The effect of inulin on new and on patent infections of *Trichuris suis* in growing pigs

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(Received 13 March 2006; revised 9 June and 12 June 2006; accepted 12 June 2006)

SUMMARY

The objective of this experiment was to investigate the potential influence of inulin on the establishment of new and patent infections of *Trichuris suis* in growing pigs. Two experimental diets were formulated based on barley flour with either added insoluble fibre from oat husk (Diet 1) or a pure inulin (16%) supplementation (Diet 2). Twenty-eight 10-week-old pigs were divided randomly into 4 groups (Groups 1–4) each of 7 pigs. After 3 weeks adaptation to the experimental diets all pigs were infected with a single dose of 2000 infective *T. suis* eggs. Group 1 was fed Diet 1 until 7 weeks post-infection (p.i.) and Group 3 until 9 weeks p.i., Group 2 was fed Diet 2 until 7 weeks p.i., Group 4 was fed Diet 1 until week 7 p.i. and was switched-over from Diet 1 to Diet 2 until week 9 p.i. Seven weeks p.i. pigs in Groups 1 and 2 were slaughtered, and pigs in Groups 3 and 4 were slaughtered at 9 weeks p.i. *Trichuris suis* worm burdens were determined for all pigs. Inulin-fed pigs (Group 2) exhibited an 87% reduction in EPG, compared to the pigs on standard diet (Group 1) ($P < 0.0001$). The number of worms recovered at week 7 p.i. from pigs on the inulin diet (Group 2) was significantly reduced by 71%, compared to the pigs on standard diet (Group 1) ($P < 0.01$). At week 9, worm recovery in pigs on the inulin diet switch protocol (Group 4) was reduced by 47% compared to the control pigs in Group 3 ($P < 0.01$). Further, the inulin-fed pigs exhibited a significant reduction in female worm fecundity and worm large intestine location was more distal compared to those from pigs on standard diet. These results demonstrate that inclusion of the highly degradable fructose polymer inulin in the diet leads to significant reductions in *T. suis* establishment, egg excretion, and female worm fecundity and can be used as a treatment for patent infections.

Key words: *Trichuris suis*, inulin, nutrition, pigs.

INTRODUCTION

Our previous studies have shown that dietary carbohydrates which differ in their fermentability have a significant influence on the establishment, localization and fecundity of established infections of the nodular worm *Oesophagostomum dentatum* (Petkevičius *et al.* 1999, 2000, 2001, 2003a) in the large intestine of pigs. Diets with carbohydrates resistant to fermentation in the large intestine provided favourable conditions for the establishment and fecundity of *O. dentatum*. However, carbohydrates that were non-digestible in the small intestine but highly fermentable in the large intestine (inulin and sugar beet fibre (SBF)) decreased the establishment and fecundity of nodular worms. Recent results have shown that inclusion of 16%

inulin as a single component in a normal barley flour based diet reduced established *O. dentatum* infection in growing pigs by 97% (Petkevičius *et al.* 2003a). Inulin is recognized as a prebiotic, which escapes digestion in the upper intestinal tract and is utilized selectively in the large intestine by a restricted group of micro-organisms that are associated with certain health-promoting properties (Bornet *et al.* 2002). Other than our studies there are no other reports on the negative influence of inulin on the gastrointestinal parasites.

It is well documented that *Oesophagostomum* and *Trichuris* have the same predilection site inhabiting the colon and caecum of the pig (Beer, 1973). The whipworm *Trichuris suis* (Shrank, 1788) is a widely occurring intestinal nematode parasite of pigs (Pattison *et al.* 1980; Morris *et al.* 1984) and has an economic importance in young and growing pigs due to its effects on growth rate, feed efficiency, utilization and retention of nutrients (Stewart and Hale, 1988). Recent results indicate that the mixture of fermentable carbohydrates (inulin and SBF)

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Table 1. Composition of the plant material and chemical composition of experimental diets

(LMW sugars, low molecular weight sugars; NSP, non-starch polysaccharides; NCP, non-cellulosic polysaccharides; FUp, Feed Units for pigs. Values in parentheses are soluble NSP.)

