The Influence of Lipids on Exocrine Pancreatic Secretions in Pigs - Review -

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ABSTRACT : The characteristics of the exocrine pancreatic secretions in pigs and its hormonal regulation as influenced by dietary lipids are reviewed. There is clear evidence that the secretion of lipolytic enzymes is positively correlated with the amount of fat consumed by the pig. For example, there was an increase in the specific lipase activity by 83% after the dietary fat content was increased from 5% to 25%. Moreover, it was shown that also the quality of fat has an influence on exocrine pancreatic secretions. Peroxidized canola oil stimulated total lipase secretion much more than non-peroxidized oil. The influence of fatty acid composition on exocrine pancreatic secretions is discussed equivocally. Some authors showed that saturated fats stimulated the exocrine pancreatic secretions more than unsaturated. Others showed that the chain length of fatty acids had a strong influence on pancreatic secretions as well. Due to the different surgical methods used for sampling of pancreatic juice and wide variety of fats and oils used in these studies, direct comparisons between studies are extremely difficult to make. Plasma levels of hormones such as cholecystokinin (CCK), neurotensin (NT) and peptide YY (PYY) are influenced by the nutrient composition of the diet. With increasing amounts of fat present in the small intestine, the release of these hormones was stimulated. There is evidence that CCK release is dependent on the chain length of the fatty acids. Medium chain triglycerides stimulated the CCK release more than long chain triglycerides. Neurotensin was released more by unsaturated than by saturated fatty acids; similar results were observed for the PYY release. However, results are contradictory and further investigations are warranted that focus on the underlying mechanisms involved in the regulatory response of the exocrine pancreas to lipids of different origin. (*Asian-Aus. J. Anim. Sci. 2000. Vol. 13, No. 5 : 711-719*)

Key Words : Pancreatic Secretions, Pigs, Lipids

INTRODUCTION

The understanding of the complex physiological digestive processes plays a major role in optimizing feeding strategies for farm animals. As the pancreas is an important part of the digestive system and the main source of digestive enzymes, knowledge about its physiological processes is important. The pancreas consists between 90 to 95% of exocrine and between 2 to 3% of endocrine tissue (Brannon, 1990); it secretes enzymes for digestion of lipids, carbohydrates and proteins either in an active or inactive form, as well as bicarbonate for the neutralisation of hydrochloric acid from the stomach and other components (table 1).

The development of pancreatic fistulation techniques for several animal species including the pig (Wass, 1965; Pekas et al., 1966; Aumaitre, 1972; Corring et al., 1972; Partridge et al., 1982; Zebrowska et al., 1983; Hee et al., 1985; Pierzynowski et al., 1988) gave researchers the opportunity to study *in vivo* the various physiological mechanisms which regulate pancreatic secretions. The response of the pancreas to dietary factors and different mechanisms controlling the secretions of the exocrine pancreas is of particular interest. This review will focus mainly on the effects of lipids of different origin on quantitative and qualitative aspects of pancreatic secretions in pigs and on the regulation of the exocrine pancreas mediated by gastrointestinal hormones.

Table 1. Composition of pancreatic juice

Enzymes		
	Proteases	Trypsinogen 1, 2, 3
		Chymotrypsinogen A, B, C
		Proelastase 1, 2
		Kallikreinogen
		Procarboxypeptidase A1, A2, B1, B2
	Glycosidase	α-Amylase
	Lipases	Triglyceride lipase
		Colipase
		Carboxylester hydrolase
		Phospholipase A2
	Nucleases	DNase I
		RNase
Electrolytes		Chloride
		Sodium
		Potassium
Bicarbonate		
Mucins		
Urea		

After: Kidder and Manners (1987); Schulz, (1987); Lowe, (1994b).

