Chapter 8
Carbohydrate digestion and absorption

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This chapter will provide a:

- Defintion and classification of the diffrent groups of carbohydrates
- Proximate analysis of carbohydrates
- Description of how the different classes of carbohydrates are digested and absorbed
- Quantification of carbohydrates digestion in the small intestine and fermentation in the large intestine
- Description of the factors that influence the quantitative absorption of carbohydrates
- Description and a quantification of the absorption of carbohydrates in diets used for growing pigs and sows.

1. Introduction

Carbohydrates are naturally occurring compounds that consist of carbon, hydrogen and oxygen in the ratio C_n:H_{2n}:O_n. Carbohydrates are the single most abundant feed energy in diets for piglets, growing pigs and sows comprising 60-70% of the total energy intake. The carbohydrate fraction represents a diverse group of compounds; from simple monosaccharides and disaccharides to complex organised compounds that make up the cell walls. The linkages between the carbohydrate components and the way the different carbohydrate molecules are interrelated have a great impact on where the carbohydrates are digested and how they influence the physiology of the gastrointestinal tract. Almost all the α-linked carbohydrates are degraded to monosaccharides (glucose, fructose or galactose) by endogenous enzymes that are either secreted into the intestinal lumen or located on the epithelial brush border. Others, those with β-linkages, have to be degraded by microbial enzymes and are further processed through different metabolic pathways to short-chain fatty acids (SCFA, primarily acetate, propionate and butyrate) and gases. These processes, which all occur in the lumen or on the interface between the lumen and the gut epithelium, break down the carbohydrates to small organic molecules of sizes less than 180 Dalton. All the degradation products are water-soluble and can pass the intestine either through active absorption or facilitated diffusion. A part of the carbohydrates that makes up the fibre fraction will not be degraded, but will have an impact on the physiology of the gut due to its physical presence in the gut lumen.

The main purpose of the present chapter is to provide the reader with knowledge about the composition of carbohydrates in feeds and how the different carbohydrate components are degraded and absorbed in the different segments of the gastrointestinal tract.

2. An historic view on carbohydrates in nutrition

The digestibility of nutrients in feed is to a great extent determined by the chemical composition of the feed. The first determining factor is the concentration of digestible and non-digestible components, but the presence of some organic structures may also limit the digestibility of the components with which they are associated. Calculation of the amount of available energy in a feed requires a system of analyses that estimates the digestibility. The conventional system, now in use for more than 150 years, is the so-called proximate system of analysis according to Weende [25]. It consists of the following analyses: Dry matter, ash, crude fat, crude protein (Nx6.25) and crude fibre. The latter is determined as the ash-corrected insoluble residue after reflux of the fat-extracted residue with 1.25% sulphuric acid and 1.25% sodium hydroxide, which degrade most of the carbohydrates. A residual fraction containing most of the carbohydrates is called a nitrogen-free extract (NFE). NFE is calculated as the amount of dry matter not accounted for by the sum of ash, protein (Nx6.25), fat and crude fibre (Figure 8.1).

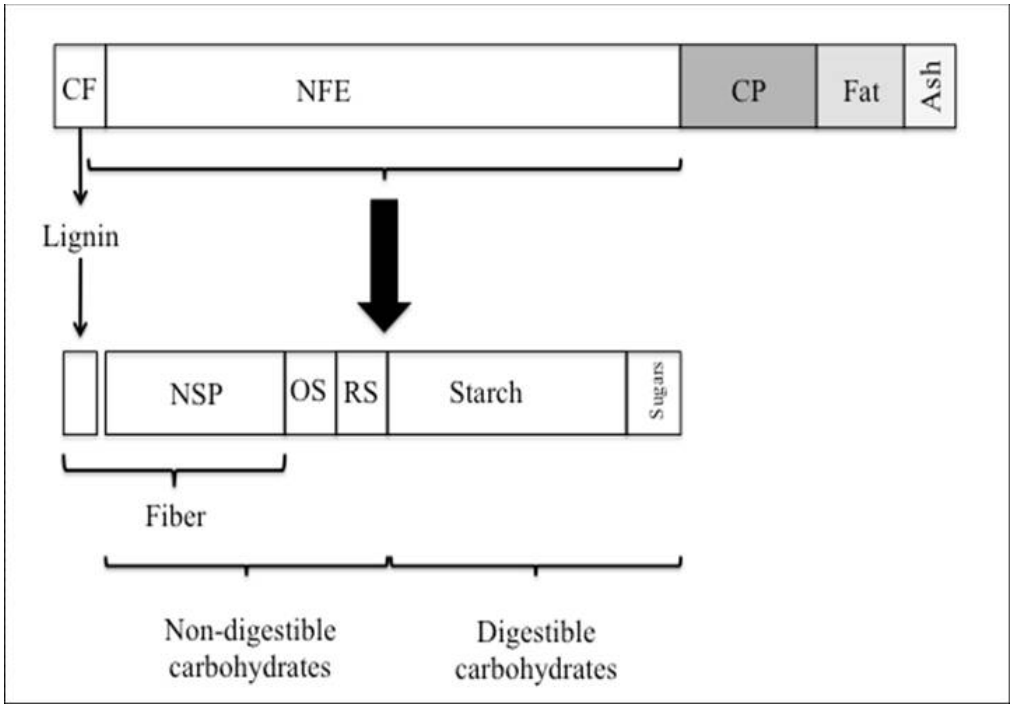


Figure 8.1. Carbohydrates and lignin making up the crude fibre (CF) and nitrogen-free extract (NFE) of the proximate (Weende) analysis and the division of carbohydrates in digestible and non-digestible carbohydrates.

The system of Weende gives a crude separation of the macronutrients, and particularly the carbohydrates are not very well defined in this system. The crude fibre will account for most of the cellulose and a variable proportion of the non-carbohydrate lignin. The NFE fraction, on the other hand, contains a very heterogeneous mix of the remaining carbohydrate structures. In some feeds, i.e. concentrated cereal feeds, the major part of the NFE fraction consists of sugars and starch, while the NFE fraction mainly contains complex fibrous polysaccharides in high-fibre feedstuffs such as sugar beet and potato pulps.

3. Carbohydrate terminology and classification

Carbohydrates are very diverse molecules that chemically can be classified according to their molecular size (degree of polymerization, DP) as sugars (DP, 1-2), oligosaccharides (DP, 3-9) and polysaccharides (DP, ≥10) with the latter consisting of starches and non-starch polysaccharides (NSP) and glycosidic bonds [16],[19]. Based on the chemical classification, it is possible to group the carbohydrates nutritionally: digestible carbohydrates represent the carbohydrates that can be digested by the host's enzymes and absorbed in the small intestine (monosaccharides, disaccharides and most starches) while non-digestible carbohydrates (NDC) are the carbohydrates that cannot be degraded by the host's endogenous enzymes, but potentially can be degraded by microbial fermentation. This group of carbohydrates comprises most oligosaccharides, enzyme-resistant starch (RS) and NSP.

