Nutritional implications of L-arabinose in pigs

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The pentose sugar L-arabinose is one of the most abundant components released by complete hydrolysis of non-starch polysaccharides of feed ingredients of vegetable origin. Two studies were conducted to investigate the apparent ileal digestibility and urinary excretion of L-arabinose at dietary inclusion levels of 50 and 100 g/kg, and 25, 50, 75 and 100 g/kg respectively, in pigs. As a reference, D-glucose was included in the studies. Water intake, ileal flow of volatile fatty acids and ileal and faecal digestibilities of dietary nutrients in pigs fed on the different diets were also examined. Castrated pigs were prepared with a post-valvular *T*-caecum cannula to measure ileal digestibility. Faecal digestibility was measured in non-cannulated pigs. Apparent ileal digestibility of L-arabinose was found to be approximately 70%. The presence of L-arabinose in the diet increased ileal flow of volatile fatty acids and lactic acid, suggesting the occurrence of microbial degradation of L-arabinose in the pig small intestine. L-arabinose was partly excreted in the urine. The extent of this urinary excretion as a percentage of intake increased linearly ($P < 0.01$) as the dietary level increased. In pigs fed on the 25 g L-arabinose/kg diet, 10·9% of the L-arabinose consumed appeared in the urine. This level was increased to 14·7% when pigs were fed on a diet containing 100 g L-arabinose/kg diet. Faecal digestibility and retention of nitrogen decreased significantly in pigs fed on the L-arabinose diets.

L-arabinose: Digestion: Excretion: Pig

Traditional pig diets are mainly composed of feed ingredients of vegetable origin. The carbohydrate fraction of these ingredients contains two broad classes of polysaccharides, starch and cell-wall polysaccharides; the latter may be conveniently referred to as non-starch polysaccharides (NSP). Starch, a storage carbohydrate, can be hydrolysed by pancreatic α-amylase and may, therefore, be digested in the small intestine of pigs and absorbed as glucose. NSP are complicated compounds from the point of view of both physical structure and chemical composition, and they include cellulose, hemi-cellulose, pectin and oligosaccharides. It is well recognized that NSP are resistant to the digestive enzymes of pigs and pass to the hind-gut where microbial degradation takes place. The end-products of a microbial degradation of NSP, lactic acid and volatile fatty acids (VFA), are rapidly absorbed into the blood and can be utilized by the pig as an energy source, but with a lower efficiency than, for example, glucose (Agricultural Research Council, 1981; Just *et al.* 1983; van Es, 1987).

Improving the utilization of NSP may be attained by treatment with enzymes capable of hydrolysing these carbohydrate fractions to monosaccharides. However, a complete hydrolysis of the NSP will release not only glucose but also other sugars of which, in quantitative terms, the pentose sugar L-arabinose is one of the most important (Carré &

Table 1. *Composition of the basal diet (g/kg)*

Maize meal	287
Wheat starch	287
Soya-bean oil	40
Animal fat	40
Isolated soya-bean protein	223·3
Cellulose*	60
Monocalcium phosphate	24
Limestone	10
Potassium bicarbonate	15
Iodized salt	3
Mineral mix†	5
Vitamin mix‡	5
DL-methionine	0·7

* Arbocel B 800 (Rettenmaier, Germany).

† Provided (mg/kg diet): magnesium 400, zinc 110, copper 25, manganese 45, iron 80, cobalt 0·5, selenium 0·1.

‡ Provided (mg/kg diet): thiamin 2, riboflavin 5, nicotinamide 30, pantothenic acid 12, pyridoxine 3, cyanocobalamin 0·04, biotin 0·1, folic acid 1, menadione 3, ascorbic acid 50, retinol 3·1, cholecalciferol 0·045, vitamin E 40, choline chloride 1000.

Brillout, 1986; Brillout *et al.* 1988). The studies reported so far on the absorption and utilization of L-arabinose relate to animal species other than pigs. These studies have shown that L-arabinose is absorbed from the intestinal tract in rats (Cori, 1925; Arnal-Peyrot & Adrian, 1974) and chicks (Bogner, 1961; Wagh & Waibel, 1967), but at a lower rate than glucose. The study reported by Arnal-Peyrot & Adrian (1974) showed that part of the ingested arabinose is excreted in the urine. Both the low absorption rate and the urinary excretion of L-arabinose may have nutritional and physiological implications for the animal, as indicated in chicks by Wagh & Waibel (1966) and Schutte (1990). From these studies it appears that in chicks the metabolizable energy value of L-arabinose was not only lower than that of D-glucose but also decreased when the dietary level was increased. Moreover, these investigators found that inclusion of L-arabinose resulted in wet droppings.