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Table 2. Fatty acid composition (% of total fatty acid content) of lipids present in feedstuffs

Fatty acid	Corn oil	Sunflower oil	Rapeseed oil	Olive oil	Lard	Fish oil	Coconut oil
C 8:0							5-10
C 10:0							5-10
C 12:0							44-51
C 14:0	0.5 - 3	0 - 1	0 - 1.5		1- 4	1- 8	13-19
C 16:0	8 -15	4 - 8	1 - 6	12	21-31	10-28	7-12
C 16:1	0.2 - 0.5	0.1- 1	0 - 2		1- 5	7-13	
C 18:0	1 - 4	2 - 5	1 - 4	2	11-21	0- 3	1- 4
C 18:1	27 -43	14 -50	11 -39	61	40-52	6-24	5- 8
C 18:2	35 -62	33 -77	10 -22	15	2- 8	1-12	1- 2
≥ C 20 unsaturated			32 -57			22-58	

after: Kirchgessner, (1987); Yago et al. (1997c).

CHEMICAL COMPOSITION OF LIPDS AND LIPOLYTIC ENZYMES

Lipids have a very high energy density. Consequently, they are a valuable component of pig diets. In addition, because of the high energy content of lipids, there is a margin for inclusion of other components. This is of special interest from an economical point of view as other dietary components can be chosen to lower feed costs and/or to increase the nutritive value of the diet. Lipids contain three essential fatty acids, namely linoleic, γ-linolenic and arachidonic acid which are important for the biosynthesis of phospholipids. These lipids are important components of cell membranes and essential for the formation of prostaglandins, which are involved in the regulation of various metabolic processes (Kirchgessner, 1987).

Lipids used in animal nutrition are triacylglycerols with fatty acids in positions one, two and three of glycerol. Lipids used in animal nutrition differ widely in chemical structure with respect to fatty acid composition. For example, vegetable oils, such as olive, soybean, canola or sunflower, consist mainly of unsaturated fatty acids with a chain length of C18, whereas tropical plant oils, such as palm and coconut oil, contain saturated fatty acids with a chain length of C12 to C14. Fats derived from marine animals, such as fish oil, contain polyunsaturated fatty acids with a chain length longer than C20, whereas lard or tallow contain saturated fatty acids with a chain length of C16 and C18 (table 2). These differences in fatty acid profiles of fats and oils may influence the physiology of the pancreas in different ways.

Jensen et al. (1997) showed that most of the lipids in diets for piglets are digested by enzymes secreted by the exocrine pancreas; in younger animals gastric lipase is capable to hydrolyze lipids. Fats are non-soluble in water and therefore fat must be emulsified before being cleaved. Digestion is carried out by means of bile salts and phospholipids which are secreted with bile into the duodenum. The exocrine pancreas secretes three different lipolytic enzymes into the duodenum: lipase, carboxylester hydrolase and phospholipase A_2. Lipase is the most important fat-cleaving enzyme. This enzyme is capable to cleave linkages at positions one and three whereas carboxylester hydrolase cleaves all linkages. Prophospholipase A_2 is activated by trypsin to phospholipase A_2 which cleaves phospholipids such as phosphatidylcholine (lecithin) and sphingomyelin specifically at position two (Rinderknecht, 1993; Lehninger et al., 1994; Lowe, 1994a; Lowe, 1994b).

Colipase, secreted by the pancreas, is an essential cofactor involved in the digestion of lipids as it catalyses the attachment of lipase to emulsified lipids (Rinderknecht, 1993).

EFFECT OF LEVEL OF FAT IN THE DIET ON THE SECRETIONS OF THE EXOCRINE PANCREAS

Several authors have demonstrated that an increase in dietary fat level is closely correlated with a higher secretion of lipase (Corring et al., 1989). According to Sabb et al. (1986) the specific pancreatic lipase activity in the young rat adapts primarily to the amount of dietary fat. A diet with a high fat content (>57% energy from fat) increased specific lipase activity by 200% compared to diets in which less than 47% of the energy was derived from fat. Mourot and Corring (1979) showed similar results in pancreatic tissue of pigs. The animals were fed a diet containing either 5 or 25% peanut oil. The specific lipase activity was 83% higher when the diet containing 25% fat was fed. An increase in the specific lipase activity by 700% was observed by Corring (1980) in pigs after increasing the daily triacylglyceride intake from 30 to 220 g. Hee et al. (1988) also showed in pigs that the total lipase activity increased 6-fold when the level of dietary fat (tallow) was increased from 2 to 10%. Ozimek et al. (1995) reported in studies with pigs an increase in the total lipase activity by 340% after 15% starch in the diet was replaced by 15% canola oil.