It is the glycosidic bond that determines whether a carbohydrate is digestible or non-digestible. A glycosidic bond joins two carbohydrate monomers to form a disaccharide as, for instance, the linkage of glucose and fructose to create sucrose. More complex polysaccharides, such as starch and cellulose, consist of numerous monosaccharide units joined by glycosidic bonds. The way (α or β) the monomeric units are linked together has a great influence on the fate of the carbohydrates in the gut. Amylose and cellulose are both glucose polymers. In the case of amylose, the linkages are α(1-4) whereas in the case of cellulose, they are β(1-4). This seemingly small difference has a great impact on the nutritional properties of the polysaccharides. While the endogenous enzymes secreted to the lumen of the small intestine can degrade the α-linkages in amylose, there are no endogenous enzymes that are able to cleave the β-linked cellulose. Cellulose, however, can to a variable degree be degraded by the microflora colonising the gastrointestinal tract, especially in the large intestine.

There is a huge diversity in chemical bondings, and along with that carbohydrate-rich feeds vary substantially in structure, appearance and fate during digestion. Table 8.1. provides an overview of the digestion fates and end-products formed during the digestion processes.

Table 8.1. Classes of feed carbohydrates and their likely fates in the intestinal tract of pigs.

Class	DP	Example	Endogenous enzymes	Absorbed molecules
Monosaccharides	1	Glucose		Glucose
	1	Fructose		Fructose
Disaccharides	2	Sucrose	+	Glucose + fructose
	2	Lactose	+	Glucose + galactose
Oligosaccharides	3	Raffinose	-	SCFA
	4	Stachyose	-	SCFA
	3-9	Fructooligosaccharides	-	SCFA
Polysaccharides	≥ 10	Starches	+	Glucose
	≥ 10	Non-starch polysaccharides	-	SCFA

DP: Degree of polymerization. SCFA: Short-chain fatty acids.

3.1. Sugars

Sugars (DP 1-2) are water-soluble components composed of monosaccharides and disaccharides (Figure 8.2). Sucrose, a disaccharide composed of glucose and fructose, is the most abundant sugar in plant products [1]. Lactose, consisting of glucose and galactose, is the main carbohydrate component in milk, while maltose, made up of two glucose units, is found in sprouted cereals, but not in non-germinated cereals. In most feedstuffs, however, monosaccharides are present in low concentrations.

3.2. Oligosaccharides

Oligosaccharides (DP 3-9) are water-soluble compounds composed of 3-9 monomers linked together by either α or β bonds. The most commonly present oligosaccharides in feedstuffs are raffinoseoligosaccharides and fructooligosaccharides. Raffinoseoligosaccharides are a homologous series consisting of 1-4 galactose β-linked units linked to sucrose. They are present in a wide variety of plant materials. Fructooligosaccharides are a homologous series that consist of 1-7 fructose β-linked with a terminal sucrose unit primarily found in roots of chicory and tubers of Jerusalem artichoke. Other types of oligosaccharides, such as xylooligosaccharides and transgalactooligosaccharides, are occasionally used as ingredients in diets for piglets.

3.3. Starch

Native starch is a water-insoluble semi-crystalline material located as granules in many plant tissues (Figures 8.2 and 8.3) [22]. Pure starch predominantly consists of α-glucan (approximately 99 % of dry matter) in the form of amylose and amylopectin. Amylose is roughly a linear α(1-4)-linked molecule (~99%) with a molecular weight of ~$1x10^5$-$1x10^6$ Da. Amylopectin is a much larger molecule (molecular weight ~$1x10^7$-$1x10^9$ Da) that is heavily branched due to the presence of ~5% of the total linkages as α(1-6)-. The two α-glucans are present in various proportions in the starch granules. The starches are defined as ‘waxy’ when the amylose-to-amylopectin ratio is low (~<15%), normal when amylose represents ~16-35% of the starch and ‘high-amylose’ (or ‘amylo-‘) when the proportion of amylose exceeds ~36% [33]. Based on the kind of X-ray diffraction pattern given by their amylopectin crystalline lattices, the starch can be divided into types A, B, and C starch [10]:

- A starch is present in cereals and has in general an open structure;
- B starch is more compact and is found in tubers such as e.g. potato;
- C starch is a combination of A and B starch and is present in legumes.

The crystallization pattern is related to the chain length of the amylopectin fragments.

In grains and legumes, the starch is always present in association with proteins, many of which are relatively hydrophobic, and the protein-starch network is surrounded by cell walls (Figure 8.3). Therefore, the starch tends to be maintained in the interior of the ingested particles protected from water. Starch from tubers and legumes is particularly well protected from the polar environment of luminal fluids, but even in cereals the starch may not be accessible for α-amylase degradation unless it has been physically processed – milled, cracked, etc.

In resistant starch (RS), the molecular linkages are the same as for digestible starch, but RS is unavailable for enzymatic degradation in the small intestine for various reasons. RS is divided into four different categories [18]:

- RS_1 is a physically enclosed starch within intact cell wall structures as for example when coarsely ground materials are fed.
- RS_2 is raw starch granules, and the digestibility of type A starch is higher than that of type C and particularly type B starch.
- RS_3 is retrograded amylase, which is formed by re-crystallization during cooling of gelatinised starch.
- RS_4 is a chemically modified starch, which is normally not used in pig feed.

