NUTRITIONAL VALUE AND PHYSIOLOGICAL EFFECTS OF D-XYLOSE AND L-ARABINOSE IN POULTRY AND PIGS

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PROEFSCHRIFT
ter verkrijging van de graad van
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Schutte, J.B., 1991. Nutritional value and physiological effects of D-xylose and L-arabinose in poultry and pigs. (Nutritionele waarde en fysiologische effecten van D-xylose en L-arabinose bij pluimvee en varkens). The main sugars other than glucose, which will be released from a hydrolysis of nonstarch polysaccharides, are D-xylose and L-arabinose. The results of studies on the fate of both pentose sugars after oral administration in poultry and pigs are presented. Digestibility of L-arabinose at the end of the ileum was found to be lower than that of D-xylose. The presence of D-xylose or L-arabinose in the diet increased the ileal flow of volatile fatty acids in pigs, suggesting microbial degradation of both sugars in the small intestine. Both pentose sugars were partly excreted in the urine. The extent of this urinary excretion, as a percentage of intake, increased as the dietary inclusion of either of the two sugars was increased. At equal dietary levels, more xylose than arabinose was excreted in the urine. Feeding of D-xylose and L-arabinose to pigs and poultry caused some physiological changes. In chicks these changes resulted in wet droppings. The net energy value of both pentose sugars was calculated to be approximately 25 to 35% of that of D-glucose. Doctoral Thesis, Wageningen Agricultural University. TNO-Institute of Animal Nutrition and Physiology (ILOB). P.O. Box 15, 6700 AA Wageningen, The Netherlands.

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STELLINGEN

1. Het feit dat varkens en pluimvee niet over een enzymsysteem beschikken voor het afbreken van niet-zetmeelkoolhydraten, berust niet geheel op toeval.
(Dit proefschrift)

2. De ileale verteerbaarheid en de benutbaarheid van suikers kunnen sterk uiteenlopen.
(Dit proefschrift)

3. De waarde van de xylose absorptietest als indicator voor een verstoorde darmfunktie dient ter discussie te worden gesteld.
(Dit proefschrift)

4. In het onderzoek naar de toepassingsmogelijkheden van enzymen in de voeding van pluimvee dient de nadruk te liggen op het elimineren van de anti-nutritionele effekten van niet-zetmeelkoolhydraat frakties.
(Dit proefschrift)

5. Volwassen hanen voorzien van een ileostomie canule, kunnen als model dienen voor het schatten van de ileale verteerbaarheid van eiwit en aminozuren van grondstoffen voor het varken.

6. Toepassing van vrije aminozuren in voeders voor varkens en pluimvee kan een wezenlijke bijdrage leveren tot het reduceren van de N emissie.

7. De bewering van Pinchasov et al., dat bij kuikens minder goede produktie resultaten worden bereikt met vrije aminozuren dan met eiwit-gebonden aminozuren is onterecht, daar deze gebaseerd is op een onvolledige toevoeging van vrije aminozuren aan het rantsoen.
(Pinchasov et al., 1990. Poultry Sience 69: 1950-1955)

8. De stelling in de Consumentengids van september 1991, dat veel veevoer bestaat uit afvalprodukten van de voedings- en genotmiddelenindustrie en zodoende leidt tot goedkoop voer, is onvolledig en dient uitgebreid te worden met "en tot goedkopere levensmiddelen voor de mens".

9. Veel van de huidige problemen in de dierlijke produktiesektor kunnen worden opgelost door de varkensstapel te vervangen door pluimvee. Het enige bezwaar van deze vervanging is dat er een tekort aan poten kan ontstaan.

10. De suggestie dat een linolzuur-rijk ei gezonder is dan een normaal ei, berust op een misverstand.

11. Met tuinieren als hobby loopt men zelden persoonlijk gezichtsverlies op; de schuld van een slechte oogst ligt immers altijd bij het uitgangsmateriaal en/ of het weer.

12. De bevolking in het westen van ons land dient zich meer bewust te worden van het feit, dat zij haar welvaart voor een belangrijk deel te danken heeft aan de in Drente en Groningen aanwezige bodemschatten.

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Wageningen, 16 december, 1991.

Aan Anny
Aan Irma, Hans en Astrid
Aan mijn moeder
Ter nagedachtenis aan mijn vader

VOORWOORD

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Het onderzoek was zeer gevarieerd. Bij de aanvang van het onderzoek (eind 1987) had ik nog geen vermoeden van de problemen die zich zouden kunnen voordoen. Eén van deze problemen lag op het vlak van het analyseren van de suikers xylose en arabinose in darminhoud, urine en faeces. Dankzij de inspanningen van de voormalige IGMB-TNO afdeling Chemie en Granen werd dit probleem tot een oplossing gebracht. Beste Rob Hamer, Maarten van Oort, Wim Lichtendonk en Henk van Lonkhuijsen, ik heb het jullie niet altijd even gemakkelijk gemaakt met mijn twijfels aangaande de nauwkeurigheid van de analyses. Bedankt voor jullie bijdragen aan het onderzoek. De overige analyses en het onderzoek met varkens en pluimvee werden uitgevoerd op het ILOB.

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Ben Schutte

CONTENTS

GENERAL INTRODUCTION

GENERAL INTRODUCTION

Traditionally pig and poultry diets are mainly based on cereals and soyabean meal. However, for economical or political reasons, the use of alternative products such as peas, beans, sunflower meal, rapeseed meal, lupins, cereal by-products and sugarbeet pulp has received increasing interest in recent years. In principle, these products have the potential to replace wholy or partly cereals and/or soyabean meal in pig and poultry diets. Several factors such as the presence of harmful compounds or low digestibility, however, limit the level of their inclusion in the diet. The harmful compounds are mainly anti-nutritional factors (ANF) such as trypsin inhibitors, lectins, tannins and antigenic proteins. These ANF, which are mainly found in legumes, can depress protein digestion and performance of pigs and poultry (Huisman, 1990). In products such as sunflower meal, rapeseed meal, lupins, cereal by-products and sugarbeet pulp, the low digestibility often limits their inclusion in pig and poultry diets in appreciable quantities. This low digestibility is associated with the composition of the carbohydrate fraction in these products, which mainly consists of nonstarch polysaccharides (NSP). As the term implies, these NSP exist in a form other than starch. It is well known that starch can be hydrolysed by pancreatic α-amylase and may therefore be digested in the small intestine of pigs and poultry, and absorbed as glucose. However, NSP are not susceptible to pancreatic enzymes (Trowell et al., 1976) and can only be utilized after fermentation by gut bacteria. This fermentation process is not only coupled with considerable losses in energy, but dietary NSP may also induce a depression of the digestibility of other dietary components. In principle both problems, the low digestibility of NSP, and their negative effect on the digestibility of other dietary components can be overcome by a treatment with enzymes which can hydrolyse the NSP. As will be discussed in more detail in this chapter, this hydrolysis will not only release D-glucose, but also other sugars (e.g. D-xylose and L-arabinose) of which the nutritional value for pigs and poultry is not fully understood.

NATURE OF NONSTARCH POLYSACCHARIDES

The nonstarch polysaccharides (NSP) are complicated compounds, both from the point of view of physical structure and chemical composition, and include cellulose, hemicelluloses, pectins, oligosaccharides and lignin

(Figure 1). In fact, lignin is not a polysaccharide but a polymer of oxygenated phenylpropane units including coniferyl, sinapyl, and p-coumaryl alcohols. Because of the low levels of lignin in common feed ingredients, its encrustration with structural carbohydrates and for the sake of simplicity, this fraction is also included in the group of NSP. The basic structural material of plant cell walls is cellulose. It is composed of linear chains of ß-(1-4) glycosidically bound glucose, arranged in fibrils in a crystalline or amorphous region. Before they can be degraded enzymatically, the crystalline regions have to be converted into amorphous ones. Hemicelluloses are made up of a complex of pentoses and hexoses and frequently show branched as well as linear chains. The chain structure varies in the different feedstuffs of plant origin. Moreover hemicelluloses are often encrustrated with lignin. This encrustration in particular seems to prevent attack by enzymes as well as by microbes. Depending on their structure, hemicelluloses can be present in soluble or insoluble forms. In cereals, the hemicelluloses mainly consist of arabinoxylans, often referred to as pentosans. Pectins in plants form the so called middle lammela between cells. The main component of pectine is α-(1-4)-glycosidically linked galacturonic acid. Oligosaccharides of the raffinose family (e.g. raffinose,stachyose, verbascose) can form an

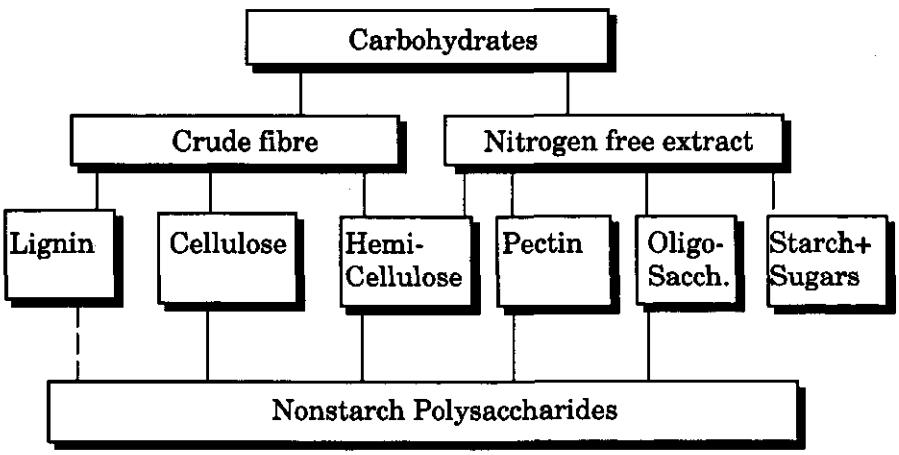


FIGURE 1. Classification of carbohydrates in vegetable feeds

important constituent of the NSP in legume seeds. The raffinose family is constituted of sugars related to raffinose by the fact that they have one or more α-D-galactopyranosyl groups in their structure. The basic unit of the raffinose family is sucrose, and α-galactose units are bound to glucose.

The contents of NSP in feed ingredients of vegetable origin vary widely (Table 1). From the data presented in this Table, it is obvious that the carbohydrate fraction of maize and wheat is predominantly starch-based. This is in contrast to the carbohydrate fraction of the protein-rich products sunflower meal, soyabean meal, groundnut meal and rapeseed meal which exists mainly as NSP. The same is true for the cereal by- products, lupins and sugarbeet pulp. Compared with these products, the contents of NSP in beans and peas are relatively low.

Regarding the composition of NSP in the various feed ingredients, there is still a lack of precise analytical data on the quantitative amounts. Information about the contents of cellulose, hemicellulose and lignin from plant residues can be derived from the acid and neutral detergent methods developed and modified by Van Soest and co-workers (Robertson & Van Soest, 1981). The acid-detergent fibre (ADF) residue provides an estimate of the cellulose and lignin content. Estimates of hemicellulose content are obtained by difference using the amounts of ADF and neutral-detergent fibre (NDF) present. Lignins must be determined in an additional step. Van Soest's method does not measure soluble substances, such as pectins, which are extensively removed by NDF extraction. Broadly, it can be said that cellulose and hemicellulose are the most important constituents of the NSP fraction in cereal by-products (Theander et al., 1989). In products such as sunflower meal, soyabean meal, beans and peas, the NSP fraction mainly consists of pectins, oligosaccharides and cellulose, and in sunflower meal also of lignin (Täufel et al., 1960; Rackis, 1974; Cerning et al., 1975; Vose et al., 1976; Reichert, 1981; Brillouet & Carré, 1983; Carré & Brillouet, 1986). The NSP fraction of lupins and sugarbeet pulp is characterized by high contents of pectins (Carré & Leclercq, 1985; Beldman,1986).

TABLE 1. Contents of carbohydrates, starch (+ sugars) and NSP in some feedstuffs (% of product)[1)]

Ingredient	Total carbohydrates	Starch (+ sugars)	NSP
Maize	72	64	8
Wheat	71	63	8
Maizegluten feed	62	20	42
Wheat bran	62	18	44
Beans (Phas.vul.)	60	43	17
Peas	58	40	18
Lupins	44	7	37
Soyabean meal	36	9*	27
Sunflower meal (dehulled)	44	+	44
Groundnut meal	45	15*	30
Rapeseed meal	45	13*	32
Sugarbeet pulp	70	15	55

1) Values derived from figures given by Anonymous (1988).
*) Vervaeke et al., (1989).

DEGRADATION OF NSP

The absence of indigenous NSP degrading enzymes and the low density of micro-organisms in the small intestine of pigs and poultry, mean that the NSP largely pass to the hind gut. Here the NSP are degraded to a greater or lesser extent by the microbes for which they are the major carbon source. The end products of this microbial degradation (lactic acid, volatile fatty acids) are readily absorbed and can be used as an energy source by the animal (Imoto & Namioka, 1978; Kass et al., 1980; Van Es, 1987; Vervaeke et al., 1989). This fermentation process, however, is coupled with considerable losses in energy, assumed to vary in pigs between 33% (Agricultural Research Council, 1981) and 50% (Just et al., 1983; Van Es, 1987). No

literature data for poultry are available, but energy losses of a similar magnitude are assumed.

The extent of fermentation of NSP in the hind gut is quite variable between various constituents of NSP. Lignin and cellulose are poorly degraded, whereas pectin, oligosaccharides and to some extent, hemicelluloses are reported to be easily fermented (Keys et al., 1969, 1970; Cummings et al., 1978; Nyman & Asp, 1982; Stanogias & Pearce, 1985; Longland & Low, 1988; Trevino et al., 1990). It also appears that microbial degradation of NSP in poultry is less important than in pigs (Longstaff & McNab, 1989). As demonstrated by Carré et al. (1990), birds can only digest the water soluble fraction of the NSP in significant amounts through bacterial fermentation, but in pigs also a significant part of the water insoluble NSP fraction can be digested (Dierick et al., 1989).

Apart from the low digestibility and utilization of NSP by pigs and poultry, the NSP-induced microbial activity may decrease ileal and faecal digestibility (Sauer et al., 1980; Dierick et al., 1983; Just et al., 1983; Graham et al., 1986; Siriwan et al., 1990). In addition NSP may inhibit lipid absorption (Just et al., 1980; Kay, 1982; Kies, 1985) and decrease digestibility of minerals (Partridge, 1978; Graham et al., 1986; Ward & Reichert, 1986). Viscous polysaccharides, such as pectin substances and ß-glucans have been shown to depress chick performance and to cause sticky, wet droppings (Wagner & Thomas, 1977; Gohl et al., 1978; Day & Thomas, 1980; White et al., 1981; Annison, 1990).

HYDROLYSIS PRODUCTS OF NSP

From a literature review, Rexen (1981) and Chesson (1987) concluded that the digestibility of NSP can be improved by treatment with enzymes which can hydrolyse the NSP to monosaccharides. This has been confirmed in a recent study at our institute (Schutte et al., 1990). Our study showed that in addition to an increase of the digestibility of cell wall components, the digestion of protein and fat was also improved in pigs when wheat bran was treated with a cellulolytic enzyme preparation. The benefits of a hydrolysis of NSP, however, are not determined only by an improvement in digestibility, but also by the potential of the animal to utilize the hydrolysis products. In addition to glucose, other sugars and uronic acids will also be released by a complete hydrolysis of NSP (Table 2). From the products of hydrolysis listed in Table 2, the sugars glucose and fructose are well utilized in monogastric animals (Demetrakopoulos & Amos, 1978; Miles et al., 1987). The same is true for galactose, but in chicks only at low dietary inclusion levels (Rutter

et al., 1953; Longstaff et al., 1988); at high dietary concentrations galactose caused kidney damage, convulsions and death (Sondergaard et al., 1957; Rigdon et al., 1963). The nutritional value of uronic acids has been reported to be very low in chicks (Longstaff et al., 1988). This was supported by our own data, (J.B. Schutte, unpublished data). We found also that administering galacturonic acid to chicks resulted in increases in water intake and caeca weights. No literature data on the utilization of uronic acids in pigs are available.

TABLE 2. The most important sugars which will be released from a complete hydrolysis of the NSP fractions.

NSP fraction	Hexoses (C_6 H_{12} O_6)	Pentoses (C_5 H_{10} O_5)	Other
Cellulose	D-glucose		
Hemicellulose	D-glucose	D-xylose L-arabinose	
Pectins	D-galactose	L-arabinose	Uronic acids*
Oligosaccharides	D-glucose D-fructose D-galactose		

* Mainly as galacturonic acid (= derived form of D-galactose of which the CH_2 OH-group is oxidized to -COOH).

In addition to glucose, the pentose sugars xylose and arabinose are in quantitative terms the most important ones which will be released from a complete hydrolysis of the NSP. Carré & Brillouet (1986) determined the composition of NSP of various feedstuffs commonly used in diets for monogastric farm animals (Table 3). From their data it can be calculated that in practical diets for growing pigs a complete hydrolysis of NSP will result in the release of each of both pentose sugars (D-xylose and L-arabinose) in quantities equal to about 4% of the diet. In Dutch practical poultry diets this amounts to about 2 to 3% for each of these two pentose sugars.

TABLE 3. Composition of NSP isolated from various feed ingredients (%)[1].

	Glucose	Xylose	Arabinose	Galactose	Mannose	Uronic acids	Lignin
Maize	24.2	24.0	19.1	4.1	0.8	6.0	5.4
Wheat	26.0	28.9	17.4	0.9	0.7	3.4	7.2
Barley	30.4	31.9	14.6	0.9	1.0	2.1	6.6
Oats	32.5	29.0	5.0	0.9	0.3	3.3	7.8
Wheatbran	24.4	18.3	18.3	1.1	0.2	4.2	7.2
Soyabean meal	18.9	5.4	13.6	24.9	5.4	15.2	1.9
Sunflower meal	27.9	13.0	7.7	2.2	3.4	11.5	21.1
Rapeseed meal	17.3	4.8	12.8	4.2	0.3	17.3	25.2
Peas	41.6	7.9	19.7	1.7	+	15.5	2.4
Field beans	37.4	5.2	8.9	1.6	+	15.0	8.2
White lupins	32.4	11.4	9.7	21.9	0.5	10.8	2.3
Lucerne meal	42.2	11.7	3.2	1.7	1.2	13.0	17.2

1)Data from Carré & Brillouet (1986). In the dicotyledonous plant materials, a small amount (0.1 - 1.7%) of rhamnose and fucose was also found. Data regarding the contents of starch, protein and ash in the NSP fractions are omitted.
+ Traces.

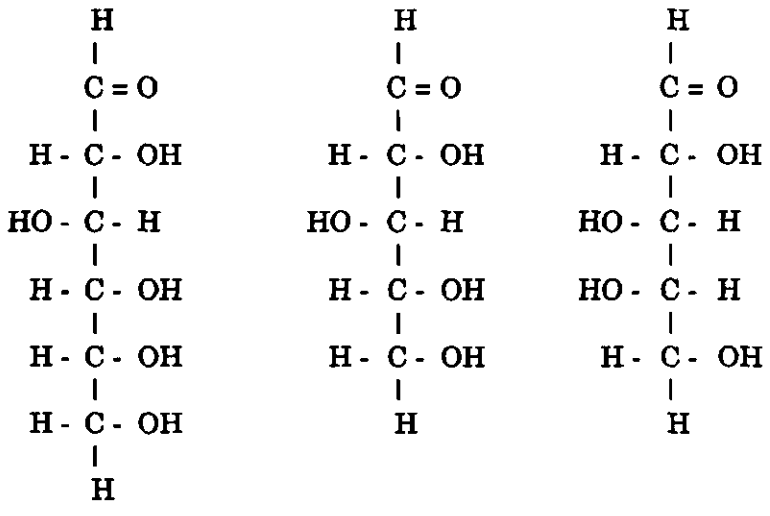
ABSORPTION AND UTILIZATION OF D-XYLOSE AND L-ARABINOSE

Knowledge about the nutritional value of D-xylose and L-arabinose in pigs and poultry is incomplete. This is not surprising, since in their free form both sugars, having five carbon atoms (Figure 2), are normally present in the small intestine in only very low concentrations. It is well known that both pentose sugars are absorbed from the intestinal tract of monogastric animals (Cori, 1925; Miller & Lewis, 1932; Bogner, 1961; Wagh & Waibel, 1967a; Arnal-Peyrot & Adrian, 1974). It appears, however, that both pentose sugars, in spite of their identical molecular size, have a different mode of transport in the small intestine. It is generally accepted that L-arabinose is passively absorbed from the small intestine of animals (Crane, 1960; Herman, 1974). However, the mode of transport of D-xylose from the intestinal tract is still controversial. The idea that D-xylose crosses the

intestinal mucosa by simple diffusion was initially reported (Cori, 1925; Wilson & Vincent, 1955; Crane, 1960). The bulk of evidence, however, suggests that this sugar shares the same transport mechanism with D-glucose (Salomon et al., 1961; Csâky & Lassen, 1964; Alvarado, 1966; Caspary, 1972; Ohkohchi & Himukai, 1984). This will mean that glucose, galactose and xylose will compete for the same transport system, so that absorption of xylose, which has the least affinity for this system, will be inhibited (Kidder et al., 1968).

Research on the rate and extent of xylose and arabinose absorption from the intestinal tract of monogastric animals is limited. Bogner (1961) and Wagh & Waibel (1967a) studied the absorption rate of D-xylose and L-arabinose in young chicks by analysing the gastro-intestinal contents 30 minutes after oral administration by crop tube. Their data showed that L-arabinose was absorbed at a lower rate than glucose and xylose, whereas the rate of absorption of xylose was only slightly lower than that of glucose. Similar results were found in rats by Cori (1925), reporting rates of absorption of various sugars in the sequence galactose > glucose > fructose > mannose > xylose > arabinose. This sequence would be the same for man, rabbit and the dog (Herman, 1974).

FIGURE 2. Structural formulae of D-glucose, D-xylose and L-arabinose



The metabolic pathways of both pentose sugars is still under discussion. It is well recognized that both pentose sugars are partly excreted in the urine of man and monogastric animals (Wise et al., 1954; Segal & Foley, 1959; Finlay et al., 1964; Arnal-Peyrot & Adrian, 1974; Haeney et al., 1978; Craig & Atkinson, 1988). Considering the literature, there are indications that renal excretion of D-xylose is affected by several factors. These factors include intestinal bacterial growth, dietary level and age. Beck et al. (1962) reported low xylose excretion in patients with intestinal diverticulli, suggesting that part of the ingested xylose is consumed by the intestinal microbes. This hypothesis is supported by data of Schiffer et al. (1962), Cooke et al. (1963) and Goldstein et al. (1970), who reported an increased urinary xylose excretion after antibiotics in patients with small intestinal diverticulosis. Wagh and Waibel (1966) reported that in chicks, the metabolizable energy (ME) value of xylose decreased when the dietary level increased. Their finding may provide some evidence of an increased urinary excretion of xylose in percentage of intake when the dietary level of this sugar is increased, since Longstaff et al. (1988) reported that apparent digestibility of D-xylose in chicks was almost 100%. It has been reported that renal xylose output in man declines with age (Fowler & Cooke, 1960; Finlay et al., 1964). The reason for this is unknown, but it has been postulated that renal function, and consequently xylose excretion, is affected by the ageing process (Kendall, 1970). On the other hand altered intestinal mucosal function associated with ageing, and/ or a decrease in arterial bloodflow through the small bowel due to atherosclerosis has been suggested (Sapp et al., 1964). No literature data are available on factors which may affect renal excretion of arabinose.

The xylose absorption test is widely used in the diagnosis of malabsorption in man and animals. This test, in which the renal excretion of xylose is measured after an oral dose of the sugar, is based on the assumption that D-xylose is not metabolized to any significant extent in the body. In man, the xylose absorption test is often standardized to an oral administration of 25 g D-xylose followed by a 5 hour urine collection. A low renal excretion of xylose has been connected with mucosal diseases. The validity of the D-xylose absorption test has been questioned (Sladen & Kumar, 1973; Kwawitt & Beeken, 1975; Hindmarsh, 1976). According to Craig & Atkinson (1988) this is not surprising since the xylose test has been derived empirically and only a few formal kinetic studies have been made to provide a rational physiological basis for their interpretation. The assumption that D-xylose is not metabolized in the body does not hold when considering the data of Wyngaarden et al. (1957). These investigators observed a rise in blood glucose level after infusion of D-xylose in man. The same was true after

infusion of L-arabinose in man. Hiatt (1957) observed in mice a slight conversion of D-xylose-1-C14 to glycogen via the pentose phosphate scheme, but virtually no conversion of L-arabinose.

The known biochemical pathways of metabolizing D-xylose, suggest conversion to D-xylulose followed by the phosphorylation to xylulose-5-phosphate, with subsequent conversion to hexose via the pentose phosphate pathway. Enzyme systems responsible for such metabolic pathways have been demonstrated to be present in bacteria (Hochster, 1955; Stumpf & Horecker, 1956; McCormick & Touster, 1957), but not in pigs and poultry. Considering the data of Wijngaarden et al. (1957), metabolism of D-xylose in higher organisms seems to be possible. These investigators reported that from an intravenous dose of C14 labeled D-xylose given to man, about 14% could be recovered as carbon dioxide in the expired air. Similar results were reported by Segal & Foley (1959) who found that 16% of an intravenous dose of C14 D-xylose given to man was metabolized to carbon dioxide. Radioisotope studies with D-xylose in monogastric animals have only been done with chicks. Wagh & Waibel (1967b) reported that from a subcutaneous dose of C14 labeled D-xylose, 4% was recovered in expired carbon dioxide.

According to Segal & Foley (1959), metabolism to carbon dioxide for arabinose is of lower magnitude than for xylose. When an intravenously infused dose of C14 L-arabinose was given to man, only 0.8% could be recovered as carbon dioxide in the expired air. In bacteria, the pathway L-arabinose -> L-arabinolactone -> L-arabonic acid -> α ketoglutarate has been described (Weimberg & Doudoroff, 1955). Since α ketoglutarate gives rise to carbon dioxide, if this pathway were operative in monogastric animals the end product would be prior to the keto acid. Apparantly, the sequence L-arabinose -> L-ribulose -> D-xylulose-5-phosphate reported in bacteria (Heath et al., 1958), seems to be absent in monogastric animals, for this would give rise to C14 carbon dioxide via the pentose phosphate pathway. Another alternative for the fate of L-arabinose may be its conversion to L-arabitol, a substance which has been isolated from pentosuric urine of man (Touster & Harewell, 1958). The L-xylulose formed from the oxidation of L-arabitol may be reduced to D-xylitol and then oxidized to D-xylulose, as found in animal cells (Hollman & Touster, 1957).

