4. THE INFLUENCE OF POTATO FIBRE ON EXOCRINE PANCREATIC SECRETIONS AND ON PLASMA LEVELS OF INSULIN; SECRETIN AND CHOLECYSTOKININ IN GROWING PIGS

4.1. Summary

The effect of a potato fibre preparation on exocrine pancreatic secretions and on gastrointestinal hormone levels in plasma was studied in three 8 wk old piglets that were surgically fitted with a jugular vein catheter for blood sampling, a pancreatic duct catheter and a T-shaped duodenal cannula for collection of pancreatic juice. The animals were fed for 2 wk a control diet (experimental period 1), thereafter for 2 wk the control diet supplemented with 2% potato fibre (experimental period 2) and for another 2 wk the control diet again (experimental period 3). Additionally, intraduodenal (i.d.) infusions of the experimental diet, the control diet and potato fibre as well as intraveneous (i.v.) infusions of a solution containing Cholecystokinin (CCK) and secretin were administered.

Potato fibre in the diet evoked in tendency ($P<0.1$) an increase in the volume of secretion of pancreatic juice and a significant ($P<0.05$) increase both in the mean values of the total protein content and total activities of lipase, trypsin and α-amylase when compared to the control diet. The i.d. infusion of the control diet , experimental diet and fibre infusate as well as the i.v. administration of the hormone infusate led to a spontaneous secretory response of the exocrine pancreas. Besides gastrointestinal hormones, such as CCK, other factors such as short chain fatty acids may be involved in the regulation of the exocrine pancreas.

4.2. Introduction

It can be derived from various studies related both to animal and human nutrition that the dietary inclusion of plant fibre will affect the function of the gastrointestinal tract and the health status of the whole organism as well. Since the exocrine pancreas represents a major source of endogeneous secretions into the gastrointestinal tract, several studies have been

performed that focus on the effect of dietary fibre (DF) on the secretions of the exocrine pancreas in different species including humans.

In studies with growing pigs, Mosenthin and Sauer (1991) and Mosenthin et al. (1994) reported no effect of level and source of dietary fibre (DF) on the total activities of enzymes secreted in pancreatic juice when 10% cellulose, 10% strawmeal or 7.5% pectin were included in the diets. These results are in agreement with those of Zebrowska and Low (1987). The authors found that the replacement of 50% of wheat in a wheat-based diet (88.7% wheat) by 50% wheat bran did not affect the volume of secretion and the total activities of trypsin, chymotrypsin, carboxypeptidase A and B and of α-amylase in pancreatic juice.

However, these results are in contrast to those obtained by Langlois et al. (1987) in growing pigs who found an increase ($P<0.05$) in the volume (+115%) and protein content (+36%) of pancreatic juice when 40% wheat bran was included in a cereal-based diet at the expense of wheat. In contrast to the results reported by Zebrowska and Low (1987) total enzyme activities in pancreatic juice were increased ($P<0.05$) when wheat bran was included in the diet.

The effect of DF on exocrine pancreatic secretions in humans is contradictory. Dukehart et al. (1989) observed no influence of DF on exocrine pancreatic secretions, whereas Sommer and Kasper (1980) reported a decrease in the volume of pancreatic secretion ($P<0.025$) when carrageenan and guar meal were included in the diets; there was a trend ($P<0.1$) towards a lower secretion of protein and the specific α-amylase activity. A possible explanation of these results was provided by Dunaif and Schneeman (1981) in *in vitro* experiments. The incubation of human pancreatic juice with cellulose or xylan resulted in a substantial loss in the activities of all enzymes that were estimated. Similarly, incubation with wheat bran as well as with oat bran caused a decrease in the specific activities of α-amylase and chymotrypsin whereas the incubation with pectin increased ($P<0.05$) the specific activities of these enzymes. However, possible mechanisms underlying the regulatory effect of DF on enzyme activities under *in vitro* conditions are still unknown.