	Diet 1		Diet 2	
<i>g per kg</i>				
Barley flour	501		570	
Oat hull meal	300			
Sugar beet fibre				
Inulin (Raftiline®)			160	
Soybean meal	180		250	
Vitamin and mineral mixture	17		18	
Marker	2		2	
<i>g per kg⁻¹ dry-matter</i>				
Protein (N × 6.25)	149		159	
Fat	19		16	
LMW-sugars				
Glucose and fructose	3		1	
Sucrose	14		32	
Total sugars	17		33	
Inulin (fructan)	6		208	
Starch	497		388	
NSP:				
Cellulose	65		5	
NCP:	142	(40)	116	(71)
Rhamnose	1	(0)	1	(1)
Fucose	1	(0)	1	(0)
Arabinose	19	(4)	16	(9)
Xylose	60	(0)	37	(29)
Mannose	5	(2)	5	(2)
Galactose	12	(5)	12	(6)
Glucose	35	(26)	36	(18)
Uronic acids	9	(4)	10	(6)
Total NSP	207	(40)	119	(71)
Klason lignin	37		11	
Dietary fibre	244		130	
FUp per 100 kg dry matter	99		136	

does not affect the establishment of *T. suis* in naïve pigs, but results in earlier expulsion and reduced growth of the established worms (Thomsen *et al.* 2005). The present study investigated whether fermentable carbohydrate inulin can affect both the establishment of a new infection and an already established whipworm infection in growing pigs.

MATERIALS AND METHODS

Experimental diets

Two experimental diets were formulated based on barley flour with added insoluble fibre from oat husk (standard diet – Diet 1) and on barley flour with a pure inulin (16%) supplementation (inulin diet – Diet 2). Both diets were supplemented with soybean meal, synthetic lysine, vitamins and minerals to balance the concentrations of essential

nutrients (Table 1). The diets were not specifically analysed but, based on results from our previous study (Petkevičius *et al.* 2003a), they can be expected to contain 0.99 and 1.36 Feed Units for pigs (FUp) per kg dry matter, respectively. The pigs were fed the same amount of digestible energy (DE) per day divided into 2 daily meals according to weight development. The average intake of dry matter per day during the entire study period was 2.37 kg for Diet 1 and 1.98 kg for Diet 2, and the amount of digestible protein per day was 322 g and 316 g for Diet 1 and 2, respectively.

Experimental design

Twenty-eight pigs of Landrace/Yorkshire Danish crosses (females, castrates) were divided by stratified random sampling according to weight, sex and litter into 4 groups (1–4) with 7 pigs in each group. All experimental pigs were infected by oral inoculation with 2000 infective *T. suis* eggs after 3 weeks of feed adaptation.

Groups 1, 3 and 4 were fed Diet 1 and Group 2 was fed Diet 2 (inulin). Seven weeks p.i. Groups 1 and 2 were slaughtered and Group 4 was changed to Diet 2. Nine weeks p.i. Groups 3 and 4 were slaughtered.

The pigs were weighed on arrival, then every other week, and at slaughter. The pigs were weighed at the same time of the day relative to feeding time. The average live weight (standard deviation, s.d.) of the pigs at the start of the experiment was 26.0 kg (2.3). The pens were thoroughly disinfected and dried prior to introduction of the pigs and excreta were removed twice daily. The pigs were kept without bedding and had free access to water via drinking nipples.

Parasitological assays

Faecal samples were collected from the rectum for *T. suis* egg counts the day after arrival, the day before inoculation, and twice a week after week 6 p.i. Faecal egg counts were determined using a modified McMaster technique (Roepstorff and Nansen, 1998) which has a lower sensitivity of 20 eggs per gram (EPG) faeces. At slaughter the entire large intestine was immediately removed and separated from the mesenteries. The large intestine was divided into the caecum (Ce) and 4 segments of the colon (Co1-0–20%, Co2-21–40%, Co3-41–60%, and Co4-5-rectum-61–100%). For recovery of *T. suis* the mucosa of the large intestine sections were rinsed several times and looked through carefully for the presence of worms. The suspension of intestinal contents and intestinal wall washings was washed through a 212 µm sieve. *Trichuris suis* worms were collected and counted. The sex of *T. suis* was recorded.

Table 2. The average weight gains of pigs fed normal and inulin diet and infected with *Trichuris suis* (S.D., standard deviation.)

