotic artificial saliva and insertion of a balloon (RRIAS-RIB) treatment during sham feeding conditions, respectively, according to a cross-over design.

In both the RRIAS-NIB control and the RRIAS-RIB treatment, at the commencement of feeding, 3.4±0.07 L of

iso-osmotic artificial saliva was intraruminally infused to replenish saliva removed from the esophageal fistula using a bath tub pump. The iso-osmotic artificial saliva had osmolality of 274.8 mOsmol/L, pH 8.6, and its concentrations of Na^+, K^+, Cl^-, HCO_3^-, and HPO_4^- were 142.8 mmol/L, 8.8 mmol/L, 7.0 mmol/L, 145 mmol/L, and 40 mmol/L, respectively.

In the RRIAS-NIB control, a balloon was not intraruminally inserted. However, in the RRIAS-RIB treatment, a balloon was intraruminally inserted before the commencement of feeding and 6.6±0.51 L of water was infused into the balloon concurrently with the commencement of feeding using a bath tub pump.

The volume of iso-osmotic artificial saliva that was replenished into the rumen in experiment 2 was approximately equal to the total volume of secreted saliva recorded during the 2 h feeding period in the NIB control of experiment 1. The weight of water that was infused into the balloon in the rumen in experiment 2 was equivalent to the weight of feed boluses removed via an esophageal fistula during the 2 h feeding period.

Before starting experiment 1 (in both the NIB control and the RIB treatment) and experiment 2 (in both the RRIAS-NIB control and the RRIAS-RIB treatment), the plug for closing the esophageal fistula was removed and a cannula for collecting boluses was fitted into the fistula. Therefore, all swallowed boluses of dry forage and secreted saliva were collected in the cannula through the fistula. In both experiments, the controls and the treatments were carried out with each group at 1 week intervals to ensure that animals had recovered and to minimize any compounding effects from the previous treatments.

In order to ascertain the physiological state of animals, heart rate, respiration rate, and rectal temperature were measured daily prior to the morning feeding period. Heart rate was measured by counting heart sounds with a stethoscope placed 5 cm behind the left olecranon. Respiration rate was measured by counting respiratory sounds with a stethoscope, and observing and counting thoracic movement that occurs in conjunction with respiration. Rectal temperature was measured using a veterinary thermometer inserted 10 cm into the rectum for about 10 min.

One day before the beginning of each treatment in each experiment, a polyethylene cannula (o.d. 1.50 mm, No.5, Imamura Gomu, Tokyo) was inserted into the jugular vein on one side of each goat for collecting blood samples. A three-way tap was attached to the end of each cannula. The cannula was sewn to the skin on the animal's neck and back to secure it and filled with heparin-saline (50 IU/ml) to prevent coagulation of the blood.

During the experiments, feed consumption was measured at intervals of 10 min for the duration of the 2 h feeding period (11:00 to 13:00 h). The animals were deprived of water during feeding in both the controls and the treatments. Following the completion of feeding, 5 kg of water was provided for a period of 30 min.

The parameters measured in the present study were rate of eating, cumulative dry forage intake, rate of bolus output, cumulative bolus output, rate of salivary secretion, cumulative salivary secretion, thirst level, hematocrit, plasma total protein concentration, plasma osmolality, ruminal fluid osmolality, and ruminal fluid pH. The rate of eating (g dry matter (DM)/10 min) and the cumulative dry forage intake (g DM) were measured during the 2 h of feeding (11:00 to 13:00 h). Eating rate was determined by placing the roughly crushed alfalfa hay cubes (1.5 to 2.5 kg) in a feed box attached to 8 kg measuring scales and measuring the weight of the remaining feed every 10 min for the duration of the 2 h feeding period. Rate of bolus output from the esophageal fistula (g/10 min) was measured during the 2 h of feeding (11:00 to 13:00 h) by using a feed box attached to 12 kg measuring scales and weighing the bolus output from the esophageal fistula every 10 min. The esophageal bolus consisted of a mixture of ingested feed and saliva. Rate of salivary secretion was measured by subtracting the rate of eating from the rate of bolus output at the same time so that cumulative salivary secretion was determined every 10 min. Fluid intake is regulated by thirst mechanisms (Guyton and Hall, 1996; Prasetiyono et al., 2000). In the present study, the thirst level (g/30 min) was evaluated quantitatively using water intake for 30 min upon conclusion of the 2 h feeding period.

Blood samples (4 ml) were collected at 8:55, 10:55, 11:15, 11:30, 12:00, 12:30, 13:00 and 13:30 through the polyethylene cannula. Prior to drawing the samples, a drop of heparin solution (1,000 IU/ml) was placed into a test tube. The blood samples were transferred to these test tubes, which were then placed in ice until plasma separation was carried out by centrifugation (16,260×*g*, 10 min, 4°C).

Ruminal fluid samples (30 ml) were collected at 8:55, 10:55, 11:15, 11:30, 12:00, 12:30, 13:00 and 13:30 through the polyvinyl tube fitted in the ruminal fistula and put into test tubes placed in ice until ruminal fluid separation from sediments was carried out by centrifugation (12,320×*g*, 10 min, 4°C).

All surgical and experimental procedures were approved by the Animal Experimental Ethics Committee of the University of the Ryukyus and were in compliance with the Japanese code of practice for the care and use of animals for scientific purposes.

Biochemical analysis

Blood samples were placed in capillary tubes and centrifuged using a hematocrit centrifuge (HC-12A, Tomy Seiko, Tokyo; 5 min, 12,851×*g*) to determine hematocrit by

hematocrit reader (Tomy Seiko, Tokyo). Plasma total protein concentration and osmolality were measured using a refractometer (Atago, Tokyo) and an osmometer (OM-6010, Kyoto Daiichi Kagaku, Kyoto), respectively.