The two experiments reported herein were undertaken to obtain information on the quantitative aspects of digestion and utilization of L-arabinose in pigs. In the first experiment ileo-cannulated pigs were used in order to measure the disappearance rate of L-arabinose at the end of the terminal ileum at dietary inclusion levels of 50 and 100 g/kg. The second experiment was performed with intact animals to determine the urinary excretion of L-arabinose at dietary levels of 25, 50, 75 and 100 g/kg. In addition, in these trials the effect of L-arabinose on ileal and faecal digestibilities of other dietary nutrients was investigated. D-glucose was included in the experiments as a reference material.

MATERIALS AND METHODS

Animals and diets

Two separate trials were conducted with growing castrated male pigs (Dutch Landrace × Dutch Yorkshire): one trial with cannulated pigs (Expt A) and one with non-cannulated pigs (Expt B). In both trials the pigs were individually housed in metabolism cages under a 12 h light–12 h twilight cycle throughout. The nutritionally complete basal diet used was based on maize, wheat starch and isolated soya-bean protein. The composition of the basal diet and its chemical characteristics are shown in Tables 1 and 2 respectively. The test sugars (D-glucose and L-arabinose), supplied as anhydrous monosaccharides, were substituted by weight for wheat starch.

Table 2. *Chemical composition of the basal diet (analysed; g/kg)*

Constituent	Expt A	Expt B
Dry matter	901	894
Ash	53	52
Crude protein (nitrogen × 6·25)	221	223
Crude fibre	59	57
Crude fat	84	83
Gross energy (MJ/kg)	17·8	17·7
Calcium	9·8	9·6
Phosphorus	8·6	8·3

In both trials the experimental diets were fed at a daily rate of approximately 0·9 MJ metabolizable energy (ME)/kg metabolic body-weight ($BW^{0.75}$), assuming that L-arabinose has the same ME content as D-glucose. The daily amount of feed was offered as four equal meals at intervals of 6 h, and adjusted weekly according to body-weight. The feed was mixed with water (1 part feed + 1 part water). In addition, water was freely available.

Experimental protocol

Expt A. The ileal digestibility of L-arabinose and the effect of this pentose sugar on ileal digestibility of dry matter (DM), organic matter (OM), gross energy (GE) and nitrogen were determined. Moreover, ileal flow of volatile fatty acids (VFA) and lactic acid was measured.

Four pigs, 9 weeks old at the start of the trial, were involved. The pigs were surgically fitted with a post-valvular *T*-caecum cannula (PVTC) according to the procedure described by Van Leeuwen *et al.* (1988). Post-operative care included keeping the pigs warm (25°) and withholding feed for 24 h. During the 3-week post-operative period the pigs were fed on the basal diet (Table 1). The experimental period originally involved three phases during which time each pig was fed consecutively on diets containing 100 g D-glucose/kg (Gluc 100), 50 g L-arabinose/kg (Arab 50) and 100 g L-arabinose/kg (Arab 100), with a 7 d adaptation period and a 4 d collection period for each diet. During the first 3 d of each adaptation period pigs were gradually changed to the next diet. After termination of the third phase a fourth phase was included in the trial in order to investigate whether or not the observed increase in ileal digesta output in pigs fed on the Arab 100 diet returned to a normal level when they were changed to the Gluc 100 diet. The fourth phase consisted of a 1 d adaptation period and a 4 d collection period. At the start of the experimental period the pigs weighed on average 26·4 (SD 1·6) kg and at the end of the fourth phase 51·2 (SD 5·2) kg.

Expt B. The objectives of this trial were to determine the urinary excretion of L-arabinose, and to study the effect of this sugar on faecal digestibility of DM, OM, GE and N, and N retention. This trial, involving ten 9-week-old pigs, was performed after termination of Expt A. The pigs were accustomed to the cages and basal diet (Table 1) for 3 weeks before starting the experimental period. The basal diet was composed of the same batches of feed ingredients as used in Expt A. At the start of the experimental period two groups of five pigs, each of similar average body-weight, were formed and fed on diets containing either D-glucose or L-arabinose according to a scheme as outlined in Table 3. As illustrated in Table 3, the experimental period consisted of four phases. Each of the four phases consisted of a 7 d adaptation period and a 4 d collection period. During the first 3 d of the adaptation period pigs were gradually changed to the next diet containing a higher level of the same sugar.

Table 3. *Expt B. Experimental design*

Treatment	Sugar	Phase	Dietary sugar level (g/kg) 1 (days 1–11)	2 (days 12–22)	3 (days 23–33)	4 (days 34–44)
1	D-glucose		25	50	75	100
2	L-arabinose		25	50	75	100

At the start of the experimental period the pigs weighed 27·5 (SD 1·5) kg and the end of this period 55·8 (SD 3·0) kg.