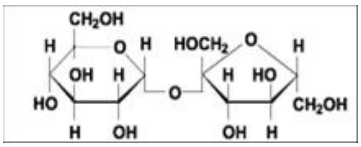
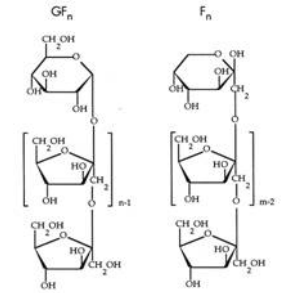
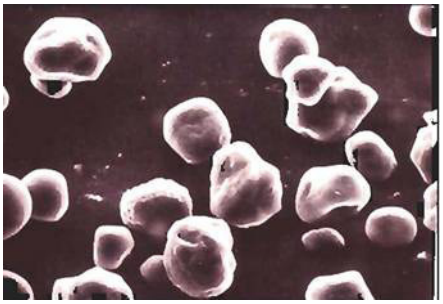
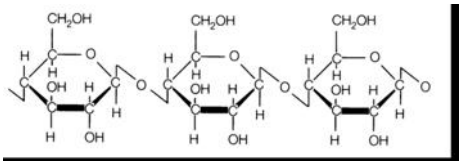
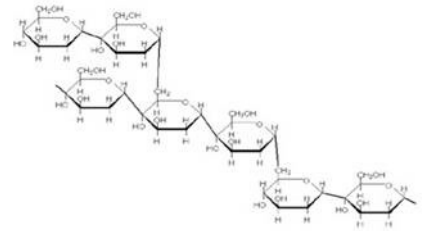
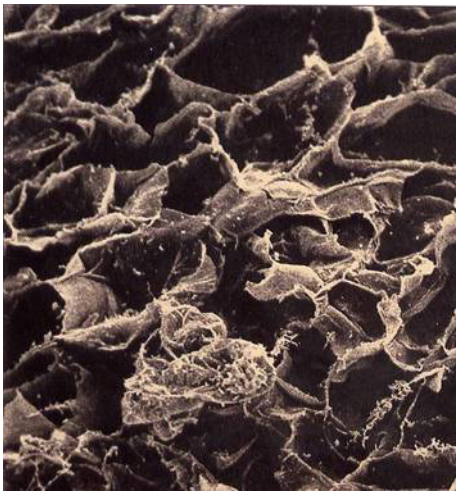
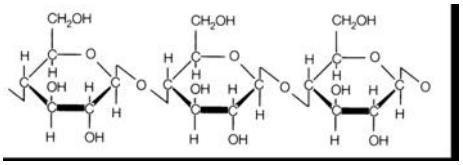
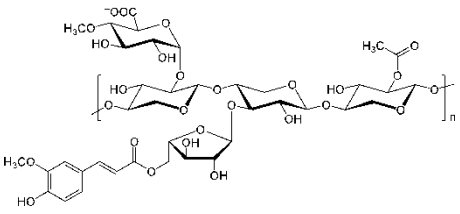
Physical structure	Chemical components
	 Sucrose
	 Fructooligosaccharides
	 Amylose  Amylopectin
	 Cellulose  Xylans

Figure 8.2. An example of the physical form and the structural organisation of the components making up the carbohydrate fraction.

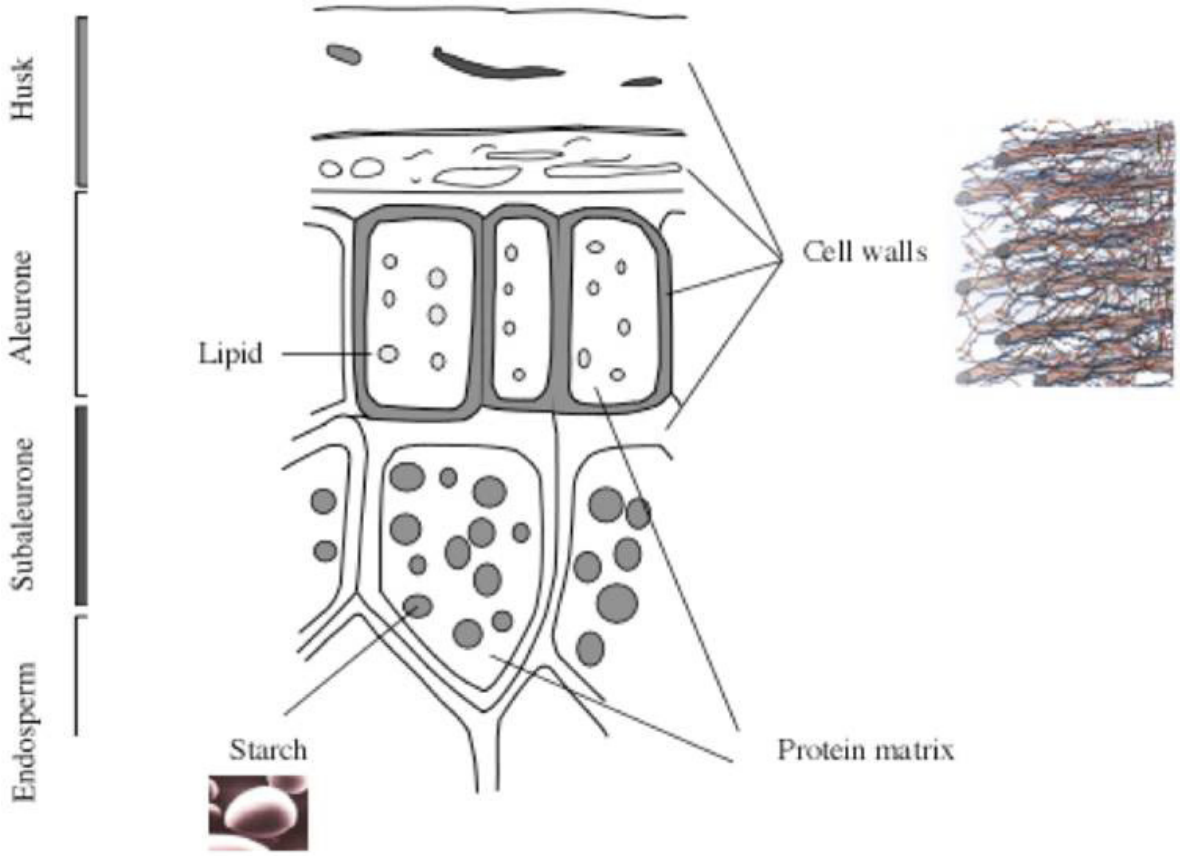


Figure 8.3. A cross-sectional cut of the husk, aleurone, subleurone and endosperm of oats and an example of the three-dimensional network of of polysaccharides building up the cell walls and the starch granule embedded in the protein matrix of the endosperm. Each tissue layer will have a different polysaccharide composition.

3.4. Non-starch polysaccharides

NSPs consist of a range of soluble and insoluble polysaccharides predominantly present in primary and secondary plant cell walls [15], [30], [34]. It is by far the most complex part of the carbohydrate fraction because of a large number of different building blocks and a great diversity in linkages to different hydroxyl groups and orientations. The building blocks of NSP are the pentoses arabinose and xylose, the hexoses glucose, the galactose and mannose, the 6-deoxyhexoses rhamnose and fucose and the uronic acids glucuronic and galacturonic acids (or their 4-O-methyl ethers). Therefore, when compared to sugars, oligosaccharides and starch, there are more different building blocks (10 common monosaccharides) that can exist in two ring forms (pyranose and furanose), and these residues can be linked through glycosidic bonds at any one of their 3, 4 or 5 hydroxyl groups available and in 2 (α or β) orientations (Figure 8.2). As a result, NSP can adopt a huge number of three-dimensional shapes and thereby offer a vast range of functional surfaces. NSP make up the major part of the cell walls where they typically represent 90-95% [34].