Studies performed by Darby & Day (1939) and Booth et al. (1953) with rats, and Wise et al. (1954) with pigs, indicated that xylose can cause cataracts, diarrhea and severe anorexia when fed at high dietary inclusion levels. Wise et al. (1954) also observed that retention of N was significantly decreased when pigs were fed a diet containing 560 g D-xylose/kg. They believed that this was a result of an energy deficiency on the D-xylose diet, and consequently greater N catabolism. This is supported by data of Wagh & Waibel (1966)

who found that plasma uric acid was significantly increased when chicks were fed on diets containing 200 and 400 g D-xylose/kg. Similar results were found when feeding diets containing 200 and 400 g L- arabinose/kg to chicks. They reported also that feeding diets containing these high levels of xylose or arabinose to chicks resulted in decreased liver weights.

AIM AND OUTLINE OF THE STUDY

The aim of the studies described in this thesis was to investigate the fate of D-xylose and L-arabinose after oral administration in poultry and pigs. The main emphasis has been on the digestion of these sugars in the different parts of the gastro-intestinal tract and on the renal excretion. From the results of the studies, the metabolizable energy value of the sugars could be estimated, and the potential of the animals to utilize the energy of these sugars is discussed. In addition some other nutritional implications of xylose and arabinose in diets for poultry and pigs have been examined.

A total of six studies were performed, three with poultry and three with pigs. The basal diet in most of these studies was composed of feed ingredients of semi-purified origin. The reason for this was to avoid interference with xylose and arabinose from dietary NSP material. To determine the ileal digestibility of xylose and arabinose in pigs, a post valvular T-caecum cannula (PVTC) was used (Van Leeuwen et al., 1988). This cannulation technique was developed at ILOB as an alternative for the re-entrant ileocaecal cannula. Before starting the present pig studies, both cannulation techniques were compared in which D-xylose was used as test sugar. No significant differences in apparent ileal digestibility of D-xylose, dry matter, N and energy between either cannulation technique were observed. Based on these results, it was decided that the PVTC cannula should be used in the present pig studies.

In part A (Chapters 1, 2 and 3), the results of the studies with poultry are presented. In the first study, the effect of graded dietary levels (25 to 150 g/kg) of either D-xylose or L-arabinose on chick performance, bloodsugar concentrations, caeca length and weight, and liver weight was investigated. In addition, the metabolizable energy value of both pentose sugars was determined. The second study mainly focussed on the determination of the ileal apparent digestibility and urinary excretion of both pentose sugars by using ileostomized adult roosters. The third study deals with two experiments in which the nutritional value of both pentose sugars and their effect on body composition was investigated by using two different types of basal diet.

The results of the experiments with pigs are presented in part B (Chapters

4, 5 and 6). The main objective of the first study was to determine the ileal and faecal digestibility of D-xylose. In addition, urinary excretion of D-xylose was examined, and the effect of this pentose sugar on ileal flow of volatile fatty acids, and ileal and faecal digestibility of other dietary components was investigated. The second study was carried out with L-arabinose of which the design was similar to that done with D-xylose. In the third study, the effects of some factors which may affect urinary excretion of xylose were investigated. The factors tested included frequency of feeding, age of the pigs and dietary inclusion level of D-xylose.

In the general discussion, various aspects of the results relating to animal species differences, and the practical consequences of the application of enzymes in pig and poultry diets are discussed.

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PART A

STUDIES WITH POULTRY

CHAPTER 1

NUTRITIONAL IMPLICATIONS AND METABOLIZABLE ENERGY VALUE OF D-XYLOSE AND L-ARABINOSE IN CHICKS

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NUTRITIONAL IMPLICATIONS AND METABOLIZABLE ENERGY VALUE OF D-XYLOSE AND L-ARABINOSE IN CHICKS

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An experiment was conducted to examine the effects of graded dietary levels (2.5, 5.0, 7.5, 10.0 and 15.0%) of dietary D-xylose or L-arabinose on chick performance. As reference D-glucose was included in the experiment. A second experiment was performed to determine the AME_n of D-xylose and L-arabinose. Results of Experiment 1 showed a significant linear decrease ($P < 0.05$) in weight gain and efficiency of feed utilization when the dietary level of either D-xylose or L-arabinose was increased. The same was true for daily feed intake of the D-xylose treatments. Water intake was linearly ($P < 0.05$) increased as dietary level of both pentose sugars increased and, as a result, dry matter content of the droppings decreased. Results of Experiment 2 showed that the AME_n value of either pentose sugar was dose related. The AME_n values for D-xylose at 5 and 10% dietary inclusion were 2,660 and 2,020 kcal/kg, respectively. Those for L-arabinose at these inclusion levels were 2,300 and 1,360 kcal/kg, respectively. Feeding equal dietary levels of either pentose sugar resulted in higher concentrations of xylose than of arabinose in blood plasma. Concentration of glucose in blood was not affected by feeding either D-xylose or L-arabinose. Cecal length and weight were markedly increased by feeding L-arabinose and intermediately by D-xylose. (Key words: pentose sugars, D-glucose, D-xylose, L-arabinose, chicks)

INTRODUCTION

The protein-rich ingredients used in poultry diets are mainly of vegetable origin. The carbohydrate fraction of these ingredients consists mainly of nonstarch polysaccharides (cellulose, hemicellulose, pectins, etc.) which are practically indigestible by poultry because birds do not possess the appropriate gastrointestinal tract enzymes. The microflora in the large intestine of birds seem to play only a minor role, thus digestibility of

nonstarch polysaccharides (NSP) by microbial fermentation is also low. Apart from the low digestibility, higher dietary inclusion of some NSP fractions like cellulose, betaglucans and pectins may also reduce digestibility of other dietary components and performance of chicks (Saito et al., 1959; Wagner & Thomas, 1977; Gohl et al., 1978; Day & Thomas, 1980; Nahm & Carlson, 1985).

Improvement of the digestibility and utilization of NSP could be attained by including enzymes in the diets that can hydrolyze the NSP to monosaccharides. However, a complete hydrolysis of the NSP will release not only glucose, but also other sugars such as xylose, arabinose and galacturonic acid. The nutritive value of these sugars in poultry are reported to be low (Wagh and Waibel, 1966, 1967a,b, Baker, 1977; Longstaff et al., 1988) at dietary inclusion ranging from 10 to 60% of the diet. Little information is available from research done with lower inclusion levels.

The two experiments reported herein were carried out to study the effect of D-xylose and L-arabinose in comparison with D-glucose at dietary inclusion ranging from 2.5 to 15% on chick performance and to determine the metabolizable energy value of both pentose sugars.

MATERIALS AND METHODS

Experiment 1: Growth.

This experiment was designed to compare the effects of graded (2.5, 5.0, 7.5, 10.0 and 15.0%) dietary D-glucose, D-xylose or L-arabinose on body weight gain, feed consumption, feed utilization, water consumption, and dry matter content of excreta. Day-old female broiler chicks ("Hybro", Euribrid BV, Boxmeer, Holland) were used. The birds were housed in electrically heated battery cages of 975 cm^2 of floor space with wire floors. The cages were situated in an insulated room with facilities for control of temperature and humidity. Chicks were subjected to continuous artificial fluorescent illumination. A standard diet was fed for the first three days, followed by another three days of a mixture of the standard diet and the basal diet used in this experiment. At six days of age, fourteen birds were allotted to each of 60 cages such that average body weight (156 g) and weight range (135 to 180 g) were similar. Treatment groups consisted of four cages arranged in a randomized block design.

The nutritionally complete basal diet used was based on corn, corn starch and isolated soya protein (Table 1). The three sugars (D-glucose, D-xylose

TABLE 1. Composition of the basal diet.

Ingredient	%
Corn	28.65
Corn starch	28.70
Soy oil	4.00
Animal fat	4.00
Isolated soya protein (88% CP)	22.33
Cellulose ("Akufloc")	6.00
Ground limestone	1.25
Monocalcium phosphate	2.10
Salt, iodized	0.30
Potasium bicarbonate	1.50
Vitamin-mineral premix[1)]	1.00
DL-methionine	0.17
Calculated contents:	
ME, kcal/kg	3460
Crude protein, %	22.5
Calcium, %	0.90
Phosphorus, %	0.70
Lysine, %	1.33
Methionine plus cystine, %	0.90

1) Supplied per kilogram of diet: vitamin A, 10,000 IU; vitamin D , 2,000 ICU; dl-α-tocopheryl acetate, 30 mg; menadione, 5 mg; thiamin, 2.5 mg; riboflavin, 5.5 mg; d-pantothenic acid, 15 mg; niacinamide, 50 mg; cobalamin, 15 µg; choline chloride, 1,850 mg; pyridoxine, 3 mg; biotin, 0.15 mg; folic acid, 0.75 mg; ascorbic acid, 50 mg; inositol, 100 mg; para-amino-benzoic acid, 2.5 mg; ethoxyquin, 100 mg; avoparcin, 15 mg; Mg, 420 mg; Mn, 95 mg; Zn, 50 mg; Fe, 40 mg; Cu, 40 mg; Co, 2 mg; Se, 0.1 mg.

and L-arabinose), supplied as anhydrous monosaccharides were substituted by weight for corn starch. The rations were pelleted utilizing a labor-monoroll press (Simon Heesen, Boxtel, Holland) at an approximate temperature of 50 ^{0} C. Both feed and water were available for ad libitum consumption during the days 6 to 25 posthatching growth period.

At the end of the trial, chicks were weighed individually and feed con -

sumption for each cage was recorded. During the last two days of the experimental period water consumption was measured, and excreta were collected, both for each cage at intervals of 12 h. Water intake was measured as the difference between a predetermined volume of water in the water pans and that remaining in the pans. Excreta were collected quantitatively into containers and stored at 4 C. Immediately after the two-day collection period the excreta were pooled per treatment group and analyzed for dry matter content.

Experiment 2: Balance

This experiment was conducted to estimate the AME of D-xylose and L-arabinose at 5 and 10% dietary inclusion levels. In addition, blood samples were collected from the birds for glucose, xylose and arabinose analyses; gross morphological observations on the gastrointestinal tract, liver and kidneys were performed.

The balance trial was carried out with birds from Experiment 1 consuming rations containing 10% D-glucose, 5 or 10% D-xylose and 5 or 10% L-arabinose, respectively. During the balance trial, rations with the same type and level of sugar were fed (Table 2). Thirty-two birds (25 days of age)

TABLE 2. Design of experiment 2 (balance trial)

Treatment	Diets fed in the preceding period	Diets fed in the balance period
A	10% D-glucose	Basal *
B	5% D-xylose	95% basal + 5% D-xylose
C	10% D-xylose	90% basal + 10% D-xylose
D	5% L-arabinose	95% basal + 5% L-arabinose
E	10% L-arabinose	90% basal + 10% L-arabinose

* Contained 10% D-glucose

from each of the five preceding treatment groups were selected such that the differences in body weight between these groups at the end of the growth trial were maintained. In the balance trial each treatment group included four cages, each with 8 birds.

The birds were housed in conditions similar to those described in the growth trial. The experimental diets were again freshly prepared. The 10%

D-glucose diet was used as a control (basal) diet. In the other diets a proportional part of the basal diet was subsituted by D-xylose or L-arabinose (Table 2).

The balance trial included a pretest period of 10 days and a test period of 4 days. During the last 3 days of the pretest period and the 4 days test period, equal amounts of feed were fed to all cages (800 g feed per cage per day). Feed was supplied as pellets four times daily. These portions were quantitatively consumed within half an hour. During the 4 x 24 h test period, the excreta were collected quantitatively from glass trays at intervals of 12 h. Contaminants, such as down and scales, were carefully removed and the excreta were then stored in closed containers at - 25 C. In addition to feed, water intake was also recorded during the test period. The latter was done according to the same procedure as followed in Experiment 1.

The five experimental diets and the excreta were analyzed for dry matter, nitrogen and gross energy (GE). The AME of each diet was calculated from the figures for GE of the feed and excreta; each replicate of 8 birds was assessed separately. The AME values were corrected to zero nitrogen balance (AME_n). The correction factor of 8.22 kcal/g of retained nitrogen as proposed by Hill and Anderson (1958) was used.

When the balance trial was finished, blood samples were taken from 8 randomly selected birds per treatment group. This was done twice, the first time without fasting and the second time after a 12-h feed deprivation (water remained available during the feed deprivation). The blood samples were obtained from the ulnar vein using heparinized syringes. Plasma was analyzed for glucose, xylose and arabinose.

Furthermore 16 randomly selected birds per treatment group were killed after a feed deprivation period of 12 h. Water remained available during this period. The birds were killed by injection of T61 (Embutramide-Mebezoniumiodide-Tetracainhydrochloride mix, Hoechst, F.R.G.). The small intestine and the ceca were removed immediately and their length was measured. In addition, the cecal weight (including contents) was determined. Gross pathological examination of the liver and kidneys was carried out, and weight of the liver was recorded.

Chemical analysis

An IKA-C4000 adiabatic bomb colorimeter was used to determine the gross energy energy content of the diets and excreta. The nitrogen content of diets and excreta were determined by the Kjeldahl procedure (Association of Official Analytical Chemists, 1975) using an automatic analyzer (Technicon Instruments systems, Tarrytown, NY).

Plasma sugar concentrations were determined as silyl derivatives of monosaccharides by gas-liquid chromatography (Sweeley et al., 1963). One ml of plasma was diluted with distilled water (1:10), deproteinized with potassium ferrocyanate and zinc-acetate and desalted by passing through a mixture of anion (Biorad AG 3x4) and cation (Biorad AG 50 W x 4) exchanger. Next, the samples were derivatized in pyridine with hexamethyldisilazane and trimethylchlorosilane and analyzed by using a Hewlett-Packard (Model HP 5890) gas-liquidchromatograph with a Chrompack capillary WCOT fused silica column coated with CP sil 5 CB of 50 m length.

Statistical analysis

A two-way ANOVA was used for Experiment 1, which had a factorial arrangement of treatments. A one-way ANOVA was used for Experiment 2. For experiment 1, the sum of squares for levels was partitioned into a set of orthogonal linear and quadratic polynomial regression components. The interaction sum of squares was partitioned by the same set of components. The computer program GENSTAT 5 (Reference Manual 1987, Oxford University Press, New York) was used to calculate the ANOVA. The significance of differences between treatment means was tested by using the Least Significance Difference test (Snedecor & Cochran, 1980). All statements of significance are based on a probability of less than 0.05.

RESULTS

Experiment 1: Growth.

The results of this experiment are summarized in Table 3. At all dietary levels of D-glucose, almost identical growth rate and feed conversion were achieved. Water intake and dry matter content of the excreta also were not affected by the added level of D-glucose in the diet.

Weight gain and efficiency of feed utilization decreased linearly ($P < 0.05$) as the level of D-xylose or L-arabinose increased (Table 3).

TABLE 3. The effect of dietary inclusion levels of D-glucose, D-xylose and L-arabinose on chick performance from 6 to 25 days of age with ANOVA summary (Experiment 1).

Sugar	Dietary level (%)	Weight gain (g)	Feed intake (g/bird per day)	Feed/ gain (g:g)	Water intake (g/bird per day)[1]	Dry matter content excreta(%)[2]
D-glucose	2.5	860	65.8	1.46	154	26.6
	5.0	852	66.3	1.48	144	26.0
	7.5	860	67.4	1.49	151	26.3
	10.0	870	67.6	1.48	148	26.4
	15.0	858	66.6	1.48	146	25.2
D-xylose	2.5	817	63.6	1.48	186	19.1
	5.0	802	62.6	1.49	203	16.4
	7.5	770	61.4	1.51	246	13.3
	10.0	726	61.1	1.60	252	13.0
	15.0	671	58.1	1.64	291	9.7
L-arabinose	2.5	826	65.0	1.50	209	17.1
	5.0	802	63.8	1.51	222	16.6
	7.5	781	63.9	1.56	281	12.9
	10.0	761	63.6	1.59	303	12.1
	15.0	739	65.4	1.68	377	10.0

ANOVA summaries.

Source of variation	Df	Probability			
Sugar(S)	2	**	**	**	**
Level(L)	4	**	**	**	**
Linear	1	**	**	**	**
Quadratic	1	NS	NS	NS	NS
S x L	8	**	**	**	**
Linear	2	**	**	**	**
Quadratic	2	NS	*	NS	NS
Residual MS	45	369	1.76	0.0006	637

1 Means of four pens per treatment of Days 24 plus 25.
2 Pooled samples per treatment of Days 24 plus 25; figures not analysed statistically.
* $P < 0.05$.
** $P < 0.01$.

The same was true for the daily feed intake by birds fed diets containing D-xylose, but not for intake of chicks fed L-arabinose. The differences in weight gain between both pentose sugars were small up to a dietary level of 7.5%, but at 10 and 15%, weight gain of the birds fed the L-arabinose diets was significantly ($P < 0.05$) greater than those fed the D-xylose diets. However, feed conversion efficiency, was somewhat better with D-xylose than with L-arabinose. On a composite basis the differences in feed conversion efficiency between the two pentose sugars were significant ($P < 0.05$).

A significant linear increase ($P < 0.05$) in daily water intake occurred as the dietary level of either D-xylose or L-arabinose increased (Table 3). However, at each dietary level, water intake of the birds fed the L-arabinose diets was much higher than that of the birds fed the D-xylose diets. On a composite basis, the difference in water intake between the two pentose sugars was significant ($P < 0.01$). As a result of the increase in water intake from increasing dietary D-xylose or L-arabinose, dry matter content of the excreta decreased steadily.

Mortality rate was very low; only 1% of the birds died. No appreciable differences in mortality among the treatments were observed.

Experiment 2: Balance.

The values determined for the AME_n of the experimental diets are presented in Table 4. From these values the AME_n content of D-xylose and

TABLE 4. Determined AME_n values of the experimental diets (Experiment 2).

Diets	AME_n (kcal/kg)
Basal	3505 ± 2^a
95% basal + 5% D-xylose	3463 ± 12^b
90% basal + 10% D-xylose	3357 ± 14^c
95% basal + 5% L-arabinose	3445 ± 10^b
90% basal + 10% L-arabinose	3291 ± 25^d

[a-d]Means (± SD) with no common superscript differ significantly ($P < 0.05$).

L-arabinose was derived by comparing the AME_n of xylose and arabinose containing diets with that of the basal diet (Table 5). The AME_n value of both pentose sugars was dose-related. At any specific dietary level, a higher AME_n value was observed for D-xylose than for L-arabinose, but only the difference at the 10% dietary inclusion was significant.

TABLE 5. Derived AME_n values for the sugars (Experiment 2).

Sugar	Dietary (%) inclusion	AME_n (kcal/kg)
D-xylose	5	2660 ± 243[a]
	10	2020 ± 141[b]
L-arabinose	5	2300 ± 204[a]
	10	1360 ± 251[c]

[a-c]Means (± SD) with no common superscript differ significantly ($P < 0.05$).

Data regarding body live weight, daily water intake, dry matter content of excreta, length of small intestine and ceca, weight of liver and ceca and sugar concentrations in blood plasma are shown in Table 6. Results for daily water intake and dry matter content of excreta agree well with those obtained in the growth trial. The length of the small intestine was not affected by feeding diets containing either D-xylose or L-arabinose. The ceca from chicks fed diets containing D-xylose or L-arabinose were not only longer but also heavier than those from chicks fed the basal diet. The length and weight of the ceca of the birds fed the L-arabinose diets was dose-related; cecal length and weight of the 10% L-arabinose group were significantly different from those of the 5% L-arabinose group. Also, there was a tendency for ceca weight of the birds fed the D-xylose diets to increase as dietary level increased from 5 to 10%.

Relative liver weights of the birds fed either D-xylose or L-arabinose were not significantly different from that of chicks fed the basal diet (Table 6).

TABLE 6. Effect of dietary inclusion of D-xylose and L-arabinose on water intake, dry matter content of excreta, and physical and biochemical characteristics of chicks (Experiment 2).

Parameter	Basal	D-xylose 5	D-xylose 10	L-arabinose 5	L-arabinose 10
Live weight at the end of the experiment, g	1750[a]	1661[b]	1593[c]	1663[b]	1526[d]
Daily water intake, g/bird	179[a]	226[b]	292[c]	274[c]	365[d]
Dry matter content excreta, %	26.6[a]	19.0[b]	15.4[c]	16.1[c]	11.6[d]
Small intestine length, cm	124[a]	129[a]	129[a]	126[a]	135[a]
cecal length, cm	29[a]	31[b]	31[b]	30[ab]	35[c]
cecal weight (incl. contents),					
g	7.4[a]	9.2[ab]	10.6[b]	10.3[b]	14.5[c]
% of LW	0.42[a]	0.55[ab]	0.67[b]	0.62[b]	0.95[c]
Liver weight,					
g	45.0[a]	40.4[ab]	42.2[ab]	47.5[a]	35.1[b]
% of LW	2.6[ab]	2.4[b]	2.6[ab]	2.9[a]	2.3[b]
Blood plasma values, mmol/l					
Without feed deprivation					
Glucose	12.9[a]	12.6[a]	13.5[a]	13.5[a]	13.4[a]
Xylose	0	4.6[a]	8.2[b]	0	0
Arabinose	0	0	0	0.9[a]	1.5[b]
After 12 h feed deprivation					
Glucose	10.6[a]	11.2[a]	11.1[a]	10.9[a]	11.2[a]
Xylose	0	0	0	0	0
Arabinose	0	0	0	0	0

[a-d] Means with no common superscripts within a row differ significantly ($P < 0.05$).

Gross pathological examination of the liver and kidneys did not show abnormalities in any of the treatments. No indications were observed that the D-glucose level of the blood plasma was influenced by feeding diets containing D-xylose or L-arabinose. However, when equal levels of D-xylose or L-arabinose were fed, concentrations of xylose in the plasma were significantly higher than those for arabinose. Xylose plasma concentrations were almost doubled by increasing the level of dietary inclusion from 5 to 10%. The same was true for arabinose. After 12 h feed deprivation, the xylose and arabinose levels were reduced to zero.

DISCUSSION

The results of Experiment 1 show that even at the very low dietary inclusion of 2.5%, both D-xylose and L-arabinose affected performance adversely. This could be expected since the AME_n value for D-xylose and L-arabinose are much lower than the AME_n value of D-glucose (3640 kcal/kg, Anderson et al., 1958). Furthermore, the AME_n value of both pentose sugars decreased when the dietary level was increased. This finding is in agreement with those of Wagh & Waibel (1966), showing that the AME_n values for D-xylose and L-arabinose were reduced to zero kcal/kg at dietary inclusion of 40%. The decrease in energy value of both pentose sugars by increasing the dietary levels may have resulted from decreased absorption capacity, or an increased urinary excretion, or both of these. A decrease in the utilization of the other energy bearing components in the diet may be a further possibility, resulting in a lower derived AME_n value for both pentose sugars. Results of a recently performed study (Schutte et al., unpublished data) indicate that all three factors are more or less responsible for the decrease in energy as dietary of D-xylose or dietary L-arabinose were increased. However, in that study the increase in sugar excretion with the urine was the most important factor. This may also be the reason for the excessive water consumption of birds fed the higher dietary levels of either D-xylose or L-arabinose observed in the present studies.

The AME_n value of D-xylose was higher than for L-arabinose. The feed conversion efficiency data of Experiment 1 were consistent with this finding, showing a better efficiency of feed utilization of the birds fed the D-xylose diets than those fed the L-arabinose diets. The higher AME_n value of D-xylose was not reflected in the results for weight gain due to the depression in feed intake caused by dietary D-xylose. Depressed feed intake as a result of feeding D-xylose diets to chicks also was observed by Baker (1977).

Results were similar when D-xylose diets were fed to pigs (Wise et al., 1954).

The appearance of higher concentrations of xylose than arabinose in plasma observed in the present study agrees with the data of Wagh & Waibel (1967a), suggesting a faster absorption of the former. This is supported by the gastrointestinal absorption data of Wagh & Waibel (1967b), showing that D-xylose was more efficiently absorbed from the small intestine than L-arabinose. The more efficient absorption of D-xylose over L-arabinose is supported further by the heavier cecal weights of birds fed the L-arabinose diets than those fed the d-xylose diets, indicating that a greater part of the former is fermented by the cecal microflora.

The observation that blood glucose was not affected in chicks when D-xylose or L-arabinose were included in the diet, agrees with the finding of Wagh & Waibel (1967a). These investigators also studied the effect of feeding D-xylose and L-arabinose diets on liver weight and liver glycogen. At dietary inclusion of 10 to 40%, liver weight and liver glycogen decreased, indicating a depletion of liver glycogen as a reflection of energy deprivation. The results of the present study (Experiment 2) do not support this conclusion. In Experiment 2, relative liver weight was only slightly reduced when 10% L-arabinose was included in the diet.

In conclusion, the nutritional values of D-xylose and L-arabinose are less than that of D-glucose and are dose-dependent. In addition both pentose sugars may induce unwanted nutritive problems and wet droppings.

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CHAPTER 2

ILEAL DIGESTIBILITY AND URINARY EXCRETION OF D-XYLOSE AND L-ARABINOSE IN ILEOSTOMIZED ADULT ROOSTERS

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An experiment with ileostomized adult roosters was conducted to determine the ileal digestibility and urinary excretion of D-xylose and L-arabinose. As a reference D-glucose was included in the experiment. The sugars were tested at graded dietary levels of 2.5, 5.0, 7.5 and 10.0%. Mean ileal digestibility of D-glucose and D-xylose was nearly 100%. Ileal digestibility of L-arabinose decreased linearly ($P < 0.05$) with increasing dose level. The corresponding ileal digestibilities for L-arabinose at dietary levels of 2.5, 5.0, 7.5 and 10.0% were 95.5, 93.6, 80.3 and 74.6%. Both pentose sugars were partly excreted in the urine. The extent of this urinary excretion in percentage of intake increased linearly ($P < 0.05$) as the dietary level increased. In roosters fed the 2.5% D-xylose diet, 7.2% of the D-xylose consumed appeared in the urine. This level increased to 20.2% when roosters were fed a diet containing 10.0% D-xylose. Corresponding values for L-arabinose at these dietary inclusion levels were 8.7 and 16.6%. (Key words: pentose sugars, D-xylose, L-arabinose, ileal digestibility, urinary excretion, adult roosters).

INTRODUCTION

The feed ingredients used in poultry diets are mainly from vegetable origin. The carbohydrate fraction of many of these feed ingredients, including soybean meal, sunflower meal, rapeseed meal, lupins and wheatbran, consists mainly of non-starch polysaccharides (Carré & Brillouet, 1986; Brillouet et al., 1988; Schutte et al., 1990), which are resistant to the digestive enzymes. Moreover, degradation of non-starch polysaccharides (NSP) in the hindgut of birds by microbes is also low (Vogt & Stute, 1971;

Carré & Leclercq, 1985; Longstaff & McNab, 1986, 1989). From a literature review, Chesson (1987) concluded that the digestibility of feed ingredients containing high levels of NSP can be improved by treatment with enzymes which can hydrolyze the NSP to monosaccharides. However, hydrolysis of NSP will release not only glucose, but also sugars such as xylose and arabinose which are normally not encountered in the small intestine.