Digesta collection

Ileal digesta from individual animals was collected quantitatively from the PVTC cannula over a 12 h period per d during each 4 d collection period (08.00–20.00 hours). Previous studies have shown that ileal digesta collection is almost complete by using this type of cannula with the same type of basal diet as in the present trial (Köhler *et al.* 1991). Previous studies also showed that there were no significant differences in ileal digestibility between digesta collected over 12 h per d and that collected over a 24 h period (E. J. van Weerden, J. Huisman and P. van Leeuwen, unpublished results).

The digesta were collected continuously in dry ice, weighed daily and stored at −20°. At the end of the experiment the four 12 h collections were pooled for each pig, homogenized and sampled. VFA and lactic acid determinations were performed on the pooled digesta sample, while the other measurements were made on freeze-dried samples which were kept at −20° until required for analysis.

Faeces and urine collection

Faeces were collected directly into a bag fitted around the anus, and urine was collected using a funnel fitted under the cage. Total collection of faeces and urine from the individual animals was carried out during the four 24 h collection periods; the faeces were collected at intervals of 12 h and stored at −20°. All faeces produced during each collection period were pooled for each pig, homogenized and sampled, and the samples freeze-dried.

Urine was collected in containers at intervals of 4 h. At the start of each collection period the containers were provided with merthiolate sodium (Thiomersal; BDH Chemicals Ltd, Poole, UK) as a preservative to inhibit bacterial activity. Before inclusion, this preservative was dissolved in an ethanol solution (40 g/l), and added in an amount of 0.4 ml/container. This amount was based on a urine production of 200 ml/4 h. The urine from each interval was pooled daily for individual animals. A representative sample of 100 ml/l of the pooled urine was taken and frozen at −20°. The 4 d sub-samples of urine were pooled for each animal, homogenized and sampled. Faeces and urine were kept at −20° until required for analysis.

Analytical methods

Samples of feed and freeze-dried digesta and faeces were milled to pass through a 1·0 mm screen (Retsch mill ZM1; Retsch B.V., Ochten, Holland) before analysis. All analyses were carried out in duplicate. DM was determined by drying the samples to a constant weight at 101°. Inorganic matter and N were determined by standard methods (Association of Official Analytical Chemists, 1975); GE was determined using an IKA-C 4000 adiabatic bomb calorimeter.

Concentrations of VFA and lactic acid in wet digesta were determined by a modification

of the gas–liquid chromatographic method of Imoto & Namioka (1978). A known portion (about 20 g) of the digesta was centrifuged and immediately afterwards the supernatant fraction (5 ml) was acidified with 500 μl phosphoric acid (850 ml/l) and 3 ml of an aqueous solution of isocapronic acid (4·0193 g/l) was added as an internal standard. Distilled water was then added to the mixture to obtain a final volume of 10 ml. A 1 μl sample of the final solution was injected into the column of the gas–liquid chromatograph. The gas–liquid chromatograph was fitted with a flame-ionization detector (Packard 419, V. Hewlett Packard Co., Palo Alto, USA). A glass column (1850 × 2 mm i.d.) packed with Chromosorb 101 of 80/100 mesh was used. The carrier gas (N_2) was saturated with formic acid, and had a flow-rate of 25 ml/min. The oven temperature was set at 190°, and the inlet and detector temperature at 225°. Standard solutions containing acetic acid, propionic acid, butyric acid, isobutyric acid, valeric acid and isovaleric acid were prepared for gas–liquid chromatography in the same way as described for isocapronic acid. Calibration curves for these acids were then made by obtaining the ratios for peak-height of each acid to that of isocapronic acid. Recoveries between 95 and 100 % were found for the individual VFA and the internal standard. Total VFA was represented as the sum of all six acids. Lactic acid concentrations were determined enzymically (Anonymous, 1986).