Potato fibre as a source of DF in diets for growing pigs was used in recent studies by Siljander-Rasi et al. (1998).The supplementation of a basal diet with 2% potato fibre reduced daily body weight gain (Siljander-Rasi et al., 1998). However, the influence of potato fibre on exocrine pancreatic secretions remains unclear and it can be speculated that potato fibre may stimulate the production of pancreatic enzymes thus facilitating digestion and subsequent absorption of nutrients; Botermans and Pierzynowski (1999) reported that an increase in body weight gain in growing pigs was positively correlated with an increase in exocrine pancreatic secretions.

The first objective of this study was to obtain further information on the effect of potato fibre in the diet of growing pigs on the exocrine pancreatic secretions. The second objective was to study the spontaneous response of the exocrine pancreas as influenced either by i.d. infusion of different dietary substrates including potato fibre or by i.v. infusion of gastrointestinal hormones, such as cholecystokinin (CCK) and secretin, that are known to stimulate exocrine pancreatic secretions .

4.3. Materials and Methods

4.3.1. Animals

A total of three 8 wk old piglets were obtained 4 wk after weaning from a Swedish Landrace herd (Odarslov's Research Farm, Swedish University of Agricultural Sciences, Lund). The average body weight (BW) was 12.4 kg at the time of surgery. The pigs were housed individually in pens under 12 h light : 12 h dark cycles (lights were on from 08.00 h to 20.00 h).

4.3.2. Surgical procedures

The pigs were surgically fitted with a chronic pancreatic duct catheter and a T-shaped duodenal cannula for collection and subsequent return of pancreatic juice into the duodenum according to Pierzynowski et al. (1988) and modified as described by Thaela et al. (1995). Additionally, a permanent jugular vein catheter for blood sampling was implanted according to procedures adapted from Pierzynowski et al. (1988).

4.3.3. Experimental procedures

The pigs were fed semi-ad libitum twice daily at 10.00h and 16.00h. Two different diets, a barley-based control diet (Växfor, Lantmännen, Stockholm, Sweden) and an experimental diet based on the control diet and supplemented with 2% potato fibre preparation (Povex^{TM}, Lyckeby Stärkelsen, Lyckeby, Sweden) were fed. The animals had free access to water. The chemical composition of the control diet and the potato fibre preparation is shown in Table 1 and 2, respectively. The chemical composition of the control diet was determined according to Naumann et al. (1976).

Table 1 Chemical composition of the control diet:

	Nutrients (g/kg DM)
Organic matter	937.0
Crude protein	177.8
Crude fat	52.1
Crude fibre	45.8
N- free extract	661.3
Starch	415.0
NDF	243.9
ADF	63.0
ADL	13.7

Table 2 Chemical composition of potato fibre (g/kg DM)[1]

Crude fibre	Cellulose	Pectin + hemicellulose	Lignin	Starch	Protein	Fat
700	230	450	20	100	70	3

[1]Data from Lyckeby Stärkelsen, Lyckeby, Sweden

After surgery, the pigs were allowed an 8-d recuperation period followed by three experimental periods, each lasting 14d. The experimental design is illustrated in Figure 1. The control diet was fed to all 3 pigs during the first and third experimental period whereas the experimental diet (control diet supplemented with potato fibre) was provided exclusively during the second period. Each of the experimental periods consisted of an 8-d adaptation period to the diet. Thereafter, within a period of 6 d, the secretory response of the exocrine pancreas to the i.d.. infusion of different dietary substrates and the i.v. infusion of a solution of two gastrointestinal hormones was studied. The infusates that were infused i.d. consisted of (1) 2% potato fibre and 98% saline (w/v), (2) 20% of the control diet and 80% saline (w/v) and (3) 20% of the experimental diet and 80% saline (w/v), which are referred to as the fibre, control diet and experimental diet infusates, respectively. In addition, a solution containing of 1 IDU (Ivy Dog Unit) CCK-33 (corresponding to 254 pmol CCK-33) and 1 CU (Clinical Unit) secretin (corresponding to 110 pmol secretin) dissolved in saline with 0.5% BSA (bovine serum albumin, Sigma, St. Louis, MO, US) was prepared which in the following is referred to as hormone infusate. According to Pierzynowski et al. (1999) the level of hormones in the infusate corresponds to physiological concentrations with the potential to stimulate the exocrine pancreas up to 50% of its capacity.