3.5. Lignin

Chemical lignin is not a carbohydrate, but will be mentioned anyway as it is closely associated with the NSP in the cell walls in plant material, and many of the older and still commonly used analytical methods for fibre determination include lignin (see section 3.6). Lignification of the cell walls has a huge impact on the physicochemical properties and digestibility of NSP. Lignin is formed by the polymerisation of coniferyl, ρ-coumaryl and sinapyl alcohols [17]. Lignin may be covalently linked to polysaccharides both directly through sugar residues and indirectly via ferulic acid esterified to polysaccharides. Lignin stabilises the polymers and will consequently cement and anchor the cellulose microfibrils and other matrix polysaccharides. In this way, it stiffens the cell walls making them very rigid and difficult to degrade by the microorganisms in the large intestine [34]. The outer

husk layer of the different botanical layers presented in Figure 8.3 is highly lignified, whereas the endosperm, the subaleurone and the aleurone layers are not. In these layers, however, the polysaccharides may be cross-linked to phenolic acids.

3.6. Fibre

Fibre has a long story within nutrition as the organic structure that limited the digestibility of nutrients. Fibre is not a well-defined chemical entity, but a term that has been defined by the methods applied for its analysis both in human and animal nutrition. The fibre methods used for the analysis of fibre in feedstuff are e.g. the crude fibre method, the detergent methods developed by Van Soest and co-workers, the enzymatic or non-enzymatic gravimetric AOAC (Association of Official Analytical Chemists) procedures and the enzymatic-chemical Englyst and Uppsala procedures. It is beyond the scope of this chapter to make an in-depth presentation of the different fibre analytical methods, but it is important to know that the analytical values and components analysed in different feedstuffs will vary depending on the method applied (Figure 8.4).

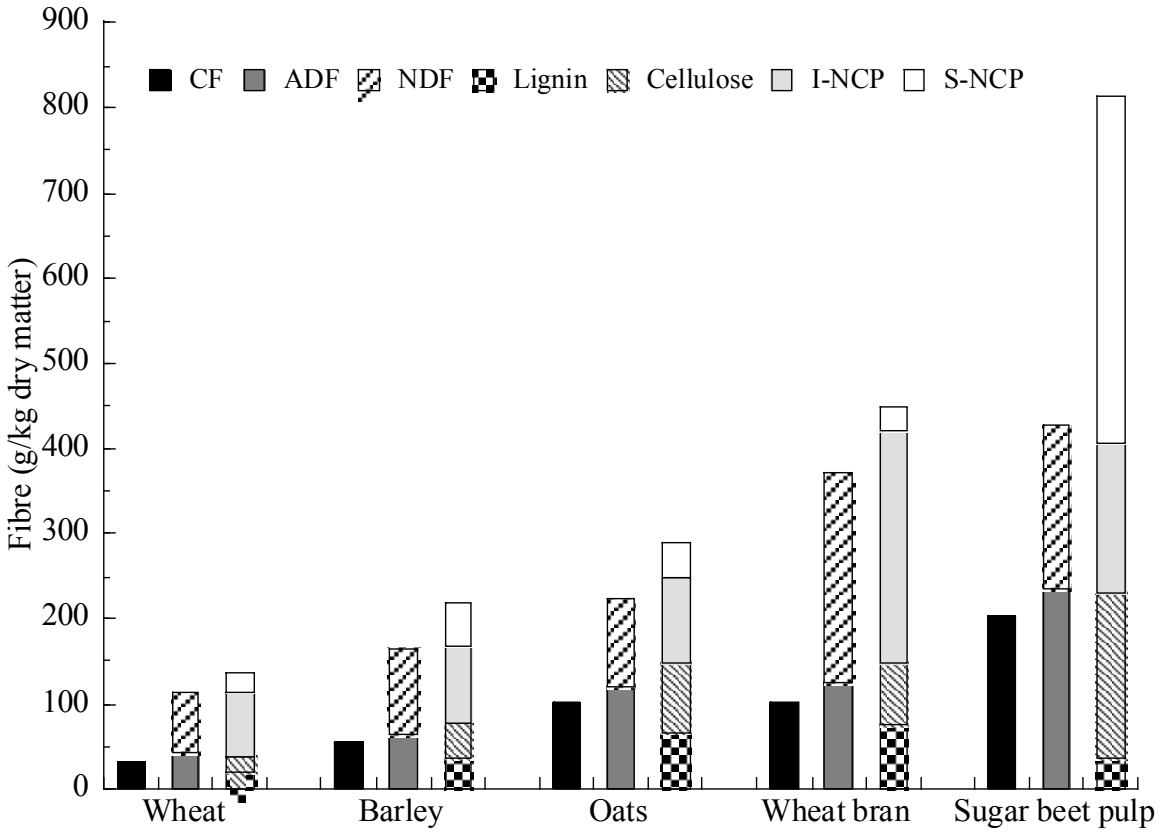


Figure 8.4. Analytical fibre values in different feedstuffs measured by the crude fibre (CF) method, the acid detergent fibre method (ADF) and the neutral detergent fibre (NDF) methods of Van Soest and the enzymatic-chemical Uppsala and Englyst methods (lignin (Klason)), cellulose, insoluble non-cellulosic polysaccharides (I-NCP) and soluble non-cellulosic polysaccharides (S-NCP).

4. Physicochemical properties of fibre

The diverse composition and structure of the fibre fraction influence the physicochemical properties (hydration and viscosity[1]) of the feed and the behaviour of the fibres in the digestive system. The physicochemical properties of a feed are important and may interfere with the digestion and

1 Viscosity is a measure of the resistance of a fluid that is being deformed to either shear stress or tensile stress. In everyday terms, viscosity is “thickness” or “internal friction”. Thus, water is “thin” having a low viscosity, while honey is “thick” having a high viscosity. Put simply, the less viscous the fluid is, the greater its ease of movement (fluidity).

absorption processes in all segments of the gastrointestinal tract. In this respect, the fibre content and the composition of a feed are major determinants. The ability of a feed to hydrate is characterised by its solubility, swelling, and water-binding capacity. The latter two are used interchangeably in the literature since both reflect the ability of a fibre source to immobilise water within its matrix.