Concentrations of glucose and arabinose in digesta and urine were determined as the silyl derivatives of the monosaccharides by gas–liquid chromatography (Sweeley *et al.* 1963). A known amount of wet digesta (1 g) or urine (1 ml) was diluted with distilled water (1:10, v/v). The diluted sample was then deproteinized with potassium ferrocyanate and zinc acetate, and desalted by passing through a mixture (1:1, w/w) of anion (Biorad AG 3 × 4) and cation (Biorad AG 50 W × 4)) exchangers. After centrifugation, 200 μl of the supernatant fraction was freeze-dried. Phenylglucopyranoside (0·4 mg in a 1 ml pyridine solution) was added to the freeze-dried sample as an internal standard. The sample was then derivatized by the addition of 0·6 ml hexamethyldisilazane and 0·3 ml trimethylchlorosilane. The contents were mixed using a Vortex stirrer and after an incubation period of 30 min at room temperature the reagents were removed by evaporation with N_2 at 40°. The residue was then redissolved in 0·5 ml ethyl acetate. From this sample 2 μl was analysed using a Hewlett Packard HP 5890 equipped with a flame-ionization detector and a Hewlett Packard 3396A integrator. The carbohydrate derivatives were separated with a chrompack capillary WCOT fused silica column coated with CP sil 5 CB of 50 m length. H_2 was used as carrier gas. The oven temperature was held for 3 min at 190°, then raised at the rate of 5°/min to a final temperature of 265°, which was held for 5 min. The temperatures of the injector and detector were 240 and 300° respectively.

Statistical analysis

The results of both experiments were analysed by means of analysis of variance as a randomized block design (Cochran & Cox, 1957). Treatments were confounded by time and age, but it was assumed that differences were due to the test sugar or an increase in dietary sugar. This assumption will be elucidated further in the discussion.

In Expt A the treatment factors were type and dietary level of sugar. All four phases of Expt A were included in the statistical analysis despite the differences in the length of the adaptation period between the first three phases and the fourth phase. This can be justified because the differences in results obtained on the Gluc 100 diets in the first and fourth phase were not statistically significant. Moreover, the ratio wet ileal digesta output:intake of DM was similar in both D-glucose phases. This suggests that an adaptation period of 1 d was sufficient to stabilize the conditions in the gastrointestinal tract when pigs were changed from the arabinose to the glucose diet.

In Expt B the treatment factors were type of sugar and the dietary level of sugar. The

Table 4. *Expt A. Intake (g/12 h) of dry matter (DM) and water, output (g/12 h) of wet digesta, and DM content (g/kg) of digesta, measured in cannulated pigs fed on* D-*glucose (Gluc) and* L-*arabinose (Arab) diets*

(Mean values for four pigs per treatment)

Phase*.....	1	2	3	4	
Sugar.....	Gluc	Arab	Arab	Gluc	SED
Dietary level† (g/kg)...	100	50	100	100	(df 9)
Intake of DM (A)	370[a]	432[b]	496[c]	528[d]	5·4
Intake of water (B)	800[a]	1300[b]	1900[c]	1250[b]	82·9
B:A	2·16[a]	3·03[b]	3·85[c]	2·37[a]	0·19
Output of wet ileal digesta	517[a]	874[b]	1491[c]	753[ab]	142·9
DM content ileal digesta	120[a]	94[b]	72[c]	117[a]	6·1

SED, standard error of difference between means.

[a, b, c] Within a row, mean values with unlike superscript letters were significantly different ($P < 0·05$).

* Phases 1–3, 7 d adaptation period and 4 d collection period; phase 4, 1 d adaptation period and 4 d collection period; for details, see p. 197.

† For details of diets, see pp. 196–197 and Table 1.

between-animal error term was used for testing the effect of type of sugar and the within-animal error term for testing the effect of sugar levels as well as the type of sugar × level interaction.

The sum of squares for each of the levels was partitioned into a set of orthogonal linear and quadratic polynomial regression components. All statements of significance are based on a probability of $P < 0·05$.

RESULTS

The pigs were healthy and consumed their daily feed allowance completely for all experimental treatments.

Expt A

Intakes of DM and water, output of digesta, and DM content of digesta measured in cannulated pigs on D-glucose or D-arabinose diets are given in Table 4. Since the output of digesta was measured over 12 h/d, intake of DM and water is also presented over a 12 h period. There were significant differences in DM intake between the treatments. These differences were caused by the feeding system applied, since this system was based on the live weight of the pigs. Water intake of pigs during phase 1 (Gluc 100 diet) was on average 2·16 times their daily DM intake. This ratio increased significantly when pigs were fed on the Arab 50 (phase 2) and Arab 100 (phase 3) diets, by 40 and 78% respectively. When pigs were changed from the Arab 100 to the Gluc 100 diet (phase 4), the water:DM intake decreased significantly to 2·37, a value which was similar to that obtained in phase 1. Output of wet digesta was increased significantly when pigs were changed successively to the Arab 50 and Arab 100 diet. However, when pigs were changed from the Arab 100 to the Gluc 100 diet the ileal output of digesta was decreased significantly.

The increase in digesta output in pigs fed on the arabinose diets was associated with a decrease in DM content of the digesta. However, similar to water intake and ileal output of digesta, this was more pronounced on the Arab 100 diet than on the Arab 50 diet.

