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Influence of Rumen Escape Starch on α-Amylase Activity in Pancreatic Tissue and Small Intestinal Digesta of Lambs

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ABSTRACT : Two slaughter experiments were conducted to determine the effects of rumen escape starch, by altering dietary starch concentration and corn particle size, on α-amylase activity in the pancreas and the small intestinal digesta of lambs. In experiment 1, 18 wether lambs (28.5±1.6 kg) were fed low, medium or high starch diets for 35 d and slaughtered. Dietary starch concentrations linearly increased rumen escape starch ($p<0.05$). Pancreatic α-amylase activity was lower ($p<0.05$) in lambs fed the low starch diet. When expressed per gram of digesta, α-amylase activity was lower in lambs fed the low starch diet. However, expressed as total activity, α-amylase in the digesta was greater in lambs fed the medium starch diet. In experiment 2, 12 wether lambs (23.5±0.3 kg) were fed diets with finely cracked corn, coarsely cracked corn and whole corn. These dietary treatments continued for 35 d before tissue collection. Rumen escape starch increased with increasing corn particle size ($p<0.05$). α-Amylase activity in the pancreas and the small intestinal digesta was significantly greater ($p<0.05$) in lambs fed the coarsely cracked corn. These data suggest that increasing rumen escape starch results in a quadratic increase in total α-amylase activity in the pancreas and the small intestinal digesta. Maximum α-amylase activity is reached when rumen escape starch is about 100-120 g/d in 25-30 kg lambs. (**Key Words** : Starch, α-Amylase, Pancreas, Digesta, Lamb)

INTRODUCTION

Modern feeding systems of ruminants promote the consumption of high-starch diets. It has been demonstrated that there are limits to small intestinal starch assimilation in ruminants fed high-starch diets (Owens et al., 1986; Harmon, 2004), and insufficient activity of pancreatic α-amylase is possible cause (Kreikemeier et al., 1991; Swanson et al., 2000). Many researchers have reported increased pancreatic α-amylase activity in steers and sheep fed high-concentrate diets compared to forage diets (Clary et al., 1969; Janes et al., 1985). In contrast, abomasal infusion of partially hydrolyzed starch decreases pancreatic α-amylase secretion in steers (Walker and Harmon, 1995; Swanson et al., 2002b, 2004). Thus the action of rumen escape starch (RES) on pancreatic α-amylase activity is particularly intriguing.

Ruminal infusion of partially hydrolyzed starch does not affect pancreatic α-amylase secretion (Walker and Harmon, 1995). Therefore, the objective of the experiments was to determine the effect of RES, by altering dietary starch concentration and corn particle size, on α-amylase activity in the pancreas and the small intestinal digesta of lambs.

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MATERIALS AND METHODS

Animals and diets

Experiment 1 : Eighteen Saanen wether lambs (28.5±1.6 kg) were randomly allocated to diets containing low, medium or high starch concentration (6 lambs per diet; Table 1). Corn was cracked to pass through a 3-mm screen. Because the small intestinal protein flow affects α-amylase activity in the pancreas (Swanson et al., 2002a), diets were formulated so that all lambs would receive the same amount of metabolizable protein using the calculations described by the NRC (2001) for dairy cattle.

Experiment 2 : Twelve Saanen Wether lambs (23.5±0.3 kg) were used in a completely randomized design experiment with three treatments. Corn was cracked to pass through a 3-mm screen (finely cracked corn) or without the screen (coarsely cracked corn), or was not processed (whole corn). Diets were formulated to contain 35% starch which was the same starch content as that of the medium diet in Experiment 1 (Table 1).

Lambs were placed in individual metabolism crates in a

Table 1. Diet composition

Composition	Experiment 1			Experiment 2
	Low starch diet	Medium starch diet	High starch diet	
Ingredient % of dry matter				
Corn silage	68.30	54.20	34.90	54.55
Corn grain	15.90	30.95	50.60	28.35
Wheat bran	-	-	-	9.00
Soybean meal	14.00	13.00	12.60	6.30
Dicalcium phosphate	0.50	0.50	0.50	0.50
Limestone	0.50	0.55	0.60	0.50
Vitamins and minerals permix[1]	0.50	0.50	0.50	0.50
Chromic oxide	0.30	0.30	0.30	0.30
Nutrient % of dry matter[2]				
Dry matter	29.87	34.40	44.05	40.86
Starch	27.62	35.20	45.61	35.53
Crude protein	14.56	14.58	14.55	12.93

[1] Contained 96.5% NaCl, 0.35% Zn, 0.30% Fe, 0.20% Mn, 0.10% Cu, 0.010% I, 0.010% Co, 0.010% Se, 6,000IU/g Vitamin A, 1,500 IU/g Vitamin D, and 1.00 IU/g Vitamin E.