During the first and third experimental period the control diet, fibre and the hormone infusates were infused. However, during the second experimental period in which the experimental diet (with potato fibre) was fed, the control diet infusate was replaced by the experimental diet infusate. Within each experimental period the infusion treatments followed a randomised order with two repetitions.

The pigs received the last meal 17 h before the infusions started at 09.00h on d 9 to d 14 of each experimental period. The dietary infusates were infused i.d. over a period of 30 min at a rate of 5 ml/kg BW/h. Before the start and after the completion of these infusions pure saline was infused as control infusion at the same rate over a period of 60 min each (Figure 2). The hormonal infusate was infused i.v. over a period of 30 min and at a rate of 2 ml/kg BW/h. A control infusion containing saline with 0.5% BSA (Sigma, St. Louis, MO, US) was infused at the same rate over a period of 60 min before and 60 min after the hormonal infusion was received. The infusions were carried out by means of a syringe pump (Pompa Infuzyina Typ 340B, Unipan, Warsaw, Poland).

Pancreatic juice was collected quantitatively during both control infusion periods (2 x 60 min) and over a period of 30 min when the dietary and hormonal infusates were administered. It was collected by free drainage into a glass bottle at the right side of the animals attached to a belt allowing the animal to move freely during collections. The volume of secretion was recorded and the whole samples were stored at –20°C until analyses. Blood samples of 2 ml were taken 45, 90 and 150 min after the start of the control infusion. After the addition of 4 mmol EDTA and 1000 KIU (Kallikrein Inhibitor Units) Trasylol (Bayer, Leverkusen, Germany) as a proteinase-inhibitor, the blood samples were ice-chilled immediately and centrifuged at 4000 rpm. The plasma samples were stored at –20° C until analyses.

Figure 1 Experimental design (Experimental periods)

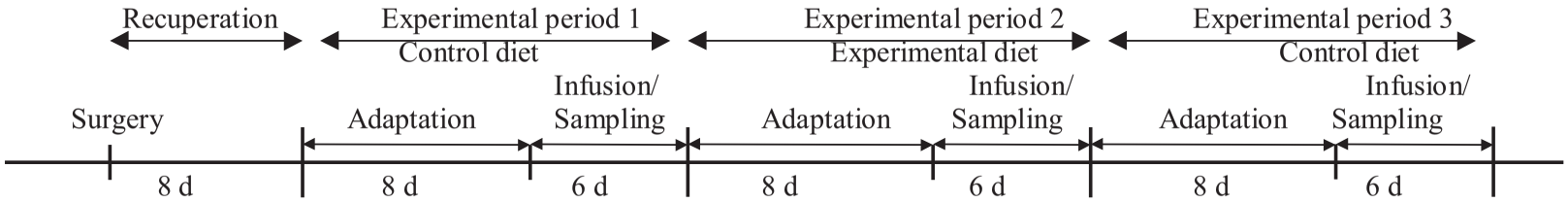
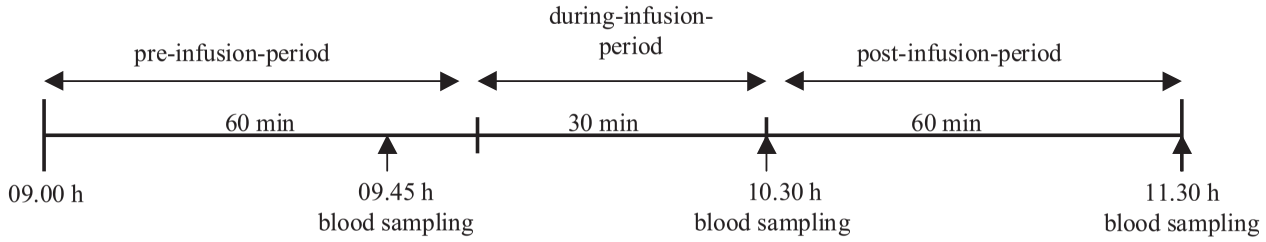


Figure 2 Experimental design (Infusions)