Apparent ileal digestibility values for DM, OM, GE, N, D-glucose and L-arabinose are shown in Table 5. In pigs fed on the Gluc 100 diet (phases 1 and 4), similar digestibility coefficients for DM, OM, GE, N and D-glucose were observed. However, in pigs fed on the arabinose diets lower digestibility coefficients for DM, OM and GE were observed; the

Table 5. *Expt A. Apparent ileal digestibility coefficients of dry matter (DM), organic matter (OM), gross energy (GE), nitrogen, D-glucose and L-arabinose, measured in cannulated pigs fed on D-glucose (Gluc) and L-arabinose (Arab) diets*

(Mean values for four pigs per treatment)

Phase*	1	2	3	4		
Sugar	Gluc	Arab	Arab	Gluc		
Dietary level† (g/kg)	100	50	100	100	SED	df
DM	83·3[a]	81·8[a]	79·3[b]	83·4[a]	1·10	9
OM	84·5[a]	82·9[ab]	81·0[b]	84·9[a]	0·93	9
GE	84·9[a]	83·6[ab]	81·9[b]	85·1[a]	0·94	9
N	88·5[a]	88·0[a]	88·0[a]	88·6[a]	1·51	9
D-glucose	99·4[a]	—	—	99·3[a]	1·55	3
L-arabinose	—	70·2[a]	66·8[a]	—	2·36	3

SED, Standard error of difference between means.

[a,b] Within a row, mean values with unlike superscript letters were significantly different ($P < 0·05$).

* Phases 1–3, 7 d adaptation period and 4 d collection period; phase 4, 1 d adaptation period and 4 d collection period; for details, see p. 197.

† For details, see pp. 196–197 and Table 1.

Table 6. *Expt A. Ileal flow of volatile fatty acids (VFA) and lactic acid (mg/12 h), measured in cannulated pigs fed on D-glucose (Gluc) and L-arabinose (Arab) diets*

(Mean values for four pigs per treatment)

Phase*	1	2	3	4	
Sugar	Gluc	Arab	Arab	Gluc	SED
Dietary level† (g/kg)	100	50	100	100	(df 9)
Total VFA	985[a]	1233[ab]	1567[b]	987[a]	166·2
Individual VFA					
Acetic acid	713[a]	957[a]	1297[b]	823[a]	139·6
Propionic acid	108[a]	44[a]	79[a]	65[a]	30·8
Butyric acid	50[a]	35[a]	28[a]	34[a]	12·9
Isobutyric acid	106[a]	188[b]	141[ab]	41[c]	27·8
Valeric acid	8[a]	9[a]	22[b]	24[b]	5·0
Isovaleric acid	‡	‡	‡	‡	
L-lactic acid	511[a]	632[a]	863[a]	548[a]	176·9

SED, Standard error of difference between means.

[a,b] Within a row, mean values with unlike superscript letters were significantly different ($P < 0·05$).

* Phases 1–3, 7 d adaptation period and 4 d collection period; phase 4, 1 d adaptation period and 4 d collection period; for details, see p. 197.

† For details of diets, see pp. 196–197 and Table 1.

‡ Below the detection level of 1 mg/100 g wet digesta.

values for the Arab 100 diet being significantly different from those of pigs fed on the Gluc 100 diet. There was a tendency for digestibility of N to be less in pigs fed on the arabinose diets than in pigs fed on the glucose diet. Apparent ileal digestibility of D-glucose was found to be close to 100%. However, ileal digestibility of L-arabinose was only approximately 70%. Digestibility of L-arabinose was not significantly affected by the dietary level of L-arabinose.

Values for ileal flow of VFA and lactic acid are given in Table 6. In pigs fed on the arabinose diets the ileal flow of VFA was higher than that of pigs fed on the glucose diet,

Table 7. *Expt B. Intake (g/24 h) of dry matter (DM) and water, output (g/24 h) of faeces and urine, and DM content (g/kg) of faeces, measured in non-cannulated pigs fed on* D*-glucose (Gluc) and* L*-arabinose (Arab) diets**

(Mean values for five pigs per treatment)

		Intake			Output		
Sugar	Sugar level (g/kg)	DM (A)	Water (B)	B:A	Urine	Faeces	DM content faeces
Gluc	25	670	1470	2·19	730	162	426
	50	797	1650	2·07	790	186	442
	75	917	2040	2·22	1050	215	443
	100	1081	2490	2·30	1360	236	440
Arab	25	675	1420	2·10	690	182	393
	50	802	1750	2·18	860	192	435
	75	926	2230	2·41	1320	227	423
	100	1085	2890	2·66	1940	247	417
SED (df 32)†		8·8	139	0·16	139	19·9	15·6
SED (df 24)‡		24·4	176	0·21	167	24·2	17·7
		Mean results per sugar					
Gluc		866	1912	2·20	982	200	438
Arab		872	2072	2·34	1202	212	417
SED (df 8)		23·2	128·4	0·16	115·5	17·1	11·4

SED, standard error of difference.