The first part of the solubilisation process of polymers is swelling in which incoming water spreads the macromolecules until they are fully extended and dispersed [39]. This is illustrated in Figure 8.5 and is accomplished by an expansion of the cell walls in the three-dimensional space. Solubilisation, however, is not possible when polysaccharides adopt regular, ordered structures, which is the case e.g. with the cellulose and arabinoxylans present in the husk layer of the oats in Figure 8.3.

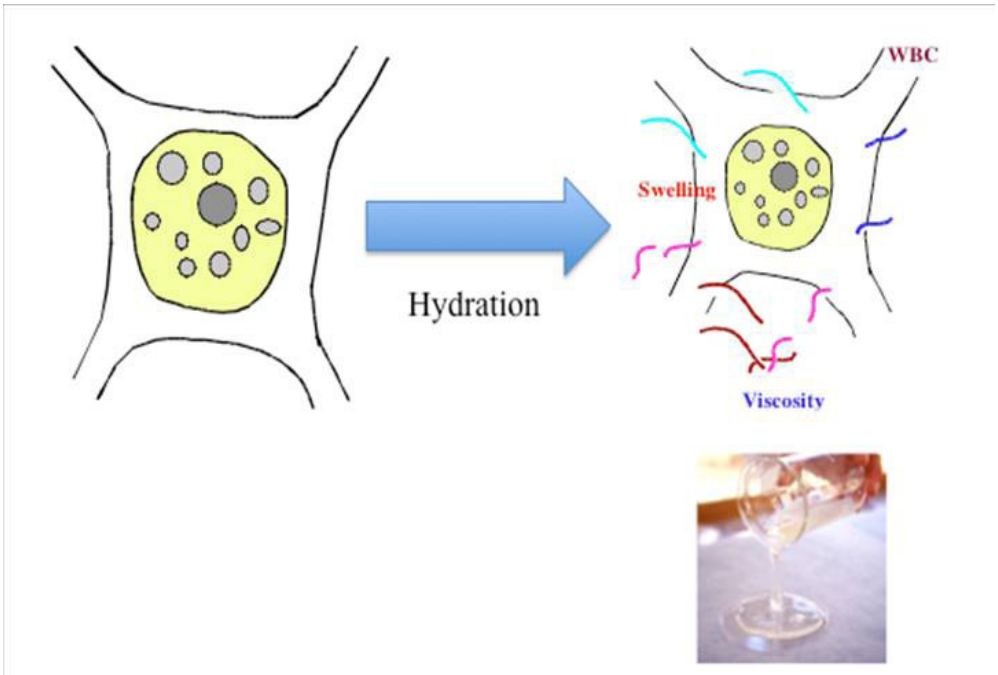


Figure 8.5. The hydration processes of fibre. Incoming water spreads the macromolecules, which expand in the fibre matrix in the three-dimensional space. During this process, some of the polysacchraides will be solubilised from the matrix thereby increasing the viscosity of the liquid phasse.

The reason is that the linear structure increases the strength of the non-covalent bonds that stabilize the ordered conformation. Under these conditions, only swelling can occur [39]. The majority of polysaccharides that are dissolvable in water give viscous solutions [32]. This may interfere with the digestion and absorption processes in the foregut as high viscosity can reduce the rate of gastric emptying and impair the diffusion and absorption of nutrients in the small intestine. The ability of fibres to increase viscosity is dependent on the primary structure, the concentration and the molecular weight of the polymer.

5. Carbohydrate composition of feedstuffs

Carbohydrates are not present as pure chemical entities as described above. In feed, they are present as a mix of sugars, oligosaccharides and polysaccharides. Furthermore, polysaccharides are mostly linked to other biopolymers such as proteins and lignin (Figure 8.3) [1], [38]. The modern pig industry in Denmark and in other important pig producing countries relies on relatively few feedstuffs - mostly from cereals (corn, wheat, barley, oat, rye and rice), cereal co-products (different milling fractions, residues from biofuel and alcohol industries etc.), cereal substitutes (tapioca, manioca), legumes (peas, beans, lupin), protein concentrates (meal or cake of soybean, rape,

sunflower, cotton) and co-products from the sugar and starch industries to produce compounds feeds (Table 8.2).

Table 8.2. Typical carbohydrate and ligning contents (g/kg DM) of feedstuffs (data from [1] and unpublished).

	Digestible CHO		Non-digestible CHO							
Feedstuff	Sugars	Starch	OS	Fructans[1]	RS	S-NCP[2]	I-NCP[3]	Cellulose[3]	KL[3]	Fibre
Rice	2	837	2	<1	3	9	1	3	8	22
Corn	17	680	3	6	10	9	66	22	11	108
Wheat	13	647	6	15	4	25	74	20	19	138
Barley	16	585	6	4	2	56	88	43	35	221
Oats	13	466	5	3	2	40	110	82	66	298
Wheat bran	37	220	16	20	2	29	273	72	75	449
Barley hulls	21	172	12	7	2	20	267	192	115	594
DDGS-corn	-	35	ND	ND	ND	25	183	68	47	323
DDGS-wheat	-	92	ND	ND	ND	55	135	61	86	337
Peas	39	432	49	ND	22	52	76	53	12	192
Faba beans	32	375	54	ND	32	50	59	81	20	210
Soybean meal	77	27	60	ND	ND	63	92	62	16	233
Rapeseed cake	72	15	16	ND	ND	43	103	59	90	295
Cotton seed cake	12	18	54	ND	ND	61	103	92	83	340
Pea hull	15	88	ND	5	ND	121	148	452	9	677
Potato pulp	<1	122	ND	ND	127	280	95	202	35	612
Sugar beet pulp	38	5	ND	0	ND	290	27	203	37	737
Chicory roots	156	ND	ND	470	ND	76	24	48	11	158

CHO: Carbohydrates; OS: Oligosaccharides; RS: Resistant starch; S-NCP: Soluble non-cellulosic polysaccharides; I-NCP: Insoluble non-cellulosic polysaccharides; KL: Klason ligning; ND: Not determined; DDGS: Destillers dried grain with solubles.
1) Fructans are a mix of oligosaccharides (DP 3-9) and polysaccharides (DP ≥ 10)
2) S-NCP is synonymous with insoluble fibre.
3) The sum of I-NCP, cellulose and KL is insoluble fibre.