4.3.4. Chemical Analyses

Pancreatic juice samples were analysed for total protein content using the Lowry method (Lowry et al., 1951), performed on 96-well microwell plates, and BSA (Sigma, St. Louis, MO, USA) as a standard. Trypsin activities were estimated after enterokinase (Sigma, St Louis, MO, US) activation using N-α-benzoyl-DL-arginine-p-nitroanilide (Sigma, St Louis, MO, US) as a substrate (Pierzynowski et al, 1990). Lipase activities were determined by a pH-stat titration method using tributyrin as a substrate, as described by Borgström and Hildebrand (1975). Activities of α-amylase were determined by the method of Ceska et al. (1969) using the Phadebas amylase reagent as a substrate (Pharmacia Diagnostics, Uppsala, Sweden). One unit (U) of enzyme activity is defined as the amount of enzyme hydrolysing 1 μmol substrate per min. Total enzyme activities in pancreatic juice were expressed as U per 1 h of secretion per kg metabolic BW ($U/h/kg^{0.75}$). Blood samples were analysed for the plasma insulin levels using a radio-immuno-assay (RIA) with guinea pig antiporcine insulin (Milab, Malmö, Sweden), ^{125}I-labelled insulin and porcine insulin as a standard (Novo Novo Nordisk A/S, Bagsvaerd, Denmark) according to a method by Thaela et al. (1995). Plasma secretin concentrations were measured with a RIA according to Schaffalitzky de Muckadell and Fahrenkrug (1977). CCK levels in plasma were determined with a RIA according to Cantor and Rehfeld (1985). Plasma glucose levels were analysed by the glucose oxidase method described by Bruss and Black (1978).

4.3.5. Statistical analyses

Data were analysed using Statview software (1992, Abacus Concepts, Berkeley, CA, US). with 2-factorial ANOVA, Tukey range test (with experimental period in the model) and Student's t-test (with infusates in the model). The results were expressed as mean values + SEM.

4.4. Results

Pigs fed the diet containing potato fibre (experimental period 2) showed in tendency ($P>0.1$) an increase in the volume of secretion of pancreatic juice and a significant ($P<0.05$) increase both in the mean values of the total protein content and total activities of lipase, trypsin and α-amylase when compared to corresponding values in period 1 (Table 3). These values remained at that level after feeding the pigs the control diet in period 3 resulting in an 1.5-fold increase in the volume of secretion, although not significant, and in a 2.2-fold increase ($P<0.05$) in the total protein content compared to those values obtained in period 1. Similar differences were obtained for total trypsin and lipase activities which increased ($P<0.05$) 2.2-fold and 2.4-fold, respectively. No significant differences between period 2 and 3 were obtained for the volume of secretion, total protein content and total activities of trypsin and lipase. The total α-amylase activity increased ($P<0.05$) 2.8-fold from period 1 to period 2 and decreased ($P<0.05$) 1.9-fold in period 3 as compared to period 2. However, the total α-amylase activity in period 3 is still 1.5-fold higher ($P<0.05$) than in period 1.

Table 3 The influence of diet on the volume of secretion, protein secretion and total enzyme activities in pancreatic juice in experimental periods 1, 2 and 3

Experimental Period	1		2		3	
Diet	Control		Experimental		Control	
	Mean	SEM[1]	Mean	SEM	Mean	SEM
Volume, (ml/h/kg$^{0.75}$)	3.9	0.8	6.3	0.8	5.7	0.8
Protein, (mg/h/kg$^{0.75}$)	6.3^{a}	0.4	10.9^{b}	0.6	13.9^{b}	2.0
Trypsin, (U/h/kg$^{0.75}$)	4.6^{a}	0.3	8.6^{b}	0.8	10.0^{b}	1.4
Lipase, (U/h/kg$^{0.75}$)	1.2^{a}	0.3	2.6^{b}	0.4	2.9^{b}	0.3
α-amylase, (U/h/kg$^{0.75}$)	320^{a}	20	890^{b}	30	480^{c}	180

[1] Standard error of the mean within a experimental period

^{a,b,c} Means in the same row not followed by the same superscript are significantly different ($P<0.05$)

As is shown in Table 4, the mean values for plasma insulin tended to be higher (P<0.1) in pigs adapted to the diet supplemented with potato fibre; there was a 2.1-fold increase compared to period 1 and 1.3-fold increase in comparison to period 3. The plasma glucose and secretin levels were not affected (P>0.1) by the different dietary treatments whereas the CCK levels decreased (P<0.05) following feeding of pigs with the control diet in period 3.