However, this adaptation of the exocrine pancreas to the amount of dietary fat was not observed in dogs fed either a high fat or a high starch-containing diet (Manas et al., 1996). In the rabbit it was shown that pancreatic lipase activity increased 2-fold when the amount of dietary fat was increased from 2.7% to 12% (Borel et al., 1991).

EFFECT OF QUALITY OF FAT ON THE EXOCRINE PANCREAS

There is a scarcity of information on the effect of quality of fat on the secretory activity of the pancreas in pigs. It is known that hydroperoxides, which are the primary products resulting from oxidative processes of unsaturated fat during storage and processing, are involved in the production of rancidity, odours, bad flavours and even toxic compounds. Ozimek et al. (1995) compared the effect of peroxidized versus non-peroxidized canola oil in a diet for growing pigs. After replacement of 15% canola oil by 15% peroxidized canola oil (heated at 180℃ for 12 h) the total lipase activity increased 2.5-fold.

EFFECT OF FATTY ACID COMPOSITION ON THE EXOCRINE PANCREAS

Several studies have been conducted to investigate the response of the exocrine pancreas to changes in the fatty acid profile of dietary or intraduodenally infused lipids. However, most of these studies were based on slaughter investigations, in particular with rats. These studies do not allow for the measurement of total enzyme activities since long-term collections of pancreatic juice are not possible. According to Sauer and Mosenthin (1999) only results expressed in total rather than specific activities are a true reflection of the effect of dietary treatments on the exocrine pancreas since differences in specific activities may simply reflect dilution by pancreatic juice.

The results obtained in studies with rats are contradictory with respect to the influence of the degree of saturation and/or chain length of fatty acids on lipase activities. Lanckman et al. (1971) showed that the lower the degree of saturation, the higher the specific lipase activity. Corn oil with a high content of saturated fatty acids (polyunsaturated/ saturated (p/s) ratio was 0.1) had a less pronounced effect on the specific lipase secretion in the rat than the same amount of sunflower oil in the diet (p/s ratio is 6.5). These observations were confirmed by Sabb et al. (1986) and Ricketts and Brannon (1994). According to these authors the inclusion of polyunsaturated fatty acids increased specific lipase activities more than saturated fatty acids. However, as was pointed out by Saraux et al. (1982), specific lipase and colipase activities were not affected by the degree of saturation or the chain length of fatty acids when rats were fed a diet containing 40% fat. It should be emphasized, however, that estimates of specific enzyme activities in pancreatic homogenates do not provide information on the diurnal variation. From experiments with fistulated calves (Zabielski et al., 1993; Zabielski et al., 1997a) it was shown that the secretory response of the exocrine pancreas can change within minutes. This has to be taken into consideration when interpreting results obtained by means of slaughter investigations.

Only a few studies have been conducted with pigs in which the effect of fatty acid composition on pancreatic secretion of lipolytic enzymes was determined. Simoes (1986) investigated the influence of sunflower oil and lard on exocrine pancreatic secretions in the growing pig. A control group received a starch-based diet whereas two experimental groups were fed diets in which 21% lard or 21% sunflower oil were included at the expense of starch. The pigs were slaughtered on d 12 after the start of the experiment and pancreatic tissue homogenates were obtained. Although the pancreatic protein content was similar in all groups, the specific lipase activity was 60% higher in the pigs fed lard and about 300% higher in the pigs fed sunflower oil compared to the control treatment. These significant differences between the treatments indicate that the degree of saturation or the chain length of the fatty acids may influence specific lipase activity.