The commonly used compound feed in Denmark for growing pigs is based on wheat, barley and soybean meal (see section 10 for details), but other cereals (rye, oat) and protein concentrates (pea, rapeseed cake, sunflower) are also used. However, based on the ingredients in Table 8.2, a wide variety of compound feeds with a very diverse composition can be produced. For instance, low-fibre diets can be produced with rice as the primary feedstuff providing carbohydrates whereas co-products from the vegetable food and agro industries and the biofuel industry can be used to produce high-fibre diets especially for gestating sows. Because the biofuel industry is expected to expand substantially in coming years, more co-products will most likely be used in the feeding of pigs. Roughages, however, are rarely used to a large extent except in organic pig production.

6. Qualitative digestion and absorption

The transport processes in the intestinal enterocytes cannot accommodate anything larger than monosaccharides [23], [31]. As only a negligible part of the feed carbohydrates are present in this form, the majority of carbohydrates need to be degraded to low molecular weight compounds prior to absorption (Figure 8.6). These processes involve the secretion of salivary and pancreatic a-amylases, which digest α-1,4-glucosidic linkages in starches and oligosaccharidases, and sucrases located on the brush border, which degrade the starch degradation products to glucose [11], [12], [23], [31] (Chapter 5). The final glucose product can then be transported by the specific glucose carrier, an integrated brush border glycoprotein expressed only in the small intestine and with a high affinity for monosaccharides. The driving force for uphill transport of glucose into the enterocyte is provided by the sodium-potassium ATPase that pumps the intracellular Na^+ across the basolateral membrane.

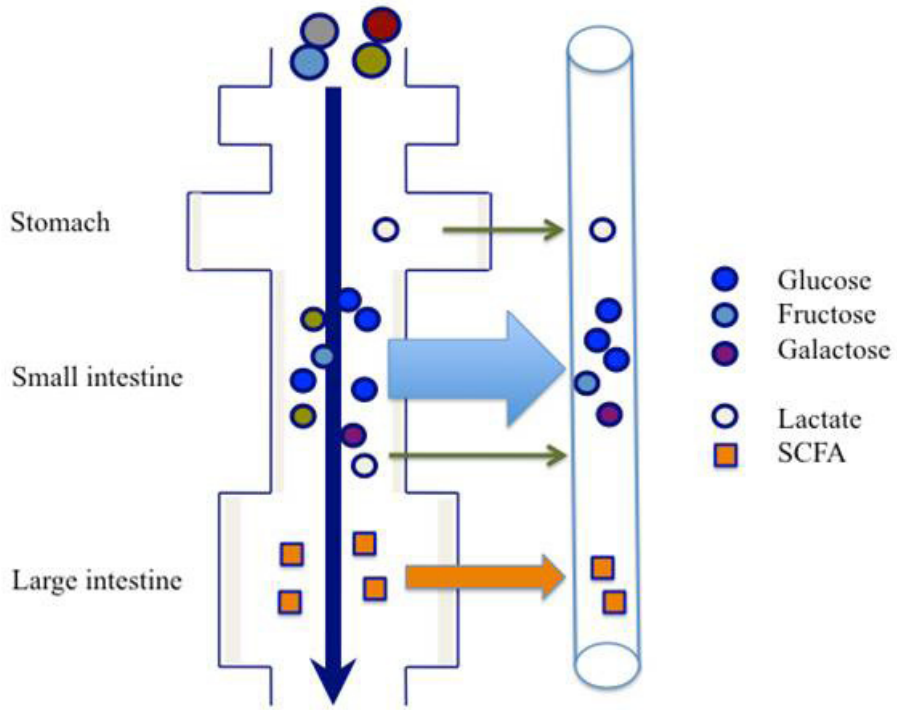


Figure 8.6. Assimilation of carbohydrate derived from products from the digestion process in the stomach, small intestine and large intestine of pigs.

Microbial fermentation occurs to a varying degree in all segments of the gastrointestinal tract of pigs. The transit of fluids and solids through the stomach and small intestine is generally rapid (3-4 hours) with little or no accumulation at any point. These conditions are unfavourable for bacterial growth, and most studies reveal a relatively low microbial activity in these segments [5], [26]. However, lactic acids (LA) are present in significant quantities in the stomach and the distal small intestine, which reflects some microbial activity in these segments. The large intestine is, on the other hand, characterised as an anaerobic fermentation chamber with a low oxygen concentration, a low flow rate and a high moisture content, which are all factors that favour bacterial growth, and the microbial density may reach 10^{11}-10^{12} viable counts per gram fresh material [21], [29] (Chapter 6). The microbial ecosystem contains hundreds of species of anaerobic bacteria, each species occupying a particular niche and with numerous interrelationships. In this segment of the gastrointestinal tract, NSP are degraded by the microflora at varying speeds and to varying extents. The end products of this fermentation in the large intestine are SCFA, gases and a microbial biomass, whereas a certain fraction of NSP in lignified cell walls along with lignin will not be degraded and is passed to the faeces (Figure 8.7). Based on a theoretical rumen fermentation balance, Wolin [40] came up with the following equation:

$$57.5\ (C_6H_{12}O_6) \rightarrow 65\ \text{acetate} + 20\ \text{propionate} + 15\ \text{butyrate} + 60\ CO_2 + 35\ CH_4 + 25\ H_2O \quad (1)$$

Although the equation is based on fermentation in the rumen, the equation fits reasonably to the condition in the large intestine of pigs, and it can be estimated that approx. 25% of the energy present in the carbohydrate is lost as fermentation gases. The molar proportion will vary depending on the composition of NDC because the different carbohydrates will stimulate different groups of microroganisms and because butyrate can be formed from acetate as influenced by the conditions in the large intestine. A concentration and proportion gradient from the caecum/proximal colon to the distal colon is also seen.