* For details of diets and procedures, see pp. 197–199 and Tables 2 and 3.

† Within each sugar.

‡ Both sugars.

being significant in pigs fed on the Arab 100 diet. The increase in ileal flow of VFA in pigs fed on the arabinose diets was caused mainly by an increase in acetic acid. Ileal flow of lactic acid followed the same pattern of response as that for VFA when pigs were fed on the arabinose diets. However, the differences in ileal flow of lactic acid between the treatments were not significant.

Expt B

The mean values for DM and water intake, output of urine and fresh faeces, and DM content of faeces in pigs fed on D-glucose (Gluc) or L-arabinose (Arab) diets are given in Table 7. There were significant differences in DM intake between the treatment groups. However, as already stated for Expt A, these differences were caused by the feeding system applied. Water intake as a percentage of DM intake of pigs fed on the glucose diets was not significantly affected by the dietary level of this sugar. When pigs were fed on the arabinose diets, water intake as a percentage of DM intake increased linearly ($P < 0·01$) as the level of this sugar was increased. Output of urine and fresh faeces on both types of sugar diet followed the same pattern of response as for DM and water intake. On a composite basis the differences in output of urine and fresh faeces between pigs fed on the glucose diets and those fed on the arabinose diets were not significant ($P > 0·05$). The DM content of faeces was not significantly affected by the type and dietary level of the sugar.

Apparent faecal digestibility coefficients for DM, OM, GE and N are given in Table 8. Similar results for apparent faecal digestibility of DM, OM and GE were achieved in pigs fed on the glucose and arabinose diets. However, the average digestibility of N was significantly lower in pigs fed on the arabinose diets than in those fed on the glucose diets.

Table 8. *Expt B. Apparent faecal digestibility coefficients of dry matter (DM), organic matter (OM), gross energy (GE) and nitrogen, measured in non-cannulated pigs fed on* D*-glucose (Gluc) and* L*-arabinose (Arab) diets**

(Mean values for five pigs per treatment)

Sugar	Sugar level (g/kg)	Digestibilities			
		DM	OM	GE	N
Gluc	25	89·8	91·0	90·9	93·8
	50	89·7	91·0	91·2	94·3
	75	89·6	91·1	91·1	94·2
	100	90·5	91·7	91·5	94·4
Arab	25	89·5	90·4	90·2	93·0
	50	89·6	90·9	90·9	93·9
	75	89·6	90·9	90·9	93·2
	100	90·4	91·3	91·0	93·6
SED (df 32)†		0·85	0·61	0·55	0·34
SED (df 24)‡		1·00	0·99	0·86	0·39
		Mean results per sugar			
Gluc		89·9	91·2	91·2	94·2
Arab		89·8	90·9	90·8	93·4§
SED (df 8)		0·68	0·84	0·72	0·26

SED, standard error of difference.

* For details of diets and procedures, see pp. 197–199 and Tables 2 and 3.

† Within each sugar.

‡ Both sugars.

§ Mean value was significantly different from that for the Gluc diets ($P < 0·05$).

Results for urinary excretion of arabinose, energy and N, and retention of N are given in Table 9. Arabinose was partly excreted via the urine. The extent of the urinary excretion of this sugar, as a percentage of intake, was significantly dose-related ($P < 0·01$). As a result of the arabinose losses into the urine, urinary excretion of energy also increased in pigs fed on the arabinose diets. Urinary excretion of N and retention of N are both affected by age (McConnell *et al.* 1972; Carr *et al.* 1977). Since the experimental diets were fed in sequence, the increase in urinary excretion of N and the decrease in N retention as the dietary sugar levels were increased is due to an age effect rather than to the dietary level (Carr *et al.* 1977). Retention of N, being approximately 55% of N intake, was high in the present trial when compared with practical values. This high N retention value will be the result of both a well-balanced highly digestible protein basal diet and the relatively low daily feeding level applied (Agricultural Research Council, 1981). When pigs were fed on the arabinose diets, less ($P < 0·05$) N was retained than when feeding the glucose diets. This is due to both a lower N digestibility and a higher amount of N excreted in the urine in pigs fed on the arabinose diets.