Only one study in which the influence of fats differing in chain length and degree of saturation on exocrine pancreatic secretions was conducted with pigs fitted with permanent pancreatic cannulas allowing the determination of both specific and total enzyme activities. Gabert et al. (1996) conducted two experiments using two different surgical procedures to collect pancreatic juice. Three barrows were fitted with a pancreatic duct catheter according to Pierzynowski et al. (1988) and three barrows according to the pouch method as described by Hee et al. (1988). The animals of each group received three different wheat-based diets containing 15% fish oil, rapeseed oil and coconut oil, respectively. In pigs fitted with the pouch no differences between the parameters measured were observed. The coconut and fish oil treatments evoked an increase in total activity of chymotrypsin and carboxylester hydrolase, however, this was only observed in pigs fitted with a pancreatic duct catheter. As considerable differences between both surgical methods exist, Gabert et al. (1996) claimed that these differences may be explained by different physiological changes induced by the two methods. The implantation of a catheter into the pancreatic duct bypasses the *sphincter oddi* and the formation of a duodenal pouch involves anastomosis of the duodenum and

Table 3. Effect of different lipids on exocrine pancreatic secretions in different species

Species	Lipids	Pancreatic secretions	Reference
Pig	sunflower oil, lard	unsaturated long chain fatty acids (sunflower oil) increased specific lipase activities more than lard	Simoes, 1986
	fish-, rapeseed-, coconut oil	unsaturated, long chain fatty acids (fish oil) increased total carboxylester hydrolase activities more than rapeseed and coconut oil	Gabert et al., 1996
Dog	sunflower, olive oil	polyunsaturated fatty acids (sunflower oil) increased total lipase activities more than mono-unsaturated fatty acids (corn oil)	Ballesta et al., 1990
Rat	sunflower oil, corn oil	polyunsaturated fatty acids (sunflower oil) increased specific lipase activities more than saturated fats (corn oil)	Deschodt Lanckman et al., 1971
	safflower-, corn,- olive-, coconut oil, butter, lard	polyunsaturated fatty acids (safflower oil) increased specific lipase activities more than corn,- olive-, coconut oil, butter and lard	Sabb et al., 1986
	medium chain triglycerides (C8-C10), coconut oil	no influence of degree of saturation or chain length	Saraux et al., 1982
	safflower oil, lard	polyunsaturated fatty acids (safflower oil) increased specific lipase activities	Ricketts and Brannon, 1994
Human	sunflower-, olive oil	monounsaturated fatty acids (olive oil) increased total lipase activities more than saturated fatty acids (sunflower oil)	Yago et al., 1997a

duodenal-pancreatic neural reflexes may be distorted (Zabielski et al., 1997b). However, it should be mentioned that the number of observations was relatively small in this study which, in turn, limits the interpretation of these results. Studies on the influence of different lipids on exocrine pancreatic secretions in different species, including humans, are summarized in table 3.

DIETARY FAT AND STAGE OF DEVELOPMENT

Jensen et al. (1996) showed in the suckling piglet that the level of pancreatic lipase is relatively low and increases with age of the piglet until weaning (figure 1). However, Cranwell and Moughan (1989) reported that suckling piglets are able to digest sows milk very efficiently; they reported an apparent fat digestibility of 96%. This supports the idea by Jensen et al. (1996) that during the suckling period gastric lipase may play a major role in the hydrolysis of fat. Moreover, Jensen et al. (1996) observed an increase in lipolytic enzyme activity until weaning. They concluded that the low pancreatic lipase activities in suckling piglets are compensated by high carboxylester hydrolase activities (figure 1). Interestingly, carboxylester hydrolase is similar in structure to the bile-salt stimulated lipase, which is found in human milk and plays an important role in the nutrition of premature born infants (Hernell and Blackberg, 1994a; Hernell and Blackberg, 1994b).

HORMONAL REGULATION OF PANCREATIC SECRETIONS MEDIATED BY DIFFERENT LIPIDS

It has been shown that intestinal perfusions with fatty acids stimulate pancreatic secretions (Solomon, 1987). In addition, there is evidence that they mediate the release of hormones and regulatory peptides (Olsen et al., 1989). The gastrointestinal hormones secretin