[2] Values based analysis.

temperature and light controlled environment at 10°C to 15°C with a 14-h light: 10-h dark cycle. Each day, feed allowances were weighted out, divided into 3 equal portions, and fed at 0800, 1400 and 2000 h.

Sample collection

Dietary treatments continued for 35 d in each experiment. Feed samples were collected on the final 5 d, and pooled within animal across sampling days and stored at -30°C until further analysis. At the conclusion of the feed period, each lamb was weighted, and then stunned by captive bolt, bled and eviscerated before the morning feeding. The pancreas was removed, weighed and placed on ice. The caudal portion of the pancreas was removed, and sampled for analysis of pancreatic α-amylase activity. The pyloric junction was cut to separate the small intestine from the abomasum, and the mesentery was cut to separate the entire small intestine from the viscera, then total weight of the small intestine was determined. To rapidly determine length, the small intestine was laid out on a table and looped around pegs that were securely anchored to each end of the table as described by Bauer et al. (2001). Small intestinal sampling began immediately distal to the pylorus and terminated immediately proximal to the ileal-cecal junction. Six equally spaced 30-cm segments were removed and these sections are referred to as the relative site of 0, 20, 40, 60, 80 and 100 of the small intestine. The digesta in lumen of each small intestinal site was removed, weighed and then stored at -80°C until analysis. After these tissues were collected, the entire small intestinal digesta was emptied into an insulated container, and total digesta weight was determined. The abomasal digesta was removed, sampled and then stored at -80°C until analysis. The entire process, animal stunning through tissue collection, generally took less than 25 min.

Sample analysis

Dietary, abomasal and some ileum digesta samples were dried in a 55°C oven, ground to pass through a 2-mm screen. Diet was analyzed for dry matter and nitrogen content according to the procedures of the AOAC (1990). Feed and digesta starch were analyzed using the method of Herrera-Saldana and Huber (1989). Chromium in the feed and the digesta was determined using the atomic absorption spectrophotometry (TAS-986(F); PGENERAL Corporation, Beijing, China) according to Poore et al. (1991). Samples (1 g) were dried at 550°C and solubilized with a 6N mixture of HCl and HNO_3. Amounts of starch delivered to and disappearing in the small intestine were calculated from chromium concentration in feed and digesta. The distribution of corn particle size was measured by dry sieving. Dry sieving was performed with a system that equipped with seven sieves (sieve apertures of 4,000, 2,500, 1,500, 1,000, 750 and 500 μm and bottom pan). Mean particle size was calculated according to the method of Yu et al. (1998).

The small intestinal digesta (1.0 g) was combined with 10 ml of saline, and 2.5 g pancreatic tissue was homogenized in 250 ml of saline. The homogenate was centrifuged at 3,000 r/min for 10 minutes according to Russell et al. (1981), and then stored at -80°C until analysis for α-amylase activity within one week. Activity of α-amylase in the digesta and the pancreas was measured as described by Walker and Harmon (1996) and Jang et al. (2004). The homogenate was incubated with potato amylopectin for 6 min at 39°C. The amount of glucose was determined by comparison with maltose standards. One unit (U) of α-amylase activity is defined as 1 μmol of glucose produced per minute.

Table 2. Daily intake, apparent flow and disappearance of starch in the small intestine of lambs

Item	Experiment 1					Experiment 2				
	LS[1]	MS[1]	HS[1]	SEM[2]	p value	FC[1]	CC[1]	Whole[1]	SEM[3]	p value
Dry matter intake (g/d)	1,000	1,000	1,000	-	-	760	760	760	-	-
Starch intake (g/d)	276.2	352.0	456.1	-	-	270.0	270.0	270.0	-	-
Abomasal flow of starch (g/d)	57.3^{b}	117.3^{b}	141.3^{a}	14.08	0.015	83.4^{h}	99.9^{g}	134.7^{f}	6.89	<0.001
Ileum flow of starch (g/d)	18.9^{b}	25.0^{b}	37.3^{a}	2.85	0.007	28.8^{h}	36.1^{h}	65.3^{f}	5.73	0.003
Disappearance in the small intestine (g/d)	38.5	92.3	104.0	13.40	0.054	54.6	63.8	69.4	3.09	0.064

[1] LS = Low starch diet; MS = Medium starch diet; HS = High starch diet; FC = Finely cracked corn; CC = coarsely cracked corn; Whole = Whole corn.
[2] SEM = Standard error of means; N = 18.
[3] SEM = Standard error of means; N = 12.
[a, b, f, g, h] Row means with different superscripts differ ($p<0.05$).