Group	Diet	No. of pigs	Average weight (S.D.) of pigs (kg)*				
			Week 0	Week 2	Week 5	Week 7	Week 9
1	Normal	7	25.7 (2.6)	34.1 (3.3)	46.7 (5.5)	57.6 (6.4)	—
2	Inulin	7	26.1 (1.9)	34.5 (2.9)	47.0 (4.6)	57.2 (7.0)	—
3	Normal	7	25.9 (2.5)	34.0 (3.5)	47.5 (5.2)	56.8 (5.0)	68.1 (8.0)
4	Normal/Inulin	7	26.3 (2.2)	35.2 (3.2)	48.0 (4.3)	58.8 (5.6)	69.5 (7.4)

* Note: no statistical differences were detected in columns at the 5% significance level.

Statistical analysis

Parasitological data were analysed using the SAS software package (Version 8.2, SAS® Institute Inc.). Differences between groups were tested using analysis of variance. The effect of diet on faecal egg counts was assessed using $\log_{10}$ (EPG + 1) transformed counts for each pig. The pig-to-pig variation in EPG in a given week was described using a 95% reference interval, roughly covering 95% of egg counts from pigs in each group. The comparisons made were (a) inulin (Group 2) versus normal diet (Groups 1, 3 and 4) in week 7 p.i. and (b) a diet change to inulin (Group 4) versus continued normal diet (Group 3) from weeks 7.5 to 9 p.i.

The effect of diet on *T. suis* worm burdens was contrasted for each intestinal section and analysed using $\log_{10}$ (worm burden + 1) transformed counts. The basic data were the number of female and male worms in a given intestinal section of a given pig. The $\log_{10}$ -transformed worm counts were thus classified according to diet group, pig, section and sex, allowing for the simultaneous assessment of the influence of these factors. The sex ratio (females/males) was calculated from this model by anti-log transformation of worm sex estimates.

The mean position of the *T. suis* worms along the large intestine in each pig was calculated according to Petkevičius *et al.* (1995) using the section number (1–5) as a proxy for geometrical position along a line. Worm fecundity was defined as the number of eggs excreted (EPG) divided by the number of female worms per pig at week 7 or week 9.

Ethical consideration

The experiment was designed not to cause a higher parasite load in the animals than under average natural conditions. The infection course was sub-clinical. The experiment was approved by the Danish Animal Ethical Committee (Experimental Animal Permission License: 2000/561-321). Meetings were held with the agricultural and laboratory technicians to explain the purpose of the experiment

and what was required from the persons handling the pigs.

RESULTS

Animal health and performance

There were no clinical signs of parasitic disease in any of the pigs during the experiment. All pigs had normal appetites during the experiment (daily feed allowance was completely consumed), and weight gains and general appearance was similar in all diet groups. There were no significant differences in the weight gain of pigs between two diet groups or the sex of the pigs. In all experimental groups, the average weight (S.D.) of pigs increased gradually at 2, 5, 7 and 9 weeks p.i. and reached weights of 34.5 kg (3.2), 47.3 kg (4.9), 57.6 kg (6.0) and 68.8 kg (7.7), respectively (Table 2).

Parasitological findings

Eggs were observed in the faeces of most pigs from week 6 and onwards (see Fig. 1); levels were similar until week 7 p.i., when the geometric mean EPG was significantly lower in pigs fed with the inulin diet compared to the pigs in the remaining groups that were fed with the standard diet ($P < 0.0001$) (Table 3). At week 7 this amounted to an 87% lower EPG in the inulin group (Group 2) compared to pigs fed with a normal diet (Group 1).

In Group 4, *T. suis* egg counts started to decline immediately after the diet switch and remained at a nearly constant, low level (< 1000 EPG) from week 7.5 until slaughter, while in the matched control pigs continuing on the normal diet (Group 3), EPGs remained at a high level until week 8 at which time they declined in 3 out of 7 pigs. As a result, the egg excretion level in Group 4 was reduced significantly ($P < 0.05$) compared to Group 3 in weeks 7.5, 8 and 8.5, but not at slaughter ($P > 0.10$) (see Table 3). Inclusion of inulin in the diet resulted in a reduction in EPG of at least 65%, depending on week post-infection, compared to a normal diet.

Fig. 1. Geometric mean *Trichuris suis* egg counts of pigs 7 weeks fed Diet 1 (●), 7 weeks fed Diet 2 (○), 9 weeks fed Diet 1 (■) and 7 weeks changed Diet 1 > Diet 2 (□).