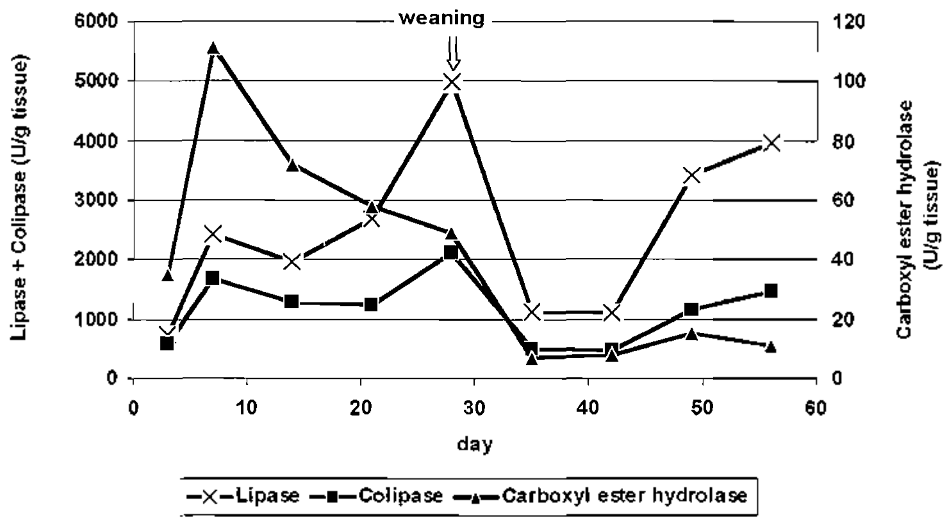

Figure 1. Development of lipolytic enzyme activities in pancreatic tissue of piglets (after: Jensen et al. (1997))

and cholecystokinin (CCK) are considered to be the most potent stimulators of the secretions of the exocrine pancreas. Whereas secretin mediates mainly the secretion of bicarbonate, water and electrolytes, CCK stimulates the acini of the pancreas, which release pancreatic enzymes (Brannon, 1990).

CCK is released after contact with digesta in the duodenum. Several authors showed in studies with different species (rats, dogs and pigs) that CCK release is stimulated after contact of the duodenal mucosa with either protein, carbohydrate or fat (Corring et al., 1986; Rhodes et al., 1988; Corring et al., 1989; Lluis et al., 1989; Greenberg, 1993; Jakob et al., 2000). Comparative studies with rats showed that fat and carbohydrate stimulate the exocrine pancreatic secretions less than protein (Douglas et al., 1988). In contrast, Hopman et al. (1985) showed in studies with humans that the consumption of equal amounts of fat and protein increased plasma CCK concentrations to the same extent, whereas starch consumption stimulated the release of CCK to a lesser extent than other nutrients. Corring and Chayvialle (1987) demonstrated, in pigs fitted with a permanent pancreatic cannula, adaptation of the specific lipase activity to the amount of dietary fat, but there was no effect on plasma CCK levels.

It can be concluded from results of Douglas et al. (1990) that medium-chain triglycerides with a chain length smaller than C12 stimulated CCK release more than long-chain triglycerides. The consumption of medium-chain triglycerides (caprylic acid) evoked a 2.8-fold higher CCK release than the consumption of long-chain triglycerides (corn oil). In dogs with pancreatic cannulas no differences in plasma CCK levels were observed after consumption of diets containing either olive or sunflower oil (Yago et al., 1997b).

Other gastrointestinal hormones are considered to be influenced by fat in the diet as well. Lluis et al. (1989), in studies with dogs, reported an increase in the level of neurotensin (NT) after intraduodenal application of corn oil. Sagher et al. (1991) demonstrated that the composition of fat may influence the level of NT in the distal part of the small intestine to a different extent. Rats were fed for 8 wk three different experimental diets in which 40% of the energy content was derived from butter (mainly saturated fatty acids), olive oil (mainly unsaturated fatty acids) and corn oil (polyunsaturated fatty acids), respectively. The control diet was low in fat (10% of the energy from fat). The consumption of olive and corn oil resulted in an increase in the concentrations of NT compared to the control treatment. However, this increase in NT plasma levels was not observed after consumption of butter. The authors postulated that the increased levels of NT after consumption of olive and sunflower oil could be explained by a better absorption of unsaturated fatty acids. In contrast to results obtained in studies with dogs and pigs, Wood et al. (1988) showed in studies with rats, that NT, injected at three different levels subcutaneously, increased the fresh weight of the pancreas by 16%. However, an increase in the specific lipase activity was not observed. This was confirmed by Beck et al. (1992) in studies with rats who also did not show an effect of a diet high in fat content on plasma levels of NT.