Ruminal fluid was analyzed for osmolality with an osmometer (OM-6010, Kyoto Daiichi Kagaku, Kyoto) and for pH by a pH/Ion meter F-53 (Horiba Ltd., Kyoto).

Statistical analysis

The present study was conducted in accordance with a cross-over design. The values collected were subjected to an analysis of variance (ANOVA). Fisher's LSD was used to determine the significance of treatment effects. In the ANOVA table for cross-over design, the sources of variance included animals (A), group of animals (G), treatments (T) and error (E). For statistical analysis, General Linear Model (GLM) procedures (SAS Inst., Inc., Cary, NC, 1990) were adopted.

All data were analyzed using the following model:

$$Y_{ijkl} = \mu+G_i+A_{ij}+T_k+E_{ijkl}$$

Where Y_{ijkl} = the measured variable on the l^{th} replication of the j^{th} animal within the i^{th} group and the k^{th} treatment; μ = the overall mean; G_i = the effect of the i^{th} group; A_{ij} = the effect of the j^{th} animal within the i^{th} group; T_k = the effect of the k^{th} treatment; E_{ijkl} = the random error.

RESULTS

Experiment 1 : The effect of intraruminal insertion of a balloon on dry forage intake in large-type goats during sham feeding

Physiological parameters : The mean values of heart rate, respiration rate, and rectal temperature in the NIB control and the RIB treatment were 69.6±3.06 and 74.4±4.07 beats/min, 19.2±0.80 and 16.8±0.49 breaths/min, and 38.5±0.06 and 38.4±0.08°C, respectively.

Rate of eating and cumulative dry forage intake : Figure 1 shows the effect of intraruminal insertion of a balloon (RIB) on rate of eating and cumulative dry forage intake. Eating rates in the NIB control slightly decreased in the first 30 min of feeding (0 to 10 min, 370.9±52.78 g; 10 to 20

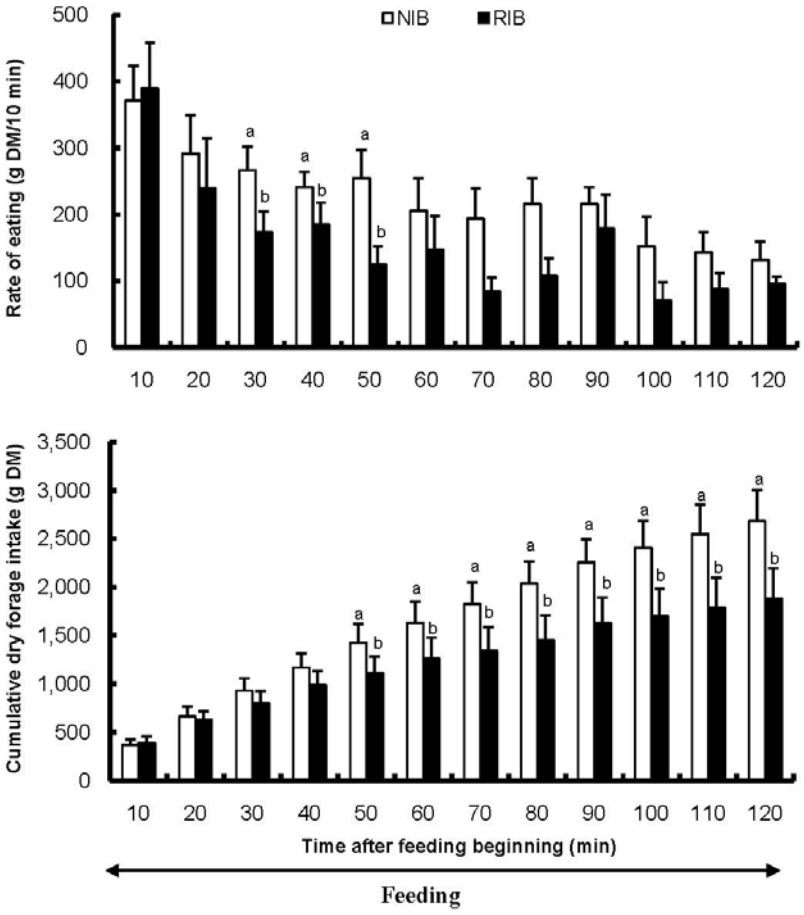

Figure 1. The effect of intraruminal insertion of a balloon (RIB) on rate of eating and cumulative dry forage intake. Values are means±SE of 5 large-type goats. [a, b] Means with different superscript are significantly different ($p<0.05$) from intraruminal non-insertion of a balloon (NIB).

min, 291.7±57.65 g; 20 to 30 min, 266.4±35.43 g) and subsequently maintained at high levels. Meanwhile, the eating rates in the RIB treatment sharply decreased in the first 30 min of feeding (0 to 10 min, 389.5±69.23 g; 10 to 20 min, 239.4±75.10 g; 20 to 30 min, 173.7±30.58 g) and subsequently declined gradually to very low eating rates (the lowest at 90 to 100 min, 70.8±26.74 g) in the remaining time of the 2 h feeding period. Eating rates in the RIB treatment from 30 min after the commencement of feeding to the conclusion of the 2 h feeding period tended to be lower than those in the NIB control.

From the commencement of feeding until a 40 min interval had elapsed, cumulative dry forage intake was not significantly different between the NIB control and the RIB treatment. However, the cumulative dry forage intake in the RIB treatment was smaller than that in the NIB control from 50 min after the commencement of feeding to the conclusion of the 2 h feeding period. In comparison with the NIB control (2,682.4±321.76 g/2 h), cumulative dry forage intake in the RIB treatment (1,884.9±310.72 g/2 h) was a significant 29.7% less ($p<0.05$) upon conclusion of the 2 h feeding period.