Table 3. Pancreatic weight and α-amylase activity in lambs

Item	Experiment 1					Experiment 2				
	LS[1]	MS[1]	HS[1]	SEM[2]	p value	FC[1]	CC[1]	Whole[1]	SEM[3]	p value
Body weight (kg)	30.23	30.46	30.42	1.38	0.953	26.2	24.0	25.2	0.53	0.115
Pancreas weight										
g	39.6^{b}	46.2^{a}	35.3^{b}	2.02	0.033	31.8	30.7	33.5	1.17	0.406
g/kg body weight	1.34^{ab}	1.55^{a}	1.17^{b}	0.07	0.026	1.23	1.28	1.33	0.06	0.584
Pancreatic α-amylase activity										
U/g pancreas	293.65^{b}	497.73^{a}	620.88^{a}	45.82	0.002	389.35^{fg}	489.34^{f}	341.74^{g}	25.24	0.014
KU/pancreas	12.07^{b}	23.59^{a}	21.48^{a}	2.10	0.026	12.44^{fg}	15.00^{f}	11.17^{g}	0.76	0.048
U/pancreas/kg body weight	369.1^{b}	785.1^{a}	711.7^{a}	66.88	0.008	481.5^{fg}	626.4^{f}	442.5^{g}	36.03	0.039

[1] LS = Low starch diet; MS = Medium starch diet; HS = High starch diet; FC = Finely cracked corn; CC = coarsely cracked corn; Whole = Whole corn.
[2] SEM = Standard error of means; N = 18.
[3] SEM = Standard error of means; N = 12.
[a, b, f, g, h] Row means with different superscripts differ ($p<0.05$).

Statistical analysis

Data were analyzed as a completely randomized design using the GLM procedures of SAS (SAS Inst., Inc., Cary, NC). Lamb was used as the experimental unit. Statistical significance was declared at $p<0.05$. If the main effect from treatment was significant, means were separated by Duncan's multiple range tests.

RESULTS

Experiment 1: Dietary starch concentration

Dietary starch concentrations linearly increased ($p<0.05$) starch flow to the abomasum and the distal ileum, and tended to increase ($p = 0.054$) starch disappearance in the small intestine of lambs (Table 2).

Final body weight was not different among treatments (Table 3). Pancreas weight was greater ($p<0.05$) when comparing lambs fed the medium starch diet with the low and high starch diets. Pancreatic α-amylase activity was lower ($p<0.05$) in lambs fed the low starch diet.

α-Amylase activity in the digesta tended to be higher in proximal segments of the small intestine (Table 4). When expressed per gram of digesta, α-amylase activity was lower in lambs fed the low starch diet compared with others. However, there was a lower amount of small intestinal digesta in lambs fed the high starch diet ($p = 0.069$). Total α-amylase activity in the digesta was greater in lambs fed the medium starch diet, and paralleled that in the pancreas.

Experiment 2: Corn particle size

Mean particle size of corn was 0.76 and 2.57 mm for fine cracking and coarse cracking, respectively. Starch flow to the abomasum and the distal ileum ($p<0.05$), and disappearance in the small intestine ($p = 0.064$) increased progressively with increasing corn particle size (Table 2).

There was no effect of corn particle size on final body weight and pancreas weight (Table 3). Pancreatic α-amylase activity was greater ($p<0.05$) in lambs fed the coarsely cracked corn compared with finely cracked corn and whole corn.

The site pattern of α-amylase activity in the small intestinal digesta paralleled that in Experiment 1; it was greater in proximal segments (Table 4). Average α-amylase activity and total α-amylase activity in the digesta were significantly greater in lambs fed coarsely cracked corn ($p<0.001$).