In each group, adult *T. suis* were distributed over the 5 sections of large intestine as shown in Fig. 2. To 'normalize' residual variation in worm burdens in the statistical analysis, section 5 (which contained only a minor fraction of the total number of worms per pig) was excluded from the analysis, as well as sections without worms. The number of worms recovered at week 7 from pigs fed with an inulin diet (Group 2) was reduced significantly by 71% compared to control pigs in Group 1 ($P < 0.0001$), see Table 3. At week 9, worm recovery in inulin-fed pigs (Group 4) was reduced by 47% compared to control pigs in Group 3 ($P < 0.01$) (Table 3). This smaller reduction at week 9 p.i., compared to week 7, was most likely due to an increased variation in worm counts in Group 3 at slaughter, as can be seen from the 95% reference interval in Table 3. In pigs fed inulin for 7 weeks (Group 2) worms were located more distally in the large intestines ($P < 0.01$, Table 3) compared to pigs in any of the other groups.

The *T. suis* sex ratio was not influenced by diet or diet change (Table 3), and did not differ significantly from 1.

Inulin had a statistically significant effect on female worm fecundity. Fecundity was reduced significantly in inulin Groups 2 and 4 at week 7 p.i. ($P < 0.001$), compared to normal diet Groups 1 and 3, (Table 3). Furthermore, fecundity in inulin-fed pigs at week 7 p.i. (Group 1 versus 2) or at week 9 p.i. (Group 3 versus 4), was reduced statistically significantly ($P < 0.001$) (Table 3).

DISCUSSION

This experiment demonstrated that the highly fermentable carbohydrate inulin has a significantly negative effect on the establishing and on the already established *T. suis* infection in growing pigs. These results extend our previous findings that this carbohydrate can markedly reduce patent infections of another pig parasite *O. dentatum* (Petkevičius *et al.* 2001, 2003a). In previous experiments we demonstrated that diets containing 16% inulin caused pigs

to expel 97% of their *O. dentatum* worm burden and the fermentative activity of the microflora of the large intestine was suggested to play an important role in this anti-parasitic effect (Petkevičius *et al.* 2003a). Inulin is a glycosidic fructan (Phelps, 1965) which, because of its chemical characteristics, resists digestion by the small intestinal enzymes of mono-gastric animals and humans (Bach Knudsen and Hesso, 1995), thus becoming available as a substrate for microbial fermentation in the large intestine (Cummings *et al.* 1997). Inulin occurs as a reserve material in roots, stems and leaves of a variety of plants (Robertfroid *et al.* 1998). Because pigs harbour a more active microflora in the stomach and small intestine, the recovery of inulin at the end of the small intestine is consequently lower, with recoveries at the terminal ileum of approximately 60% (Bach Knudsen, 2001). Other than our studies there are no reports on anti-parasitic effects of highly degradable carbohydrates (inulin and SBF) on the gastrointestinal parasites.

Whipworms in the caecum and colon are known to reduce daily live weight gain and feed conversion efficiency at low levels of infection in pigs and can cause mortalities at higher levels (Stewart and Hale, 1988). *T. suis* is very similar to the human whipworm *T. trichuria* (Holland, 1987), therefore experimental whipworm infection in the pig is considered to be a model for *T. trichuria* in humans, a parasite which infects at least one billion people worldwide (Crompton, 1999). Most of the studies related to the whipworm-nutrition interactions in relation to the host's nutritional status were designed to investigate the population biology of *T. suis*. It was estimated that a low dietary level of iron (Pedersen, 2002) and decreased content of protein/energy (Pedersen and Saeed, 2002) in the diet increases the severity of *T. suis* infection in pigs, while a marginal vitamin A status leads to earlier worm loss (Pedersen, 2002). The use of diets high in dietary fibre was associated with an increased risk of *T. suis* infection and it was concluded that dietary fibre intake (particularly in form of insoluble fibre) for

Table 3. The effects of inulin on *Trichuris suis* worm burdens, sex-ratio, worm location, worm fecundity and egg excretion (EPG)

Group	Diet	No. of pigs	Worm burden*			Sex ratio*	Location*	Fecundity*	Geometric mean EPG*						
			Geometric mean	95 % confidence interval	95 % reference interval				Week 7	Week 7.5	Week 8	Week 8.5	Week 9		
1	Normal	7	1426 ^a	1176–1729	857–2374	1.04 ^a	2.02 ^a	6.11 ^a	3824 ^a	—	—	—	—		
2	Inulin	7	410 ^b	252–666	104–1616	1.20 ^a	2.73 ^b	2.55 ^b	532 ^b	—	—	—	—		
3	Normal	7	1050 ^a	592–1861	231–4773	1.03 ^a	2.14 ^a	10.22 ^a	3636 ^a	4104 ^a	5018 ^a	4147 ^a	2194 ^b		
4	Normal/Inulin	7	555 ^b	400–769	234–1318	1.12 ^a	2.27 ^a	2.7 ^b	5425 ^a	1448 ^b	956 ^b	975 ^b	745 ^b		

* Note: column estimates with different superscripts differ statistically at the 5% significance level.