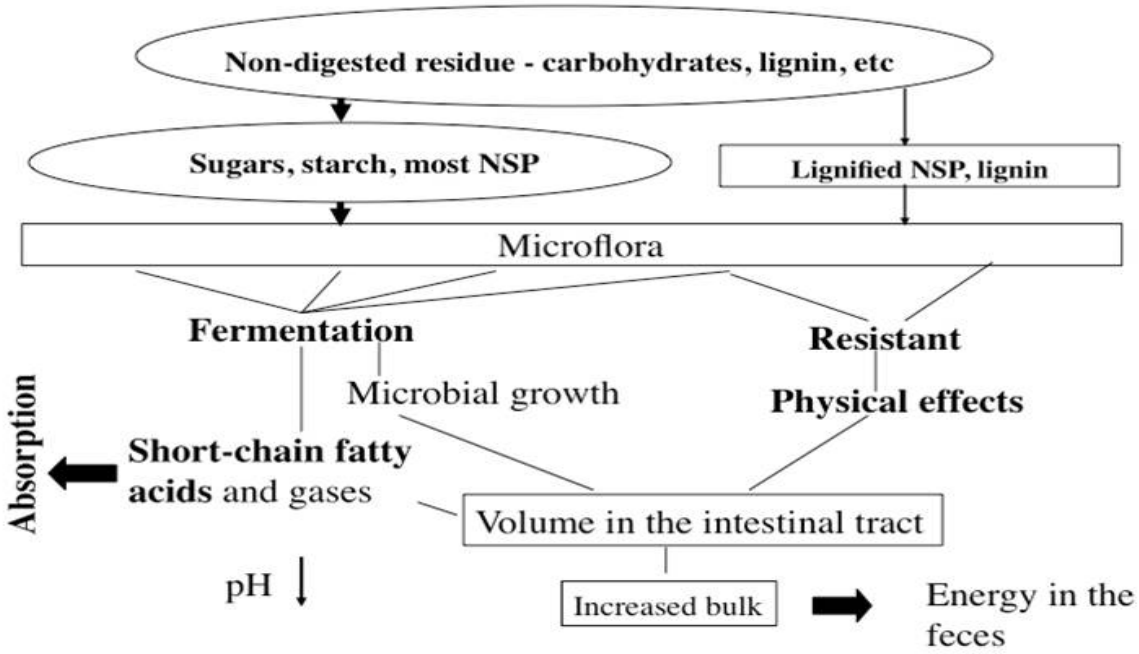


Figure 8.7. Schematic illustration of the carbohydrate degradation in the large intestine, absorption products formed and influence on the colonic and faecal weight, bulk and energy (NSP = non-starch polysaccharides).

The products of the enzymatic digestion along with end products of microbial fermentation (LA and SCFA) are absorbed and transported via mesenteric veins to the portal vein that enters the liver. The glucose response in the portal vein after a meal is very rapid (Figure 8.8) with a significant rise in the portal glucose concentration compared to the basal level. Ten minutes after a meal, the blood glucose increases significantly and peaks after 20-30 minutes. From this point onwards, there is a steady decline in the glucose absorption until the next meal. The absorption of SCFA occurs at a more constant rate and with much less diurnal variation in the SCFA concentration in the portal vein [3]. The variation in the SCFA concentration in the portal vein is limited and much lower than that of glucose even when feeding diets giving rise to relatively large variations in the SCFA production in the large intestine. The absorption of LA is better synchronised with the absorption profile of glucose than that of SCFA most likely because the LA primarily is formed in the stomach (major) and the small intestine (minor).

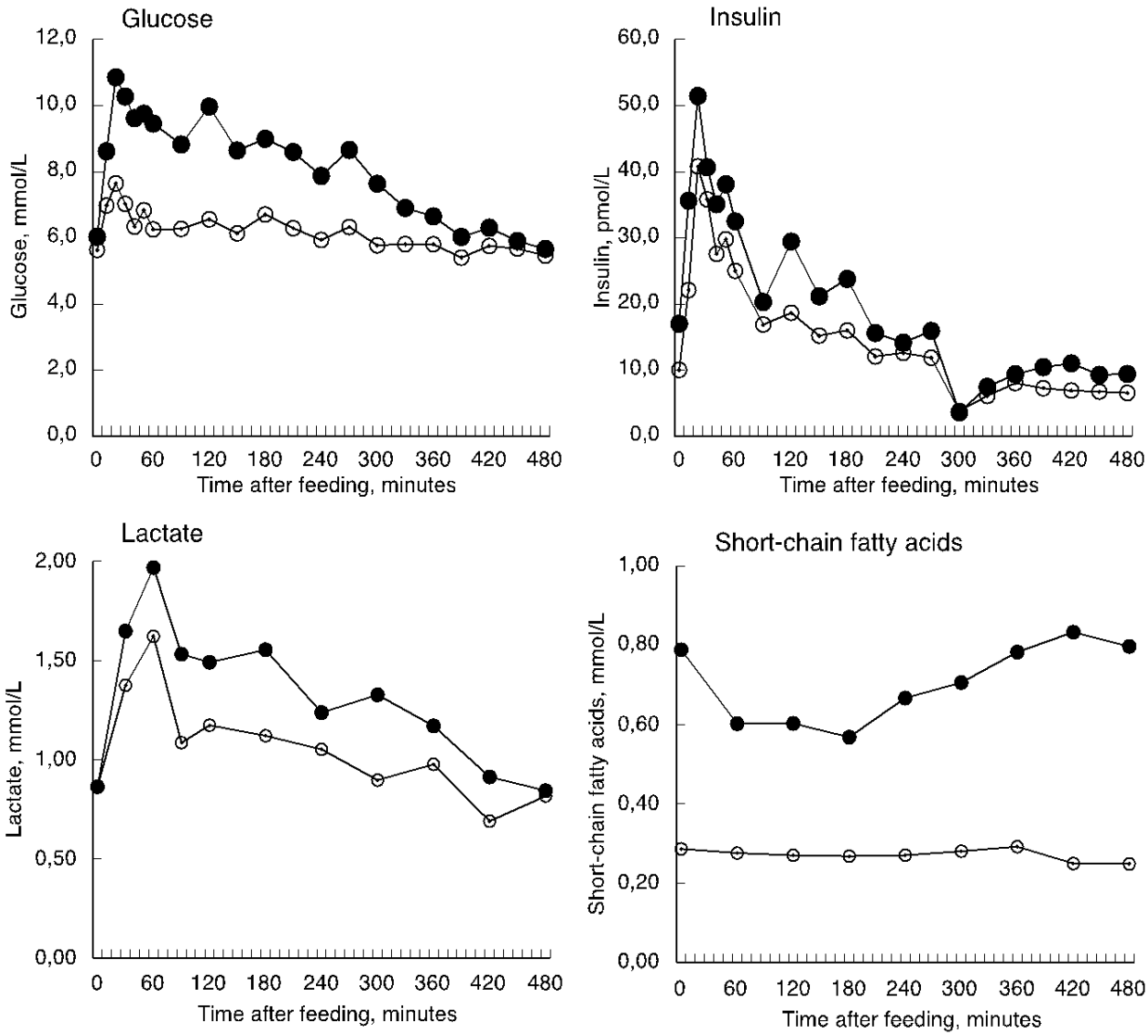


Figure 8.8.The change in glucose, insulin, lactate and short-chain fatty acids in the three mesenteric artery (open circle) ndthe portalvein (closed circle) of pigs. The meals were divided into 3 equal meals and fed 3 times a day at eight hours' interval. The values are means of 3 diets.