DISCUSSION

In our experiment, greater pancreas weight was observed when the medium starch diet was fed. This is in agreement with others in which pancreatic weight is

Table 4. α-Amylase activity in the small intestinal digesta of lambs

Item	Experiment 1					Experiment 2				
	LS[1]	MS[1]	HS[1]	SEM[2]	p value	FC[1]	CC[1]	Whole[1]	SEM[3]	p value
α-Amylase activity in the small intestinal digesta (U/g)										
0[4]	6.62	9.52	10.47	0.98	0.140	6.01^{f}	6.73^{f}	2.61^{g}	0.73	0.015
20[4]	9.44	12.32	13.11	1.04	0.245	6.45^{g}	9.19^{f}	4.02^{h}	0.75	0.001
40[4]	9.66	14.03	12.49	1.00	0.112	11.15^{g}	14.32^{f}	6.59^{h}	1.06	<0.001
60[4]	6.01^{b}	11.39^{a}	11.06^{a}	1.08	0.045	9.12^{fg}	11.77^{f}	5.89^{g}	1.00	0.014
80[4]	3.06^{b}	8.14^{a}	8.76^{a}	1.04	0.021	4.06^{g}	9.29^{f}	5.17^{g}	0.95	0.021
100[4]	1.71^{b}	2.04^{b}	3.18^{a}	0.25	0.012	2.57^{g}	7.31^{f}	2.93^{g}	0.77	0.003
Average activity[5]	6.08	9.57	9.85	-	-	6.56^{g}	9.77^{f}	4.53^{g}	0.74	<0.001
Digesta weight (g)	637.0	602.8	433.2	43.80	0.069	287.2	295.2	340.0	16.02	0.228
Total α-amylase activity, (Ku/digesta)[6]	3.87	5.77	4.26	-	-	1.88^{g}	2.85^{f}	1.43^{g}	0.21	<0.001

[1] LS = Low starch diet; MS = Medium starch diet; HS = High starch diet; FC = Finely cracked corn; CC = Coarsely cracked corn; Whole = Whole corn.
[2] SEM = Standard error of means; N = 18.
[3] SEM = Standard error of means; N = 12.
[4] The relative site of the small intestine is 0 for pylorus and 100 for ileo-cecal junction and the site of the small intestine is the proportion of the small intestine length.
[5] The α-Amylase activity in digesta of different site of the small intestine was summed, and then obtained average activity.
[6] Total α-Amylase activity (KU/digesta) = average activity (U/g digesta)×digesta weight (g)/1,000.
[a,b,f,g,h] Row means with different superscripts differ ($p<0.05$).

unaffected when ruminants are fed very high-concentrate diets (concentrate: forage = 90:10) compared to those fed forage diets (Kreikemeier et al., 1990; Swanson et al., 2000). Pancreatic weight is a function of body weight differences (Wang et al., 1998). Differences in pancreatic weight were observed among treatments in Experiment 1 even when pancreatic weight was expressed as g/kg body weight. This difference may have been related to the different amount of RES or starch digested in the small intestine. In Experiment 2, pancreatic weight was not affected by RES. We speculate that the amount of digested starch in the small intestine, not of RES, controls the pancreatic weight in ruminants.

α-Amylase activities in the pancreas and the small intestinal digesta in the present study agree with values reported by Liu et al. (2004) and Zhang et al. (2005) in lambs and Kreikemeier et al. (1990) in calves. The highest activity of α-amylase was in proximal sites of the small intestine. Similar distribution of α-amylase activity in the small intestinal digesta was reported by Liu et al. (2004) and Zhang et al. (2005) in lambs. Mechanisms controlling the distribution pattern of α-amylase activity along the length of the small intestine are still unknown.

In our experiments, increased α-amylase activity in the pancreas was associated with increased total α-amylase activity in the small intestinal digesta. Total α-amylase activity in the pancreas and the small intestinal digesta was lower in lambs fed the low starch diet compared with the medium and high starch diets. This is supported by the work of Swanson et al. (2000).

Total α-amylase activity in the pancreas and the small intestinal digesta is elevated as ruminant increases their forage intake (Kreikemeier et al., 1990; Wang et al., 2000), but is unaffected by forage intake when metabolizable protein intake is the same among different treatments (Swanson et al., 2000). These results have shown that energy itself does not affect pancreatic α-amylase activity except with changes in protein supply. In addition, infusion of partially hydrolyzed starch into the rumen does not affect pancreatic α-amylase secretion (Walker and Harmon, 1995). Therefore, RES instead of energy affecting pancreatic α-amylase activity was considered in present experiments. In agreement with others, RES increased linearly along with increasing starch intake (Karr et al., 1966; Elizalde et al., 1999) and corn particle size (Knowlton et al., 1996; Rémond et al., 2004).