Table 4 The influence of diet on the plasma levels of insulin, glucose, secretin and cholecystokinin (CCK)

Experimental Period	1		2		3	
Diet	control		experimental		control	
	Mean	SEM[1]	Mean	SEM	Mean	SEM
Glucose, mmol, L	3.82	0.2	4.00	0.2	3.78	0.1
Insulin, pmol/l	8.3^{A}	2.0	17.3^{B}	1.0	13.6^{A}	2.0
Secretin, pmol/L	8.0	3.1	9.4	3.5	9.9	4.3
CCK, pmol/L	4.3^{a}	0.6	3.8^{ab}	0.5	2.9^{b}	2.9

[1] Standard error of the mean within a experimental period

^{A,B} means in the same row not followed by the same superscript are (P<0.1)

^{a,b} means in the same row not followed by the same superscript are different (P<0.05)

The time of infusion had a major effect on the volume of secretion of pancreatic juice in all three periods; the mean values of the infusates were higher (P<0.05) when measured during the period (30 min.) of infusion of the different infusates than during the pre- and post-infusion periods when the control infusions with saline were administered (Table 5). Moreover, the hormone infusate induced in period 1 during all three infusion periods a higher (P<0.05) volume of secretion of pancreatic juice as compared to the control diet infusate and also in comparison to the fibre infusate except for the pre-infusion period. However, during periods 2 and 3 this stimulatory effect of the hormone infusate was less pronounced and in most cases not significant (P>0.05).

In period 2 the mean values for total protein content in pancreatic juice were higher (P<0.05) during the period (30 min.) in which the different infusates were administered compared to the

pre- and post-infusion periods with saline as control; they were also higher ($P<0.05$) compared to the pre-infusion period in period 3 (Table 6).

In periods 1-3 total trypsin activities were numerically higher for all infusates compared to the control infusions in the pre- and post-infusion periods (Table 7). These differences were significant ($P<0.05$) for period 2. In addition, the control diet infusate induced in period 1 higher ($P<0.05$) total trypsin activities when determined during the period of infusion as compared to the pre- and post-infusion periods.

Total lipase activities were higher ($P<0.05$) in periods 2 and 3 for all infusates compared to the control infusions in the pre- and post-infusion periods (Table 8). Furthermore, the fibre infusate caused higher ($P<0.05$) total lipase activities in pancreatic juice as compared to the control diet in period 1.

As shown in Table 9, the mean values for total α-amylase activities in pancreatic juice were equal or higher during the period of infusion of the different infusates than during the pre- and post-infusion periods, the difference being significant ($P<0.05$) for period 2. Extremely low total α-amylase activities for the post- and pre-infusion period of the control diet infusate were obtained in periods 1 and 3, respectively. These differences were significant ($p<0.05$) compared to corresponding values for the fibre and hormone infusate obtained in the post-infusion period of period 1 and the pre-infusion period of period 3.

Table 5 The effect of time period of infusion of control diet, experimental diet, fibre or hormone infusate on the volume of secretion of pancreatic juice in pigs.

Experimental Period	1			2			3		
Infusion Period	Pre-	During-	Post-	Pre-	During-	Post-	Pre-	During-	Post-
Infusate									
Control diet[1]	2.1^{ab}	2.8^{b}	1.3^{a}				6.3^{cd}	5.0^{c}	6.3^{cd}
Experimental diet[1]				5.2^{bcd}	5.6^{cd}	4.1^{c}			
Fibre[1]	3.9^{bc}	3.8^{bc}	5.2^{c}	6.5^{cd}	7.9^{cd}	6.1^{d}	4.3^{ab}	6.2^{cd}	3.1^{bc}
Hormone[1]	4.5^{c}	8.5^{d}	3.6^{b}	5.6^{bcd}	10.8^{de}	4.6^{abc}	5.2^{c}	10.3^{e}	4.6^{c}
Mean[2]	3.5^{a}	5.0^{bc}	3.4^{a}	5.8^{bc}	8.1^{e}	4.9^{bc}	5.3^{bc}	7.1^{de}	4.7^{bc}
SEM[3]	0.7	1.0	0.6	0.4	0.9	0.3	0.6	0.9	0.6