It is well recognized that both pentose sugars are absorbed from the intestinal tract in rats (Cori, 1925; Miller & Lewis, 1932; Arnal-Peyrot & Adrian, 1974). The study reported by Arnal-Peyrot & Adrian (1974) also showed that part of the ingested xylose and arabinose is excreted in the urine. Studies performed by Darby & Day (1939) and Booth et al. (1953) with rats, and Wise et al. (1954) with pigs, indicated that xylose can cause cataracts, diarrhea and severe anorexia when fed at high dietary inclusion levels. In the studies reported on the utilization of both pentose sugars in chicks, mainly feed intake, weight gain, and metabolizable energy were measured (Wagh & Waibel, 1966; 1967a; Longstaff et al., 1988; Schutte, 1990). From these studies, it appears that both pentose sugars are less well utilized than glucose by poultry and may induce unwanted nutritive problems together with wet droppings. Research on the absorption of xylose and arabinose from the intestinal tract of chicks is limited. Bogner (1961) and Wagh & Waibel (1967b) studied absorption of xylose and arabinose in young chicks by analyzing the gastrointestinal contents at 30 minutes after oral administration by crop-tube. Their data showed that arabinose was absorbed at a lower rate than glucose and xylose, whereas absorption velocity of xylose was only slightly lower than that of glucose.

The present trial was designed to get more information on the quantitative aspects of digestion and utilization of D-xylose and L-arabinose at dietary inclusion levels of 2.5, 5.0, 7.5 and 10.0% in fowl. For this purpose ileostomized adult roosters were used in order to measure the disappearance rate of D-xylose and L-arabinose at the end of the terminal ileum, and to determine the urinary excretion of these sugars. D-glucose was included in the trial as a reference.

MATERIALS AND METHODS

Birds and Housing

Adult ileostomized roosters ("Lohmann Meat", Lohmann GmbH, Cuxhaven, Germany) of 3.5 to 4.0 kg body weight were used. The birds were housed individually in wire-mesh cages (40 x 75 x 60 cm, width x height x depth), which were provided with a feed and water bowl. The cages were

situated in an insulated room with facilities for control of temperature and light. Birds were maintained under a 16 h light: 8 h twilight cycle throughout. The temperature in the room was kept at approximately 20 °C.

Surgical procedures

Birds were ileostomized by a modification of the simple T-cannula procedure of Raharjo & Farrell (1984). Prior to the surgery, birds were starved for 12 h and premedicated for anesthesia by intramuscular injection of 0.8 mL/bird of ROMPUN (Bayer AG, Leverkusen, Germany). Anesthesia was induced and maintained by inhalation of halothane evaporated in 0_2 and N_2 0. All feathers were removed from the abdominal wall caudal to the sternum, and the area was desinfected with a Betadine solution. Laparotomy was performed by a 3 cm incision ventral to the tip of the right pubic bone. The distal ileum was exteriorized and transected about 5 cm anterior to the ileocaecal junction. Next, the stumps were closed using Vicryl surgical gut (size 4). A longitudinal incision of minimum length, to receive the ileal flange, was made in the antimesenteric border of the ileum near the sealed stump. Next a purse string suture of size 00 surgical gut was incorporated into the sub-mucosa of the ileum proximal to the incision. The silicone rubber cannula, with an inside diameter of approximately 8 mm, was inserted in the intestinal lumen through the incision, and the purse string suture was drawn snugly around the barrel of the cannula. A second purse string placed about 1 mm from the first one, completed the inversion of the secretory mucosa. The intestine was then replaced in the body cavity and the muscle tissue was sutured using Vicryl surgical gut (size 4). Finally the skin was closed with non-absorbable sutures (size 4). A rubber "O" ring was placed at the base of the cannula to prevent movement of the cannula. For collection of digesta, a screw-cap vial was attached to the end of the cannula barrel. For collection of urine, a funnel was fitted into a flask and placed directly beneath each cage.

Postoperative care included keeping the birds warm and withholding feed for 24 h. Birds were allocated to the test 4 weeks after surgery.

Diets

The basal diet used was based on corn, wheat starch and isolated soya protein (Table 1) and calculated to be adequate in all nutrients following the recommendations of Agricultural Research Council (1975) and National Research Council (1984). The three sugars (D-glucose, D-xylose and L-arabinose) were tested at dietary inclusion levels of 2.5, 5.0, 7.5 and 10%.

The sugars, supplied as anhydrous monosaccharides, were substituted by weight for wheat starch. The feed was supplied as dry mash and fed at a daily rate of 140 g (= 125.6 g of dry matter) to each bird throughout. The daily amount of feed was offered as two equal meals at 08.00 h and 20.00 h. Water was available ad libitum access.

TABLE 1. Composition of the basal diet.

Ingredient	Percentage
Corn	39.00
Wheat starch	38.75
Soy oil	2.00
Animal fat	2.00
Isolated soya protein (88% CP)	12.00
Ground limestone	1.25
Monocalcium phosphate	2.10
Salt, iodised	0.30
Potassium bicarbonate	1.50
Vitamin-mineral premix[1]	1.00
DL-methionine	0.10
Calculated contents:	
ME, kcal/kg	3390
Crude protein, %	14.40
Calcium, %	0.90
Phosphorus, %	0.70
Lysine, %	0.78
Methionine plus cystine, %	0.59

[1]Supplied per kilogram of diet: vitamin A, 10,000 IU; vitamin D_3, 2,000 ICU; dl-α-tocopheryl acetate, 30 mg; menadione, 5 mg; thiamin, 2.5 mg; riboflavin, 5.5 mg; d-pantothenic acid, 15 mg; niacinamide, 50 mg; cobalamin, 15 µg; choline chloride, 1,850 mg; pyridoxine, 3 mg; biotin, 0.15 mg; folic acid, 0.75 mg; ascorbic acid, 50 mg; inositol, 100 mg; para-amino-benzoic acid, 2.5 mg; ethoxyquin, 100 mg; avoparcin, 15 mg; Mg, 420 mg; Mn, 95 mg; Zn, 50 mg; Fe, 40 mg; Cu, 40 mg; Co, 2 mg; Se, 0.1 mg.

Experimental design

As is illustrated in Table 2, during the experimental period the same type of sugar was fed to each bird in the sequence of 2.5 (phase 1), 5.0 (phase 2), 7.5 (phase 3) and 10.0% (phase 4) of the diet. Each of the four phases consisted of a pre-test period of 7 days and a test period of 4 days. During the first 3 days of the pre-test period, birds were gradually changed to the next diet containing a higher inclusion level of the same sugar. During the 4 x 24 h test period digesta and urine were collected quantitatively for each bird separately at intervals of 2 h. The digesta and urine were weighed daily and stored at -25 C.

TABLE 2. Experimental design

Treat-ment	Sugar	Number of birds	Dietary sugar level (%)			
			phase 1 (1-11days)	phase 2 (12-22days)	phase 3 (23-33days)	phase 4 (34-44days)
A	D-glucose	3	2.5	5.0	7.5	10.0
B	D-xylose	3	2.5	5.0	7.5	10.0
C	L-arabinose	3	2.5	5.0	7.5	10.0

Chemical Analysis

Each diet was analyzed for dry matter and nitrogen (N); the diets containing 5 and 10% of the test sugars also were analyzed for gross energy (GE). Digesta and urine were analyzed for the content of N, glucose, xylose and arabinose. The digesta were analysed for dry matter. In addition, digesta and urine of birds fed diets containing 5 and 10% of the test sugars were analyzed for GE. The analyses of digesta and urine were done separately for each bird.

Dry matter and N analyses were performed according standard methods (Association of Official Analytical Chemists, 1984). GE was determined by using an IKA-C4000 adiabatic bomb calorimeter (IKA-Analysentechnik GmbH, 8044 Unterschleissheim, Germany).

Sugar concentrations in digesta and urine were determined as silylderivatives of monosaccharides by gas liquid chromatography (Sweeley et al,

1963). A known amount of wet digesta (1g) or urine (1 mL) was diluted with distilled water (1 : 10). 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 x 4) and cation (Biorad AG 50 W x 4 exchanger. After centrifugation, 200 µL of the supernatant was freeze dried. To the freeze dried sample phenylglucopyranoside (0.4 mg in a 1 mL pyridine solution) was added as an internal standard. The sample was then derivatized by the addition of 0.6 mL hexamethyldisilazane and 0.3 mL trimethylchlorosilane. Next the contents were stirred on a Vortex stirrer. After an incubation period of 30 min at room temperature, the reagents were removed by evaporation with nitrogen at 40 ° C. The residue was redissolved in 0.5 mL ethylacetate. From this sample, 2 µL was analyzed by using a gas liquid chromatograph (Model HP 5890, Hewlett-Packard Co., Palo Alto, CA.), equipped with a flame ionization detector and integrator (Model 3396A, Hewlett-Packard Co., Palo Alto, CA.). The carbohydrate derivatives were separated with a Chrompack capillary WCOT fused silica column (Chrompack, Middelburg, The Netherlands.) coated with CP sil 5 CB of 50 m length. Hydrogen was used as carrier gas. The oven temperature was held for 3 min at 190 ° C, then raised at the rate of 5 °C/min to a final temperature of 265 ° C, which was held for 5 min. The temperature of the injector and detector was 240 ° and 300 ° C, respectively.

Calculations

Ileal digestibilities of sugars, dry matter, nitrogen and energy were expressed as digestibility coefficients (DC) using the equation:

$$DC = \frac{\text{Nutrient consumed - nutrient excreted in digesta}}{\text{Nutrient consumed}} \times 100$$

Rates of urinary excretion of sugars and energy were expressed as percentage of the intake of sugars and energy, respectively.

Statistical analysis

All data were analyzed by analysis of variance using a split-plot design model, in which the animals are the whole plots (Cochran & Cox, 1957). The computer program GENSTAT 5 (Reference Manual 1987, Oxford University Press, New York) was used to calculate the analysis of variances. The treatment factors were type of sugar and the dietary level of sugar. If the

number of dietary sugar levels was greater than two, the sum of squares for levels was partitioned into a set of orthogonal linear and quadratic polynomial regression components. The dietary level was confounded with time and age. It was assumed however, that differences between treatment groups were due to the increase in dietary sugar. Statements of statistical significance were based on $P < 0.05$.

RESULTS

The mean values for dry matter and water intake, output of wet digesta and urine, and dry matter content of digesta in birds fed the D-glucose, D-xylose and L-arabinose diets are given in Table 3. The birds consumed their

TABLE 3. Intake of dry matter and water, output and dry matter content of digesta, and output of urine in adult roosters fed on D-glucose, D-xylose, or L-arabinose diets.

Sugar	Dietary level	Intake of dry matter	Intake of water	Output of wet digesta	Dry matter content digesta	Output of urine
	%	_____	(g/bird/day)	_____	(%)	(g/bird/day)
D-glucose	2.5	115.8 ± 7.0	888 ± 219	110.4 ± 26.4	12.0 ± 3.3	622 ± 214
	5.0	123.6 ± 3.0	862 ± 48	122.0 ± 32.8	10.8 ± 2.3	663 ± 114
	7.5	124.9 ± 2.2	898 ± 219	124.3 ± 16.2	10.9 ± 1.8	661 ± 148
	10.0	122.0 ± 4.5	859 ± 220	125.8 ± 25.1	10.7 ± 1.0	603 ± 119
	$\bar{X}$	121.6[a]	877[a]	120.6[a]	11.1[a]	637[a]
D-xylose	2.5	113.8 ± 2.1	933 ± 190	113.2 ± 30.0	11.8 ± 3.8	616 ± 170
	5.0	116.4 ± 8.2	1054 ± 152	125.9 ± 29.9	10.2 ± 1.8	733 ± 94
	7.5	119.2 ± 5.6	1144 ± 150	136.2 ± 25.5	9.9 ± 1.5	767 ± 130
	10.0	122.3 ± 6.0	1375 ± 41	160.8 ± 15.2	8.6 ± 1.2	915 ± 93
	$\bar{X}$	117.9[a]	1127[a]	134.0[a]	10.1[a]	758[a]
L-arabi-nose	2.5	113.1 ± 2.8	744 ± 147	136.8 ± 15.7	10.4 ± 3.1	448 ± 168
	5.0	121.0 ± 2.1	939 ± 100	182.8 ± 21.0	8.7 ± 1.9	555 ± 169
	7.5	120.0 ± 2.4	1020 ± 211	223.0 ± 35.4	8.1 ± 1.8	542 ± 151
	10.0	118.2 ± 4.3	1086 ± 172	277.9 ± 23.8	6.7 ± 1.0	565 ± 100
	$\bar{X}$	118.0[a]	947[a]	205.1[b]	8.5[a]	528[a]

[a,b] Means (± SD) within a column with no common supercript differ significantly (P 0<.05).

daily feed allowance of 125.6 g dry matter per bird well. Water intake, output of wet digesta and urine, and dry matter content of digesta were not affected significantly by the dose level of D-glucose. When roosters were fed diets containing D-xylose, the water intake and output of wet digesta and urine were linearly ($p < 0.05$) increased, whereas dry matter content of digesta was linearly ($p < 0.05$) decreased as the level of this pentose sugar increased. The same pattern of response were observed for water intake, output of wet digesta and dry matter content of digesta when roosters were fed diets containing L-arabinose. The output of urine was not affected by the dose level of L-arabinose.

Ileal digestibilities of D-glucose, D-xylose and L-arabinose, and the urinary excretion of these sugars are shown in Table 4. Digestibility of D-glucose and D-xylose was nearly 100%. However, ileal digestibility of L-arabinose decreased linearly ($P < 0.05$) as the dietary level of this pentose sugar increased. The mean difference in digestibility between L-arabinose and the other two sugars was significant ($P < 0.05$). Data for urinary excretion of sugars are also shown in Table 4. Small traces of glucose were found in the urine of all experimental treatments, suggesting that these originated from the basal diet. Both pentose sugars were partly excreted via the urine. The extent of the urinary excretion of D-xylose and L-arabinose, in percentage of intake, was linearly ($P < 0.05$) related to dose. In birds fed the 2.5% D-xylose diet, 7.2% of the xylose consumed appeared in the urine. This level increased to 20.2% when the 10% D-xylose diet was fed. The urinary excretion of L-arabinose, as a percentage of intake, increased from 8.7 to 16.6% when the dietary level of this pentose sugar was increased from 2.5 to 10%.

Ileal digestibilities of dry matter and N are shown in Table 5. Ileal digestibility of dry matter in birds fed diets containing L-arabinose was consistently lower as compared to birds fed D-glucose or D-xylose diets. Digestibilities of the latter two were not different. Dry matter digestibility of the birds fed L-arabinose decreased linearly ($P < 0.05$) as the dietary level was increased. The mean difference in dry matter digestibility between L-arabinose and the other two sugars was significant ($P < 0.05$). The differences in N digestibility among the sugar treatments were not significant.

Results for ileal digestibility and urinary excretion of energy are shown in Table 6. Ileal digestibility of energy of the diets containing either D-glucose or D-xylose was very high with no appreciable differences between

TABLE 4. Ileal digestibility and urinary excretion of glucose, xylose and arabinose in adult roosters fed the experimental diets.

Sugar	Dietary level	Digestibility sugars	Urinary excretion		
			Glucose	Xylose	Arabinose
	(%)	(%)		(% of intake)	
D-glucose	2.5	98.0 ± 0.3	+1)	-	-
	5.0	99.3 ± 0.0	+	-	-
	7.5	99.5 ± 0.2	+	-	-
	10.0	99.8 ± 0.1	+	-	-
	$\bar{X}$	99.2[a]			
D-xylose	2.5	99.7 ± 0.4	+	7.2 ± 2.2	-
	5.0	100.0 ± 0.0	+	13.1 ± 1.9	-
	7.5	99.7 ± 0.2	+	16.9 ± 2.7	-
	10.0	99.6 ± 0.5	+	20.2 ± 2.0	-
	$\bar{X}$	99.8[a]		14.4	
L-arabinose	2.5	95.5 ± 4.0	+	-	8.7 ± 3.9
	5.0	93.6 ± 5.4	+	-	11.2 ± 3.6
	7.5	80.3 ± 7.9	+	-	13.9 ± 7.1
	10.0	74.6 ± 7.0	+	-	16.6 ± 5.2
	$\bar{X}$	86.0[b]			12.6

1) Small traces (0.09 - 0.13%) of glucose were found in the urine of all experimental treatments.

[a,b] Means (± SD) within a column with no common superscript differ significantly ($P < 0.05$).

TABLE 5. Ileal digestibility of dietary dry matter and nitrogen in adult roosters fed the experimental diets

Sugar	Dietary level	Digestibility	
		Dry matter	Nitrogen
	(%)	(%)	
D-glucose	2.5	89.0 ± 1.2	89.6 ± 1.5
	5.0	89.7 ± 1.4	90.0 ± 0.8
	7.5	89.1 ± 2.3	90.0 ± 1.4
	10.0	89.1 ± 1.0	90.1 ± 1.1
	$\bar{X}$	89.2[a]	89.9[a]
D-xylose	2.5	88.9 ± 0.7	89.2 ± 0.7
	5.0	89.2 ± 0.9	90.3 ± 0.2
	7.5	88.7 ± 0.8	89.8 ± 0.5
	10.0	88.7 ± 1.9	90.3 ± 2.4
	$\bar{X}$	88.9[a]	89.9[a]
L-arabinose	2.5	87.7 ± 2.7	88.0 ± 4.1
	5.0	87.1 ± 2.2	87.1 ± 3.6
	7.5	85.2 ± 1.7	87.1 ± 3.7
	10.0	84.5 ± 1.2	88.1 ± 2.8
	$\bar{X}$	86.1[b]	87.6[a]

[a,b] Means (± SD) within a column with no common superscript are significantly different ($P < 0.05$).

TABLE 6. Ileal digestibility and urinary excretion of dietary energy in adult roosters fed the experimental diets

Sugar	Dietary level(%)	Ileal digestibility energy	Urinary excretion of energy
	(%)	(%)	(% of intake)
D-glucose	5	91.7 ± 0.2	2.8 ± 0.8
	10	91.6 ± 0.9	2.4 ± 0.9
	$\bar{X}$	91.6[a]	2.6[a]
D-xylose	5	91.7 ± 0.3	4.3 ± 0.9
	10	91.4 ± 1.6	5.2 ± 0.4
	$\bar{X}$	91.6[a]	4.7[b]
L-arabinose	5	88.9 ± 2.9	3.7 ± 1.2
	10	87.9 ± 1.6	4.3 ± 1.8
	$\bar{X}$	88.4[b]	4.0[ab]

[a,b] Means (± SD) within a column with no common superscript are significantly different ($P < 0.05$).

the D-glucose and D-xylose diets. Compared to these diets, significantly ($P < 0.05$) lower digestibility values for dietary energy were found when diets containing L-arabinose were fed. The urinary excretion of energy of birds fed diets with either D-xylose or L-arabinose was greater than that of birds fed diets supplemented with D-glucose. However, only the difference between the D-xylose and D-glucose treatments was significant ($P < 0.05$).

DISCUSSION

The choice of the experimental design needs to be considered first. Latin squares are often used as an experimental design in balance studies with animals, in which the diets are fed in sequence, with 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 when there are no carry-over

effects. The results of a previous study (Schutte, 1990) showed that water intake and ceca weight of birds fed on D-xylose or L-arabinose diets increased markedly. Thus, carry-over effects of both pentose sugars can not be completely excluded. Therefore, in the present trial, each bird was fed the same type of sugar in increasing dietary levels during the experimental period. Moreover, in previous studies performed at the authors' institute (Schutte, J.B. & P. van Leeuwen, unpublished data), no indications were found that digestibility of nutrients in ileostomized adult roosters was changed with increasing age. The results of ileal N digestibility (Table 5) showing that the coefficients in each sugar block were almost constant, also indicate that the present data for digestibility were not confounded by time.

The main objectives of the present trial were to determine the ileal digestibility and urinary excretion of D-xylose and L-arabinose in birds. The dietary inclusion levels chosen (2.5 to 10.0%) were approximately one to four times higher than the levels which would be released by complete hydrolysis of the NSP in poultry diets based on cereals, soybean oilmeal and cereal by-products. The ileal digestion data of the test sugars (Table 4) indicated that D-xylose was as well absorbed from the small intestine of birds as D-glucose. The ileal digestibility values for dry matter and energy (Tables 5 and 6) were consistent with this finding, because there were no differences between the D-glucose and D-xylose treatment groups. The ileal digestibility data of the present study also demonstrated that L-arabinose was not absorbed completely from the small intestine. In addition, absorption of L-arabinose was dose related. The ileal digestibility values for dry matter and energy (Tables 5 and 6) were in agreement with this finding, showing a decrease in dry matter and energy digestibility when the dietary level of L-arabinose was increased. The decrease in ileal digestibility of L-arabinose, as the dietary level increased, was associated with an increase in output of wet digesta. Similar results were found in a study performed recently with pigs (Schutte, J.B. et al., unpublished data). This phenomenon of increased output of wet digesta caused by increasing the dietary level of L-arabinose may be connected with the osmotic properties of unabsorbed arabinose resulting in an inflow of water into the intestinal lumen. However, the presence of unabsorbed arabinose in the intestinal tract may stimulate microbial activity, which also may result in an increased output of wet digesta. The increase in wet digesta output by increasing the dietary level of D-xylose (Table 3) may provide some evidence of an increased microbial activity when including pentose sugars in the diet. Longstaff et al. (1988) and Schutte (1990) reported that ceca of birds fed L-arabinose diets were heavier than those of birds fed diets containing D-glucose. The same was

true when birds were fed diets containing D-xylose, but the effects were less pronounced than on diets containing L-arabinose. Thus, these results suggest that inclusion of either L-arabinose or D-xylose in the diet may result in an increased microbial activity in the intestinal tract of birds.

The digestibility data collected in the present study agree with the absorption data reported by Bogner (1961) and Wagh & Waibel (1967b) despite the differences in experimental technique. However, their data are not strictly comparable with the results of the present study, because their observations are based on an absorption period of only 30 min. Studies performed with rats (Cori, 1925: Miller & Lewis, 1932) suggested that absorption of sugars will not be completed fully during this period.

The results discussed, suggest that D-xylose and L-arabinose, in spite of their identical molecular size, have a different mode of transport in the small intestine of birds. It is generally accepted (Crane, 1960; Herman, 1974) that L-arabinose is passively absorbed in the small intestine of animals. However, the mode of transport of D-xylose from the animal intestine is still controversial. The idea that D-xylose crosses the intestinal mucosa by simple diffusion (Wilson & Vincent, 1955; Crane, 1960; Finlay et al., 1964) was initially reported; however, the bulk of evidence suggests that this sugar shares the same transport mechanism with D-glucose (Salomon et al., 1961; Csâky & Lassen, 1964; Alvarado, 1966; Bihler et al., 1969).

It is generally accepted that D-glucose can be utilized almost completely in human and animals (Demetrakopoulos & Amos, 1978), so only negligible amounts of glucose will be found in the urine. The latter is in agreement with the finding in the present study. It is well recognized that in man, rats and pigs, part of the ingested D-xylose and L-arabinose appears in the urine (Loos, 1954; Wise et al., 1954; Arnal-Peyrot & Adrian, 1974; Haeney et al., 1978). However, little information is available on the relationship between the dietary concentration of D-xylose or L-arabinose and the urinary excretion of these pentose sugars. In the present study, this relationship was clearly demonstrated and supported by the results of the urinary excretion of energy (Table 6). The results of an energy balance study with chicks of Wagh & Waibel (1966) are consistent with this, showing a decrease in metabolizable energy of the two pentose sugars with increasing dietary inclusion level. The latter was confirmed in a recent study of Schutte (1990).

Only a few reports are available concerning the metabolism of pentose sugars in birds. Longstaff et al. (1988) reported that chicks were able to grow well on diets containing D-xylose or L-arabinose at dietary concentrations of 5%. Radioisotope studies of Wagh and Waibel (1967a) showed that L-arabinose was better metabolized than D-xylose by chicks, but neither pentose sugar was metabolized to CO_2 as rapidly as D-glucose.

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CHAPTER 3

NUTRITIONAL VALUE OF D-XYLOSE AND L-ARABINOSE FOR BROILER CHICKENS

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Two experiments were conducted to examine the effect of feeding D-xylose and L-arabinose on broiler performance, body composition, caecal length and weight, and liver weight. Graded amounts (25, 50 and 75 g/kg) of D-xylose or L-arabinose were added to either a practical type (Expt A) or a semi-purified (Expt B) basal diet. As reference, a diet containing 75 g D-glucose/kg was included in the experiments. Both experiments were conducted in battery brooders, and birds received the isocaloric (on ME basis) diets as dry mash ad libitum from 6 to 27 days of age. A negative dose-dependent effect of both pentose sugars on weight gain and feed utilization was observed. The same was true for daily feed intake of the D-xylose treatments. Water intake increased linearly ($P < 0.05$) as the dietary level of both pentose sugars was increased. Consequently, dry matter content of the droppings decreased. Fat content of the chick body tended to decrease when either D-xylose or L-arabinose was included in the diets. Caecal weight was increased markedly by feeding L-arabinose. Liver weight was not affected by feeding either D-xylose or L-arabinose to birds. From data for ME intake and gain in body energy it was estimated that utilization of the ME of both pentose sugars was inferior to that of D-glucose. (Key words: pentose sugars, D-xylose, L-arabinose, nutritional value, chicks)

INTRODUCTION

In monogastric animals, the major part of digestion takes place in the small intestine by the digestive enzymes of the host. These enzymes hydrolyze most of the alimentary components with the exception of the nonstarch polysaccharides (cellulose, hemicellulose, pectins, oligosaccharides, etc.). The absence of nonstarch polysaccharide (NSP) degrading enzymes in the host and the low density of microorganisms in the small intestine mean that the NSP will largely pass to the hindgut. In the hindgut the NSP are degraded to a greater or lesser extent by the microbes for which they are the major carbon source. The end products of this microbial degradation (lactic acid, volatile fatty acids) are readily absorbed and can be a potential

energy source for the animal. Contrary to pigs, in poultry microbial degradation of NSP in the caeca and colon appears to be low (Vogt and Stute, 1971; Carré and Leclercq, 1985; Longstaff and McNab, 1989; Carré et al., 1990).