Rate of bolus output and cumulative bolus output : Rates of bolus output in both the NIB control and the RIB treatment (Table 1) sharply decreased in the first 20 min of feeding and then gradually reduced for the remaining time of the 2 h feeding period. Compared with the NIB control, rate of bolus output in the RIB treatment was lower from 30 min after the commencement of feeding to the end of the 2 h feeding period.

The cumulative bolus outputs in both the NIB control and the RIB treatment (Table 1) gradually increased after beginning of the feeding to the end of the 2 h feeding period. Compared with the NIB control (6,804±469.92 g), the cumulative bolus output in the RIB treatment (5,716±803.89 g) was smaller upon conclusion of the 2 h feeding period.

Rate of salivary secretion and cumulative salivary secretion : Table 1 presents the effect of intraruminal insertion of a balloon (RIB) on rate of salivary secretion and

Table 1. The effect of intraruminal insertion of a balloon (RIB) on rate of bolus output, cumulative bolus output, rate of salivary secretion and cumulative salivary secretion

Time after feeding beginning (min)	Rate of bolus output (g/10 min)		Cumulative bolus output (g)		Rate of salivary secretion (g/10 min)		Cumulative salivary secretion (g)	
	NIB	RIB	NIB	RIB	NIB	RIB	NIB	RIB
10	1,096 ±117.46	1,014 ±114.44	1,096 ±117.46	1,014 ±114.44	656 ±84.95	552 ±39.92	656 ±84.95	552 ±39.92
20	696 ±137.13	734 ±156.48	1,792 ±180.43	1,748 ±261.29	350 ±79.81	450 ±133.08	1,006 ±87.61	1,002 ±168.30
30	718 ±86.74[a]	602 ±94.20[b]	2,510 ±259.36	2,350 ±347.33	402 ±45.87	396 ±78.65	1,408 ±125.68	1,398 ±238.25
40	622 ±48.00	544 ±110.75	3,132 ±303.50	2,894 ±454.00	336 ±22.49	324 ±79.79	1,744 ±145.83	1,722 ±316.12
50	612 ±56.07	430 ±86.02	3,744 ±351.78	3,324 ±533.39	310 ±6.32	282 ±66.74	2,054 ±151.15	2,004 ±373.24
60	510 ±32.86	406 ±106.42	4,254 ±353.05	3,730 ±637.94	266 ±31.87	232 ±53.05	2,320 ±149.16	2,236 ±426.13
70	530 ±80.50	290 ±57.36	4,784 ±384.90	4,020 ±692.41	300 ±42.90	190 ±39.62	2,620 ±147.34	2,426 ±462.32
80	498 ±43.86	332 ±45.21	5,282 ±391.26	4,352 ±711.14	242 ±9.16	204 ±18.60	2,862 ±155.38	2,630 ±464.21
90	478 ±49.64	470 ±94.02	5,760 ±412.42	4,822 ±686.69	222 ±38.00	258 ±35.41	3,084 ±153.05	2,888 ±442.58
100	346 ±63.84	264 ±99.48	6,106 ±452.61	5,086 ±775.47	166 ±28.74	180 ±70.92	3,250 ±163.52	3,068 ±510.91
110	360 ±37.82	280 ±41.71	6,466 ±470.75	5,366 ±812.31	190 ±27.02	176 ±37.63	3,440 ±141.53	3,244 ±538.01
120	338 ±66.51	350 ±35.36	6,804 ±469.92	5,716 ±803.89	182 ±46.52	236 ±33.25	3,622 ±104.13	3,480 ±533.41

NIB = Intraruminal non-insertion of a balloon; RIB = Intraruminal insertion of a balloon.

Values are means±SE of 5 large-type goats. [a, b] Means in the same row bearing different superscripts differ ($p<0.05$).

cumulative salivary secretion volume. In the NIB control, the rate of salivary secretion rapidly decreased in the first 20 min of feeding and subsequently declined gradually for the remaining time of the 2 h feeding period. In the RIB treatment, the rate of salivary secretion decreased gradually from 10 min after feeding to the conclusion of the 2 h feeding period. There were no significant differences between the two treatments in the salivary secretion rate.

Cumulative salivary secretion volumes in the NIB control and the RIB treatment upon conclusion of the 2 h feeding period were 3,622±104.13 g/2 h and 3,480±533.41 g/2 h, respectively. There were no significant differences between the two treatments. The secreted saliva weight in the NIB control and the RIB treatment during the 2 h feeding period was 53.2% and 60.9% the total weight of the bolus output, respectively.

Thirst level : In the NIB control, while all animals drank water, the amount of water consumed was low and thirst level was 1,360±467.02 g/30 min upon conclusion of the 30 min drinking period. However, four out of five animals in the RIB treatment did not drink water so thirst level was only 30±30.00 g/30 min upon conclusion of the 30 min drinking period. In comparison with the NIB control, thirst level in the RIB treatment was a significant 97.8% less ($p<0.05$) upon conclusion of the 30 min drinking period.

Hematocrit, plasma total protein concentration and plasma osmolality : Table 2 presents the effect of intraruminal insertion of a balloon (RIB) on hematocrit, plasma total protein concentration, and plasma osmolality. In the NIB control and the RIB treatment, hematocrit and plasma total protein concentrations increased rapidly due to increased salivary secretion during the first 15 min after the commencement of feeding. Subsequently, hematocrit and plasma total protein concentrations in both the NIB control and the RIB treatment remained at high levels for the remainder of the feeding period. On the other hand, the values in hematocrit and plasma total protein concentrations were not significantly different between the NIB control and the RIB treatment during the 2 h feeding period.