[1] Mean values for pre-infusion, during-infusion and post-infusion periods (ml/h/kg$^{0.75}$) within an infusion period
[2] Mean values of control diet, experimental diet, fibre and hormone infusates (ml/h/kg$^{0.75}$) within an infusion period
[3] Standard error of the mean within an infusion period
[a,b,c,d,e] Means in the same row or in the same column not followed by the same superscript are different ($P<0.05$)

Table 6 The effect of time period of infusion of control diet, experimental diet, fibre or hormone infusate on total protein content of pancreatic juice in pigs.

Experimental Period	1			2			3		
Infusion Period	Pre-	During-	Post-	Pre-	During-	Post-	Pre-	During-	Post-
Infusate									
Control diet[1]	5.1 ^{ab}	8.7 ^{bc}	3.5 ^{a}				14.9 ^{cd}	15.0 ^{cd}	21.6 ^{e}
Experimental diet[1]				7.9 ^{bc}	14.3 ^{cd}	10.1 ^{c}			
Fibre[1]	8.3 ^{bc}	5.6 ^{ab}	6.7 ^{b}	10.0 ^{c}	14.8 ^{cd}	10.5 ^{c}	9.8 ^{bc}	17.2 ^{de}	9.0 ^{bc}
Hormone[1]	6.3 ^{b}	7.8 ^{b}	4.6 ^{a}	8.8 ^{bc}	14.9 ^{cd}	6.6 ^{bc}	11.5 ^{cd}	17.2 ^{de}	9.1 ^{bc}
Mean[2]	6.6 ^{a}	7.4 ^{a}	4.9 ^{a}	8.9 ^{b}	14.7 ^{c}	9.1 ^{b}	12.1 ^{c}	16.4 ^{d}	13.3 ^{cd}
SEM[3]	0.9	0.6	0.6	0.6	0.1	0.7	1.5	0.4	2.4

[1] Mean values for pre-infusion, during-infusion and post-infusion periods (mg/h/kg$^{0.75}$) within an infusion period
[2] Mean values of control diet, experimental diet, fibre and hormone infusates (mg/h/kg$^{0.75}$) within an infusion period
[3] Standard error of the mean within an infusion period
^{a,b,c,d,e} Means in the same row or in the same column not followed by the same superscript are different ($P<0.05$)

Table 7 The effect of time period of infusion of control diet, experimental diet, fibre or hormone infusate on total trypsin activity of pancreatic juice in pigs.

Experimental Period	1			2			3		
Infusion Period	Pre-	During-	Post-	Pre-	During-	Post-	Pre-	During-	Post-
Infusate									
Control diet[1]	4.1^{ab}	7.5^{c}	2.9^{a}				10.5^{cd}	10.3^{cd}	15.6^{e}
Experimental diet				5.9^{abc}	10.8^{cd}	7.3^{bcd}			
Fibre[1]	5.9^{bc}	4.5^{ab}	5.0^{b}	8.9^{bcd}	12.5^{cd}	8.7^{cd}	7.0^{cd}	14.7^{de}	6.8^{b}
Hormone[1]	4.2^{ab}	5.7^{bc}	2.6^{a}	7.7^{bcd}	11.0^{cd}	5.2^{abc}	7.3^{bcd}	11.7^{cd}	5.8^{bc}
Mean[2]	4.7^{b}	5.9^{b}	3.5^{a}	7.5^{c}	11.4^{d}	7.1^{c}	8.3^{cd}	12.2^{d}	9.4^{cd}
SEM[3]	0.6	0.5	0.5	0.9	0.3	0.7	1.1	0.8	2.0

[1] Mean values for pre-infusion, during-infusion and post-infusion periods (U/h/kg$^{0.75}$) within an infusion period
[2] Mean values of control diet, experimental diet, fibre and hormone infusates (U/h/kg$^{0.75}$) within an infusion period
[3] Standard error of the mean within an infusion period
[a,b,c,d,e] Means in the same row or in the same column not followed by the same superscript are different ($P<0.05$)

Table 8 The effect of time period of infusion of control diet, experimental diet, fibre or hormone infusate on total lipase activity of pancreatic juice in pigs.