Fig. 2. The mean location of *Trichuris suis* worm burdens in the intestine of pigs slaughtered 7 and 9 weeks post-inoculation. Sections of the large intestine: 1-Ce-caecum; 2-Co1-0–20%; 3-Co2-21–40%; 4-Co3-41–60% and 5-Co4,5-61–100%.

growing pigs provide favourable conditions for *T. suis* infection in pigs (Pearce, 1999). In a recent study we have shown that a mixture of fermentable carbohydrates (inulin and SBF) do not affect the establishment of *T. suis* in naïve pigs, but result in earlier expulsion and reduced growth of the established worms (Thomsen *et al.* 2005). In this study only the prophylactic effect of inulin and SBF was investigated. In the present study it was shown that inulin had a significant anti-worm effect on new and on patent infections of *T. suis* in growing pigs. Those results on *T. suis* are in concert with data on the influence of carbohydrates on *O. dentatum*, which have shown that dietary carbohydrate source and time of intervention is very important. In our previous study (Petkevicius *et al.* 2003a) it was estimated, that the inclusion of inulin to pig diets had a significantly higher effect on the establishment and on already established experimental *O. dentatum* infections compared to that of SBF or a mixture of inulin and SBF. In addition, it was demonstrated that diets containing 16% inulin caused pigs to expel 97% of their *O. dentatum* worm burden (Petkevicius *et al.* 2003a) and in the present study the number of *T. suis* worms was reduced by 71%. The higher anti-worm effect of inulin could be explained by the fact that nodular worms spent most of their entire life in the lumen of the large intestine, whereas whipworms are connected to the mucosa by the embedded anterior end, and may therefore be better protected against luminal changes due to fermentation.

It is well established that the main metabolic products from the microbial fermentation of inulin in the large intestine are short-chain fatty acids (SCFA) and lactic acids (LA) (Sobotka *et al.* 1997; Bach Knudsen, 2001). Recently, we demonstrated that the caecal infusion of SCFA and LA into the caecum of cannulated pigs in amounts and

proportions that mimicked the caecal level (150 mmol/kg digesta SCFA and 60 mmol/kg digesta LA) in inulin-fed pigs (Bach Knudsen *et al.* 2003) has a strong anti-worm effect on the established *O. dentatum* infection, as reflected by highly reduced egg excretions, worm burdens and female fecundity (Petkevičius *et al.* 2004). These data are thus supporting our conclusion that rapid degradation of carbohydrates and thereby accumulation of LA in the caecum and raised SCFA concentration (>150 mmol/kg digesta compared to a normal level of 100–130 mmol/kg digesta) throughout the length of the large intestine is a key factor controlling *O. dentatum* infection (Petkevičius *et al.* 2001, 2003a). The marked increase in levels of SCFA and LA also decreased the pH of digesta to 5.0 in the caecum and to 5.5 in the proximal colon (Petkevičius *et al.* 2003a). The specific mode of action of fermentation products in regulating whipworm populations is not yet clear, but the parallel effects of infusion of SCFA and LA (Petkevičius *et al.* 2004) to that obtained with inulin diets on nodular worms (Petkevičius *et al.* 2003a), also suggest that there are direct effects of SCFA and LA on worm physiology, especially the females. The close association between increased levels of SCFA and LA and low pH with expulsion of worms suggests that the alteration of pH has a major role in the SCFA and LA and inulin effect on nodular worms creating an unsuitable environment for mature and immature helminths. The same mechanism also seems to be applicable to whipworm infections. This provided support to the hypothesis raised in our earlier papers (Petkevičius *et al.* 1995, 1997, 1999, 2000, 2001, 2003a; Thomsen *et al.* 2005), that the strong anti-worm effect of dietary inulin is the result of the production of fermentation products produced by the microflora in the large intestine.