Plasma osmolalities in both treatments were slightly higher than the pre-feeding levels. Compared with the NIB control, plasma osmolality in the RIB treatment was not significantly different during the 2 h feeding period.

Ruminal fluid osmolality and pH : Ruminal fluid osmolalities in both the NIB control and the RIB treatment (Table 2) were mostly remained unchanged during the 2 h feeding period. Compared with the NIB control, ruminal fluid osmolality in the RIB treatment was not significantly different for the duration of the 2 h feeding period.

Ruminal fluid pH in both the NIB control and the RIB treatment (Table 2) slightly increased compared to the pre-feeding levels during the 2 h feeding period. Compared with the NIB control, ruminal fluid pH in the RIB treatment was not significantly different for the duration of the 2 h feeding period.

Table 2. The effect of intraruminal insertion of a balloon (RIB) on hematocrit, plasma total protein concentration, plasma osmolality, ruminal fluid osmolality, and ruminal fluid pH

Time after feeding beginning (min)	Hematocrit (%)		Plasma total protein (g/dl)		Plasma osmolality (mOsmol/L)		Ruminal fluid osmolality (mOsmol/L)		Ruminal fluid pH	
	NIB	RIB	NIB	RIB	NIB	RIB	NIB	RIB	NIB	RIB
-120	27.2 ±1.12	27.2 ±1.21	7.0 ±0.16	6.8 ±0.10	290.8 ±2.27	292.0 ±1.34	264.2 ±5.83	276.6 ±6.18	7.09 ±0.09	6.97 ±0.11
0	28.5 ±1.31	26.9 ±1.28	7.1 ±0.18	7.0 ±0.08	289.2 ±2.42	290.4 ±1.03	269.8 ±5.54	276.0 ±5.90	7.25 ±0.09	7.07 ±0.09
15	34.6 ±0.89	34.9 ±1.62	8.6 ±0.18	8.3 ±0.21	292.6 ±2.46	293.8 ±0.97	264.4 ±4.86	268.2 ±4.88	7.31 ±0.09	7.14 ±0.09
30	36.4 ±0.68	35.2 ±1.35	8.8 ±0.23	8.5 ±0.24	294.0 ±1.70	294.4 ±0.60	264.4 ±4.45	265.2 ±5.09	7.32 ±0.09	7.17 ±0.10
60	36.8 ±1.79	35.4 ±2.27	8.9 ±0.20	8.8 ±0.40	297.2 ±1.28	294.8 ±0.58	261.6 ±5.37	261.4 ±4.67	7.35 ±0.09	7.21 ±0.09
90	36.9 ±1.61	35.7 ±2.27	9.1 ±0.19	8.6 ±0.28	297.2 ±1.66	295.0 ±0.45	262.6 ±5.76	262.2 ±5.56	7.36 ±0.09	7.23 ±0.10
120	35.9 ±1.74	35.3 ±2.02	9.1 ±0.19	8.6 ±0.26	298.2 ±1.53	295.6 ±0.68	262.8 ±6.13	259.6 ±5.65	7.34 ±0.09	7.23 ±0.07
150	33.0 ±1.33	32.0 ±1.62	8.4 ±0.11[a]	7.8 ±0.15[b]	294.6 ±1.36	294.4 ±0.51	220.0 ±15.55	266.2 ±7.12	7.32 ±0.08	7.25 ±0.06

NIB = Intraruminal non-insertion of a balloon; RIB = Intraruminal insertion of a balloon.

Values are means±SE of 5 large-type goats. [a, b] Means in the same row bearing different superscripts differ ($p<0.05$).

Experiment 2 : The effect of intraruminal replenishment of iso-osmotic artificial saliva and insertion of a balloon on dry forage intake in large-type goats during sham feeding

Physiological parameters : The mean values of heart rate, respiration rate, and rectal temperature in the RRIAS-NIB control and the RRIAS-RIB treatment were 73.2±2.94 and 76.8±2.94 beats/min, 18.8±0.80 and 18.0±1.41 breaths/min, and 38.5±0.03 and 38.4±0.13°C, respectively.

Eating rate and cumulative dry forage intake : Figure 2 shows the effect of intraruminal replenishment of iso-osmotic artificial saliva and insertion of a balloon (RRIAS-RIB) on eating rate and cumulative dry forage intake. Eating rates in the intraruminal replenishment of iso-osmotic artificial saliva and non-insertion of a balloon (RRIAS-NIB) control and the RRIAS-RIB treatment sharply decreased in the first 30 min of feeding (0 to 10 min, 389.5±60.58 g and 300.1±67.79 g; 10 to 20 min, 313.6±41.16 g and 209.1±67.51 g; 20 to 30 min, 261.3±34.35 g and 151.7±52.51 g, respectively). These levels subsequently declined slightly in the RRIAS-NIB control but continuously decreased to a very low rate in the RRIAS-RIB treatment for the remainder of the 2 h feeding period. Eating rates in the RRIAS-RIB treatment from 30 min to the conclusion of the 2 h feeding period except 70, 80, 90, and 120 min intervals after feeding were significantly lower ($p<0.05$) than those in the RRIAS-NIB control.

The values in cumulative dry forage intake in the RRIAS-RIB treatment were significantly lower ($p<0.05$) than those in the RRIAS-NIB control from 30 min after the commencement of feeding to the conclusion of the 2 h feeding period. The cumulative dry forage intake in the RRIAS-RIB treatment (1,559.6±380.43 g/2 h) was a significant 45.5% less ($p<0.05$) compared with that in the RRIAS-NIB control (2,861.1±316.50 g/2 h) upon conclusion of the 2 h feeding period.