Experimental Period	1			2			3		
Infusion Period	Pre-	During-	Post-	Pre-	During-	Post-	Pre-	During-	Post-
Infusate									
Control diet[1]	0.7^{a}	0.4^{a}	0.2^{a}				3.2^{bd}	2.8^{bd}	3.4^{bd}
Experimental diet[1]				2.5^{b}	2.2^{b}	1.2^{ab}			
Fibre[1]	2.1^{b}	1.7^{b}	1.4^{b}	3.1^{bc}	3.8^{bc}	3.1^{bc}	1.5^{b}	3.7^{bc}	1.8^{b}
Hormone[1]	1.1^{ab}	1.5^{ab}	1.1^{ab}	2.2^{b}	3.2^{bc}	1.7^{ab}	3.0^{bd}	4.7^{c}	1.9^{b}
Mean[2]	1.3^{a}	1.3^{a}	0.9^{a}	2.6^{b}	3.1^{c}	2.0^{b}	2.6^{b}	3.7^{c}	2.4^{b}
SEM[3]	0.4	0.2	0.2	0.3	0.3	0.3	0.5	0.3	0.3

[1] Mean values for pre-infusion, during-infusion and post-infusion periods (U/h/kg$^{0.75}$) within an infusion period
[2] Mean values of control diet, experimental diet, fibre and hormone infusates (U/h/kg$^{0.75}$) within an infusion period
[3] Standard error of the mean within an infusion period
[a,b,c,d] Means in the same row or in the same column not followed by the same superscript are different ($P<0.05$)

Table 9 The effect of time period of infusion of control diet, experimental diet, fibre or hormone infusate on the total α-amylase activity of pancreatic juice in pigs.

Experimental Period	1			2			3		
Infusion Period	Pre-	During-	Post-	Pre-	During-	Post-	Pre-	During-	Post-
Infusate									
Control diet[1]	450^{bc}	460^{bc}	80^{a}				70^{a}	170^{ab}	150^{b}
Experimental diet[1]				670^{bcd}	1470^{cd}	560^{bc}			
Fibre[1]	590^{bc}	290^{b}	340^{bc}	920^{cd}	1080^{cd}	810^{cd}	450^{bc}	950^{bc}	440^{bc}
Hormone[1]	280^{b}	560^{bc}	240^{b}	820^{cd}	1170^{cd}	490^{bc}	420^{bc}	1260^{cd}	450^{bc}
Mean[2]	440^{b}	440^{b}	220^{a}	800^{c}	1240^{d}	620^{b}	310^{ab}	800^{bc}	350^{ab}
SEM[3]	90	50	50	70	100	50	120	200	70

[1] Mean values for pre-infusion, during-infusion and post-infusion periods (U/h/kg$^{0.75}$) within an infusion period
[2] Mean values of control diet, experimental diet, fibre and hormone infusates (U/h/kg$^{0.75}$) within an infusion period
[3] Standard error of the mean within an infusion period
[a,b,c,d] Means in the same row or in the same column not followed by the same superscript are different ($P<0.05$)

4.5. Discussion

It has been shown that the principal effect of dietary fibre on the exocrine pancreas of pigs is an increase in the volume of secretion (Zebrowska and Low, 1987, Mosenthin and Sauer, 1991). The results of the present study confirm that native potato fibre stimulates the secretion of pancreatic juice when the pigs were changed from the control diet in period 1 to the experimental diet in period 2. These results support findings by Mosenthin et al. (1994) who also reported a higher secretion of pancreatic juice when pectin as highly viscous fibre source was fed to growing pigs. Moreover, the feeding of the control diet without potato fibre resulted in a significant decrease in α-amylase activity in period 3 compared to period 2. However, the volume of secretion, the total protein content as well as the total activities of trypsin and lipase remained at the same level when the pigs were switched back from the experimental diet in period 2 to the control diet in period 3. As the volume of secretion in growing pigs increases with age (Makkink, 1993) it can be speculated if the higher volume of secretion in period 3 compared to period 1 is related to an increase in BW and/or age of the pigs.