From a literature review, Chesson (1987) concluded that the digestibility of feed ingredients containing high levels of NSP can be improved by treatment with enzymes which can hydrolyze the NSP to monosaccharides. However, hydrolysis of NSP will release not only glucose, but also other sugars such as D-xylose and L-arabinose, which are normally not encountered in the small intestine. Knowledge about the utilization of these pentose sugars in poultry is incomplete. It is well recognized that both pentose sugars are absorbed from the intestinal tract in birds (Bogner, 1961; Wagh and Waibel, 1967; Schutte et al., 1991a). Our data (Schutte et al., 1991a) also showed that part of the ingested xylose and arabinose is excreted in the urine. The extent of this urinary excretion of both pentose sugars, in % of intake, was increased linearly as the dietary level of these sugars was increased (Schutte et al., 1991a). This may explain the decrease in metabolisable energy (ME) value of D-xylose and L-arabinose in chicks by increasing the dietary inclusion level, as observed by Wagh and Waibel (1966) and Schutte (1990). This dosage-related ME value of both pentose sugars in chicks was reflected in the results for weight gain and feed conversion efficiency (Schutte, 1990).

The main objective of the present study was to investigate the effect of dietary inclusion levels of 25, 50 and 75 g/kg of both pentose sugars on chick performance, whereby the dosage-related ME content of these sugars was taken into account. Performance was studied by using two different types of basal diet; a practical type and a semi-purified basal diet. In addition, the effect of dietary D-xylose and L-arabinose on caecal length and weight, and liver weight were examined. Furtheron body composition of birds fed on the practical diets was determined.

MATERIALS AND METHODS

Experimental

The composition of the two basal diets is presented in Table 1 and calculated to be adequate in all nutrients following the recommendations of the National Research Council (1984). With both basal diets seven treatment groups were formed containing 75 g D-glucose/kg (reference diet) and 25, 50 and 75 g of either D-xylose or L-arabinose/kg, respectively.

The sugars, supplied as anhydrous monosaccharides, were on a ME basis, exchanged for tapioca and cellulose in basal diet A and for corn starch and cellulose in basal diet B. The ME value of the pentose sugars was derived from those determined in a previous study with chicks (Schutte, 1990) at dietary inclusion levels of 50 and 100 g/kg. Based on these values, the ME content of D-xylose at dietary levels of 25, 50 and 75 g/kg was estimated to be 12.6, 11.1 and 9.8 MJ/kg, respectively. The corresponding values for L-arabinose at these dietary levels were estimated to be 11.7, 9.6, and 7.7 MJ ME/kg. The ME value of D-glucose was assumed to be 15.1 MJ/kg (Anderson et al, 1958). The diets were fed ad libitum as dry mash. Water was also available for ad libitum consumption.

The two trials (coded as Expt A and Expt B) were run parallel. Day-old female broiler chicks ("Hybro") were used. The birds were housed in electrically heated battery cages of 0.975 square metres of floor space each with wire floors. The cages were situated in an insulated room with facilities to control of temperature and humidity. Chicks were subjected to continuous artificial fluorescent illumination. A standard diet of practical composition was fed for the first three days, followed by another three days of a mixture of the standard diet and the basal diet fed during the experimental period. At 6 days of age, 14 birds were allotted to each of 56 cages such that average body weight (130 g) and weight range (120 to 150 g) were similar. Treatment groups consisted of four cages, each with 14 birds, arranged in a randomized block design. The experimental diets were fed for a period of 21 days (from 6 to 27 days of age).

At the end of the trials, chicks were weighed individually, and feed consumption of each cage was recorded. During the last 2 days of the experimental period, water consumption was measured, and excreta were collected, both for each cage separately at intervals of 12 h. Water intake was measured as the difference between a predetermined volume of water in the water pans and that remaining in the pans. Excreta were collected quantitatively from glass trays into containers and stored at 4 °C. Immediately after the 2 day collection period the excreta were pooled per treatment group and analyzed for dry matter content.

After termination of the trials, 100 chicks of Expt A and 40 chicks of Expt B were killed by injection of T 61 (Hoechst, Germany) after a feed deprivation of 12 h. Water remained available during this period. The sacrificed chicks originated from the treatments fed diets containing 75 g/kg of D-glucose, and 25 g and 75 g/kg of either D-xylose or L-arabinose. The birds were selected in such a way that they represented the population of the treatment groups. From 40 chicks of each experiment (= 8 chicks per treatment group) the caeca were excised and their length and weight were

measured individually . Gross pathological examination of the liver and kidneys was carried out and weight of the liver was recorded individually. The remaining 60 sacrificed chicks (= 12 chicks per treatment group) of Expt A were used for determination of the dry matter, nitrogen and crude fat contents of the entire carcasses with feathers, blood and residual gut contents. Body analyses were performed in pooled samples of 3 chicks each. In order to provide initial data for body composition, at 6 days of age 20 birds were sacrificed according to the same procedure as described previously. Body analyses in these chicks were carried out in pooled samples of 5 chicks each. The chick bodies were stored at -20 °C.

Chick body sampling and analysis

The frozen chick bodies were minced in a Moerman Alexander mincer (model, SS K 45, The Netherlands). Next 30% (w/w) of diatomaceous earth (celite) was added to the mixture to aid in binding and dispersing the body fat. Then the mixture was passed through a mechanical grinder with a 2 mm die to achieve adequate mixing and desired fineness. A 500 g representative sample was taken from each mixing batch and then freeze-dried. When dry, the mass was equilibrated with air humidity, weighed and the weight corrected for celite.

TABLE 1. Composition of the basal diets (g/kg)

Ingredient	Basal Expt A	Basal Expt B
Maize	158.6	287.3
Wheat	155	-
Tapioca	160	-
Wheat starch	-	287
Soybean oil	50	40
Animal fat	20	40
Soybean oilmeal (500 g CP/kg)	240	-
Isolated soy protein (880 g CP/kg)	-	223
Sunflower meal (320 g CP/kg)	20	-
Peas (220 g CP/kg)	75	-
Herring meal (720 g CP/kg)	20	-
Meat meal tankage (580 g CP/kg)	30	-
Cellulose ("Arbocel B 800)	30	60
Molasses	10	-
Dicalcium phosphate	10	-
Monocalcium phosphate	-	21
Limestone	6	12
Iodized salt	3	3
Potassium bicarbonate	-	15
Vitamin-mineral mix[1]	10	10
DL-methionine	2.4	1.7
Contents:		
Crude protein (analysed, g/kg)	211	225
Metabolisable energy (calculated, MJ/kg)	12.4	14.1
Ca (analysed, g/kg)	9.3	8.9
P (analysed, g/kg)	6.2	5.9
Lysine (calculated, g/kg)	12.1	13.3
Methionine + cystine (calculated, g/kg)	8.8	9.0

[1] Supplied per kilogram of diet: retinol 3 mg, cholecalciferol 0.05 mg, dl-α-tocopheryl acetate 30 mg, menadione 5 mg, thiamin 2.5 mg, riboflavin 5.5 mg, d-pantothenic acid 15 mg, niacinamide 50 mg, cobalamin 0.015 mg,choline chloride 1,850 mg, pyridoxine 3 mg, biotin 0.15 mg, folic acid 0.75 mg, ascorbic acid 50 mg, inositol 100 mg, para-aminobenzoic acid 2.5 mg, ethoxyquin 100 mg, avoparcin 15 mg, Mg 420 mg, Mn 95 mg, Zn 50 mg,Fe 40 mg, Cu 40 mg, Co 2 mg, Se, 0.1 mg.

Finally the dry mass was further homogenized with a Brabander blender (model, 880802, Germany), with a 1 mm die and then analyzed for dry matter, fat and N.

Dry matter was determined by drying the samples to a constant weight at 101 °C. Fat (ether extraction) and protein (N x 6.25) were determined by standard methods (A.O.A.C., 1984). Standard methods were also used for determining the percentage of N, Ca and P in the basal diets. All analyses were carried out in duplicate.

Calculations

In Expt A, gain in energy of chicks was calculated from the differences in protein and fat composition of the chick bodies between the initial and final samples. Energy gains were computed from protein gain at 23.7 kJ per gram, and fat gain at 39.0 kJ per gram as proposed by Anderson et al. (1958). Efficiency of ME utilization for gain in the dietary treatments was calculated by using the following equation:

$$\text{ME utilization for gain} = \frac{\text{Gain in energy}}{ME_{intake} - ME_{maintenance}}$$

In this equation the chick daily maintenance need for energy was assumed at 600 kJ ME per kg metabolic weight (Scheele et al., 1987).

Statistical analysis

The results of both trials were combined in the analysis of variance (Cochran and Cox, 1957). This can be justified because both trials were run parallel in the same experimental room. The computer program SPSS/PC + V2.0 (Norusis, 1988) was used to calculate the analysis of variance. The treatment factors were type of diet and sugar, and dietary level of sugar. If the number of dietary sugar levels was higher than two, the sum of squares for 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

Expt A

Table 2 summarises performance data collected. Weight gain and feed utilization were reduced when either D-xylose or L-arabinose was included in the diet. This reduction was small at a dietary inclusion of 25 g/kg, but increased linearly ($P < 0.05$) as the level of D-xylose or L-arabinose was increased. The same was true for daily feed intake of chicks fed diets containing D-xylose, but not for intake of chicks fed L-arabinose diets. Water intake of chicks fed on diets containing the pentose sugars was at all dietary inclusion levels significantly higher than those fed on the reference diet. Moreover, water intake was increased linearly ($P < 0.05$) as the dietary level of either D-xylose or L-arabinose was increased. However, the increase in water intake of chicks fed on the L-arabinose diets was more pronounced than of chicks fed on the D-xylose diets. As a result of the increase in water intake from increasing dietary D-xylose or L-arabinose, dry matter content of the excreta decreased steadily.

Mortality rate was very low, only 1.5% of the birds died. No appreciable differences in mortality among the treatments were observed.

Dry matter, fat and protein contents of the chick bodies are presented in Table 3. There was a tendency to a decreased dry matter and fat content of the body when chicks were fed on diets containing the pentose sugars. No systematic effect of D-xylose or L-arabinose on the protein content of the body was observed. Utilization of ME for gain was decreased when birds were fed on diets containing either D-xylose or L-arabinose. This decreased ME utilization was more pronounced in chicks fed on the L-arabinose diets than in those fed diets supplemented with D-xylose. Utilization of crude protein tended to decrease when either D-xylose or L-arabinose was included in the diet. Because feed intake of birds was not recorded individually, the data for ME and protein utilization could not be analyzed statistically.

TABLE 2. The effect of dietary inclusion levels of D-xylose and L-arabinose on chick performance from 6 to 27 days of age by using a practical type basal diet (Expt A).

Sugar	Dietary level (g/kg)	Weight gain (g)	Feed intake (g/bird per day)	Feed: gain (g:g)	Water intake (g/bird per day)[1]	Dry matter content excreta (g/kg)[2]
D-glucose	75	809[a]	61.8[ab]	1.605[a]	166[a]	279
D-xylose	25	776[abc]	60.0[bc]	1.624[a]	192[b]	226
	50	751[c]	58.6[cd]	1.638[ab]	206[bc]	203
	75	716[d]	57.0[d]	1.671[bc]	216[cd]	159
L-arabinose	25	806[ab]	62.2[a]	1.620[a]	207[bc]	213
	50	775[bc]	60.2[abc]	1.632[ab]	229[d]	191
	75	750[cd]	60.3[abc]	1.686[c]	257[e]	142
SEM (df 42)[3]		11.8	0.8	0.014	5.5	

[1] Means of four pens per treatment of days 26 plus 27.

[2] Pooled samples per treatment of days 26 plus 27; figures not analysed statistically.

[3] Standard error of the mean.

[a,b,c] Mean values with no common superscripts within a column differ significantly ($P < 0.05$).

TABLE 3. Effect of dietary inclusion levels of D-xylose and L-arabinose on body composition and utilization of dietary ME and protein in chicks by using a practical type basal diet (Expt A).

Sugar	D-gluc.	D-xylose		L-arabinose		Pooled
Dietary level (g/kg)	75	25	75	25	75	SEM (df 30)
Body composition (final						
Dry matter (g/kg)	318[a]	308[a]	307[a]	304[a]	316[a]	5.3
Fat (g/kg)	107[a]	106[a]	102[a]	106[a]	102[a]	4.0
Protein (g/kg)	169[ab]	166[ab]	169[ab]	163[a]	172[b]	2.3
Utilization of ME for gain						
Intake of ME (MJ/bird)	16.1	15.6	14.8	16.2	15.7	
Maintenance (MJ/bird)	7.4	7.2	6.9	7.4	7.1	
Gain in energy (MJ/bird)[1]	6.8	6.5	5.9	6.6	6.2	
Utilization (%)[2]	78.2	77.4	74.7	75.0	72.1	
Utilization of protein						
Intake of protein (g/bird)	274	266	252	276	267	
Gain in protein (g/bird)[1]	140	131	124	134	132	
Utilization (%)[3]	51.1	49.2	49.2	48.6	49.4	

[1] Birds sacrificed at 6 days to provide initial data had following composition; average body weight 129 g, fat 78.7 g/kg, protein (Nx6.25) 149 g/kg.

[2] Calculated according to formula as described in the sub-heading "Calculations".

[3] Calculated as: $\frac{\text{protein gain}}{\text{protein intake}}$

[a,b] Mean values with no common superscripts within a row differ significantly ($P < 0.05$).

Data regarding caecal length and weight, and liver weight are shown in Table 4. There was a tendency that caecal weight was increased when chicks were fed diets containing D-xylose. The caeca from chicks fed on L-arabinose diets were not only longer but also heavier than those from chicks fed the reference diet. The differences in caecal weights between birds fed on the reference diet and those fed on the L-arabinose diets were significant. Liver weight in % of live weight was not affected significantly by the dietary treatments. Gross pathological examination of the liver and kidneys did not show abnormalities in birds fed on the different diets.

TABLE 4. The effect of dietary inclusion levels of D-xylose and L-arabinose on caecal length and weight, and liver weight of chicks by using a practical type basal diet (Expt A).

Sugar	D-gluc.	D-xylose		L-arabinose		SEM
Dietary level (g/kg)	75	25	75	25	75	(df 70)
Live weight (LW) at autopsy, g	896	874	842	901	855	20.2
Caecal length, cm	26[a]	26[a]	26[a]	28[a]	28[a]	0.81
Caecal weight (incl. contents)						
g	5.5[a]	5.6[a]	5.8[a]	7.2[b]	7.6[b]	0.47
% of LW	0.62[a]	0.64[ab]	0.69[ab]	0.80[bc]	0.89[c]	0.06
Liver weight						
g	19.9[a]	21.2[a]	20.2[a]	22.3[a]	21.2[a]	0.93
% of LW	2.2[a]	2.4[a]	2.4[a]	2.5[a]	2.5[a]	0.10

[a,b,c] Mean values with no common superscipts within a row differ significantly ($P < 0.05$).

Expt B

The performance data are summarised in Table 5. Almost similar results for weight gain, daily feed intake, feed conversion efficiency, water intake and dry matter content of excreta were obtained as in Expt A. Again weight gain and feed utilization were reduced when chicks were fed on diets containing either D-xylose or L-arabinose. Weight gain and feed utilization was decreased linearly ($P < 0.05$) as the dietary level of D-xylose was increased. Daily feed intake of birds on the D-xylose diets was not only lower as compared to birds fed on the reference diet, but also dose-dependent. Water intake of chicks fed either D-xylose or L-arabinose diets showed the same pattern of respons as in Expt A. The increases in water intake when chicks were fed the pentose sugars were reflected in the dry matter content of the excreta.

Mortality rate was again low. As a mean 0.6% of the chicks died with no appreciable differences among the treatments.

Results for caecal length and weight, and liver weight are shown in Table 6. Caecal length and weight were not clearly affected when chicks were fed on diets containing D-xylose. However, when fed diets containing L-arabinose, caecal weight increased as compared to the caecal weight of chicks fed on the reference diet. The difference in caecal weight between the reference treatment and the 75 g L-arabinosse/kg diet treatment was significant. In addition, caeca of chicks fed on the 75 g L-arabinose/kg diet were significantly longer than those of chicks fed on the reference diet. Liver weight was not affected significantly by the inclusion of either D-xylose or L-arabinose in the diet. Gross pathological examination of the liver and kidneys did not show abnormalities in any of the treatments.

TABLE 5. The effect of dietary inclusion levels of D-xylose and L-arabinose on chick performance from 6 to 27 days of age by using a semipurified basal diet (Expt B).

Sugar	Dietary level (g/kg)	Weight gain (g)	Feed intake (g/bird per day)	Feed: gain (g:g)	Water intake (g/bird per day)[1]	Dry matter content excreta (g/kg)[2]
D-glucose	75	770[a]	56.1[a]	1.531[a]	143[a]	267
D-xylose	25	737[ab]	54.0[ab]	1.538[ab]	169[b]	208
	50	719[b]	52.8[bc]	1.544[ab]	174[b]	153
	75	682[c]	51.4[c]	1.584[c]	193[c]	132
L-arabinose	25	761[a]	55.7[a]	1.537[ab]	179[bc]	174
	50	748[ab]	55.7[a]	1.565[abc]	191[c]	156
	75	738[ab]	55.4[a]	1.576[bc]	233[d]	123
SEM (df 42)		11.8	0.8	0.014	5.5	

[1)] Means of four pens per treatment of days 26 plus 27.

[2)] Pooled samples per treatment of days 26 plus 27; figures not analysed statistically.

[a,b,c] Mean values with no common superscripts within a column, differ significantly ($P < 0.05$).

TABLE 6. The effect of dietary inclusion levels of D-xylose and L-arabinose on caecal length and weight, and liver weight of chicks by using a semipurified diet (Expt B).

Sugar	D-gluc.	D-xylose		L-arabinose		SEM
Dietary level (g/kg)	75	25	75	25	75	(df 70)
Live weight (LW) at autopsy, g	866	835	818	848	832	20.2
Caecal length, cm	23[a]	23[a]	22[a]	23[a]	26[b]	0.81
Caecal weight (incl. contents)						
g	3.9[a]	4.1[a]	4.0[a]	4.7[ab]	5.8[b]	0.47
% of LW	0.45[a]	0.50[a]	0.49[a]	0.56[ab]	0.70[b]	0.06
Liver weight						
g	21.6[a]	21.0[a]	20.3[a]	20.0[a]	20.8[a]	0.93
% of LW	2.5[a]	2.5[a]	2.5[a]	2.4[a]	2.5[a]	0.10

[a,b]Mean values with no common superscripts within a row differ significantly ($P < 0.05$).

DISCUSSION

Although the experimental diets were formulated to be balanced in ME content, weight gain and feed utilization in birds fed the pentose sugars were inferior to those fed the reference (75 g D-glucose/kg) diet (Tables 2 and 5). The extent of this reduction in weight gain and feed utilization was small when birds were fed the pentose sugars at dietary levels of 25 g/kg, but became larger when fed dietary inclusion levels of 50 and 75 g/kg. This negative dosage-dependent effect of both pentose sugars on weight gain and feed conversion efficiency may have resulted from several factors.

In the case of D-xylose, one of these factors relates to feed intake, which decreased linearly ($P < 0.05$) as the dietary level of this sugar was increased (Tables 2 and 5). Consequently, weight gain of birds fed on D-xylose diets was more depressed than of those fed on diets containing L-arabinose. Depressed feed intake as a result of feeding D-xylose to chicks was also observed in a

previous study (Schutte, 1990). The birds' dislike for D-xylose had been demonstrated by Kare and Medway (1959), who showed an almost total rejection of water solutions containing this pentose sugar. In similar tests performed by these investigators, other sugars such as lactose, galactose, raffinose and arabinose had only minor effects on water consumption. Second, the pentose sugars may have had an indirect negative effect on the utilization of the ME of other dietary energy bearing components, and as a result depressed performance. Some evidence of such an effect may be provided by the data of a recent study (Schutte et al., 1991b), indicating an increased microbial fermentation of N in pigs fed on diets containing 200 g D-xylose/kg. A third factor which needs consideration relates to the utilization of the ME of both pentose sugars as compared to D-glucose. Without taking into account a possible indirect negative effect of both pentose sugars, the utilization of the ME of D-xylose and L-arabinose can roughly be estimated from the differences in ME utilization among the 75 g sugar/kg diet treatments (Table 3). This calculation pointed out that the utilization of the ME of D-xylose for gain was only approximately 20%. In this calculation the difference in ME utilization between the reference diet and the 75 g D-xylose/kg diet was fully attributed to D-xylose. Calculations similar to those for D-xylose were made for the 75 g L-arabinose/kg diet treatment. This calculation resulted in a zero utilization of the ME of L-arabinose for gain.

The estimated less well utilization of the ME of D-xylose and L-arabinose probably relates to the metabolic pathways of these sugars. It is well recognized that the ME of D-glucose is highly utilized in chicks (Anderson et al., 1958.). Knowledge about the utilization of the ME of D-xylose and L-arabinose in chicks and also in other monogastric animals is limited. In a previous study (Schutte et al., 1991a) with adult roosters it was found that about 15% of the ingested D-xylose or L-arabinose was excreted into the urine. The remaining part not accounted for may have either been metabolised to carbon dioxide or fermented in the intestinal tract, or by both of these. According to Segal and Foley (1959) metabolism of these two pentose sugars to carbon dioxide appears to be only of significant importance for D-xylose. When given an intravenously infused dose of either C14-labeled D-xylose or L-arabinose to man, 16 and 0.8 %, respectively, could be recovered as carbon dioxide. If their data are transferable to chicks, this would mean that both pentose sugars mainly might be fermented in the intestinal tract when fed orally. This hypothesis is supported by the results of previous studies with pigs (Schutte et al., 1991b,c) showing substantial increases in ileal flow of volatile fatty acids when they were fed on diets containing either D-xylose or L-arabinose. From these results it was concluded that at least part of the ingested pentose sugars was degraded microbially. It seems likely that

microbial degradation of D-xylose in chicks occurs mainly in the crop and small intestine, since ileal digestibility of this pentose sugar was found to be nearly 100% in adult roosters (Schutte et al., 1991a). In that study an ileal digestibility value of about 85 % was found for L-arabinose, indicating that this pentose sugar will be at least partly also fermented in the hind gut. This was supported by the absence of arabinose in the faeces of colostomized cockerels fed on L-arabinose diets (unpublished data, Schutte et al.). Microbial degradation of L-arabinose in the hindgut is also supported by the observed increase in caecal weight in birds fed on L-arabinose diets (Tables 4 and 6). Increased caecal weight as a result of feeding L-arabinose diets to chicks has been previously reported (Longstaff et al., 1988; Schutte, 1990).

It is well known that microbial degradation of dietary energy bearing substances is coupled with considerable losses of energy, not accounted for in the ME determination. In pigs these losses in energy are assumed to vary vary between 33 % (Agricultural Research Council, 1981) and 50 % (Just et al., 1983; Van Es, 1987). No published data for poultry are available, but energy losses of a similar magnitude may be assumed. In addition to the energy losses as a result of the fermentation process, metabolism of D-xylose and L-arabinose per se may also be associated with losses not accounted for in the ME determination.

The higher intakes of water in birds fed on either D-xylose or L-arabinose diets (Tables 2 and 5) are in agreement with the observation in a previous study with chicks (Schutte, 1990). This phenomenon may be connected with the osmotic properties of unabsorbed pentose sugars and increased volatile fatty acids concentrations in the intestinal tract resulting in an inflow of water into the intestinal lumen (Van Weerden, 1959; Hof, 1980).

Wagh and Waibel (1966) reported that plasma uric acid was significantly increased when chicks were fed on diets containing 200 and 400 g of either D-xylose or L-arabinose/kg. Their results suggest an increased N catabolism when birds are fed on D-xylose or L-arabinose diets. They reported also that feeding these diets to birds resulted in decreased liver weights. In the present study some indications were achieved that even at low dietary inclusion levels both pentose sugars may influence N utilization adversely. However, no effect on liver weight was observed at the applied dietary levels of either D-xylose or L-arabinose in the present study (Tables 4 and 6).

In conclusion it can be stated that D-xylose and L-arabinose may provide only some energy to birds. Besides, these sugars induce increases in water intake and as result wet droppings. Considering these aspects, the benefits of hydrolysing of NSP fractions which will release mainly these sugars (e.g. hemicellulose) are very doubtful.

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PART B

STUDIES WITH PIGS

CHAPTER 4

NUTRITIONAL IMPLICATIONS OF D-XYLOSE IN PIGS

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NUTRITIONAL IMPLICATIONS OF D-XYLOSE IN PIGS

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Hemicellulose consists primarily of pentose sugars, joined together in a polysaccharide chain with D-xylose as the most abundant component. Ileal digestibility and urinary excretion of D-xylose and associated effects of this pentose sugar on ileal and faecal digestibility of dry matter (DM), organic matter (OM), gross energy (GE) and nitrogen (N) were studied in pigs. Castrated pigs were prepared with a post-valvular T-caecum cannula to measure ileal digestibility. Faecal digestibility was measured in non-cannulated pigs. D-xylose was given at dietary inclusion levels of 100 and 200 g/kg, and the control sugar, D-glucose, at a rate of 200 g/kg diet. Ileal digestibility of D-xylose as well as that of D-glucose was found to be close to 100 %. The presence of D-xylose in the diet decreased ileal digesta pH and increased ileal flow of volatile fatty acids, suggesting the occurrence of microbial degradation of D-xylose in the pig small intestine. In pigs fed on the 100 g D-xylose/kg diet, 44.5 % of the D-xylose intake appeared in the urine. This percentage increased significantly to 52.6 % when pigs were fed on the 200 g D-xylose/kg diet. Ileal and faecal digestibility of DM, OM, GE and N, as well as N retention decreased significantly in pigs fed on the 200 g D-xylose/kg diet. (Key words: D-xylose, digestion, excretion, pig).

INTRODUCTION

Cellulose and hemicellulose form the bulk of the cell wall constituents of feed ingredients of vegetable origin. Both carbohydrate fractions are resistant to the digestive enzymes of pigs, and pass to the hind gut where microbial degradation takes place. The microbial degradation of cellulose and hemicellulose in the hind gut of pigs leads to the production of absorbable volatile fatty acids which provide energy to the animal (Imoto & Namioka,

1978; Agricultural Research Council, 1981; Van Es, 1987). This fermentation process, however, is coupled with considerable losses in energy, assumed to vary between 33 % (Agricultural Research Council, 1981) and 50 % (Just et al. 1983; Van Es, 1987).

Improving the utilization of cellulose and hemicellulose may be attained by an enzyme treatment which could hydrolyse these carbohydrate fractions to monosaccharides. There is little doubt that the monosaccharide units in cellulose, i.e. glucose, are an excellent source of energy for pigs. Hemicellulose primarily consists of pentose sugars, joined together in a polysaccharide chain with D-xylose as the most abundant component.