Rate of bolus output and cumulative bolus output : Table 3 shows the effect of RRIAS-RIB on rate of bolus output and cumulative bolus output. Rates of bolus output in both the RRIAS-NIB control and the RRIAS-RIB treatment rapidly reduced in the first 20 min of feeding and

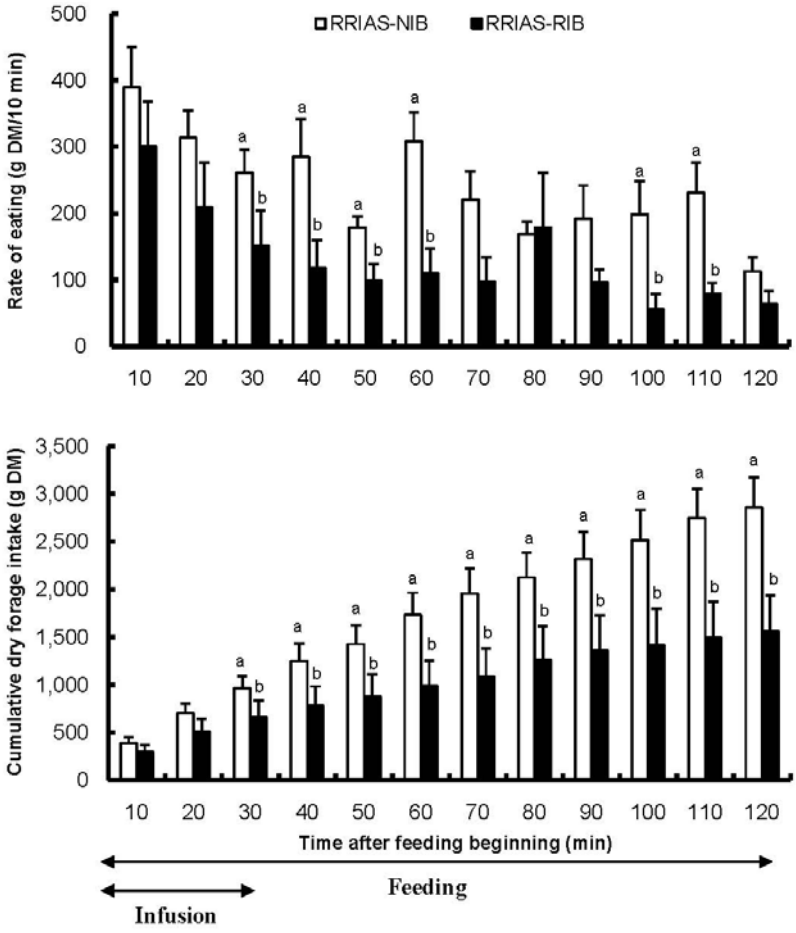

Figure 2. The effect of intraruminal replenishment of iso-osmotic artificial saliva and insertion of a balloon (RRIAS-RIB) on rate of eating and cumulative dry forage intake. Values are means±SE of 5 large-type goats. [a, b] Means with different superscript are significantly different ($p<0.05$) from intraruminal replenishment of iso-osmotic artificial saliva and non-insertion of a balloon (RRIAS-NIB).

then decreased gradually for the remaining time of the 2 h feeding period. In comparison with the RRIAS-NIB control, the rate of bolus output in the RRIAS-RIB treatment was clearly lower for the duration of the 2 h feeding period and there were significant differences ($p<0.05$) to be found at 30, 50, 70, and 110 min intervals.

The values in cumulative bolus output in the RRIAS-RIB treatment were significantly smaller ($p<0.05$) than those in the RRIAS-NIB control from 30 min after the commencement of feeding to the conclusion of the 2 h feeding period. The cumulative bolus output in RRIAS-RIB treatment (5,170±1028.95 g) was significantly smaller ($p<0.05$) than that in the RRIAS-NIB control (7,392±583.95 g) upon conclusion of the 2 h feeding period.

Rate of salivary secretion and cumulative salivary secretion : Salivary secretion rates in both the RRIAS-NIB control and the RRIAS-RIB treatment (Table 3) sharply decreased in the first 20 min after the commencement of feeding and subsequently reduced gradually for the remaining time of the 2 h feeding period. Compared with the RRIAS-NIB control, salivary secretion rates in the RRIAS-RIB treatment were numerically lower for the duration of the 2 h feeding period and significant differences ($p<0.05$) between the two treatments were only found at 30 and 70 min intervals.

Cumulative salivary secretion volumes in the RRIAS-RIB treatment (Table 3) tended to be lower than those in the RRIAS-NIB control for the duration of the 2 h feeding period. Cumulative salivary secretion volumes in the RRIAS-NIB control and the RRIAS-RIB treatment were 3,998±327.27 g/2 h and 3,320±653.18 g/2 h, respectively. The secreted saliva weight in the RRIAS-NIB control and the RRIAS-RIB treatment during the 2 h feeding period was 54.1% and 64.2% total weight of the bolus output, respectively.

Thirst level : Most of animals did not drink upon conclusion of the 2 h feeding period in both the RRIAS-NIB control (310±207.61 g/30 min) and the RRIAS-RIB treatment (30±20.00 g/30 min).