The combination of helminth infections and highly fermentable dietary carbohydrates affected the mucosal architecture, the epithelial cell proliferation and mucin secretion of the large intestine in pigs (Petkevičius *et al.* 2003b). It is claimed that whipworms are rather immunogenic in pigs causing strong protective and acquired immunity (Powers, 1959; Pedersen and Saeed, 2001), resulting in short-term infections and expulsion of worms. In our study, it is likely that inulin exhibited higher negative impact on the establishment of whipworm infection compared to the established infection due to parasite expulsion in some pigs. However, host defence functions are responsive to carbohydrate composition in the diet (Kelly-Quagliana *et al.* 2003) and an enhanced intestinal immune response has been attributed to the dietary inulin (Meyer *et al.* 2001).

In conclusion, the results from this study indicate that inulin which is highly and rapidly fermentable in the large intestine has a significant anti-worm

effect on patent and new infections of *T. suis* in pigs. These results are in concert with our previous findings on nodular worms and strongly suggest that such dietary carbohydrates have potential value for parasite control for both conventional and ecological pig production systems, especially for the control of troublesome whipworm infections. The results also show that there were no significant differences in live-weight gain between the pigs on inulin and standard diets, an important consideration in production. Future investigations should assess the influence of potential factors such as the intestinal microflora composition, mucosal barriers and inulin effects directly on host immune responses to large intestinal parasites. The data obtained on the influence of inulin on *T. suis* infection in pigs should also be of interest to those dealing with human whipworm control as a potential nutritional approach adjunct to drug treatment.

REFERENCES

- Bach Knudsen, K. E.** (2001). Development of antibiotic resistance and options to replace antimicrobials in animal diets. *Proceedings of the Nutrition Society* **60**, 291–299.
- Bach Knudsen, K. E. and Hessov, I.** (1995). Recovery of inulin from Jerusalem artichoke (*Helianthus tuberosus* L.) in the small intestine of man. *British Journal of Nutrition* **74**, 101–113.
- Bach Knudsen, K. E., Petkevičius, S., Jørgensen, H. and Murrell, K. D.** (2003). A high load of rapidly fermentable carbohydrates reduces worm burden in infected pigs. In *Manipulating Pig Production IX* (ed. Paterson, J. E.), pp. 169–170. Australasian Pig Science Association, Werribee, Australia.
- Beer, R. J., Lean, I. J., Jacobs, D. E. and Curran, M. K.** (1973). Clinical trichuriasis produced experimentally in growing pigs. Part II: Anthelmintic efficacy of dichlorvos. *Veterinary Record* **93**, 195–197.
- Bornet, F. R. J., Brouns, F., Tashiro, Y. and Duliver, V.** (2002). Nutritional aspects of short-chain oligosaccharides: natural occurrence, chemistry, physiology and health implications. *Digestive and Liver Disease* **34**, S111–S120.
- Crompton, D. W. T.** (1999). How much human helminthiasis is there in the world? *Journal of Parasitology* **85**, 397–403.
- Cummings, J. H., Robertfroid, M. B., Anderson, H., Barth, C. A., Ferro-Luzzi, A., Ghos, Y., Gibney, M., Hermansen, K., James, W. P. T., Korver, O., Lairon, D., Pascal, G. and Voragen, A. G. S.** (1997). A new look at dietary carbohydrate: chemistry, physiology and health. *European Journal of Clinical Nutrition* **51**, 417–423.
- Holland, C. V.** (1987). Neglected infections – trichuriasis and strongyloidiasis. In *Impact of Helminth Infections on Human Nutrition* (ed. Stephenson, L. S. and Holland, C. V.), pp. 161–201. Taylor and Francis, London, New York and Philadelphia.
- Kelly-Quagliana, K. A., Nelson, P. D. and Buddington, R. K.** (2003). Dietary oligofructose