The studies reported on the absorption of D-xylose relate to other animal species than pigs. These studies have shown that D-xylose is readily absorbed from the intestinal tract by rats (Cori, 1925; Miller & Lewis, 1932; Fowler & Cooke, 1960; Arnal-Peyrot & Adrian, 1974) and chicks (Wagh & Waibel, 1967a). These studies also showed that part of the ingested D-xylose is excreted in the urine. Findings on the utilization of D-xylose mainly relate to chicks. Longstaff et al. (1988) reported that chicks were able to grow well on diets containing D-xylose at a dietary concentration of 50 g/kg. Radioisotope studies by Wagh & Waibel (1967b) in chicks, showed that D-xylose was metabolized to carbon dioxide, but less rapidly than D-glucose.

The present studies were designed to obtain information on ileal digestibility (absorbability) and urinary excretion of D-xylose at dietary inclusion levels of 100 and 200 g/kg in pigs. The effects of dietary D-xylose on the ileal and faecal digestibility of dry matter (DM), organic matter (OM), gross energy (GE) and nitrogen (N) were also examined. D-glucose was included in the trials as a reference.

MATERIALS AND METHODS

Animals and diets

Two separate trials were conducted with growing castrated male pigs (Dutch Landrace x 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 en 12 h twilight cycle throughout. The nutritionally complete basal diet used was based on maize, wheat starch and isolated soya protein. The composition of the basal diet and its chemical characteristics are shown in Tables 1 and 2, respectively.

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

Maize meal	287
Wheat starch	287
Soya-bean oil	40
Animal fat	40
Isolated soya protein (880 g protein/kg)	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, FRG)

\+ 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.

TABLE 2. Chemical composition of the basal diet (analysed, g/kg unless otherwise stated)

Constituent	
Dry matter	909
Ash	47
Crude protein (nitrogen x 6.25)	218
Crude fibre	56
Crude fat	86
Gross energy (MJ/kg)	17.9
Calcium	9.2
Phosphorus	8.1

The test sugars (D-glucose and D-xylose), supplied as anhydrous monosaccharides, were substituted by weight for wheat starch.

In both trials the experimental diets were fed at a daily rate of 0.9 MJ metabolizable energy (ME)/kg metabolic body weight, assuming that D-xylose has the same ME content as D-glucose. The daily amount of feed was offered at two equal meals at 08.00 and 20.00 hours, 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 D-xylose, and the effect of this pentose sugar on ileal digestibility of DM, OM, GE and N were measured. Moreover, digesta pH, concentrations of volatile fatty acids (VFA) in the digesta, and ileal flow of VFA were investigated.

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 witholding feed for 24 h. During the 3-week post-operative period, the pigs were fed on the basal diet (Table 1). The experimental period lasted 24 d and consisted of three phases, during which time each pig was fed consecutively on a diet containing 200 g D-glucose/kg (Gluc diet), 100 g D-xylose/kg (LL-Xyl diet) and 200 g D-xylose/kg (HL-Xyl diet), with a 4 d adaptation and a 4 d collection period for each diet.

At the start of the experimental period, the pigs weighed on average 24.3 (SD 2.6) kg and at the end of this period 31.8 (SD 3.4) kg.

Expt B. The objectives of this trial were to determine the urinary excretion of D-xylose, and to study the effect of D-xylose on faecal digestibility of DM, OM, GE and N, and N retention. This trial, involving four 9-week old pigs, was run parallel with Expt A. The pigs were accustomed to cages and the basal diet (Table 1) for 3 weeks before starting the experimental period. The experimental design of Expt B was similar to that of Expt A. During the 24 d experimental period the same three diets and batches of feed were used, and fed in the same order as described for Expt A.

At the start of the experimental period, the pigs weighed on average 25.0 (SD 0.7) kg and at the end of this period 34.4 (SD 0.8) kg.

Digesta collection

Ileal digesta during each 4 d collection period were collected quantitatively from individual animals over a 12 h period per day (08.00-20.00 hours). In this procedure it was assumed that ileal digestibility was completed within 12 h. This assumption was based on previous studies (E.J. Van Weerden, J. Huisman & P. van Leeuwen; unpublished results) indicating that there were no significant differences in ileal digestibility when digesta were collected over a 12 h or over a 24 h period per day.

The digesta were collected continuously in dry ice, weighed daily and stored at -20°. At the end of the experiment, the four 12 h collected portions were pooled for each pig separately, homogenized and sampled. The pH and VFA determinations were performed in the digesta as such, the other measurements in freeze-dried samples. Until analysis all samples were kept at -20°.

Faeces and urine collection

Faeces were collected directly into a bag fitted around the anus, and the urine was collected using a funnel fitted under the cage. Total collection of faeces and urine was carried out during the four 24 h collection periods from the individual animals. 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 separately, homogenized and sampled. Then the samples were freeze-dried.

Urine was collected in containers provided with merthiolate sodium (Thiomersal, BDH chemicals Ltd, Poole, England) at intervals of approximately 4 h. The portion from each interval was pooled daily from individual animals. A representative sample of 10 % of the pooled urine was taken and frozen at -20°. The 4 d sub-samples of urine were pooled for each animal separately, homogenized and sampled. Faeces and urine were kept at -20° between sampling and before 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) 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 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. Immediately afterwards the supernatant fraction (5 ml) was acidified with 500 µl phosphoric acid (850 ml/l, reagent grade), 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, USA). A glass column (1850 mm x 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 previously. Calibration curves for these acids were then made by obtaining the peak-heights of the acids: that of isocapronic acid. Recoveries values 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.

Concentrations of glucose and xylose in digesta and urine were determined as silyl derivatives of 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 x 4) and cation (Biorad AG 50 W x 4) exchanger. After centrifugation, 200 µl of the supernatant fraction was freeze-dried. To the freeze-dried sample phenylglucopyranoside (0.4 mg in a 1 ml pyridine solution) was added as an internal standard. The sample was then derivatized by the addition of 0.6 ml hexamethyldisilazane and 0.3 ml trimethyl-chlorosilane. Then the contents were mixed using a Vortex stirrer. 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 temperature of the injector and detector was 240 and 300°, respectively.

Statistical analysis

All values were analysed by means of analysis of variance. A randomized block design was used, in which the animals were the blocks (Cochran & Cox, 1957). Although the treatments are confounded by time it is assumed that differences are due to the test sugar. The Genstat 5 package (Oxford University Press, 1987) was used to calculate the analysis of variance. The treatment factors were the combination of the type of sugar and the dietary level. Then the treatment means were compared using the Least Significance Differences test. 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

Intake of DM and water, output of digesta, and DM content of digesta measured in cannulated pigs on D-glucose or D-xylose diets are given in Table 3. 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 among the treatments. These differences were caused by the feeding system applied, since this system was coupled with live weight of the pigs. Water intake of pigs fed on the Gluc diet (200 g D-glucose/kg) was significantly lower as compared with the LL-Xyl (100 g D-xylose/kg) and HL-Xyl (200 g D-xylose/kg) diets. Pigs fed on the Gluc diet produced on average 255 g wet digesta/12 h, which value was increased to 326 and 547 g/12 h when pigs were fed on the LL-Xyl and HL-Xyl diets, respectively. The amount of digesta produced in pigs on the HL-Xyl diet was significantly different from that of pigs on the Gluc and LL-Xyl diets. The increase in digesta output in pigs on the LL-Xyl and HL-Xyl diets was associated with a decrease in DM content of the digesta. However, the latter was more pronounced on the HL-Xyl diet than on the LL-Xyl diet.

Apparent digestibility values for DM, OM, GE, N, D-glucose and D-xylose

are shown in Table 4. In pigs fed on the Gluc and LL-Xyl diets, similar digestibility coefficients for DM, OM, GE and N were observed. However, in pigs fed on the HL-Xyl diet digestibility of DM, OM, GE and N decreased significantly. The apparent ileal digestibility of D-glucose and D-xylose was found to be close to 100 %.

Digesta pH, VFA concentrations in the digesta, and ileal flow of VFA are given in Table 5. The pH decreased significantly from 6.5 in digesta of pigs on the Gluc diet to 6.2 and 6.0 when they were fed on the LL-Xyl and HL-Xyl diets, respectively; the latter two values being also significantly different from each other. The decrease in pH on the LL-Xyl and HL-Xyl diets concurred with the appearance of greater amounts of VFA in the digesta. The increase in total VFA concentrations in pigs on the LL-Xyl diet was about 50 %, but not significant. The latter due to the large differences between animals within the treatments. When pigs were fed on the HL-Xyl diet, total VFA concentrations in digesta increased significantly with about 110 % when compared with the Gluc treatment. The increase in total VFA concentrations on the HL-Xyl diet was reflected in all individual VFA fractions. In terms of ileal flow of VFA the differences between the treatments are much greater, since pigs on the LL-Xyl and HL-Xyl diets produced greater quantities of digesta than when fed on the Gluc diet.

TABLE 3. Expt A. Intake (g/12 h) of dry matter (DM) and water, output (g/12 h) of ileal digesta, and DM content (g/kg) of ileal digesta, measured in cannulated pigs fed on D-glucose and D-xylose (100 (LL-Xyl) or 200 (HL-Xyl) g/kg) diets

(Mean values of four pigs per treatment)

Diet	Gluc	LL-Xyl	HL-Xyl	SEM (df 6)
Intake of DM	316[a]	333[b]	349[c]	0.3
Intake of water	817[a]	1029[b]	1156[b]	53.4
Output of wet ileal digesta	255[a]	326[a]	547[b]	45.9
DM content ileal digesta	172[a]	151[a]	118[b]	9.0

[a,b,c] Within a row, mean values with different superscript letters were significantly different ($P < 0.05$).

TABLE 4. Expt A. Apparent ileal digestibility coefficients of dry matter (DM), organic matter (OM), gross energy (GE), nitrogen, D-glucose and D-xylose, measured in cannulated pigs fed on D-glucose and D-xylose (100 (LL-Xyl) or 200 (HL-Xyl) g/kg) diets
(Mean values of four pigs per treatment)

Diet	Gluc	LL-Xyl	HL-Xyl	SEM	df
DM	86.2[a]	85.7[a]	81.9[b]	1.00	6
OM	87.6[a]	87.2[a]	84.7[b]	0.71	6
GE	87.6[a]	87.5[a]	84.5[b]	0.62	6
N	90.3[a]	89.1[a]	87.2[b]	0.47	6
D-glucose	99.3	-	-	-	-
D-xylose	-	98.7[a]	98.6[a]	0.23	3

[a,b] Within a row, mean values with different superscript letters were significantly different ($P < 0.05$).

TABLE 5. Expt A. Digesta pH, concentrations of volatile fatty acids (VFA) in digesta and ileal flow of VFA, measured in cannulated pigs fed on D-glucose and D-xylose (100 (LL-Xyl) or 200 (HL-Xyl) g/kg) diets

(Mean values of four pigs per treatment)

Diet	Gluc	LL-Xyl	HL-Xyl	SEM (df 6)
pH, and concentrations of VFA in digesta (mg/100 g)				
pH	6.5[a]	6.2[b]	6.0[c]	0.06
Total VFA	437[a]	644[ab]	930[b]	86.6
Individual VFA				
Acetic acid	270[a]	478[ab]	654[b]	61.2
Propionic acid	77[a]	79[a]	121[a]	17.9
Butyric acid	51[a]	49[a]	75[a]	11.4
Isobutyric acid	12[a]	11[a]	22[b]	2.0
Valeric acid	13[a]	14[a]	27[b]	2.4
Isovaleric acid	14[a]	13[a]	31[b]	2.8
Ileal flow of VFA (mg/12 h)				
Total VFA	1106[a]	2062[b]	4888[c]	123.7
Individual VFA				
Acetic acid	684[a]	1508[b]	3447[c]	99.2
Propionic acid	196[a]	253[a]	630[b]	42.0
Butyric acid	125[a]	171[a]	386[b]	37.6
Isobutyric acid	31[a]	34[a]	115[b]	6.4
Valeric acid	33[a]	48[a]	146[b]	10.3
Isovaleric acid	37[a]	48[a]	164[b]	7.7

[a,b,c] Within a row, mean values with different superscript letters were significantly different ($P < 0.05$).

Expt B

The mean values for DM and water intake, output of fresh faeces, DM content of faeces and output of urine in pigs fed on the Gluc, LL-Xyl and HL-Xyl diets over a 12 h period, are given in Table 6. There were significant

differences in DM intake among the treatment groups. However, as already stated in Expt A, these differences were caused by the feeding system applied. Water intake and urine output tended to increase and the DM content of faeces tended to decrease when the pigs were fed on the LL-Xyl diet. When fed on the HL-Xyl diet, water intake as well as output of urine and fresh faeces increased significantly compared with the Gluc and LL-Xyl diets. In addition, the DM content of faeces in pigs fed on the HL-Xyl diet was significantly lower when compared with the Gluc diet.

Apparent faecal digestibility coefficients for DM, OM, GE and N, retention of N, and the urinary excretion of glucose, xylose, energy and N are given in Table 7. Similar results for apparent faecal digestibility of DM, OM, GE and N were achieved on the Gluc and LL-Xyl diets. When fed on the HL-Xyl diet, digestibilities of all four substances decreased significantly. N retention was calculated from the intake of N and the losses of N into the faeces and urine. When fed on the HL-Xyl diet, significantly less N was retained than when feeding the Gluc and LL-Xyl diets. This is due to both a lower N digestibility and a higher amount of N excreted in the urine on the HL-Xyl diet. The losses of xylose into the urine were considerable. When pigs were fed on the LL-Xyl diet, 44.5 % of the D-xylose intake was excreted in the urine. This percentage increased significantly to 52.6 % when pigs were fed on the HL-Xyl diet. As a result of the xylose losses into the urine, urinary excretion of energy also increased significantly in pigs on the LL-Xyl and HL-Xyl diets.

TABLE 6. Expt B. Intake (g/12 h) of dry matter (DM) and water, output (g/12h) of faeces and urine, and DM content (g/kg) of faeces, measured in non-cannulated pigs fed on D-glucose and D-xylose (100 (LL-Xyl) or 200 (HL-Xyl) g/kg) diets.

(Mean values of four pigs per treatment)

Diet	Gluc	LL-Xyl	HL-Xyl	SEM (df 6)
Intake of DM	322[a]	339[b]	355[c]	0.1
Intake of water	655[a]	736[a]	963[b]	36.6
Output of fresh faeces	35[a]	34[a]	68[b]	3.4
DM content faeces	482[a]	448[ab]	419[b]	14
Output of urine	326[a]	407[a]	676[b]	28.8

[a,b,c] Within a row, mean values with different superscript letters were significantly different ($P < 0.05$).

TABLE 7. Expt B. Apparent faecal digestibility coefficients of dry matter (DM), organic matter (OM), gross energy (GE) and nitrogen, retention of N (% of intake), and urinary excretion (% of intake) of glucose, xylose, energy and N, measured in non-cannulated pigs fed on D-glucose and D-xylose (100 (LL-Xyl) or 200 (HL-Xyl) g/kg) diets

(Mean values of four pigs per treatment)

Diet	Gluc	LL-Xyl	HL-Xyl	SEM	df
Digestibilities					
DM	94.9[a]	95.5[a]	92.2[b]	0.37	6
OM	95.8[a]	96.5[a]	93.5[b]	0.31	6
GE	95.2[a]	96.0[a]	92.7[b]	0.34	6
N	96.1[a]	96.1[a]	93.5[b]	0.44	6
Urinary excretion					
Glucose	+	+	+		
Xylose	-	44.5[a]	52.6[b]	1.44	3
Energy	2.2[a]	6.1[b]	9.9[c]	0.83	6
N	34.9[a]	35.1[a]	38.7[b]	0.71	6
Retention of N	61.2[a]	60.9[a]	54.8[b]	1.00	6

\+ Small traces (0.2 - 1.2 g/l) of glucose were found in the urine of all experimental treatments.

[a,b,c] Within a row, mean values with different superscript letters were significantly different ($P < 0.05$).

DISCUSSION

The choice of the experimental design needs to be considered. Latin squares are often used as an experimental design in balance studies with pigs, especially in trials in which the diets are fed in sequence, the diet sequence being different for each pig (Goedhart, 1990). The advantages of using Latin squares are that variation between animals and those arising from a common time trend between periods can be equilibrated. However, this is only true when there are no carry-over effects. For D-xylose, the results of a previous tentative study showed that carry-over effects of this pentose sugar cannot be excluded. Therefore, for the sake of safety in the present trials each pig was fed on the sugars in the sequence of D-glucose (Gluc), low-level D-xylose (LL-Xyl; 100 g/kg) and high-level D-xylose (HL-

Xyl; 200 g/kg). One disadvantage of feeding experimental diets in sequence is that faecal digestibilities may be affected by a time period x treatment interaction, because the digestive capacity of the pig large intestine increases with increasing age. Considering the results reported by McConnell et al. (1971, 1972), Hennig et al. (1979) and Goedhart (1990), the changes in faecal DM, OM, GE and N digestibilities in Expt B as affected by age would have been less than 1%. Furthermore, it should be noted that the feeding system applied in our design may have induced changes in intake of water, and output of wet digesta, fresh faeces and urine. However, when corrected for the differences in DM intake among the treatments, it can be calculated that there are still large differences in these characteristics between the D-Gluc and HL-Xyl diets.

The results obtained in the present study indicate that D-xylose was digested almost completely at the terminal ileum; this would suggest an almost complete absorption of this pentose sugar per se. On the other hand, administration of D-xylose to pigs was associated with an increase in ileal flow of VFA and a decrease in pH. Both symptoms point to a more extensive microbial activity in the small intestine of pigs on the D-xylose diets. This may have resulted from the differences in rates of absorption from the small intestine between D-glucose and D-xylose as reported by Miller & Lewis (1932) in rats, and Bogner (1961) and Wagh & Waibel (1967a) in chicks. These authors showed that absorption velocity of D-xylose was lower than that of D-glucose. The presence of unabsorbed xylose in the small intestine may stimulate microbial activity. Thus, the observed high ileal digestibility of D-xylose in the present study could partly be due to a microbial degradation of this sugar. The extent of microbial degradation of D-xylose in the pig small intestine cannot be derived simply from the differences in ileal flow of VFA between the D-glucose and D-xylose treatments, because some of the VFA will be absorbed already in the small intestine. In addition to D-xylose, other readily fermentable components in the diet may also be attacked by an increased intestinal bacterial activity. It is likely that the depression in apparent ileal digestibility of N in pigs on the 200 g D-xylose/kg diet is, at least partly, a result of the increased microbial activity with this diet. As protein is part of DM, OM and GE, this will also affect the digestibility of these substances. However, the reduction in ileal digestibility of DM, OM and GE on the HL-Xyl (200 g D-xylose/kg) diet can only partly be explained by the depression in N digestibility. Additionally, the increase in ileal digesta flow may also be responsible for the depression in digestibility of DM, OM and GE on the HL-Xyl diet. This higher ileal digesta flow can be explained by the presence of unabsorbed xylose in the small intestine which

will lead to an inflow of water into the intestinal lumen in order to keep osmolality constant (Van Weerden, 1959; Hof, 1980).

The magnitude of the difference in ileal DM, OM, GE and N digestibility between the treatments was maintained at a similar level in the faecal digestibility values (Table 4 v. Table 7). These results may suggest that microbial activity in the pig large intestine was not markedly changed when the D-xylose diets were fed. The observed depressed N retention on the HL-Xyl diet is a result of the depressed N digestibility on the one hand and of a higher urinary excretion on the other. Since the experimental diets were fed in sequence, the higher urinary excretion of N on the HL-Xyl diet could be partly due to an age effect (Carr et al. 1977).

It is well recognized that a portion of the ingested D-xylose appears in the urine of man (Loos, 1954; Folwer & Cooke, 1960), rats (Arnal-Peyrot & Adrian, 1974) and pigs (Wise et al. 1954). This observation is confirmed in the present work. However, there is a scarcity of information about the relationship between the dietary inclusion level of D-xylose and the urinary excretion of this sugar. Wagh & Waibel (1966) reported, that in chicks the ME value of D-xylose was decreased when the dietary level of this sugar was increased. Their finding may provide some evidence of an increased urinary excretion of D-xylose in percentage of intake when the dietary level of this sugar is increased, since Longstaff et al. (1988) reported that apparent digestibility of D-xylose in chicks was nearly 100 %. In the present study, urinary excretion of xylose as a percentage of intake increased when the dietary level of D-xylose was increased from 100 to 200 g/kg. When fed on the LL-Xyl (100 g D-xylose/kg) diet, 44.5 % of the D-xylose intake was excreted via the urine pathway. This percentage increased to 52.6 % when fed on the HL-Xyl (200 g D-xylose/kg) diet. This dosage dependent urinary excretion of D-xylose in percentage of intake may be connected with the low renal threshold for this sugar as suggested by Loos (1954). The differences in urinary excretion of xylose between the two D-xylose treatments are not reflected in the urinary excretion of energy. Calculations have indicated that when the increases in urinary excretion of energy over the D-glucose treatment were contributed to D-xylose, this would represent about 45 % of the D-xylose intake at both dietary levels.

In conclusion, it can be stated that utilization of D-xylose in pigs at dietary inclusion levels of 100 g and 200 g/kg is low. Apart from the great losses of D-xylose into the urine, at least part of this pentose sugar is fermented in the intestinal tract of pigs, which process is coupled with considerable losses in energy. In addition, at high dietary levels this pentose sugar may induce unwanted nutritive problems together with a higher excretion of urine and faeces. Considering these aspects, the benefits of a hydrolysis of the

hemicellulose fraction in pig diets seem to be doubtful as compared with a fermentation of this fraction in the hind-gut of pigs. There are no findings available on the extent of release of D-xylose in the gastrointestinal tract of pigs as a result of enzyme inclusion in pig diets. Carré & Brillouet (1986) determined the content and composition of various feedstuffs used by single-stomach farm animals. From their findings it can be calculated that by a complete hydrolysis of non-starch polysaccharides in pig diets based on cereals, soyabean oilmeal and cereal-byproducts, about 4 % D-xylose will be released. Considering the results of Wagh & Waibel (1966) with chicks, it might be expected that also in pigs utilization of D-xylose will be much better at low than at high dietary levels. This was confirmed in a recently performed study (J.B. Schutte, G. Beelen, G.B. Derksen & J. Wiebenga; unpublished results) with pigs, in which D-xylose was tested at graded dietary levels of 25 - 100 g/kg. The results of that study showed that ME content of D-xylose was significantly decreased when the dietary level of this pentose sugar was increased. Further studies will be required to clarify the utilization and metabolism of D-xylose in pigs in relation to the dietary inclusion level.

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CHAPTER 5

URINARY EXCRETION OF D-XYLOSE IN PIGS AS AFFECTED BY AGE, FREQUENCY OF FEEDING AND DIETARY LEVEL

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URINARY EXCRETION OF D-XYLOSE IN PIGS AS AFFECTED BY AGE, FREQUENCY OF FEEDING AND DIETARY LEVEL

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The pentose sugar D-xylose is one of the most abundant components which will result from a complete chemical or enzymatic hydrolysis of nonstarch polysaccharides of feed ingredients of vegetable origin. Because of the uncertainties about the nutritional value of D-xylose, two trials with pigs were conducted to investigate the urinary excretion of xylose in relation to the age of pigs, frequency of feeding and dietary inclusion level of D-xylose. Moreover the effect of inclusion of D-xylose in pig diets on N and energy utilization was examined. Urinary excretion of xylose was not significantly affected by age and frequency of feeding. The extent of urinary excretion of xylose in % of intake increased linearly ($P < 0.05$) as the dietary level of this sugar was increased. In pigs fed on a diet containing 25 g D-xylose/kg, about 20% of the D-xylose consumed appeared in the urine. This level increased to about 43% when pigs were fed on a diet containing 100 g D-xylose/kg. Retention of N was slightly decreased when pigs were fed 100 g D-xylose/kg diet. Urinary excretion of energy bearing components tended to increase in pigs fed on D-xylose diets. Liver and kidney weight, pH of urine and blood composition were not significantly affected by inclusion of D-xylose in the diets. (Key words: D-xylose, excretion, pigs)

INTRODUCTION

Nonstarch polysaccharides (NSP) can form a major fraction of the carbohydrate content of practical diets for pigs. These NSP include a mixture of substances such as cellulose, hemicellulose, pectin and oligosaccharides which contain hexose and pentose sugars and uronic acids. It is well known that NSP are resistant to the digestive enzymes of saliva, stomach and small intestine of pigs. As a result they pass to the hind gut where microbial degradation takes place. The end products of a microbial degradation of NSP (lactic acid, volatile fatty acids) are readily absorbed and can be utilized by the pig as an energy source, but with a lower efficiency

than e.g. glucose (Agricultural Research Council, 1981; Just et al., 1983; Van Es, 1987).

In a literature review, Chesson (1987) concluded that the digestibility of feed ingredients containing high levels of NSP can be improved by treatment with enzymes which can hydrolyse the NSP to monosaccharides. This was confirmed in a recently performed study at our institute (Schutte et al., 1990). Our study showed that in addition to an improvement of the digestibility of cell wall components, digestion of protein and fat was also improved in pigs when wheat bran was treated with a cellulolytic enzyme preparation. However, it remains an open question as to what extent pentose sugars and uronic acids can be utilized in pigs. Next to D-glucose the pentose sugar D-xylose is one of the most important components to be released in an enzymatic hydrolysis of NSP (Carré & Brillouet, 1986; Brillouet et al., 1988). It is well recognized that D-xylose is readily absorbed from the intestinal tract of monogastric animals (Cori, 1925; Miller & Lewis, 1932; Arnal-Peyrot & Adrian, 1974; Schutte et al., 1991a, 1991b). These studies also showed that part of the ingested D-xylose is excreted in the urine. The extent of urinary xylose output may be affected by several factors like intestinal bacterial growth, state of health, age and dietary level (Hindmarsh, 1976).

In the two trials reported herein the influence of frequency of feeding, age and dietary D-xylose level on urinary excretion of xylose was investigated in pigs. In addition, in these trials the effect of D-xylose on nitrogen and energy utilization was examined.

MATERIALS AND METHODS

Animals and diets

Two separate trials were conducted with growing castrated male pigs (Dutch Landrace x Dutch Yorkshire). 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 protein. The composition of the basal diet and its chemical characteristics are shown in Table 1.

The test sugars (D-glucose and D-xylose), supplied as anhydrous monosaccharides, were substituted by weight for wheat starch. In both trials the experimental diets were fed at a daily rate of approximately 0.9 MJ metabolizable energy (ME)/kg metabolic body weight, assuming that D-xylose has the same ME content as D-glucose. The daily amount of feed was adjusted weekly according to body weight. The feed was mixed with water (1 part feed + 1 part water). In addition, water was freely available.