Hematocrit, plasma total protein concentration and

Table 3. The effect of intraruminal replenishment of iso-osmotic artificial saliva and insertion of a balloon (RRIAS-RIB) on rate of bolus output, cumulative bolus output, rate of salivary secretion and cumulative salivary secretion

Time after feeding beginning (min)	Rate of bolus output (g/10 min)		Cumulative bolus output (g)		Rate of salivary secretion (g/10 min)		Cumulative salivary secretion (g)	
	RRIAS-NIB	RRIAS-RIB	RRIAS-NIB	RRIAS-RIB	RRIAS-NIB	RRIAS-RIB	RRIAS-NIB	RRIAS-RIB
10	1,066 ±94.42	894 ±143.44	1,066 ±94.42	894 ±143.44	604 ±39.70	538 ±73.17	604 ±39.70	538 ±73.17
20	792 ±83.81	608 ±175.65	1,858 ±174.77	1,502 ±306.18	420 ±38.47	360 ±96.49	1,024 ±75.47	898 ±154.09
30	696 ±80.41[a]	450 ±100.95[b]	2,554 ±243.65[a]	1,952 ±397.04[b]	386 ±52.78[a]	270 ±45.50[b]	1,410 ±122.35	1,168 ±198.46
40	678 ±93.40	486 ±144.55	3,232 ±323.87[a]	2,438 ±534.23[b]	340 ±49.70	346 ±132.69	1,750 ±164.19	1,514 ±318.91
50	526 ±35.44[a]	366 ±60.87[b]	3,758 ±355.49[a]	2,804 ±589.25[b]	314 ±28.91	248 ±40.30	2,064 ±192.53	1,762 ±352.98
60	682 ±81.63	434 ±150.42	4,440 ±429.41[a]	3,238 ±728.61[b]	316 ±39.06	304 110.16	2,380 ±230.98	2,066 ±455.00
70	574 ±68.82[a]	292 ±87.49[b]	5,014 ±478.49[a]	3,530 ±811.67[b]	312 ±27.09[a]	176 ±52.97[b]	2,692 ±254.05	2,242 ±502.63
80	458 ±55.53	478 ±148.81	5,472 ±496.72[a]	4,008 ±883.66[b]	258 ±42.83	266 ±57.32	2,950 ±288.88	2,508 ±532.40
90	510 ±54.59	268 ±68.37	5,982 ±505.51[a]	4,276 ±946.77[b]	282 ±21.77	154 ±52.02	3,232 ±284.72	2,662 ±579.71
100	472 ±113.91	344 ±69.04	6,454 ±604.69[a]	4,620 ±1009.35[b]	236 ±56.27	278 ±53.42	3,468 ±326.70	2,940 ±626.46
110	628 ±76.90[a]	282 ±38.91[b]	7,082 ±588.07[a]	4,902 ±997.51[b]	354 ±54.00	188 ±21.77	3,822 ±354.49	3,128 ±627.33
120	310 ±41.23	268 ±55.98	7,392 ±583.95[a]	5,170 ±1,028.95[b]	176 ±36.55	192 ±35.69	3,998 ±327.27	3,320 ±653.18

RRIAS-NIB = Intraruminal replenishment of iso-osmotic artificial saliva and non-insertion of a balloon.

RRIAS-RIB = Intraruminal replenishment of iso-osmotic artificial saliva and insertion of a balloon.

Values are means±SE of 5 large-type goats. [a, b] Means in the same row bearing different superscripts differ ($p<0.05$).

Table 4. The effect of intraruminal replenishment of iso-osmotic artificial saliva and insertion of a balloon (RRIAS-RIB) on hematocrit, plasma total protein concentration, plasma osmolality, ruminal fluid osmolality, and ruminal fluid pH

Time after feeding beginning (min)	Hematocrit (%)		Plasma total protein (g/dl)		Plasma osmolality (mOsmol/L)		Ruminal fluid osmolality (mOsmol/L)		Ruminal fluid pH	
	RRIAS-NIB	RRIAS-RIB	RRIAS-NIB	RRIAS-RIB	RRIAS-NIB	RRIAS-RIB	RRIAS-NIB	RRIAS-RIB	RRIAS-NIB	RRIAS-RIB
-120	26.6 ±0.58	26.8 ±1.33	6.8 ±0.22	6.7 ±0.11	293.0 ±1.38	293.8 ±1.53	276.0 ±3.41	278.6 ±9.64	7.03 ±0.09	6.92 ±0.08
0	28.0 ±1.04	27.3 ±1.71	7.0 ±0.27	6.9 ±0.09	289.8 ±0.80	291.6 ±1.60	274.8 ±4.66	277.4 ±9.19	7.19 ±0.05	7.00 ±0.08
15	35.9 ±1.31	34.3 ±1.77	8.5 ±0.29	8.1 ±0.29	294.0 ±1.23	296.2 ±1.16	267.0 ±2.70	267.8 ±6.74	7.48 ±0.07	7.34 ±0.06
30	36.4 ±1.31	33.6 ±1.67	8.6 ±0.30	8.1 ±0.30	295.2 ±1.07	295.6 ±1.40	265.4 ±2.58	267.8 ±5.29	7.54 ±0.08	7.41 ±0.07
60	37.1 ±1.81	33.6 ±1.71	8.7 ±0.30	8.1 ±0.30	295.4 ±1.57	297.8 ±2.82	263.6 ±2.77	265.4 ±5.12	7.54 ±0.07	7.45 ±0.07
90	37.2 ±1.55	34.0 ±2.08	8.9 ±0.38	8.1 ±0.35	296.2 ±1.62	298.0 ±1.76	263.6 ±3.06	265.2 ±4.94	7.53 ±0.07	7.44 ±0.07
120	36.9 ±1.03	32.4 ±2.12	8.8 ±0.34	7.9 ±0.35	296.8 ±0.97	298.0 ±1.95	263.2 ±2.71	265.4 ±4.84	7.54 ±0.07	7.42 ±0.08
150	32.5 ±1.00	29.4 ±1.24	7.8 ±0.28	7.4 ±0.26	292.6 ±1.29^{b}	297.6 ±1.44^{a}	255.4 ±6.23	267.6 ±5.41	7.48 ±0.05	7.37 ±0.07

RRIAS-NIB = Intraruminal replenishment of iso-osmotic artificial saliva and non-insertion of a balloon.
RRIAS-RIB = Intraruminal replenishment of iso-osmotic artificial saliva and insertion of a balloon.
Values are means±SE of 5 large-type goats; $^{a, b}$ Means in the same row bearing different superscripts differ ($p<0.05$).

plasma osmolality : Table 4 shows the effect of RRIAS-RIB on hematocrit, plasma total protein concentration, and plasma osmolality. In both the RRIAS-NIB control and the RRIAS-RIB treatment, rapid increases in hematocrit and plasma total protein concentrations were recorded during the first 15 min after the commencement of feeding. Subsequently, hematocrit and plasma total protein concentrations in both the control and the treatment remained at these levels for the remainder of the 2 h feeding period. Compared with the RRIAS-NIB control, hematocrit and plasma total protein concentrations in the RRIAS-RIB treatment tended to be lower for the duration of the 2 h feeding period.