DISCUSSION

In designing a study of this kind, a number of factors have to be taken into account. These factors mainly relate to the experimental design and the dietary inclusion levels of the test product. Latin squares are often used as an experimental design in balance studies with animals in which the diets are fed in sequence, the diet sequence being different for each animal. The advantages of using Latin squares are that variation between animals and those arising from a common time trend can be equilibrated. However, this is only true

Table 9. *Expt B. Urinary excretion (% of intake) of glucose, arabinose, energy and nitrogen, and retention of N (% of intake), measured in non-cannulated pigs fed on* D*-glucose (Gluc) and* L*-arabinose (Arab) diets**

(Mean values for five pigs per treatment)

Sugar	Sugar level (g/kg)	Urinary excretion: Glucose	Arabinose	Energy	N	Retention of N
Gluc	25	+	+	2·8	33·4	60·4
	50	+	+	2·8	35·7	58·6
	75	+	+	3·0	38·6	55·6
	100	+	+	3·2	41·2	53·2
Arabinose	25	+	10·9	3·3	34·3	58·7
	50	+	12·2	3·7	36·8	57·1
	75	+	13·7	4·7	41·8	51·4
	100	+	14·7	5·2	43·5	50·2
SED (df 32)†			1·29	0·20	2·19	2·15
SED (df 24)‡			—	0·29	2·25	2·19
			Mean results per sugar			
Gluc		+	+	3·0	37·4	57·0
Arab		+	12·9	4·2	39·1	54·4§
SED (df 8)			—	0·23	1·22	1·15

+ Small traces of glucose (0·2–0·4 g/l) and arabinose (0·01–0·2 g/l) were found in the urine of these experimental treatments; SED, standard error of difference.

* For details of diets and procedures, see pp. 197–199 and Tables 2 and 3.

† Within each sugar.

‡ Both sugars.

§ Mean value was significantly different from that for the Gluc diets ($P < 0·05$).

when there are no carry-over effects. The results of a previous tentative study have shown that carry-over effects of arabinose cannot be excluded completely. Moreover, the results of that study showed that water intake and ileal output of wet digesta of pigs fed on L-arabinose diets was increased markedly, especially at dietary inclusion levels above 100 g/kg. Therefore, in the present experiments the Latin squares method was not followed but the maximum dietary inclusion level of L-arabinose was set at 100 g/kg. One disadvantage of feeding experimental diets in sequence is that digestibilities may be affected by an age × treatment interaction. In the present study, however, no indications were found that our ileal and faecal digestibility data had been affected by age. This statement for ileal digestibility is based on the similar coefficients obtained with the glucose diet in phases 1 and 4 (Table 5). The results for faecal digestibility (Table 8), showing that the coefficients within the D-glucose block were almost constant, also indicate that these values were not confounded by age.

Previous studies have shown that L-arabinose is not absorbed completely from the small intestine in rats (Cori, 1925) and chicks (Bogner, 1961; Wagh & Waibel, 1967). Their observation is supported in the present study, indicating an incomplete digestion of this sugar at the terminal ileum. This incomplete digestion was reflected in the apparent ileal digestibility values for DM, OM and GE, showing a decrease in digestibility when including L-arabinose in the diets. There were no clear indications that ileal digestibility of L-arabinose was dose-related. This finding does not support that of a previous study with roosters showing that ileal digestibility of L-arabinose decreased when the dietary level was increased (Schutte *et al.* 1991*b*). In this context it seems relevant to comment on the possible

influence of the alimentary tract bacteria on the ileal digestibility of L-arabinose. It may be assumed that the presence of unabsorbed arabinose in the small intestine of poultry and pigs will lead to a microbial attack on this sugar. In poultry this microbial attack might have already started in the crop. Unfortunately, no reports are available in the literature on a possible fermentation of arabinose in the crop and small intestine of poultry and in the small intestine of pigs. However, it is highly probable that in the present study some microbial degradation of arabinose in the small intestine of pigs had taken place. This statement is based on the observed increase in ileal flow of VFA and lactic acid in pigs fed on the L-arabinose diets. This finding points to a more extensive microbial activity in the small intestine of pigs when fed on diets containing L-arabinose. Quantitatively the influence of the increased microbial activity on the ileal digestibility of L-arabinose is difficult to assess. In addition to arabinose, other readily fermentable components in the diet may also be susceptible to the increased intestinal bacterial activity. However, this hypothesis could not be confirmed by the ileal digestibility values for N, since the differences in apparent ileal digestible N between the D-glucose and L-arabinose treatments were small and not statistically significant.

Administration of L-arabinose to pigs was associated with an increase in ileal digesta flow. This finding is in agreement with the results of a previous study with roosters (Schutte *et al.* 1991*b*). This increase in ileal digesta flow can be explained by the presence of unabsorbed arabinose in the small intestine which will lead to an inflow of water into the intestinal lumen in order to maintain constant osmolality (Van Weerden, 1959; Hof, 1980).