In general, an uniform pattern both in the secretion of pancreatic juice, and the total output of protein and enzyme activities (trypsin, lipase, α-amylase) was obtained when either different substrates (control diet infusate, experimental diet infusate, fibre infusate) were administered into the duodenum or when gastrointestinal hormones such as CCK and secretin were infused i.v. These infusates stimulated the exocrine pancreas by inducing a spontaneous secretory response of the pancreas during the time period of infusion. Consequently, the volume of secretion, the total output of protein, trypsin, lipase and α-amylase were consistently and in most cases lower ($P<0.05$) in the pre- and post-infusion periods than the corresponding values determined during the infusion of the different infusates. This spontaneous response to the infusion treatments corresponds to the immediate postprandial response after feeding as reported by Thaela et al. (1995).

It can be further derived from the results of this study that the presence of substrates in the duodenum *per se* has a much more pronounced effect on the pattern of secretion of the exocrine pancreas than the source of substrates itself. The time period when the different infusates were infused was uniformingly characterised by an increased secretion of pancreatic

juice, protein and enzymes, irrespective of the source of substrate (control diet infusate, experimental diet infusate, fibre infusate) administered. These results could indicate that during this phase the acinar (producing enzymes) and ductal (producing fluid) cells of the pancreas were stimulated, probably hormonally via CCK and secretin (Pierzynowski et al., 1999) and neurally via the vagus nerve (Solomon, 1987). Considering the increased secretion of pancreatic juice, protein and enzymes during the i.v. infusion of CCK and secretin, it can be concluded that the secretory response of the pancreas to the infusion of different substrates is controlled via feed back mechanisms mediated by the plasma levels of those gastrointestinal hormones (Owyang, 1994) that are involved in the stimulation of the acinar and ductal cells of the pancreas.

According to Botermans and Pierzynowski (1999) higher exocrine pancreatic secretions are positively correlated to daily weight gain. If under the experimental conditions described herein the positive response of the exocrine pancreas to potato fibre supplementation will have a similar effect needs to be verified.

It is likely possible that potato fibre affects the microbial activity of the large intestine and, in consequence, the production of short chain fatty acids (SCFA). Kato et al. (1989) and Mineo et al. (1990) could show that the i.v. infusion of SCFA stimulated both the exocrine and endocrine pancreas in ruminants. In pigs, SCFA are involved in the regulation of stomach emptying (Malbert et al., 1994). It can be speculated if the stimulating effect of potato fibre on the pancreas could also be attributed, at least in part, to the production of SCFA in the large intestine. Moreover, SCFA are potent stimulators of insulin release in ruminants (Manns and Boda, 1967). Therefore, a stimulation of the exocrine pancreas via a well described insulin-pancreatic acinar axis is possible (Williams and Goldfine, 1985, Pierzynowski, 1990). Moreover, the plasma levels of CCK were lower ($p<0.05$) in pigs adapted to the experimental diet in period 2 and also in pigs fed the control diet again in period 3. It can be derived from these result that an increase in enzyme secretion as observed in these periods is not necessarily associated with a higher CCK level in plasma. A possible stimulating effect of SCFA on the interdigestive, postprandial and gut hormone stimulated pancreatic secretion in pigs warrants further investigations.

4.6. Conclusions

The secretory response of the exocrine pancreas can be stimulated by the presence of potato fibre in the diet. Moreover, a spontaneous secretory response of the pancreas following the i.d. infusion of different dietary substrates and the i.v. infusion of CCK and secretin resulted in higher levels of volume of secretion, protein and enzymes in pancreatic juice. Obviously, higher enzyme activities are not necessarily associated with higher CCK levels in plasma; a possible stimulating effect of SCFA on the exocrine pancreas warrants further investigation.

4.7. References

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