Plasma osmolalities in both the RRIAS-NIB control and the RRIAS-RIB treatment slightly increased for the duration of the 2 h feeding period. In comparison with the RRIAS-NIB control, plasma osmolality in the RRIAS-RIB treatment was not significantly different over the 2 h feeding period.

Ruminal fluid osmolality and pH : Table 4 shows the effect of RRIAS-RIB on ruminal fluid osmolality and pH. Ruminal fluid osmolality in both the RRIAS-NIB control and the RRIAS-RIB treatment was mostly remained unchanged during the 2 h feeding period and was not different compared with pre-feeding levels. There were no significant differences between the two treatments for the duration of the 2 h feeding period. Ruminal fluid pH in both the control and the treatment increased in the first 15 min of feeding and subsequently remained mostly the same level for the remainder of the 2 h feeding period. In comparison with the RRIAS-NIB control, ruminal fluid pH in the RRIAS-RIB treatment was not significantly different over the 2 h feeding period.

DISCUSSION

The new findings in the present study were that in ruminants fed dry forage, physiological ruminal distension itself is a major factor in suppressing dry forage intake, and that the copious volume of saliva secreted during dry forage feeding works in conjunction with the consumed feed to create the ruminal load responsible for ruminal distension.

Feeding regime

In countries such as Japan where ruminants are raised in barns, most farmers feed their livestock a diet of dry forage twice a day. In the present study, the goats were fed roughly crushed alfalfa hay cubes with any large remaining chunks removed (similar to lucerne chaff) 2 h twice daily. Because large-type goats are fast eaters and consume large amounts of dry forage in short time, they were able to satisfy their daily nutrient requirements when fed twice daily for 2 h

each time. In other words, the animal's body weight upon completion of the experiments increased compared to that prior to the experiments (pre-experiments 65.5±3.76 kg and post-experiments 72.6±4.32 kg).

Sham feeding

Under normal feeding conditions, it is difficult to determine which factor is physiologically responsible for controlling feed intake because ruminal fluid and blood parameters (ruminal distension, ruminal fluid osmolality, ruminal fluid volatile fatty acid concentrations and plasma osmolality), which are thought to suppress feed intake, change at the same time. In the present study, experiments were conducted under sham feeding conditions and feed boluses were removed before they entered the rumen during dry forage feeding. Because of this, increase in ruminal fluid osmolality, decrease in ruminal fluid pH, and increase in plasma osmolality that occur under normal feeding conditions when feed enters the rumen were not observed (Table 2; Thang et al., 2010). Furthermore, under sham feeding conditions, dry forage intake increased significantly compared to normal feeding conditions on non-experimental days (Thang et al., 2010). This indicates that under normal feeding conditions, dry forage intake is regulated by factors produced when boluses enter the rumen.

Reproduction of ruminal distension by intraruminal insertion of a balloon

To date there have been a number of papers reporting the effects of ruminal balloons on feed intake (Campling and Balch, 1961; Anil et al., 1993). However, it is unclear as to how the weight on the balloons was decided upon. According to the results of previous balloon experiments conducted under normal feeding conditions in which feed intake was suppressed, it was thought that feed boluses entering the rumen brought about increases in ruminal distension, ruminal fluid osmolality, and plasma osmolality that suppressed feed intake. Therefore, it is not clear whether or not a physiological level of ruminal distension for feed intake suppression was produced by the balloons. Anil et al. (1993) reported that in cows, if a balloon inserted into the rumen was not filled with enough water or if the increase in ruminal fluid osmolality was insufficient, the amount of dry forage or silage intake was not decreased.

In contrast to small-type goats, large-type goats consume large quantities of dry forage. Therefore, large-type goats secrete a copious amount of saliva. The secreted saliva weight in the present experiments was about 60% total weight of the bolus output (Tables 1 and 3). It is thought that this saliva worked in conjunction with consumed feed to form the ruminal load responsible for ruminal distension. In ruminants, it has been suggested that the rumen wall has tension receptors (Iggo and Leek, 1970). Rumen fill refers to the rumen reaching its volumetric capacity for feed. Feeding volume is limited by rumen capacity (Forbes, 1995). On the other hand, ruminal distension refers to the stomach being stretched downward under the weight of feed boluses in the rumen despite the rumen not being completely full of feed. The feed boluses consumed by goats during dry forage feeding are bulky, heavy, and coarse. In the present study, in order to reproduce the ruminal distension caused when boluses enter the rumen, a balloon was inserted into the rumen and water equivalent in weight to the boluses was infused into the balloon. The weight of the water in the balloon causes distension of the ruminal wall.