Previous researches have shown that postruminal infusions of partially hydrolyzed starch or glucose result in the decreases of expression (Swanson et al., 2000, 2002a, 2003) and secretion (Walker and Harmon, 1995; Swanson et al., 2002b, 2004) of pancreatic α-amylase in cattle and sheep. Intravenous infusion of glucose also inhibits pancreatic α-amylase secretion in lambs (Call et al., 1975). Partially hydrolyzed starch is made from raw starch hydrolyzed by a heat-stable α-amylase for 40 min (Walker and Harmon, 1995). Partially hydrolyzed starch and glucose are both the products, not the substrate of α-amylase. It was hypothesized that effects of partially hydrolyzed starch on pancreatic α-amylase activity may be different from native starch in the small intestine.

We found a tendency for a quadratic increase in total α-amylase activity in pancreas and the small intestinal digesta as native RES increased in both Experiment 1 and Experiment 2. Because of lower intake of metabolizable protein in Experiment 2 than Experiment 1 (Table 1), total

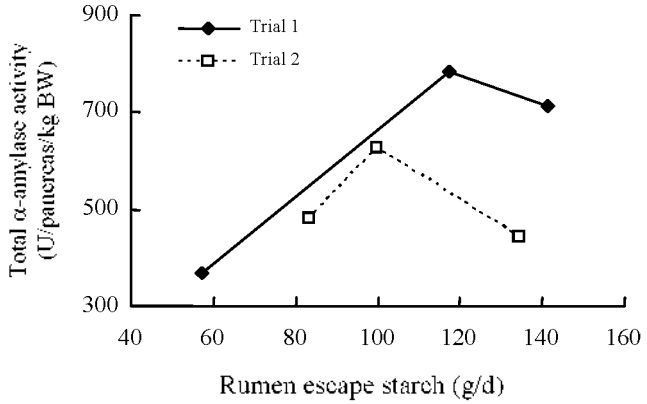

Figure 1. Effect of rumen escape starch on total pancreatic α-amylase activity in lambs.

pancreatic α-amylase activity was lower under similar RES intakes (Figure 1). The significance of the regression equation including two experiment data is poor ($p = 0.369$, regression not shown). Figure 1 show that the maximum total α-amylase activity would be reached when RES is about 100-120 g/d in 25-30 kg lambs. Duodenal infusion of more than 150 g/d raw starch decreases secretion of pancreatic α-amylase activity in sheep (Chittenden et al., 1984; Wang and Taniguchi, 1998). This is consistent with present tendency which total pancreatic α-amylase activity was decreased as RES increased when it was beyond 100-120 g/d (Figure 1). Other experiments allowing for more precise information about interactions between starch and protein supply in the small intestine are needed to show how it affects secretion and expression of pancreatic α-amylase.

Several earlier studies have shown pancreatic α-amylase activity is greater in steers and sheep fed high-concentrate diets compared with forage diets (Clary et al., 1969; Janes et al., 1985). However, steers fed alfalfa hay have greater pancreatic α-amylase activity than steers fed a grain diet (Russell et al., 1981; Kreikemeier et al., 1990). Wang et al. (2000) reported alfalfa hay tended to increase secretion of pancreatic α-amylase compared with ryegrass hay in sheep. Increases in the small intestinal protein supply enhance expression (Swanson et al., 2002a) and secretion (Wang and Taniguchi, 1998; Richards et al., 2003) of pancreatic α-amylase in ruminants. However, protein intake was not similar among dietary treatments in these experiments, making it difficult to discern whether the response was due to starch or protein supply. In the present experiments, dietary crude protein concentration was formulated to be similar metabolizable protein intakes among treatments. Differences in metabolizable protein flow among dietary treatments seemed to be small and probably did not so greatly influence pancreatic α-amylase activity.

Based on the data of these two experiments, it is concluded that the optimal RES for pancreatic α-amylase activity appears to be 100-120g/d. Further increases in RES will decrease pancreatic α-amylase activity, which may explain in part the low starch digestibility in the small intestine of ruminants fed high-starch diets and infused abomasally high level starch (Li et al. 2000; Harmon et al., 2004).

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