TABLE 1. Composition of the basal diet.

Ingredient	g/kg
Maize meal	287
Wheat starch	287
Soyabean oil	40
Animal fat	40
Isolated soya protein (880 g protein/kg)	223.3
Cellulose ("Arbocel B800")	60
Monocalcium phosphate	24
Limestone	10
Potassium bicarbonate	15
Iodized salt	10
Mineral/vitamin mix *	5
DL-methionine	0.7

Contents (g/kg)	Expt 1	Expt 2
Dry matter **	886	891
Gross energy (MJ/kg) **	17.6	17.8
Crude protein **	216	223
Calcium ***	8.4	8.4
Phosphorus ***	7.0	7.0
Lysine ***	12.6	12.6
Methionine + cystine ***	6.8	6.8
Threonine ***	8.3	8.3
Tryptophan ***	2.6	2.6

* Provided (mg/kg diet): magnesium, 400; zinc, 110; copper, 25; manganese, 45; iron, 80; cobalt, 0.5; selenium 0.1; 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.

** Analysed *** Calculated

Experimental protocol

Experiment 1. The objectives of this trial were to determine the effect of D-xylose at a dietary inclusion level of 100 g/kg on faecal digestibility of nitrogen (N) and gross energy (GE), retention of N, and urinary excretion of xylose, N and energy in relation to feeding frequency. The feeding frequencies applied were 2 and 4 times/d, respectively. The daily amount of feed was offered at two, respectively, four equal meals at intervals of 12 and 6 h, respectively.

The trial involved 12 pigs with a mean age of 8 weeks at the start of the trial. The pigs were accustomed to cages and basal diet (Table 1) for 25 days before starting the experimental period. At the start of the experimental period three groups of four pigs, each of similar average body weight, were formed and fed diets containing either D-glucose or D-xylose. As is illustrated in Table 2, the experimental period consisted of two phases. During both phases the D-glucose diet (treatment 1) was fed four times/d, whereas the frequency of feeding of pigs fed the D-xylose diets (treatments 2 and 3) was changed in phase two. Each of the two phases consisted of a 4 d adaptation and a 5 d collection period.

At the start of the experimental period, the pigs weighed 25.2 (SD 1.1) kg and at the end 34.6 (SD 1.2) kg.

TABLE 2. Design of experiment 1.

Treatment	n	Sugar*	Frequency of feeding	
			Phase 1	Phase 2
1	4	D-glucose	4 times/d	4 times/d
2	4	D-xylose	2 times/d	4 times/d
3	4	D-xylose	4 times/d	2 times/d

* Included in the diet at a level of 100 g/kg.

Experiment 2. In this trial the effect of graded dietary levels (25 to 100 g/kg) of D-xylose on N digestibility, N retention, and urinary excretion of xylose and N in relation to the age of the pigs was examined. Moreover, specific density and pH of urine, liver and kidney weight, and blood composition were examined.

This trial involved 16 pigs: 8 young pigs with an age of 7 weeks and 8 older pigs with an age of 15 weeks at the start of the trial. The pigs were

accustomed to cages and basal diet (Table 1) for 14 days before starting the experimental period. At the start of the experimental period two treatment groups each involving 4 young and 4 older pigs were formed and fed diets containing either D-glucose or D-xylose. As is illustrated in Table 3, the experimental period consisted of four phases, during which time the pigs of the two treatment groups were fed consecutively on a diet containing 25, 50, 75 and 100 g D-glucose or D-xylose /kg. The daily amount of feed was offered at two equal meals at intervals of 12 h. Each of the four phases consisted of a 3 d adaptation and a 4 d collection period. At the start of the experimental period the young and older pigs weighed on average 17.0 (SD 1.3) and 55.3 (SD 5.6) kg, respectively. At the end of this period the pigs weighed 27.9 (SD 1.8) and 74.8 (SD 8.0) kg, respectively.

TABLE 3. Design of experiment 2.

Treatment	n	Sugar	Dietary sugar level (g/kg)			
			phase 1	phase 2	phase 3	phase 4
1	8	D-glucose	25	50	75	100
2	8	D-xylose	25	50	75	100

Faeces and urine collection

Faeces were collected directly into a bag fitted around the anus, and the urine was collected using a funnel fitted under the cage. Total collection of faeces and urine was carried out during each five (Expt 1) and four (Expt 2) 24 h collection periods from the individual animals. The faeces were collected at intervals of 12 h, and stored at -20 °C. All faeces produced during each collection period were pooled for each pig separately, homogenized and sampled. Next the samples were freeze-dried. Urine was collected in containers provided with merthiolate sodium (Thiomersal, BDH, Chemicals Ltd, Poole, England) at intervals of approximately 4 h. The portion from each interval was pooled daily from individual animals. A representative sample of 10 % of the pooled urine was taken and frozen at -20 °C. The five (Expt 1) and four (Expt 2) day sub-samples of urine were pooled for each animal separately, homogenized and sampled. Faeces and urine were kept at -20 °C between sampling and before analysis.

Analytical methods

Samples of feed and freeze-dried faeces were milled to pass through a 1.0 mm screen (Retsch mill ZMI, Retsch BV, Ochten, The Netherlands) before analysis. All analyses were carried out in duplicate. Dry matter was determined by drying the samples to constant weight at 101 °C. Inorganic matter and nitrogen were determined by standard methods (Association of Official Analytical Chemists, 1975). Gross energy was determined using an IKA-C 4000 adiabatic bomb calorimeter. Concentrations of glucose and xylose in urine were determined according the procedure described by Schutte et al. (1991a).

Statistical analysis

The results of both trials were analysed by means of analysis of variance (Cochran & Cox, 1957). The computer program Genstat 5 (Reference Manual, 1987, Oxford University Press, New York) was used to calculate the analysis of variance. Although the treatments were confounded by time and age, it was assumed that differences are due to the test sugars or increase in dietary sugar. In Expt 1 the treatment factors were type of sugar, frequency of feeding and phase. The differences in results achieved on the D-xylose diets in the first and second phase at an equal feeding frequency were small and statistically not significant. Therefore, the results obtained at an equal feeding frequency were combined in the statistical analysis. In Expt 2 the treatment factors were type of sugar, dietary level of sugar and age. In this experiment the sum of squares for levels was partitioned into a set of orthogonal linear and quadratic polynomial regression components.

RESULTS AND DISCUSSION

Table 4, which incorporates values of a previous study (Schutte et al., 1991a), indicates that D-xylose was digested almost completely at the terminal ileum. This would suggest an almost complete absorption of this pentose sugar as such. However, administration of D-xylose to pigs was associated with an increased ileal flow of VFA and a decreased ileal chyme pH. Both symptoms point to a more extensive microbial activity in the small intestine. This is further supported by the decrease in apparent ileal digestibility of N in pigs fed on the D-xylose diets. From the results of this study is was concluded that at least part of the ingested D-xylose has been consumed by the intestinal microbes. This conclusion is supported by data of Schiffer et al. (1962), Cooke et al. (1963) and Goldstein et al. (1970) who

TABLE 4. Apparent ileal digestibility data of pigs fed on D-glucose and D-xylose diets *.

Sugar	D-glucose	D-xylose	
Dietary level (g/kg)	200	100	200
Digestibilities			
OM	87.6[a]	87.2[a]	84.7[b]
GE	87.6[a]	87.5[a]	84.5[b]
N	90.3[a]	89.1[a]	87.2[b]
D-glucose	99.3	-	-
D-xylose	-	98.7[a]	98.6[a]
Ileal chyme pH	6.5[a]	6.2[b]	6.0[c]
Ileal flow of VFA (mg/12h)	1106[a]	2062[b]	4888[c]

* Data from Schutte et al. (1991a).

[a,b,c] Within a row, mean values with different superscript letters were significantly different ($P < 0.05$).

reported an increased urinary xylose excretion after antibiotics in man with small intestinal diverticulosis.

The extent of microbial degradation of D-xylose in our study with pigs cannot be derived simply from the differences in ileal flow of VFA between the D-glucose and D-xylose treatments, because some of the VFA will be absorbed already in the small intestine. Wyngaarden et al. (1957) reported that approximately 15% of an intravenously infused dose of D-xylose can be recovered as carbon dioxide in the expired air. In a previous study (Schutte et al., 1991a) it was found that at a dietary inclusion level of 100 g/kg, about 45% of the ingested D-xylose was excreted in the urine of pigs. Assuming that 15% of the dose has been metabolized to carbon dioxide (Wyngaarden et al., 1957), the remaining 40% not accounted for may have been fermented by the intestinal microbes.

One of the main objectives of the present experiments was to investigate whether urinary excretion of xylose is affected by feeding frequency, age and dietary inclusion level of this pentose sugar in pigs. The results of Expt 1 (Table 5) show that urinary excretion of xylose was not clearly affected by the frequency of feeding diets containing this pentose sugar. The dietary

inclusion level of D-xylose, however, did appear to effect the urinary excretion of xylose (Expt 2, Table 6). In both young and older pigs a positive correlation between the dietary level and the urinary excretion of xylose was found. This correlation was more pronounced in the young than in the older pigs. Taking the results of both ages together it appeared that urinary excretion of xylose in % of intake was linearly ($P < 0.01$) increased when the dietary level of this sugar was increased. Similar results were found in a previous trial with ileostomized adult roosters (Schutte et al., 1991b). Wagh & Waibel (1966) reported that the ME value of D-xylose in chicks was decreased when the dietary level was increased. This observation suggests also a dosage-dependent urinary excretion of D-xylose. In the present study no VFA measurements in the ileal chyme were performed. Thus it cannot be simply stated that the observed dosage-dependent urinary excretion of xylose is exclusively due to differences in microbial degradation of this sugar at the different dietary levels. In addition the low renal threshold for this sugar as suggested by Loos (1954) may have affected our results for urinary excretion.

Fowler & Cooke (1960), Finlay et al. (1964) and Hindmarsh (1976) reported that urinary xylose output in man declines with age. The reason for this is unknown, but it has been postulated that renal function, and consequently xylose excretion, is affected by the ageing process (Kendall, 1970). In our study an age dependent urinary excretion of xylose was not clearly demonstrated (Table 6).

The losses of xylose into the urine were reflected in the urinary excretion of energy (Tables 5 and 6), but the differences in urinary excretion of energy between the D-glucose and D-xylose treatments could not be fully explained by the xylose losses. Calculations have pointed out that when the increases in urinary excretion of energy of the D-xylose treatments over the D-glucose treatments were attributed to D-xylose, this would represent about 50% of the D-xylose intake in Expt 1 (Table 5). Thus compared to the losses of xylose in the urine (40%), 10% of the energy excreted in the urine is not accounted for. In Expt 2 (Table 6) the extra losses of energy into the urine of pigs fed on the D-xylose diets would represent about 47 and 52% of the xylose intake in young and older pigs, respectively. The values found for urinary excretion of xylose in both young and older pigs were much lower, being as a mean 32 and 35%, respectively. It is obvious that other energy bearing substances than xylose have contributed to the extra losses of energy into the urine of pigs fed on the D-xylose diets. This is supported by the slight increase in urinary excretion of N when pigs were fed on diets containing 100 g D-xylose/kg (Tables 5 and 7). Wise et al. (1954) reported that N retention was significantly decreased when pigs were fed on a diet containing 560 g D-

TABLE 5. Expt 1. Influence of feeding frequency of D-xylose diets on N and energy utilization, and urinary excretion of xylose.

Sugar(100g/kg diet)	D-glucose	D-xylose		SED	
Frequency of feeding	4 times/d. (1)	4 times/d. (2)	2 times/d. (3)	1~2 1~3	2~3
DM intake (g/pig/d)	754[a]	751[a]	764[a]	9.9	4.1
Faecal digestibility (%)					
N	92.5[a]	92.9[a]	93.0[a]	0.5	0.4
Gross energy	90.3[a]	90.5[a]	nd	0.6	-
Urinary excretion (% of intake)					
Glucose	+	+	+	-	-
Xylose	+	41.0[a]	39.9[a]	-	1.8
N	32.2[a]	35.9[a]	37.4[a]	2.4	2.3
Energy	2.3[a]	7.2[b]	nd	0.6	-
N retained (% of intake)	60.4[a]	57.0[a]	55.6[a]	2.3	2.2
ME (MJ/kg DM)					
Diets *	16.7[a]	15.9[b]	nd	0.1	-
D-glucose **	15.2	-	-	-	-
D-xylose ***	-	7.8	nd	-	-

SED = standard error of difference of means.
nd = not determined.

\+ Small traces of glucose (0.1-0.3 g/L) and xylose (0.01-0.2 g/L) were found in the urine of these experimental treatments.
* Corrected to zero N balance by using the factor 31.4 kJ/g retained N.
** Calculated as 98% of GE value.
*** Derived from he differences in ME value between the D-glucose and D-xylose diets.
[a,b] Within a row, mean values with different superscript letters were significantly different ($P < 0.05$).

TABLE 6. Expt 2. Urinary excretion of xylose and energy in young (A) and older (B) pigs fed on D-glucose (Gluc) and D-xylose(Xyl) diets.

Sugar	Dietary level (g/kg)	DM intake (g/pig/d)		Xylose excreted in urine (% of intake)		Energy excreted in urine (% of intake)	
		A	B	A	B	A	B
Gluc	25	524	1142	+	+	2.76	3.61
	50	569	1220	+	+	2.92	3.36
	75	621	1291	+	+	2.75	3.41
	100	678	1362	+	+	2.96	3.34
Xyl	25	540	1100	18.4	22.6	3.87	4.34
	50	604	1254	29.2	34.1	5.04	5.96
	75	666	1326	36.6	41.3	5.51	7.60
	100	723	1435	43.2	42.5	8.18	9.19

Analysis of variance (exclusive DM intake)

Source of variation	Probability	
between animal stratum		
Age	0.41	0.01
Sugar	-	0.01
Age x sugar	-	0.14
Residual MS	110.5	0.46

+ Small traces (0.01-0.1 g/l) of xylose were found in the urine of these experimental treatments.

xylose/kg, indicating also a greater urinary excretion of N. These investigators believe that the observed reduction in N retention in pigs fed on D-xylose diets was due to an energy deficiency and consequently greater N catabolism. This is supported by data of Wagh & Waibel (1966) who found that plasma uric acid was significantly increased when chicks were fed on diets containing 200 and 400 g D-xylose/kg. Further they reported that feeding these diets to birds resulted in decreased liver weights. The data of Wise et al. (1954) and Wagh & Waibel (1966) are not strictly comparable with the results of our study since lower levels of D-xylose were included in our diets. An energy deficiency when occuring in our study, was not reflected in liver weights (Table 8).

Wagh & Waibel (1967) reported that blood hematocrit, cholesterol, serine and proline in plasma were increased and plasma glutamic acid was decreased when birds were fed on diets containing 100 to 400 g D-xylose per kg. In order to study whether or not inclusion of D-xylose in pig diets will

TABLE 7. Expt 2. Apparent faecal digestibility of N, urinary excretion of N and N retained in young (A) and older (B) pigs fed on D-glucose (Gluc) and D-xylose (Xyl) diets.

Sugar	Dietary level (g/kg)	N digestibility (%)		N excreted in urine (% of intake)		N retained (% of intake)	
		A	B	A	B	A	B
Gluc	50	92.8	93.9	38.1	51.5	54.7	42.4
	100	93.2	94.3	40.4	53.7	52.8	40.7
Xyl	50	93.0	94.3	38.5	51.4	54.5	42.9
	100	93.1	94.4	41.6	55.9	51.5	38.5

Analysis of variance

Source of variation		Probability	
between animal stratum			
Age	0.01	0.01	0.01
Sugar	0.65	0.60	0.65
Age x sugar	0.73	0.95	0.99
Residual MS	1.08	22.81	23.0

change blood composition, blood samples were collected from pigs of Expt 2. These samples were taken after termination of the last phase (phase 4) and involved the following determinations; leucocytes, hemoglobin (Hb), erythrocytes, hematocrit, mean corpuscular value, mean corpuscular Hb concentration, glucose, bilirubin, bilirubinester, cholesterol, triglycerides, albumine and total protein. The differences in these blood parameters between pigs fed on the D-glucose diets and those fed on the D-xylose were small and not significant. Further it is noteworthy that histo-pathological examination of the liver and kidneys did not show abnormalities in pigs fed on either D-glucose or D-xylose diets (Expt 2). Specific density of urine appeared to be slightly increased (Table 8) when pigs were fed on diets containing D-xylose; this will be related with the increased urinary excretion of energy on this diet. No effect of D-xylose on the pH value of urine was observed (Table 8).

TABLE 8. Expt 2. Specific density and pH of urine, and liver and kidney weight (in % of body weight) in young (A) and older (B) pigs fed on D-glucose (Gluc) and D-xylose (Xyl) diets.

Sugar	Urine values *				Organ weights			
	Spec. density		pH		Liver		Kidney	
	A	B	A	B	A	B	A	B
Gluc	1.006	1.023	7.1	6.7	1.8	1.5	0.372	0.282
Xyl	1.014	1.026	7.0	6.6	1.9	1.6	0.352	0.301

Analysis of variance

Source of variation		Probability		
between animal stratum				
Age	0.01	0.01	0.01	0.01
Sugar	0.06	0.10	0.34	0.96
Age x sugar	0.34	0.75	0.56	0.22
Residual MS	32.11	0.01	0.02	0.01

* Determined during phase 4 only; each value represents 16 individual observations (one observation/animal/d).

In conclusion it can be stated that the energy value of D-xylose is much lower than that of D-glucose. From the results of Expt 1 it was calculated that at a dietary level of 100 g/kg, D-xylose has a ME value of only 7.8 MJ/kg, which value is approximately 50% of that of D-glucose. Considering the data for urinary excretion of xylose, it may be expected that at lower dietary inclusion levels than 100 g/kg the ME value of this pentose sugar will increase. The net utilization of D-xylose in pigs is difficult to access from the present study. This because of the unknown metabolic pathway of this sugar. The results of a previous study (Schutte et al., 1991a) indicated that at least part of the xylose is fermented in the small intestine. It may even be possible that all xylose has to be fermented before it can be used as an energy source for pigs.

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CHAPTER 6

NUTRITIONAL IMPLICATIONS OF L-ARABINOSE IN PIGS

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NUTRITIONAL IMPLICATIONS OF L-ARABINOSE IN PIGS

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The pentose sugar L-arabinose is one of the most abundant components which will become free in a complete hydrolysis of nonstarch 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 digestibility 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 in 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 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. (Key words: L-arabinose, Digestion, Excretion, Pig)

INTRODUCTION

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 last one

may be conveniently referred to as nonstarch polysaccharides. Starch, a storage carbohydrate, can be hydrolyzed by pancreatic α-amylase and may therefore be digested in the small intestine of pigs, and absorbed as glucose. Nonstarch polysaccharides (NSP) are complicated compounds both from the point of view of physical structure and chemical composition, and 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 hindgut where microbial degradation takes place. The end products of a microbial degradation of NSP, lactic acid and volatile fatty acids, are rapidly absorbed into the blood and can be utilized by the pig as an energy source, but with a lower efficiency than e.g. 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 and 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 and Adrian, 1974) and chicks (Bogner, 1961; Wagh and Waibel, 1967), but at a lower rate than glucose. The study reported by Arnal-Peyrot and 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 and Waibel (1966) and Schutte (1990). From these studies, it appears that in chicks the metabolizable energy value of L-arabinose not only was 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 digestibility of the dietary nutrients was investigated. D-glucose was included in the experiments as a reference.

MATERIALS AND METHODS

Animals and diets

Two separate trials were conducted with growing castrated male pigs (Dutch Landrace x 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 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.

In both trials the experimental diets were fed at a daily rate of approximately 0.9 MJ metabolizable energy (ME)/kg metabolic body weight, assuming that L-arabinose has the same ME content as D-glucose. The daily amount of feed was offered at 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 (N) 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 witholding feed for 24 h. During the 3-week post-operative period, the pigs were fed on the basal diet (Table 1). The experimental period involved originally three

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

Maize meal	287
Wheat starch	287
Soya-bean oil	40
Animal fat	40
Isolated soya protein (880 g protein/kg)	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, FRG)

\+ 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.

TABLE 2. Chemical composition of the basal diet (analysed, g/kg unless otherwise stated)

Constituent	Expt A	Expt B
Dry matter	901	894
Ash	53	52
Crude protein (N x 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

phases during which time each pig was fed consecutively a diet 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 and a 4 d collection period for each diet. During the first three days 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 an 1 d adaptation 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.

TABLE 3. Experimental design of experiment B.

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

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 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 5 pigs, each of similar average body weight, were formed and fed diets containing either D-glucose or L-arabinose according to a scheme as outlined in Table 3. As is illustrated in Table 3, the experimental period consisted of four phases. Each of the four phases consisted of a 7 d adaptation and a 4 d collection period. During the first three days of the adaptation period, pigs were gradually changed to the next diet containing a higher level of the same sugar.

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 during each 4 d collection period was collected from the PVTC cannula quantitatively from individual animals over a 12 h period per day (8.00-20.00 hours). Previous studies had shown that ileal digesta collection is almost complete by using this type of cannula on the same type of basal diet as in the present trial (Köhler et al. 1991). Previous studies had also shown that there were no significant differences in ileal digestibility when digesta were collected over a 12 h or over a 24 h period per day (E.J. van Weerden, J. Huisman & 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 collected portions were pooled for each pig separately, homogenized and sampled. VFA and lactic acid determinations were performed in the digesta as such, the other measurements in freeze-dried samples. Until analysis all samples were kept at -20°.

Faeces and urine collection

Faeces were collected directly into a bag fitted around the anus, and the urine was collected using a funnel fitted under the cage. Total collection of faeces and urine was carried out during the four 24 h collection periods from the individual animals. 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 separately, homogenized and sampled. Then the samples were 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, BDM, Chemicals, Ltd, Poole, England) as a preservative to inhibit bacterial activity. Before inclusion, this preservative was dissolved in an ethanol solution (4 g/100 ml), and added in an amount of 0.4 ml/ container. This amount was based on an urine production of 200 ml per 4 h. The portion of urine from each interval was pooled daily from individual animals. A representative sample of 10 % of the pooled urine was taken and frozen at -20°. The 4 d sub-samples of urine were pooled for each animal separately, homogenized and sampled. Faeces and urine were kept at -20° between sampling and before 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. Immediately afterwards the supernatant fraction (5 ml) was acidified with 500 µl phosphoric acid (850 ml/l), 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, USA). A glass column (1850 mm x 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 peak-height ratios of the acids: that of isocapronic acid. Recovery values 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 enzymatically according to Anonymous (1986).

Concentrations of glucose and arabinose in digesta and urine were determined as silyl derivatives of 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 x 4) and cation (Biorad AG 50 W x 4)) exchanger. After centrifugation, 200 µl of the supernatant fraction was freeze-dried. To the freeze-dried sample phenylglucopyranoside (0.4 mg in a 1 ml pyridine solution) was added as an internal standard. The sample was then derivatized by the

addition of 0.6 ml hexamethyldisilazane and 0.3 ml trimethyl-chlorosilane. Then the contents were mixed using a Vortex stirrer. 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 temperature of the injector and detector was 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 are due to the test sugar or increase in dietary sugar. This will further be elucidated 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 between wet ileal digesta output and intake of DM were almost similar in both D-glucose phases. This suggests that an adaptation period of 1 d was sufficient to stabilize the conditions in the gastro-intestinal tract when pigs were changed from the Arab to the Gluc diet.

In Expt B the treatment factors were type of sugar and the dietary level of sugar. The 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 x level interaction. The sum of squares for 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

Intake 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 among the treatments. These differences were caused by the feeding system applied, since this system was coupled with 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 by 40 and 78 % when pigs were fed on the Arab 50 (phase 2) and

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 of 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
Ratio 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

* Standard error of difference between means.

[a,b,c] Within a row, mean values with no common superscript letters were significantly different ($P < 0.05$).

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

(Mean values of four pigs per treatment)

Phase	1	2	3	4		
Sugar	Gluc	Arab	Arab	Gluc	SED*	df
Dietary level (g/kg)	100	50	100	100		
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

* Standard error of difference between means.

[a,b] Within a row, mean values with no common superscript letters were significantly different ($P < 0.05$).

Arab 100 (phase 3) diets, respectively. When pigs were changed from the Arab 100 to the Gluc 100 diet (phase 4), the ratio between water and DM intake decreased significantly to 2.37, a value which was almost 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, ileal output of digesta was decreased significantly. The increase in digesta output in pigs fed on the Arab 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 diets (phase 1 and 4), similar digestibility coefficients for DM, OM, GE, N and D-glucose were observed. However, in pigs fed on the Arab diets, lower digestibility coefficients for DM, OM and GE were observed; the values on the Arab 100 diet being significantly different from those of pigs fed on the Gluc diets. There was a tendency for digestibility of N to be less in pigs fed on the Arab

diets than in pigs fed on the Gluc diets. 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 affected significantly by the dose level of L-arabinose.

Data for ileal flow of VFA and lactic acid are given in Table 6. In pigs fed on the Arab diets, the ileal flow of VFA was higher than in pigs fed on the Gluc diets, being significant in pigs on the Arab 100 diet. The increase in ileal flow of VFA in pigs fed on the Arab diets was mainly caused by an increase in acetic acid. Ileal flow of lactic acid followed the same pattern of response as for VFA when pigs were fed the Arab diets. However, the differences in ileal flow of lactic acid among the treatments were not significant.

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 of 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

* Standard error of difference between means.

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

[a,b] Within a row, mean values with no common superscript letters were significantly different ($P < 0.05$).

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 among the treatment groups. However, as already stated in Expt A, these differences were caused by the feeding system applied. Water intake in % of DM intake of pigs fed on the Gluc diets was not significantly affected by the dose level of this sugar. When pigs were fed the Arab diets, water intake in % 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 Gluc diets and those fed on the Arab diets were not significant ($P > 0.05$). DM content of faeces was not significantly affected by the type and dose 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 Gluc and Arab diets. However, the average digestibility of N was significantly lower in pigs fed on the Arab diets than those fed on the Gluc diets.

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 % 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 Arab 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 rather due to an age effect than to the dose level (Carr et al. 1977). Retention of N, being approximately 55% of N intake, was high in the present trial as compared to practical values. This high N retention value will be the result of both a well balanced highly digestible protein basal diet and the relative low daily feeding level applied (Agricultural Research Council, 1981). When pigs were fed on the Arab diets, less ($P < 0.05$) N was retained then when feeding the Gluc 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 Arab diets.

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 of five pigs per treatment)

Sugar	Sugar level (g/kg)	Intake DM(A)	Intake water(B)	Ratio B:A	Output urine	Output 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

* Standard error of difference between means within each sugar.