The hormone peptide YY (PYY) is considered to inhibit pancreatic secretions via a feedback mechanism. It is released from the ileum to the portal circulation approx. 30 min postprandially (Greeley et al., 1989b); it inhibits pancreatic secretions via a negative feedback

Table 4. Gastrointestinal hormones regulating the exocrine pancreatic secretion

Hormone/peptide	Effect on pancreas	Dietary stimuli for release	Releasing tissue	Reference
Cholecystokinin (CCK)	stimulates secretion of enzymes (mainly proteolytic enzymes)	protein, carbohydrates, fat	duodenal and jejunal mucosa	Douglas et al., 1988; Greenberg, 1993; Liddle, 1995
Pancreatic Polypeptide (PP)	inhibits enzyme, protein and bicarbonate secretion, minor effect on volume of secretion	fat, fatty acids	small intestine	Lonovics et al., 1981; Owyang et al., 1983; Fried et al., 1984; Langlois et al., 1989
Peptid YY (PYY)	inhibits enzyme activity and volume of secretion	fat, fatty acids, protein	distal ileum, colon	Greeley et al., 1989a; Greeley et al., 1989b; Guan et al., 1991; Lin et al., 1996
Neurotensin (NT)	stimulates enzyme, protein and bicarbonate secretion	fat, fatty acids	ileum	Walker et al., 1985; Gomez et al., 1986; Mössner, 1990
Bombesin	stimulates protein and volume of secretion	not known	gastric mucosa	Holmgren et al., 1982; Lilja et al., 1984; Ami et al., 1993
Enterostatin	inhibits pancreatic secretion	fat, protein	pancreas, fragment of pro-colipase after its activation by trypsin	Holmgren et al., 1982; Lilja et al., 1984; Ami et al., 1993
Enteroglucagon	inhibits pancreatic secretion	unabsorbed nutrients in the ileum	not known	Dowling et al., 1985; Sagher et al., 1991; Holst, 1997

mechanism (Mössner, 1990; Guan et al., 1991; Lin et al., 1996). Studies with dogs fitted with pancreatic duct catheters showed that a diet containing sunflower oil increased total activities of α-amylase and lipase compared to dogs fed a diet containing olive oil (Ballesta et al., 1990). It was demonstrated in humans that the consumption of a diet containing olive oil resulted in elevated PYY levels compared to the consumption of a diet containing sunflower oil (Yago et al., 1997b). These results were confirmed by Serrano et al. (1997). In addition, various other hormones interact with the exocrine secretions of the pancreas which emphasizes the complexity of the regulatory mechanisms involved in the secretory response of the pancreas to dietary fat (table 4).

CONCLUSIONS

It can be concluded that level as well as type and origin of dietary fat is probably the most important factor affecting the secretion of lipolytic enzymes. A close positive correlation between the amount of dietary fat and lipase activity could be shown. Moreover, there is evidence that not only the level of fat in the diet influences the exocrine pancreatic secretions, but also the type and origin of fat has to be considered as an important factor. However, results are contradictory so far and no final conclusion can be drawn if the degree of saturation and/or the chain length of fatty acids is the most effective factor involved in the regulation of the exocrine pancreas.

Furthermore, gastrointestinal hormones such as CCK, NT, PYY and secretin mediate the secretory response of the exocrine pancreas to fat supplementation, however, most of the underlying pathways are not known yet.

Thus, further investigations are warranted to elucidate the effects of fats of different composition both on the secretions of the exocrine pancreas and on the underlying hormonal regulatory processes. It has to be emphasized that most of the studies do not allow for the determination of total volume secretion, total protein output and total enzyme activities due to methodological constraints (slaughter investigations). The application of surgical techniques that permit permanent collection of pancreatic juice will provide more detailed information on the effect of dietary lipids on the function of the exocrine pancreas. Pigs are appropriate animal models not only with respect to animal nutrition, since they may also be used in human biomedicine.

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