Similar results for apparent faecal digestibility of DM, OM and GE were achieved when pigs were fed on diets containing either D-glucose or L-arabinose. These results indicate that L-arabinose not digested in the small intestine was microbially degraded in the hind-gut. This was confirmed by the absence of arabinose in a pooled sample of faeces from pigs fed on the arabinose diets. Considering the faecal digestibility values of N, it is likely that the presence of arabinose in the hind-gut of pigs was coupled with increased microbial activity. If sufficient substrate is available this will result in an increased net microbial protein synthesis. Consequently N output in the faeces will increase, thus decreasing faecal digestibility of N. Generally, an increased N output in the faeces due to an increased bacterial fermentation in the hind-gut of pigs is accompanied by a reduced urinary N output resulting in a zero or sometimes positive overall effect on N balance (Partridge *et al.* 1982; Dierick *et al.* 1983; Malmhof & Hakansson, 1984; Morgan & Whittemore, 1988). In contrast to these findings are the results of the present study. In addition to a depressed faecal digestibility of N, N losses in urine were also slightly increased when pigs were fed on diets containing L-arabinose. As a result, less N was retained in pigs fed on the L-arabinose diet. A similar finding of depressed N retention was reported in a previous study with the pentose sugar D-xylose when fed to pigs at a dietary inclusion level of 100 g/kg (Schutte *et al.* 1991*a*). Why the pentose sugars L-arabinose and D-xylose tend to decrease the efficiency of the utilization of absorbed N in pigs is unknown.

It is generally accepted that D-glucose can be utilized almost completely in humans and animals (Demetrakopoulos & Amos, 1978), thus only negligible amounts of glucose will be found in the urine. The latter finding is confirmed in the present study. Relatively little information is available on the extent to which L-arabinose will be excreted in the urine of simple-stomached animals. Arnal-Peyrot & Adrian (1974) reported the urinary loss of 7·5% of ingested arabinose when rats were fed on a diet containing 60 g L-arabinose/kg. Similar results were obtained in our previous study with roosters at a dietary inclusion level of 25 g L-arabinose/kg (Schutte *et al.* 1991*b*). The results of the latter study also showed that urinary excretion of arabinose, as a percentage of intake, increased linearly as the dietary level of this sugar increased. A similar finding was recorded in the present study.

However, this dose-dependent urinary excretion of L-arabinose could not be derived from the differences in urinary excretion of energy between the D-glucose and L-arabinose treatments. Calculations indicated that if the increase in urinary excretion of energy over the D-glucose treatments were attributed to L-arabinose, this would represent about 23% of the L-arabinose intake at all levels. The differences between the determined values for urinary excretion of arabinose (mean 12·9%) and those calculated from the urinary excretion of energy probably relate to the higher losses of other energy-bearing components in the urine of pigs fed on the L-arabinose diets. This proposal is supported by the higher losses of N in the urine of pigs fed on the L-arabinose diets.

Taken together, the two studies indicate that the nutritional value of L-arabinose in pigs is lower than that of D-glucose. In addition, administration of L-arabinose to pigs may result in depressed N retention. Quantitatively, the nutritional value of L-arabinose for pigs is difficult to assess from the present studies. This is because of the unknown metabolic pathway of this pentose sugar. The findings of the present studies only indicate that about 30% of the ingested L-arabinose entered the large intestine where it was fermented, while another 13% was excreted in the urine. The pathway of the remaining 57% of ingested L-arabinose is uncertain. This remaining L-arabinose, which disappeared from the small intestine, may have been either utilized as such or fermented to VFA, or both. Of these two mechanisms, a possible microbial fermentation of L-arabinose in the small intestine was demonstrated in the present study. Information about a possible metabolic pathway for this pentose sugar in the animal body is limited. Segal & Foley (1959) reported that when ^{14}C-labelled L-arabinose is intravenously infused in man only 0·8% is recovered in expired carbon dioxide. If their findings could be extended to pigs this would mean that L-arabinose can be used as an energy source for pigs only after microbial fermentation. Based on this assumption and taking urinary arabinose losses as 13%, it can be calculated that the net energy value of L-arabinose is at least 40% lower than that of D-glucose. In this calculation the efficiency of utilization of energy via hind-gut fermentation compared with that of precaecally digested glucose was set at 67% (Agricultural Research Council, 1981; Müller *et al.* 1989). Based on the differences in energy losses in the urine between the D-glucose and L-arabinose treatments the calculated net energy value for arabinose is an overestimate. On the other hand, findings of Close *et al.* (1989) suggest that the efficiency of utilization of energy from hind-gut fermentation is higher than that estimated by Agricultural Research Council (1981) and Müller *et al.* (1989).

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