** Standard error of difference between means of both sugars.

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

(Mean values of 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[a]
SED (df 8)		0.68	0.84	0.72	0.26

* Standard error of difference between means within each sugar.

** Standard error of difference between means of both sugars.

[a] Mean value was significantly different from the Gluc diets ($P < 0.05$).

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

(Mean values of 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
Arab	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[a]
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.

* Standard error of difference between means within each sugar.

** Standard error of difference between means of both sugars.

[a] Mean value was significantly different from the Gluc diets ($P < 0.05$).

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 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 square method was not followed, whereas 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 x 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 almost similar coefficients on both glucose diets (Table 5). The results for faecal digestibilities (Table 8), showing that the coefficiënts within the D-glucose block were almost constant, also indicate that these data 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 and 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. No clear indications were observed 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. 1991a). 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 may commence already in the crop. Unfortunately, no literature data are available 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 symptom 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 attacked by an increased intestinal bacterial activity. However, this hypothesis could not be backed up firmly 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. 1991a). 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 keep osmolality constant (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 the part of 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 of pigs fed on the Arab 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 an 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 non or sometimes positive overall effect on N balance (Partridge et al. 1982; Dierick et al. 1983; Malmhof & Hakansson, 1984; Morgan & Whittemore, 1988). Contrary to these findings are the results of the present study. In addition to a depressed faecal digestibility of N, also N losses in urine were slightly increased when pigs were fed on diets containing L-arabinose. As a result of both, less N was retained in pigs fed on the L-arabinose diet. Similar results of a depressed N retention were found 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. 1991b). Why the pentose sugars L-arabinose and D-xylose tend to decrease efficiency of the utilization of absorbed N in pigs is unknown.

It is generally accepted that D-glucose can be utilized almost completely in human and animals (Demetrakopoulos, 1978), so only negligible amounts of glucose will be found in the urine. The latter is in agreement with the

finding in the present study. Only little information is available to which extent L-arabinose will be excreted in the urine of monogastric animals. Arnal-Peyrot and Adrian (1974) reported an urinary loss of 7.5 % ingested arabinose when rats were fed 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. 1990). The results of that study also showed that urinary excretion of arabinose in % of intake, increased linearly as the dietary level of this sugar increased. The same was true in the present study. However, this dose-dependant urinary excretion of L-arabinose could not be derived clearly 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 (as a mean 12.9 %) and those calculated from the urinary excretion of energy, relate most probably to the higher losses of other energy bearing components in the urine of pigs fed on the L-arabinose diets. This is supported by the higher losses of N in the urine in 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 a 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. From the present studies it has only become clear that about 30 % of the ingested L-arabinose entered the large intestine where it was fermented, while another 13 % was excreted into the urine. The pathway of the remaining 57 % of ingested L-arabinose is uncertain. This part, which disappeared from the small intestine, may have been utilized as such or fermented to VFA, or both of these. Of these two mechanisms, a possible microbial fermentation of L-arabinose in the small intestine was demonstrated in our study. Knowledge about a possible metabolic pathway of this pentose sugar in the animal body is limited. Segal & Foley (1959) reported that when given an intravenously infused dose of C14 labeled L-arabinose to man, only 0.8% could be recovered in expired carbon dioxide. If their data are transferable to pigs, this would mean that L-arabinose only after microbial fermentation can be used as an energy source for pigs. 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 to that of praecaecally 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 rather optimistic. On the other hand, data of Close et al. (1989) suggest that the efficiency of utilization of energy from hind gut fermentation is higher than estimated by Agricultural Research Council (1981) and Müller et al. (1989).

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GENERAL DISCUSSION

GENERAL DISCUSSION

The NSP fraction of feed ingredients of vegetable origin represents the least digestible component of diets in pigs and poultry. Therefore most efforts on the use of enzymes in pig and poultry diets in order to improve digestibility of feed ingredients have focussed on the NSP fraction. The benefits of an enzymatic hydrolysis of NSP, however, are not determined solely by an improvement in digestibility, but also by the potential of the animal to utilize the products of hydrolysis. In addition to D-glucose, other sugars will also be released by complete hydrolysis of NSP, of which in quantitative terms D-xylose and L-arabinose are the most important ones. The literature review (General introduction) indicates that knowledge is incomplete on the nutritional value of these pentose sugars in pigs and poultry. The investigations described in this thesis were mainly focussed on the digestion of D-xylose and L-arabinose in the various parts of the gastrointestinal tract, and on renal excretion. Besides, the effect of both pentose sugars on some physiological characteristics in poultry and pigs was studied. The results of the investigations were compared with data from literature. In the present discussion various aspects of the results will be considered in relation to some other effects and properties of these sugars and NSP.

ILEAL DIGESTIBILITY OF XYLOSE AND ARABINOSE

Without an accurate knowledge of the extent of the removal of xylose and arabinose from the precaecal tract, it is hardly possible to follow the fate of both pentose sugars in the animal organism on a quantitative basis. Hitherto, most of the reported experiments on intestinal absorption of xylose and arabinose in monogastric animals have been performed on the whole intestinal tract of rats (Cori, 1925; Miller & Lewis, 1932;) and chicks (Bogner, 1961; Wagh & Waibel, 1967a). The principle of this method is briefly as follows. The experimental animals are fed a predetermined amount of the sugar by stomach or crop tube. After a given time, the animals are killed and the quantity of sugar remaining in the intestine is determined. The difference between the amount fed and that recovered from the intestinal tract is considered as the amount of sugar absorbed by the animal. This method is open to a number of objections, chiefly related to the length of the absorption period. The results reported by Bogner (1961) and Wagh & Waibel (1967a) are based on an absorption period of 30 min. Considering the data of Wagh & Waibel (1967a), it appears that not all the sugar administered had disappeared from the crop and gizzard during this time period. At a dose rate of 15 µm per g body weight, 16.7 % of the ingested glucose was still present in the crop and gizzard. For xylose and arabinose these percentages amounted to 20.3 and 24.5 %, respectively. Miller & Lewis (1932) reported

that in rats absorption coefficients of xylose tended to increase as the absorption period was prolonged. Mean values of 29, 39 and 46 mg of absorbed xylose per h per 100 g of body weight were obtained during absorption periods of 1, 2 and 3 h, respectively.

In our studies the ileal fistula technique was used to measure absorption of the sugars. This would permit of basing the results on a much longer absorption period, and to study possible side effects from the feeding of D-xylose and L-arabinose to pigs and poultry in more detail. As a longer absorption period could lead to an increased attack by intestinal microbes, this type of experiments does not distinguish between sugar removal by absorption and by fermentation. Both probably occur in all sections of the precaecal tract, but to greatly varying extents. The ratio between removal by absorption and fermentation depends on the velocity of absorption of the sugars and on the precaecal activity of microorganisms. From literature data it is well known that glucose is absorbed at a higher rate than xylose, the latter being superior to arabinose (General introduction). Thus, when precaecal fermentation of these sugars occurs, the sequence is likely to be of arabinose > xylose > glucose. This sequence of microbial fermentation, however, could not be confirmed in the present studies with pigs (Chapters 4 and 6). At equal dietary dose levels of 100 g/kg, ileal flow of VFA increased more in pigs fed on the xylose diet than in those fed on the arabinose diet. When ileal flow of VFA for the glucose treatment was set at 100%, the value for the xylose treatment was 186% and for the arabinose treatment 159%. These results suggest that the precaecal microbes have a preference for xylose over arabinose. While it is questionable whether both trials are comparable, in this case it can be justified since the same type of basal diet was used in both trials and the ileal flow of VFA on the glucose treatments were similar. Some evidence of a discrimination between sugars by the bacteria in the alimentary tract is provided by Luckey (1987). This investigator reviewed the capability of the human alimentary tract bacteria to utilize simple sugars. His study indicated that there are considerable differences between bacterial species in their capacity to utilize various sugars. Glucose appeared to be utilized by all of the identified intestinal bacteria. In contrast, xylose as well as arabinose were not used by **Lactobacillus acidophilus**, and arabinose also not by **Bacteroides fragilis.** Thus, it would seem that the extent of microbial degradation of sugars depends not only on the density, but also on the composition of the intestinal bacteria. In this context it seems relevant to consider also the differences in ileal digestibility of the sugars between pigs and adult roosters (Chapters 2, 4 and 6). In both animal species, D-xylose was digested almost completely at the terminal ileum. Considering the ileal digestibility data of L-arabinose, it appears that in pigs fed this pentose sugar at 50 and 100 g/kg diet, 30 and 33 %, respectively, of the ingested arabinose appeared in the ileal chyme. In adult roosters, however, at these dietary inclusions, only 5 and 25 %,

respectively, of the ingested arabinose was recovered in the ileal chyme. These results suggest that precaecal microbes in roosters are able to utilize more L-arabinose than those in pigs. However, care should be taken with this conclusion. This conclusion has to be restricted since fermentation of arabinose in fowls may already commence in the crop. While the role of the crop as a storage organ in the bird is well established, its digestive function is not well understood. Bolton (1965) demonstrated that as a sugar disappeared from the crop, the amount of lactic acid, acetic acid and ethanol in the crop increased. Bayer et al. (1978) fed broiler chicks on high and low fibre diets and noted that lactic and acetic acid were the predominant organic acids in the crop. Medl & Scharrel (1978) demonstrated an active trans-epithelial movement of sodium across the chicken's crop, suggesting that nutrients can be absorbed from the crop. This hypothesis is supported by data of Soedarmo et al. (1961), who showed that about 7% of an administered dose of C14-labeled glucose into the ligated crop disappeared from this organ. They noted also that when given C14 labeled xylose, this sugar did not leave the ligated crop in appreciable amounts. Thus, both absorption of sugars and microbial fermentation may occur in the chicken's crop, but to a relatively small extent only. On the basis of certain assumptions it is possible to estimate from the present studies the amounts of xylose and arabinose which have been removed from the precaecal tract by either absorption or fermentation. This will be discussed further in the next section.

FATE OF THE PRECAECALLY DIGESTED XYLOSE AND ARABINOSE

(1) D-xylose

The xylose absorption test is widely used in the diagnosis of malabsorption. The test is based on the assumption that xylose is not metabolized to any significant extent in the body. Thus, this would mean that the amount of xylose excreted in the urine after oral administration reflects the amount of xylose absorbed in the gastro-intestinal tract. No direct evidence is available to state whether conversion to glucose is a fate of D-xylose in monogastric animals (Segal & Foley, 1959). There is conclusive evidence, however, indicating that some of the D-xylose absorbed is metabolized in the organism. After intravenous administration of D-1-C14 xylose to man, about 14 to 16 % could be recovered as carbon dioxide in expired air (Wyngaarden et al., 1957; Segal & Foley, 1959). Similar results were reported by Weser & Laster (1968) who found that about 11 % of an intraperitoneal injection of D-xylose -1-C14 to guinea pigs was recovered as carbon dioxide in expired air. A much lower value was reported in chicks by Wagh & Waibel (1967b). These investigators found that only 4 % of a subcutaneous dose of C14-labeled D-

xylose was recovered as carbon dioxide in expired air. In addition to catabolism of D-xylose to carbon dioxide, a proportion of both orally and intravenously administered D-xylose has been shown to be converted into a four-carbon polyol (D-threitol) in the human organism (Pitkänen & Svinhufvud, 1965). Their data suggest further that D-threitol is excreted into the urine with no or very little tubular reabsorption. According to experimental data of Weser & Laster (1968), D-xylose catabolism occurs mainly in the kidney and liver. The role of the liver in the conversion of D-xylose to D-threitol has been studied more extensively by Pitkänen (1977). Urinary excretion of D-xylose and D-threitol was studied after oral administration of 25 g xylose to man with portal liver cirrhosis, with active fatty liver disease and with no liver disease, respectively. This study pointed out that 15% of the dose of D-xylose excreted in the urine was recovered as D-threitol in man without liver disease or with fatty liver disease. D-threitol excretion was decreased to 8% in cirrhotic patients. Based on these results the author concluded that a substantial proportion of the conversion of D-xylose to D-threitol conversion occurs in the liver. In order to test whether conversion of D-xylose to D-threitol is of significant importance in pigs and poultry, additional analyses were carried out in the urine of adult roosters and pigs involved in the studies reported in Chapters 2 and 5. In the urine of both pigs and adult roosters fed on D-glucose diets, D-threitol could not be detected. Considerable amounts of D-threitol were found in the urine of pigs and adult cocks fed on diets containing D-xylose (Table 1). The extent of the urinary excretion of D-threitol agrees well with the data of Pitkänen (1977). The presence of D-threitol in the urine may also partly explain the discrepancy between the renal excretion of D-xylose and the energy losses into the urine observed in our studies.

TABLE 1. Urinary excretion of D-xylose and D-threitol (% of intake) in pigs and adult roosters fed on diets containing 100 g D-xylose/ kg (mean values ± SD of 4 pigs and 3 adult roosters)

Animal species	Urinary excretion of: D-xylose	D-threitol	D-threitol/ D-xylose ratio *
Pigs	37.2 ± 7.6	7.9 ± 1.4	0.17
Adult roosters	20.2 ± 2.0	4.6 ± 0.5	0.19

* Not corrected for the differences in molecular weight.

The metabolic path for the conversion of D-xylose to D-threitol is not fully known. There is evidence that D-xylose metabolism is initiated by glucose dehydrogenase or by a more specific pentose dehydrogenase (Weser & Laster, 1968). As proposed by Pitkänen (1977), further steps in the conversion

may occur through the glucuronate cycle enzymes for which D-xylonate and D-erythrulose are intermediates. A similar direct oxidation pathway of galactose through galactose dehydrogenase and beta-L-hydroxy-acid dehydrogenase has also been demonstrated in man (Cuatrecasas & Segal, 1966; Segal & Cuatrecasas, 1968).

In our studies it was found that in both adult roosters and pigs the urinary excretion of D-xylose in % of intake was significantly increased when the dietary level of this sugar was increased from 25 g to 100 g/kg (Chapters 2 and 5). On the assumption that at these dose levels 10% of the ingested D-xylose is catabolized to carbon dioxide, and that D-threitol represents 15% of the renal D-xylose excretion, the proportion of D-xylose fermented prior to the caecum can be calculated. The results of these calculations are summarized in Table 2. In considering the data presented in this table, it should be realized that the calculations relate to a certain physiological status of the animals. Both renal excretion and precaecal microbial degradation of D-xylose may be affected by age (Hindmarsh, 1976). The data (Table 2) are based on pigs with a live weight of 20 to 80 kg. Within this period renal excretion of xylose was not affected to any extent by age (Chapter 5). Renal excretion of xylose in pigs aged 4 weeks was found to be similar to that in older pigs (Schutte et al., unpublished results). The results of that study also showed that in young pigs D-xylose was not digested completely at the terminal ileum. When fed these pigs on a diet containing 100 g D-xylose /kg, approximately 10 % of the ingested xylose was recovered in the ileal chyme.

TABLE 2. Estimated proportion of D-xylose microbially fermented in the precaecal tract of pigs and fowls.

Animal species	Dietary inclusion (g /kg)	Fate of precaecally digested D-xylose (% of intake)			
		Excreted in urine		Catabolized to CO2	Microbially degraded
		xylose *	D-threitol		
Pigs	25	20	4	10	66
	50	32	6	10	52
	75	39	7	10	44
	100	43	8	10	39
Fowls	25	7	1	10	82
	50	13	2	10	75
	75	17	3	10	70
	100	20	4	10	66

* Data from the studies presented in Chapter 5 (pigs) and Chapter 2 (adult roosters).

As stated before, in older pigs this recovery value was nearly zero. Most probably these differences in ileal apparent digestibility coefficients of D-xylose between young and older pigs are due to less microbial activity in the precaecal tract of the young pigs.

It is highly likely that there are differences in precaecal microbial degradation of D-xylose between chicks and adult roosters. The observed slight increase in ceacal weight of chicks fed on diets containing D-xylose may provide some evidence for this hypothesis (Chapters 1 and 3). The few data available on the precaecal fermentation of D-xylose in monogastric animals are conflicting. Using the everted sac technique, Heneghan (1963) investigated the absorption of D-xylose from the mid small intestine in conventional and germfree rats and mice. In the absence of microbial flora there was a twofold increase in the absorption of D-xylose. This observation was based on an absorption period of one hour, a time when both germfree and control animals had absorbed less than half of the administered dose. Tennant et al. (1970) analysed the intestinal tract of germfree and conventional rats 6 hours after administration of D-xylose. At the end of the test period, 11.3% of the D-xylose remained in the stomach of the germfree rats compared to 3.8% in conventional rats. There was no difference between germfree and conventional groups in the amount of D-xylose which remained in the small intestine. Further studies are in progress at our Institute with germfree pigs and chicks in order to clarify the role of the intestinal microbial flora on xylose digestion.

(2) L-arabinose

The literature on the metabolic pathway of L-arabinose is very scarce. Data of Segal & Foley (1959) suggest that metabolism of L-arabinose to carbon dioxide is of no significance. When given an intravenously infused dose of C14-L-arabinose to man, only 0.8% could be recovered as carbon dioxide in expired air. A slightly higher value was reported in chicks by Wagh & Waibel (1967b). These investigators observed that of a subcutaneous dose of C14 labeled L-arabinose, 4.6% could be recovered in the expired air as carbon dioxide. Inspection of our chromatography bands for urine of pigs fed on L-arabinose diets, showed that there was an unidentified peak, representing about 50% of the arabinose peak. These results suggest that L-arabinose is excreted in the urine partly in a form other than arabinose. This is supported by the higher losses of urinary energy than expected from the renal excretion of arabinose (Chapter 6). Few literature data are available on the catabolisme of L-arabinose to products other than carbon dioxide. The existence of an enzyme converting L-arabinose to L-arabitol has been suggested since this substance has been isolated from pentosuric

urine of man (Touster & Harewell, 1958). In addition some arabinose may be oxidized to L-arabonic acid as was demonstrated in bacteria (Weimberg & Doudoroff, 1955). Additional analyses performed in the urine of pigs fed on diets containing L-arabinose (Chapter 6) revealed the presence of both L-arabitol and L-arabonic acid. Further studies are in progress to quantify both metabolites in the urine of pigs and fowls fed on L-arabinose diets.

On the assumption that 4% of the ingested arabinose is catabolized to carbon dioxide and that arabinose metabolites represent 50% of the renal L-arabinose excretion, microbial degradation of L-arabinose in the precaecal tract of pigs and adult roosters was calculated (Table 3). In this calculation the incomplete ileal digestion of arabinose was taken into account. Since ileal digestion of arabinose in pigs was only measured at dietary inclusions of 50 and 100 g/kg, calculations could not be made for dose levels of 25 and 75 g/kg. It should be noted that the data in Table 3 have to be considered with some reservation, as they relate to a certain physiological status of the animals; in pigs to the live weight period of 25 to 55 kg and in fowl to adult roosters. No experimental data are available to indicate whether both renal excretion and microbial degradation of this pentose sugar are affected by age of the animal. The results of a trial on the effect of the frequency of feeding diets containing D-xylose on the renal excretion of this pentose sugar are discussed in Chapter 5. The attack of precaecal microbes on both pentose sugars may be expected to be greater in animals continuously fed on diets containing these pentose sugars. Consequently, renal excretion of D-xylose and arabinose would decrease. This hypothesis was not be supported in the trial with D-xylose because renal excretion of xylose was similar in animals fed D-xylose diets twice or four times a day. A similar study showed that renal excretion of L-arabinose was also not affected distinctly when arabinose diets were fed twice or four times a day (Schutte et al., unpublished results). Studies are now being undertaken with germfree pigs and chicks to investigate the role of the intestinal microbial flora in arabinose digestion.

TABLE 3. Estimated proportion of L-arabinose microbially fermented in the precaecal tract of pigs and fowls.

Animal species	Dietary inclusion (g/kg)	Ileal digested (%)*	Fate of precaecally digested L-arabinose (% of intake) Excreted in urine		Catabolized to CO2	Microbially degraded **
			arabin.*	metabolites		
Pigs	25	ND	11	5	4	
	50	70	12	6	4	48
	75	ND	14	7	4	
	100	67	15	7	4	41
Fowls	25	95	9	4	4	78
	50	94	11	5	4	74
	75	80	14	7	4	55
	100	75	17	8	4	46

* Data from studies presented in Chapter 6 (pigs) and Chapter 2 (adult roosters).

**Preceacally fermented. The amount of L-arabinose not digested at the terminal ileum can be considered to be fermented in the hind gut.

ENERGETIC VALUE OF D-XYLOSE AND L-ARABINOSE

From stoichiometry, it can be calculated that the content of gross energy is 2.82 MJ/mole for D-glucose and 2.34 MJ/mole for D-xylose and L-arabinose. This means that all three sugars have a similar gross energy content of 15.65 MJ / kg substance. Several systems have been devised to express the energy value of feed ingredients or diets in terms of the energy which is useful to the animal. In this respect the term metabolizable energy (ME) is commonly used, especially in poultry. In this system the losses of energy in faeces and urine are taken into account. The ME value of D-glucose can be considered to be similar to the GE content, because this sugar is absorbed and utilized almost completely in monogastric animals. (Demetrakopoulos & Amos, 1978). The results of our studies have shown that the ME value of both pentose sugars was not only lower than that of D-glucose but also dose dependent. The latter statement was based on the increase in urinary excretion of both pentose sugars when the dietary inclusion of these sugars was increased. In poultry, this dose dependent ME value was confirmed by direct measurements of the ME value of both pentose sugars at dietary levels of 50 and 100 g/kg (Chapter 1). Based on these measurements, the ME value of D-xylose for poultry was estimated to be 11.1 MJ/kg at 50 g/kg diet and 8.5 MJ /kg at 100 g/kg diet. Corresponding values for L-arabinose at

these dietary levels were 9.6 and 5.7 MJ/kg. These estimated ME values for both pentose sugars have to be considered with some caution because they concern a far extrapolation to 100%. An increase in the dietary level of the pentose sugars may also have an indirect negative effect on the ME of other dietary energy bearing components. In pigs, the direct measurement of the ME value of both pentose sugars in our studies were made for a dietary inclusion of 100 g/kg only. Based on this dose level, the ME value of D-xylose and L-arabinose for pigs was estimated to be 7.8 and 8.1 MJ/kg, respectively, (Chapter 5; Schutte et al., unpublished results). However, as already stated for poultry, also these ME values have to be considered with some caution. The results referred to above indicate that it is not possible to give a fixed ME value for D-xylose or L-arabinose because these values are dose dependent. Apart from this, the use of the ME value in predicting the energy value of both pentose sugars is questionable. From both pathways of the pentose sugars after ingestion, metabolism per se and fermentation, losses in energy can arise. As a result from these losses in energy, the ME content of these sugars overestimates the energy that is actually available to the animals as compared to D-glucose. It is well recognized that the ME of D-glucose is utilized with a great efficiency in terms of producing adenosine triphosphate (ATP). According to Van Es (1974), the energetic efficiency of utilization of the ME of D-glucose is approximately 80%, resulting in a net energy (NE) value of approximately 12.5 MJ/kg. However, the ME of both pentose sugars is mainly in the form of energy from a fermentation process, which process is coupled with considerable losses of energy. These losses arise from the heat of fermentation, the production of methane and the less efficient utilization of the absorbed end products (organic acids) as compared to D-glucose. The overall utilization of fermented ME is still under discussion. The present estimations about the utilization of fermented ME relative to that of the ME of D-glucose vary between 50 and 70% (Agricultural Research Council, 1981; Just et al., 1983; Van Es, 1987; Müller et al., 1989). No data are available to which extent the part of the absorbed pentose sugars not excreted into the urine, can be used by the animal. This uncertainty together with the discrepancies on the efficiency of utilization of fermented ME, means that the NE value of both pentose sugars can only be estimated roughly. On the assumption that metabolism of both pentose sugars is analogous to that proposed in the previous section (Tables 2 and 3), the following equation was used to estimate the NE value of both pentose sugars.

NE (in MJ/kg) = A x 0.80 + 0.80 (B x 0.60)

Where for the particular pentose sugar concerned:
A = the amount (in MJ/kg) of the ME which was calculated to arise from a metabolism of both pentose sugars per se . The energetic efficiency of utilization of this fraction was assumed to be equal to that of absorbed D-glucose (=80%)

B = the amount (in MJ/kg) of the ME which was calculated to arise from the fermentation process. The relative utilization of this fraction as compared to D-glucose was assumed to be 60% (mean value of literature data)

According to this method the NE value of D-xylose and L-arabinose at a dietary inclusion of 100 g/kg for pigs would be 4.2 and 4.0 MJ/kg. Corresponding values for poultry at this dose level are 4.4 and 2.8 MJ/kg, respectively. Notwithstanding the uncertainties involved in these estimations, there is no doubt that the energy value of both pentose sugars is considerably lower than that of D-glucose in pigs and poultry. An overall estimate of the energy value of both pentose sugars of 25 to 35 % of that of D-glucose is probably not far from the real value. The study with chicks described in Chapter 3, in which carcass energy was measured, suggests indeed that the energy of D-xylose and L-arabinose can only be utilized to a limited extent by the animal.

ASSOCIATED EFFECTS OF D-XYLOSE AND L-ARABINOSE

Like galactose, D-xylose can potentially cause cataracts on the eyes (Kinoshita, 1974). No reliable data are available as to whether L-arabinose also induces cataract formation. The cataractogenic potential of D-xylose in rats was first reported by Darby and Day (1939, 1940). Indeed, xylose cataracts have occurred only in young Wistar albino rats when fed on a regular diet enriched with 350 g or more D-xylose/kg. The cataracts appeared on the 4th and 5th dietary day and progressed up to the 8th or 9th day (Van Heynigen, 1959). Despite the discontinuation of D-xylose feeding, the lenses became completely transparent and opacities did not reoccur (Van Heynigen, 1967). Older rats did not develop cataracts when fed on diets containing 250 to 500 g D-xylose/kg (Lerman & Heggeness, 1961; Van Heynigen, 1969). Similarly, cataracts were not observed in adult rats fed on diets containing 50 to 150 g D-xylose/kg for a period of a year (Loos, 1954). There is only one report (Wise et al., 1954) available on the occurrence of cataracts in pigs. These authors produced cataracts in young piglets by feeding D-xylose at a level of 560 g/kg diet, but not when fed on a diet

containing approximately 200 g of this sugar/kg. Additionally, other detrimental effects (anorexia, vomiting and severe diarrhoea) were reported in young piglets by these investigators when fed these high dietary dose levels of D-xylose. These effects were not observed in our experiments when pigs were fed on diets containing at a maximum the lowest dietary level of D-xylose fed by Wise et al. (1954). The same holds true for L-arabinose at dietary levels upto 100 g/kg, being the maximum dietary inclusion involved in our experiments. No information is available about detrimental effects of this pentose sugar at higher dose levels.