- and inulin modulate immune functions in mice. *Nutrition Research* **23**, 257–267.
- Meyer, D. P., Tungland, B. C., Causey, J. L. and Slavin, J. L.** (2001). *In vitro*- und *in vivo*- Effekte von Inulin auf das Immunsystem. *Ernährungs-Umschau* **48**, 13–16.
- Morris, R. G., Jordan, H. E., Luce, W. G., Coburn, T. C. and Maxwell, C. V.** (1984). Prevalence of gastrointestinal parasitism in Oklahoma Swine. *American Journal of Veterinary Research* **45**, 2421–2423.
- Pattison, H. D., Thomas, R. J. and Smith, W. C.** (1980). A survey of gastrointestinal parasitism in pigs. *Veterinary Record* **107**, 415–418.
- Pearce, G. P.** (1999). Interactions between dietary fibre, endo-parasites and *Lawsonia intracellularis* bacteria in grower-finisher pigs. *Veterinary Parasitology* **87**, 51–61.
- Pedersen, S.** (2002). Population biology of *Trichuris suis* in pigs in relation to host nutritional status and its relevance to human *T. trichuria* infections. Ph.D. thesis, University of Copenhagen, Denmark.
- Pedersen, S. and Saeed, I.** (2001). Acquired immunity to *Trichuris suis* infection in pigs. *Parasitology* **123**, 95–101.
- Pedersen, S. and Saeed, I.** (2002). Host age influence on the intensity of experimental *Trichuris suis* in pigs. *Parasite* **9**, 75–79.
- Petkevičius, S., Bach Knudsen, K. E., Nansen, P. and Murrell, K. D.** (2001). The effect of dietary carbohydrates with different digestibility on the populations of *Oesophagostomum dentatum* in the intestinal tract of pigs. *Parasitology* **123**, 315–324.
- Petkevičius, S., Bach Knudsen, K. E., Nansen, P., Roepstorff, A., Skjøth, F. and Jensen, K.** (1997). The impact of diets varying in carbohydrates resistant to endogenous enzymes and lignin on populations of *Ascaris suum* and *Oesophagostomum dentatum* in pigs. *Parasitology* **114**, 555–568.
- Petkevičius, S., Bach Knudsen, K. E. and Murrell, K. D.** (2003b). Effects of *Oesophagostomum dentatum* and dietary carbohydrates on morphology of the large intestine of pigs. *Veterinary Parasitology* **116**, 125–138.
- Petkevičius, S., Bach Knudsen, K. E., Murrell, K. D. and Wachmann, H.** (2003a). The effect of inulin and sugar beet fibre on *Oesophagostomum dentatum* infection in pigs. *Parasitology* **127**, 61–68.
- Petkevičius, S., Bjørn, H., Roepstorff, A., Nansen, P., Bach Knudsen, K. E., Barnes, E. H. and Jensen, K.** (1995). The effect of two types of diet on populations of *Ascaris suum* and *Oesophagostomum dentatum* in experimentally infected pigs. *Parasitology* **111**, 395–402.
- Petkevičius, S., Murrell, K. D., Bach Knudsen, K. E., Jørgensen, H., Roepstorff, A., Laue, A. and Wachmann, H.** (2004). Effects of short-chain fatty acids and lactic acids on survival of *Oesophagostomum dentatum* in pigs. *Veterinary Parasitology* **122**, 293–301.
- Petkevičius, S., Nansen, P. and Bach Knudsen, K. E.** (2000). The influence of insoluble carbohydrates on the populations of *Ascaris suum* and *Oesophagostomum dentatum* in pigs. *Veterinarija ir Zootechnika* **10**, 15–17.
- Petkevičius, S., Nansen, P., Bach Knudsen, K. E. and Skjøth, F.** (1999). The effect of increasing levels of insoluble dietary fibre on the establishment and persistence of *Oesophagostomum dentatum* in pigs. *Parasite* **6**, 17–26.
- Phelps, C.** (1965). The physical properties of inulin solutions. *Journal of Biochemistry* **45**, 41–47.
- Powers, K. G.** (1959). Swine whipworm in Wisconsin. *Veterinary Medicine* **54**, 396–397.
- Robertfroid, M. B., Van Loo, J. A. E. and Gibson, G. R.** (1998). The bifidogenic nature of chicory inulin and its hydrolysis products. *Journal of Nutrition* **128**, 11–19.
- Roepstorff, A. and Nansen, P.** (1998). Epidemiology, diagnosis and control of helminth parasites of swine. *FAO Animal Health Manual No. 3*. FAO, Rome, Italy.
- Sobotka, L., Bratova, M., Šlemrova, M., Manak, J., Vižda, J. and Zadák, Z.** (1997). Inulin as the soluble fiber in liquid enteral nutrition. *Nutrition* **13**, 21–25.
- Stewart, T. B. and Hale, O. M.** (1988). Losses to internal parasites in swine production. *Journal of Animal Science* **66**, 1548–1554.
- Thomsen, L. E., Petkevičius, S., Bach Knudsen, K. E. and Roepstorff, A.** (2005). The influence of dietary carbohydrates on experimental infection with *Trichuris suis* in pigs. *Parasitology* **131**, 857–865.