Dry forage intake suppressed solely by a physiological level of ruminal distension

In the NIB control and the RIB treatment of experiment 1, under sham feeding conditions, increases in ruminal fluid and plasma osmolality, and a decrease in ruminal fluid pH which are normally associated with feeding were not observed (Table 2). The dry forage intake in the NIB control increased markedly compared to normal feeding conditions (Thang et al., 2010). The weight of water infused into the balloon in the rumen in the RIB treatment was equivalent to the weight of feed boluses consumed over the duration of the 2 h feeding period in the NIB control. Thus, the ruminal distension caused by insertion of a balloon in the rumen was approximately same as the level of ruminal distension caused by feed boluses entering the rumen under normal feeding conditions. The result was that the cumulative dry forage intake in the RIB treatment was smaller than those in the NIB control during the second hour of the 2 h feeding period (Figure 1). Nagamine et al. (2010) inserted a balloon into the rumen to reproduce the ruminal distension caused when feed boluses enter the rumen. They reported an increase in single unit activity in the ventromedial hypothalamic nucleus which is considered the satiety center. Therefore, the results in experiment 1 indicate that increase in ruminal distension due to the weight of feed boluses entering the rumen is a physiological factor in controlling dry forage intake in very hungry goats.

Dry forage intake suppressed by salivary secretion volume

Saliva in ruminants is secreted in large volumes during the initial stages of dry forage feeding (Sato, 1975; Sunagawa et al., 2003; Tables 1 and 3). When ruminants feed on dry forage, the animals mix saliva with the feed in order to create a bolus that can be swallowed. Saliva acts as a lubricant in the mouth and esophagus and assists in the mastication and swallowing of dry forage. Saliva also acts

as an alkali and serves to buffer the decrease in the pH of ruminal fluid due to the volatile fatty acid production of microbial fermentation in the rumen.

In the RRIAS-NIB control and RRIAS-RIB treatment of experiment 2, the iso-osmotic artificial saliva was used to replenish the saliva loss with the removal of feed boluses. In the RRIAS-RIB treatment, the effect of ruminal distension on dry forage intake brought about by a balloon inflated with water in the rumen was investigated under these conditions. Eating rates in the RRIAS-NIB control decreased less rapidly and were subsequently maintained a relatively higher level after 30 min had elapsed. Eating rates in RRIAS-RIB treatment, on the other hand, decreased rapidly and then remained at low level for the remainder of the 2 h feeding period (Figure 2). The values in cumulative dry forage intake in the RRIAS-RIB treatment were significantly smaller ($p<0.05$) than those in the RRIAS-NIB control from 30 min after the commencement of feeding to the conclusion of the 2 h feeding period. The cumulative dry forage intake in the RRIAS-RIB treatment was a significant 45.5% less compared with that in the RRIAS-NIB control upon conclusion of the 2 h feeding period. The level of decrease in dry forage intake in the RRIAS-RIB treatment of experiment 2 was larger than that in the RIB treatment of experiment 1 (Figures 1 and 2). Thang et al. (2010) has reported that in large-type esophageal-fistulated goats fed dry forage twice daily, dry forage intake during the second hour of the 2 h feeding period is regulated by factors produced when boluses enter the rumen. In the present experiment, the secreted saliva weight in the RRIAS-NIB control and the RRIAS-RIB treatment during the 2 h feeding period was 54.1% and 64.2% total weight of the bolus output, respectively.

The reason for greater dry forage intake suppression levels when iso-osmotic artificial saliva was infused was that the iso-osmotic artificial saliva infused into the rumen acted as ruminal load as in normal feeding and this is thought to have caused more ruminal distension. In other words, it indicates that the marked decrease in feed intake observed in the second hour of the 2 h feeding period under normal feeding conditions is related to ruminal distension caused by the feed consumed and the copious amount of saliva secreted during dry forage feeding. From the results of the present experiments, it is thought that while the copious amount of saliva secreted during dry forage feeding assists in mastication and swallowing of dry forage, ruminal distension in the second half of the feeding period serves to suppress dry forage intake.

Dry forage intake and thirst

The volume of iso-osmotic artificial saliva infused into the rumen in the experiment 2 was approximately equal to the total volume of secreted saliva recorded during the 2 h feeding period in the NIB control of experiment 1. The iso-osmotic artificial saliva had an osmolality of 274.8 mOsmol/L and pH 8.6. While ruminal fluid pH levels tended to increase during feeding when iso-osmotic artificial saliva was intraruminally replenished, ruminal fluid osmolality tended to decrease (Table 4).

Intraruminal replenishment of iso-osmotic artificial saliva did not alter the increases in plasma total protein concentrations and hematocrit associated with a decrease in plasma volume caused by dry forage feeding. On the other hand, the increase in plasma osmolality due to iso-osmotic artificial saliva infusion during dry forage feeding in experiments 1 and 2 tended to be small (Tables 2 and 4). However, it was observed that after the completion of the 2 h feeding period in both the RRIAS-RIB treatment and the RRIAS-NIB control, the animals did not experience thirst sensations due to dry forage feeding under sham feeding conditions.

Cumulative feed intake in the RRIAS-NIB control of experiment 2 was greater than that in the NIB control of experiment 1 (Figures 1 and 2). Sunagawa et al. (2002, 2007) reported that the intraruminal infusion of parotid saliva and the intravenous infusion of artificial saliva reduced the degree of dry forage intake suppression during the initial stages of feeding under normal feeding conditions in large-type goats. This is the reason why the rapid suppression of dry forage intake during the initial stages of dry forage feeding was caused by a feeding-induced hypovolemia (decrease in circulating plasma volume) through the accelerated secretion of saliva during the initial stages of feeding while the suppression was reduced by the intraruminal replenishment of iso-osmotic artificial saliva. These results indicate that suppression of dry forage intake due to the RRIAS-RIB treatment in goats under sham feeding conditions is not caused by thirst sensations brought about by dry forage feeding.

The results of the present study indicate that the marked decrease in feed intake observed in the second hour of the 2 h feeding period is related to ruminal distension caused by the feed consumed and the copious amount of saliva secreted during dry forage feeding.

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