Considering the data of Wagh & Waibel (1967b), other side effects from the feeding of D-xylose or L-arabinose also mainly may occur when fed at relatively high dose levels. These authors reported that in chicks, blood hematocrit, cholesterol, serine and proline in plasma increased significantly when feeding these pentose sugars at dietary levels of 200 and 400 g/kg. However, blood composition was not affected significantly when fed at a level of 100 g/kg diet. The latter results are in agreement with the results of our blood chemistry studies in pigs (Chapter 5; Schutte et al., unpublished results). A decreased liver weight of chicks fed on diets containing high levels of either pentose sugar (400 g/kg diet), and a tendency for this decrease at dietary levels of 200 g/kg, was reported by the same authors (Wagh & Waibel, 1966, 1967b). These observations together with our results in chicks (Chapters 1 and 3) indicate that below dietary levels of 200 g/kg neither D-xylose nor L-arabinose will affect liver weight.

When dietary sugars are not absorbed completely in the small intestine, there will be considerable water retention in the lumen (Cunningham et al., 1963; Kidder et al., 1968; Gray, 1983; De Groot, 1987). Consequently, diarrhoea may occur when feeding sugars with an incomplete absorption in excessive quantities (Darly & Day, 1939; Booth et al., 1953; Wise et al., 1954; Walker & Faichney, 1964; Bär, 1985; De Groot, 1987). The results of our experiments with D-xylose and L-arabinose showed an increased water intake, and a decreased dry matter content of ileal digesta and of faeces in pigs (Chapters 4 and 6). Similarly, in chicks water intake was increased and dry matter content of excreta was decreased when fed on diets containing either D-xylose or L-arabinose (Chapters 1 and 3). These disturbances in ileal digesta, faeces and excreta consistency are usually due to increased amounts of osmotically active compounds in the caudal parts of the gastrointestinal tract (Hof, 1980). The extra osmotic load may partly be the result of the unabsorbed sugars and partly of the acids produced as the end products of bacterial fermentation of the former (De Groot, 1987). Due to osmotically attracted water in the lumen, an increase in the size and weight of the caecum is a further result of increased amounts of osmotically active compounds in the intestinal tract (Leegwater et al., 1974; Walker, 1978; Bär, 1985). Caecal enlargement is considered to be an adaptive phenomenon rather than a toxic effect since no signs of tissue degeneration were observed

from an increased intestinal weight (WHO, 1974). In our chick studies, caecal enlargement was mainly observed when L-arabinose was fed. This could be expected because, unlike D-xylose, part of the ingested L-arabinose enters the hind gut for microbial fermentation.

Carbohydrates which stimulate fermentation in the hind gut usually have a negative effect on protein digestibility due to increased faecal loss of N. Generally, an increase in N excretion in the faeces due to increased fermentation is accompanied by a reduction in urine N excretion without effect on N balance (Partridge et al., 1982; Dierick et al., 1983; Malmlof & Hakansson, 1984; Morgan & Whittemore, 1988). Our studies on L-arabinose in pigs do not support these findings (Chapter 6). In addition to a depressed faecal N digestibility, N losses in urine were increased slightly in pigs fed on diets containing L-arabinose. Consequently, these pigs retained less N. This reduced N retention was observed in all L-arabinose treatments regardless the dose administered. In chicks both treatments with 25 and 75 g L-arabinose /kg diet caused a similar decrease in protein utilization (Chapter 3). A similar pattern of decrease in protein utilization was obtained when D-xylose was fed to chicks and pigs (Chapters 3 and 5). However, considering the data of our results with pigs (Chapter 5), this decrease in protein utilization from D-xylose seems to be exclusively the result of an increase in urinary N excretion. The fact that, in contrast to L-arabinose, faecal N excretion is not affected by D-xylose can be explained by the absence of a microbial degradation of xylose in the hind gut. Taking the results of both pentose sugars on protein utilization together, it can be concluded that feeding either D-xylose or L-arabinose to pigs and poultry results in an increased N excretion via the urine. The mechanism responsible for this phenomenon is not yet clear.

It has been reported that feeding D-xylose reduced voluntary feed intake in birds (Baker, 1977). This was confirmed in our studies with chicks showing that even at a low dietary level of 25 g/kg, feed intake was depressed (Chapters 1 and 3). This effect was not observed when birds were fed on diets containing L-arabinose (Chapters 1 and 3). Our observations are in agreement with those reported by Kare & Medway (1959). These authors reported an almost total rejection of water solutions containing D-xylose when offered to birds together with untreated water. In similar tests performed by these investigators, other sugars such as lactose, galactose, raffinose and arabinose had only minor effects on water consumption. After studying many variables including sweetness, viscosity, refractive index,concentration, osmotic pressure and density, Kare & Medway (1959) concluded that there was no distinct basis for the birds' selection other than an absolute specificity for the sugars involved. No reliable data are available on whether the pig discriminates between glucose, xylose and arabinose.

CONCLUSIONS

It appears that D-xylose and L-arabinose, in spite of their identical molecular size, have a different mode of transport in the small intestine of monogastric animals. The pentose sugar L-arabinose is absorbed at a lower rate than D-xylose, whereas absorption velocity of D-xylose is slightly lower than that of D-glucose. Both pentose sugars are partly excreted in the urine. The extent of this urinary excretion in percentage of intake increases as the dietary inclusion of either D-xylose or L-arabinose is increased. However, at equal dietary dose levels, more xylose than arabinose is excreted in the urine. There is no direct evidence available to state whether conversion to glucose is a fate of D-xylose and L-arabinose in monogastric animals. It appears that some D-xylose may be catabolized to carbon dioxide, but this pathway seems to be of no significance for L-arabinose. Therefore it is concluded that the energy value of both pentose sugars mainly depends on their degree of fermentation. Taking into account the losses in energy arising from this fermentation process, it was estimated that the energy value of the two pentose sugars is approximately 25 to 35% of that of D-glucose.

Feeding of D-xylose or L-arabinose to pigs and poultry causes a series of physiological changes. In some cases, these changes are similar to those observed in rats fed lactitol, lactose, xylitol and sorbitol, all of which are known to be poorly absorbed in the small intestine. Unlike well digestible sugars and starches, substantial amounts of these products are fermented microbially. Consequently, this will result in an increased production of volatile fatty acids and lactic acid, increased water retention in the intestinal contents and the faeces, and distention and increased weight of the caecum. Changes induced by D-xylose are less pronounced than those produced by L-arabinose. The latter can be explained by the difference in ileal digestibility between both pentose sugars; D-xylose is digested almost completely at the terminal ileum, while arabinose is also partly digested in the hind gut.

There are indications that both pentose sugars affect protein utilization. Both faeces N and urine N increase when L-arabinose is fed to pigs. However, in pigs fed on diets containing D-xylose only an increase in urine N was observed. When D-xylose is included in chick diets, voluntary feed intake is depressed. This phenomenon is not observed when L-arabinose is added to chick diets.

In conclusion it can be stated that not only the nutritional value of D-xylose and L-arabinose for pigs and poultry is low, but these sugars also may induce unwanted nutritive problems together with wet droppings in chicks. Considering these aspects, the benefits of a dietary application of NSP degrading enzymes which will release mainly these sugars (e.g. hemicellulose) are very doubtful. In this statement a possible improvement of the digestibility of dietary N and fat as a result from an enzymatical degradation of such NSP is not taken into account.

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SUMMARY

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Plant carbohydrates are the major energy component of pigs and poultry diets. These carbohydrates contain two broad classes of polysaccharides, starch and the polysaccharides of the plant cell wall which are conveniently referred to as nonstarch polysaccharides (NSP). Starch, a storage carbohydrate in plants such as cereal grains, is an α-linked glucan susceptible to hydrolysis by pancreatic α-amylase. Thus, it can be digested in the small intestine of monogastric animals, and absorbed as glucose. Nonstarch polysaccharides, which comprise the remainder of the dietary plant polysaccharides, are all resistant to α-amylase. They are principally cell wall structures and include a mixture of substances such as cellulose, hemicellulose, pectin and oligosaccharides which contain hexose and pentose sugars and uronic acids. In some feed ingredients including cereal by-products, soyabeans, sunflower seed, groundnuts, rapeseed and lupins, the carbohydrate fraction exists mainly as NSP. In spite of the absence of indigenous NSP degrading enzymes in the small intestine of pigs and poultry, some NSP is utilized by these animal species via microbial degradation in the hind gut. Volatile fatty acids and lactic acid formed as a result of the microbial degradation can be absorbed and utilized as a source of energy. However, in microbial conversion and the subsequent utilization of these organic acids approximately 30 to 50% of the energy is lost.

There is conclusive evidence that the digestibility of NSP can be improved by treatment with enzymes which hydrolyse the NSP to monosaccharides. The benefits of a hydrolysis of NSP, however, are not determined solely by an improvement in digestibility, but also by the potential of the animal to utilize the products of hydrolysis. In addition to glucose, other sugars will also be released by complete hydrolysis of NSP in normal practical feed compositions. In quantitative terms the pentose sugars D-xylose and L-arabinose are the most important ones. A review of the relevant literature (General Introduction) revealed that knowledge about the nutritional value of these sugars in pigs and poultry is incomplete. Most of the literature data are concerned with the rate of absorption of both pentose sugars from the intestinal tract in small laboratory animals and man. It appears that both pentose sugars can be absorbed from the intestinal tract of monogastric animals, but at a lower rate than glucose. Moreover, absorption velocity of L-arabinose appears to be lower than that of D-xylose. The literature review also indicated that both pentose sugars are partly excreted in the urine.

The present studies were designed to obtain quantitative data on the digestion and utilization of D-xylose and L-arabinose in poultry and pigs. In addition, some physiological effects of the pentose sugars in both animal species were examined. Six studies were performed, three with poultry (Chapters 1, 2 and 3) and three with pigs (Chapters 4, 5 and 6).

In Chapter 1 the effects of graded levels from 25 to 150 g/kg of dietary D-xylose and L-arabinose on chick performance and the metabolizable energy (ME) value of both pentose sugars were studied. Weight gain and feed conversion efficiency were decreased linearly when the dietary level of either D-xylose or L-arabinose was increased. The same was true for daily feed intake on the D-xylose treatments. Water intake was linearly increased as the dietary level of both pentose sugars increased, and as a result dry matter content of the droppings decreased. Caecal length and weight were markedly increased by feeding L-arabinose and intermediately by feeding D-xylose. The concentration of glucose in the blood was not affected by feeding either D-xylose or L-arabinose. The ME value of both pentose sugars was considerably lower than that of glucose and negatively related with dose.

In Chapter 2, results are reported of a study with ileostomized adult roosters in which the ileal digestibility and urinary excretion of both pentose sugars at dietary inclusions ranging from 25 to 100 g/kg, were determined. Ileal digestibility of D-xylose was found to be close to 100%. Ileal digestibility of L-arabinose was dose related and varied between 95 (at 25 g/kg diet) and 75% (at 100 g/kg diet). Both pentose sugars were partly excreted in the urine. The extent of urinary excretion in percentage of intake increased linearly as the dietary level increased. When fed 25 g D-xylose per kg diet, about 7% of the ingested xylose appeared in the urine. This level increased to 20% when roosters were fed a diet containing 100 g D-xylose/kg. Corresponding values for L-arabinose in urine at these dietary inclusion levels were approximately 9 and 17%.

In Chapter 3 the results of a study are described in which the utilization of both pentose sugars at dietary inclusion of 25, 50 and 75 g/kg in chicks was examined. Although the experimental diets were balanced for metabolizable energy content, the performance of birds fed the pentose sugars was inferior to those fed the reference diet. Based on carcass analysis it was concluded that both pentose sugars can provide only some energy to chicks. Protein utilization tended to decrease when either D-xylose or L-arabinose was included in the diets.

In Chapter 4 ileal digestibility and urinary excretion of D-xylose and the associated effects of this pentose sugar on ileal and faecal digestibility of DM, OM, GE and N were investigated in pigs. Ileal digestibility of D-xylose was found to be close to 100%. The presence of D-xylose in the diet increased the ileal flow of volatile fatty acids, suggesting the occurrence of microbial degradation of D-xylose in the small intestine. In pigs fed on diets containing 100 and 200 g D-xylose /kg, 44.5 and 52.6%, respectively, of the D-xylose intake appeared in the urine. Ileal and faecal digestibility of DM, OM, GE and N as well as N retention, were not affected in pigs fed on the 100 g D-

xylose/kg diet. At a higher inclusion level of 200 g D-xylose/kg diet, digestibility of all these parameters and retention of N was decreased significantly.

In Chapter 5, urinary excretion of xylose in relation to age, frequency of feeding and dietary inclusion of D-xylose were examined in pigs. Urinary excretion of xylose was not affected significantly by age and frequency of feeding, but certainly by dose level. In pigs fed on a diet containing 25 g D-xylose/kg, about 20% of the D-xylose consumed appeared in the urine. This level increased to about 43% when pigs were fed on a diet containing 100 g D-xylose/kg. Retention of N was slightly decreased when pigs were fed 100 g D-xylose/kg diet. Liver and kidney weight, pH of urine and blood composition were not significantly affected by the inclusion of D-xylose in the diets.

In Chapter 6 the results of a study are reported in which the ileal digestibility and urinary excretion of L-arabinose were investigated. Ileal digestibility of L-arabinose was approximately 70%. Administration of L-arabinose to pigs was associated with an increase in ileal flow of volatile fatty acids, suggesting the occurrence of microbial degradation of this pentose sugar in the small intestine. In pigs fed on a diet containing 25 g L-arabinose/kg, about 11% of the arabinose consumed appeared in the urine. This level increased to about 15% when pigs were fed on a diet containing 100 g L-arabinose/kg. Faecal digestibility and retention of N decreased significantly in pigs fed on the L-arabinose diets.

In the General Discussion, the results of these experiments were combined with data of literature on the fate of both pentose sugars in poultry and pigs. There is no direct evidence available to state whether conversion to glucose is a fate of D-xylose and L-arabinose in monogastric animals. It appears that some D-xylose may be catabolized to carbon dioxide, but this pathway seems to be of no importance for L-arabinose. Therefore, it is concluded that the energy value of both pentose sugars depends mainly on their degree of fermentation. Their energy value was estimated to be 25 to 35% of that of D-glucose. In addition to the low energy value, both pentose sugars may induce unwanted nutritive problems together with wet droppings in chicks. Therefore, the benefits of a dietary application of NSP degrading enzymes which will release mainly these sugars (e.g. hemicellulose) are considered to be very doubtful. In this statement a possible improvement of the digestibility of dietary N and fat as a result from an enzymatical degradation of such NSP is not taken into account.

SAMENVATTING

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Varkens en pluimvee zijn voor hun energie voorziening grotendeels aangewezen op de koolhydraten uit plantaardige grondstoffen. De koolhydraten kunnen globaal in twee groepen worden ingedeeld; zetmeel en de niet zetmeel-koolhydraten. De laatste groep wordt gemakshalve afgekort tot NSP. Deze afkorting is afgeleid van de engelse benaming voor de niet zetmeel-koolhydraten (nonstarch polysaccharides). Voorzover de koolhydraat fraktie uit zetmeel bestaat (b.v. in granen) levert de vertering bij varkens en pluimvee veelal geen bijzondere problemen op. Beide diersoorten beschikken nl. over een enzymsysteem dat het zetmeel kan afbreken tot glucose; een suiker die zeer goed wordt benut door varkens en pluimvee. De niet-zetmeel koolhydraten (NSP) zijn gecompliceerde verbindingen, zowel uit het oogpunt van hun fysische structuur als hun chemische samenstelling. Tot de NSP worden gerekend de koolhydraat komponenten cellulose, hemicellulose, pectine en oligosacchariden. In sommige veevoedergrondstoffen zoals sojaschroot, zonnebloemzaadschroot, raapzaad en graan bijprodukten bestaat de koolhydraatfraktie vrijwel geheel uit NSP. Varkens en pluimvee beschikken niet over enzymen die de NSP frakties kunnen afbreken. Als gevolg hiervan komen deze frakties vrijwel onverteerd in de blinde en dikke darm terecht, waar ze microbieel afgebroken kunnen worden. De eindprodukten van dit fermentatie proces (vluchtige vetzuren en melkzuur) worden door het dier geresorbeerd in het bloed en vervolgens benut als energie bron. In vergelijking met een enzymatische vertering treden bij een microbiële fermentatie van voeder-componenten echter aanzienlijke verliezen aan energie op. De schattingen omtrent de hoogte van deze verliezen lopen uiteen van 30 tot 50%.

Verbetering van de vertering van NSP is in principe mogelijk door het opnemen van enzymen in de voeders die de NSP frakties kunnen afbreken. Dit wordt bevestigd door literatuur gegevens en eigen onderzoekingen. Betreffende de kennis van de toepassingsmogelijkheden van enzymen, vooral gericht op de Nederlandse situatie, zijn er nog vele leemten. Deze leemten in kennis doen zich met name voor op het gebied van de benutting van de produkten die vrijkomen bij een enzymatische afbraak van NSP. Bij een volledige hydrolyse van NSP worden naast glucose nl. tevens monosacchariden vrijgemaakt die normaliter niet vóórkomen in de dunne darm bij varkens en pluimvee. De belangrijkste in dit opzicht zijn de pentose suikers D-xylose en L-arabinose. De literatuur (Algemene Inleiding) betreffende het metabolisme en de benutting van deze pentose suikers door varkens en pluimvee is beperkt en verwijst meestal naar inzichten geba-

seerd op humaan-medisch onderzoek. Volgens de literatuur kunnen beide suikers geresorbeerd worden uit de dunne darm, maar met een lagere efficiëntie dan glucose. Daarnaast blijkt D-xylose slechter te worden geresorbeerd dan L-arabinose. Uit het literatuur onderzoek kwam eveneens naar voren dat beide pentose suikers voor een deel weer worden uitgescheiden via de urine.

Het doel van de in dit proefschrift beschreven experimenten was tweeledig. Enerzijds was het gericht op het verkrijgen van inzicht in de vertering en benutting van de betreffende pentose suikers bij varkens en pluimvee. Anderzijds werd onderzocht in hoeverre bij het opnemen van beide suikers in het rantsoen, fysiologische veranderingen bij deze twee diersoorten optraden. Beide pentose suikers werden onderzocht in doseringen variërend tussen de 25 en 150 g/kg rantsoen. Als referentie suiker werd steeds D-glucose meegenomen. In totaal werden zes studies uitgevoerd waarvan drie met pluimvee (Hoofdstukken 1, 2 en 3) en drie met varkens (Hoofdstukken 4, 5 en 6). Voor het meten van de ileale verteerbaarheid werd gebruik gemaakt van varkens en volwassen hanen die waren voorzien van een darm canule aangebracht aan het eind van het ileum.

In hoofdstuk 1 worden de resultaten van een onderzoek behandeld, waarin het effect van oplopende doseringen (25 - 150 g/kg) aan D-xylose en L-arabinose in het rantsoen op een aantal parameters bij kuikens werd bestudeerd. Het opnemen van D-xylose of L-arabinose in de voeders resulteerde in een verslechtering van de groei en voederconversie en een verhoging van de waterconsumptie. Dit laatste leidde tot een daling van het droge stof gehalte in de excreta. Door D-xylose werd verder de voeropname negatief beinvloed. De mate van voornoemde negatieve effecten nam toe bij het oplopen van de dosering aan de pentose suikers in het rantsoen. De omzetbare energie (OE) waarde van beide pentose suikers was niet alleen aanzienlijk lager dan van D-glucose doch tevens negatief gecorreleerd met de dosering. Het glucose gehalte in het bloed werd niet beinvloed door de aanwezigheid van D-xylose of L-arabinose in het rantsoen. Er werden geen aanwijzigingen verkregen dat onder invloed van de pentose suikers bepaalde veranderingen in de organen optraden. Dit laatste met uitzondering van de blinde darm gewichten, welke met name bij het verstrekken van rantsoenen met L-arabinose sterk toenamen.

In een volgend onderzoek (Hoofdstuk 2) werd de ileale verteerbaarheid en de renale uitscheiding aan D-xylose en L-arabinose bij volwassen hanen bepaald. Aan het einde van de dunne darm werd vrijwel geen xylose meer aangetroffen, hetgeen inhoudt dat deze pentose suiker vrijwel volledig ileaal was verteerd. De ileale verteerbaarheid van L-arabinose was dosis afhankelijk. Opgenomen in een dosering van 25 g/kg rantsoen bleek L-

arabinose voor ongeveer 95% ileaal te zijn verteerd. Dit percentage liep terug tot ongeveer 75% bij een dosering van 100 g/kg rantsoen. Een belangrijk deel van de oraal verstrekte pentose suikers werd via de urine weer uitgescheiden. De mate van deze uitscheiding was sterk positief gecorreleerd met de dosering. D-xylose werd bij doseringen van 25 en 100 g/kg rantsoen voor respektievelijk 7 en 20% uitgescheiden via de urine. De corresponderende waarden voor L-arabinose bij deze doseringen waren 9 en 17%.

In het laatste onderzoek met pluimvee (Hoofdstuk 3) lag het accent op het bestuderen van de benutting van de twee pentose suikers door kuikens bij doseringen van 25, 50 en 75 g/kg rantsoen. De voeders werden op isocalorische (OE) basis verstrekt aan de dieren. Desondanks werden slechtere groei en voederconversie resultaten gemeten op de rantsoenen met D-xylose of L-arabinose. Gebaseerd op karkas analyses werden aanwijzingen verkregen dat de energie van beide pentose suikers slechts in beperkte mate kan worden benut door kuikens. Daarnaast bleken beide pentose suikers de eiwit retentie negatief te beinvloeden.

In hoofdstuk 4 worden studies beschreven welke in hoofdzaak waren gericht op het bestuderen van de ileale verteerbaarheid en de renale excretie van D-xylose bij varkens. D-xylose bleek vrijwel volledig ileaal te worden verteerd. De aanwezigheid van D-xylose in het rantsoen ging gepaard met een sterke verhoging van de passage aan vluchtige vetzuren aan het eind van de dunne darm. Dit verschijnsel werd in verband gebracht met een gedeeltelijke fermentatie van D-xylose in de dunne darm. Opgenomen in doseringen van 100 en 200 g/kg rantsoen, werd respektievelijk 44,5 en 52,6% van de opgenomen hoeveelheid D-xylose uitgescheiden via de urine. Ileale en faecale verteerbaarheid van de droge stof, organische stof, bruto energie en eiwit alsmede de eiwit-retentie werden niet duidelijk beinvloed door D-xylose bij een dosering van 100 g/kg rantsoen. Opgenomen in een hogere dosering van 200 g/kg rantsoen, werden de verteringscoefficiënten van voornoemde parameters en de eiwit-retentie sterk negatief beinvloed.

In het volgende onderzoek met varkens (Hoofdstuk 5) werd de invloed van enkele faktoren die mogelijk de renale uitscheiding aan xylose kunnen beinvloeden, onderzocht. De mate van de uitscheiding aan xylose via de urine was sterk positief gecorreleerd met de dosering. Opgenomen in een dosering van 25 g/kg rantsoen werd 20% van de opgenomen hoeveelheid D-xylose uitgescheiden in de urine. Dit percentage liep op tot 43% als varkens een rantsoen kregen verstrekt met 100 g D-xylose/kg. De leeftijd van de dieren en de frequentie van de voederverstrekking hadden geen duidelijke invloed op de renale uitscheiding aan xylose. Lever- en niergewichten, pH van de urine en de samensteling van het bloed werden niet significant

beinvloed door D-xylose.

In hoofdstuk 6 tenslotte zijn de resultaten van een onderzoek met L-arabinose bij varkens beschreven. Op ileaal niveau bleek L-arabinose voor ongeveer 70% te worden verteerd. Verstrekking van rantsoenen met L-arabinose ging gepaard met een verhoging van de passage aan vluchtige vetzuren aan het eind van de dunne darm. Dit verschijnsel werd in verband gebracht met een gedeeltelijke fermentatie van L-arabinose in de dunne darm. De renale uitscheiding aan L-arabinose was positief gecorreleerd met de dosering. Bij een dosering van 25 g/kg rantsoen werd van de opgenomen hoeveelheid L-arabinose ongeveer 11% via de urine uitgescheiden. Bij een dosering van 100 g/kg rantsoen bedroeg dit 15%. Faecale verteerbaarheid van het eiwit en de eiwit-retentie werden door L-arabinose negatief beinvloed.

De resultaten van de hier beschreven proeven werden tesamen met gegevens uit de literatuur nader geëvalueerd (Algemene Discussie). De literatuur levert geen direkt bewijs dat D-xylose en L-arabinose gemetaboliseerd kunnen worden tot glucose. Een andere mogelijke route van beide suikers, omzetting tot CO2, lijkt alleen in beperkte mate van toepassing te zijn op D-xylose. Op basis van deze twee uitgangsstellingen werd geconcludeerd dat de energiewaarde van beide pentose suikers voor pluimvee en varkens in hoofdzaak wordt bepaald door de mate van hun fermentatie in het maag-darmkanaal. Een globale berekening leerde dat de energiewaarde van beide pentose suikers hooguit gesteld kan worden op 25 à 35% van die van D-glucose. Dit betekent dat beide pentose suikers slechts in geringe mate een bijdrage kunnen leveren aan de energievoorziening bij varkens en pluimvee. Gezien dit laatste en mede gelet op het feit dat beide pentose suikers aanleiding kunnen geven tot het optreden van ongewenste neveneffekten, lijkt een volledige enzymatische afbraak van NSP frakties, waarbij in hoofdzaak xylose en arabinose vrijkomen (b.v. hemicellulose), voor monogastrische landbouw-huisdieren geen bijzondere voordelen op te leveren. Hierbij is geen rekening gehouden met een eventueel positief effekt van een enzymatische afbraak van deze NSP frakties op de verteerbaarheid van eiwit en vet.

CURRICULUM VITAE

Johannes Bernardus Schutte werd geboren op 21 mei 1936 ter gemeente Odoorn. Achtereenvolgens behaalde hij het diploma van de lagere en middelbare landbouwschool, de MULO en de praktijkschool voor de pluimveeteelt. In 1976 slaagde hij cum laude voor het diploma Register Ingenieur. In 1988 werd aan hem vrijstelling verleend voor het doctoraal examen aan de Landbouwuniversiteit Wageningen. Van 1958 tot 1984 was hij verbonden aan het ILOB (Instituut voor Landbouwkundig Onderzoek van Biochemische produkten). Sinds 1 mei 1984 is het ILOB opgenomen in de TNO organisatie onder de naam TNO Instituut voor Diervoeding en Fysiologie. Zijn huidige funktie is wetenschappelijk medewerker en hoofd van de sectie voedingsonderzoek pluimvee en varkens.