6.1. Sugars

Sucrose is readily degraded and absorbed from the gut lumen of pigs, and there is no limitation of the digestibility even at very high concentrations in the feed (Table 8.3). The same applies to glucose that is directly available for absorption without prior enzymatic breakdown. In contrast, fructose, which is absorbed by facilitated transport, is not absorbed completely [8]. The lactase activity is high in piglets, but decreases after weaning to a level that is not sufficient to degrade high amounts of lactose in the diet. Overall, most of the sugars in feedstuffs are well digested and absorbed in the small intestine, and the amount of sugars fermented in the large intestine is limited.

6.2. Oligosaccharides

Pigs lack the enzymes capable of cleaving the bonds of most feed oligosaccharides. In spite of this, independent studies with raffinose oligosaccharides from soybean meals, lupins and peas, fructans (a mix of oligosaccharides and inulin), fructooligosaccharides and transgalactoologosaccharides all show variable and relatively high digestibility coefficients in the small intestine (Table 8.3). The reason is that these oligosaccharides are readily fermentable substrates for the microflora residing in stomach and small intestine [8]. However, feeding diets containing large amounts of e.g. chicory roots or Jerusalem artichoke or diets supplemented by oligosaccharides will overload the fermentative capacity in the stomach and small intestine and result in significant quantities

of oligosaccharides reaching the large intestine. An important property of some oligosaccharides is the stimulation of health promoting microorganisms, i.e. lactobacilli and bifidobacteria [20]. As for sugars, the conversion of oligosaccharides to SCFA is rapid and complete.

Table 8.3. Digestibility (% of intake) of sugars, oligosaccharides, starch and non-starch polysaccharides in the small intestine and total tract of weaners, growing pigs and sows (after [7] and [8]).

		Small intestine		Total tract	
	N	Mean	Range	Mean	Range
Sugars					
Glucose	1	98	-	100	-
Fructose	1	87	-	100	-
Sucrose	6	93	87-98	100	-
Oligosaccharides					
Raffinose olig.	3	52	42-66	100	-
Fructans	2	36	33-40	100	-
Starch					
Weaners, 0-14 d post-weaning	9	75	49-96	99	97-100
Weaners, 14-28 d post-weaning	8	95	89-99	100	98-100
Growing pigs	78	96	79-99	100	97-100
Sows	3	93	91-96	99	97-100
Non-starch polysaccharides					
Weaners, 0-14 d post-weaning	5	3	-24-36	57	31-82
Weaners, 14-28 d post-weaning	4	14	1-30	67	55-76
Growing pigs	78	21	-10-63	70	14-96
Sows	3	30	23-41	64	48-78

6.3.Starch

Digestibility of starch varies substantially and is influenced by the age of the animals and the type of starch (types A, B and C) consumed (Table 8.3). A compromised α-amylase secretion during the first two weeks after weaning results in a lower starch digestibility than is the case for older piglets, growing pigs and sows [8]. For growing pigs, the digestibility of starch can also vary substantially depending on the type of starch, the amylase-to-amylopectin ratio, thermal heat treatment, particle size of the feed, and the content of soluble NSP and antinutritional compounds (e.g. α-amylase inhibitors) in the feed. For instance, the digestibility of raw cereal starches (type A) is typically in the order of 95-97%, whereas it is somewhat lower for legume starches (type C) with values in the interval 84-88%. The digestibility of raw potato starch (type B) can be as low as 40-50%, but raw potato starch is only occasionally used in limited amounts in practical pig production [9]. Section 7 provides an in-depth discussion of two of these factors: particle size and thermal processing. Although the soluble NSP may have an impact on the viscosity of the gastrointestinal content, the influence of the digestibility of starch is marginal. A few studies have demonstrated a negative impact of soluble fibre on starch digestibility, but the majority of studies show no effect. Antinutritional compounds, which can interfere with the activity of α-amylase, can reduce the digestibility of starch, but the level found in most common feeds in Denmark is insufficient for any significant effects.

Undigested starch from a finely ground diet that reaches the large intestine is easily degraded in the proximal part of the large intestine. The same is the case with RS_2 from peas. There are examples, however, that starch may be degraded more slowly when very coarsely ground diets are fed. For example, starch can be detected in faeces when intact whole kernels are fed demonstrating incomplete total tract digestion [9].

6.4. Non-starch polysaccharides

NSP represents the most complex part of the carbohydrate fraction (section 3). In spite of that, approx. 21% of the NSP is digested before the digesta reaches the terminal ileum, but with large variations between the different NSP [8]. For instance, two-thirds of the β-glucan in barley and oats are degradable in the small intestine, whereas arabinoxylans are only modestly degraded (2-8%). These differences have a significant influence on the physicochemical properties of digesta; barley and oats, with high levels of soluble fibre from β-glucan [27], have only a minor impact on the luminal viscosity, whereas rye increases the viscosity and water-binding capacity much more [10].

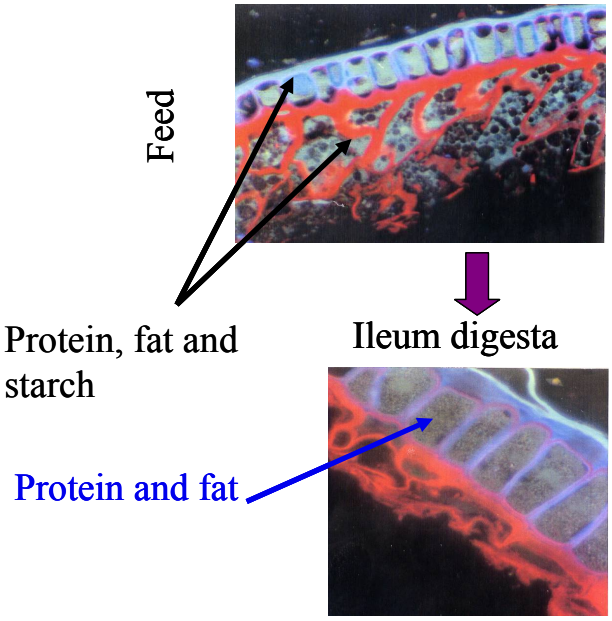


Figure 8.9. An example of encapsulation of nutrients within cell structurs. The feed illustrates the subleurone (red cell walls) and aleurone (blue cell walls) in the feed after passage of the small intestine. In ileal effluent, the aleurone cell walls encapsulate potentially available nutrients, ie. protein and fat.

Fibre is the dietary component with the most significant negative effect on the ileal digestibility of organic matter (OM). This is primarily because most of the NSP are not digested and thereby contribute to the undigestible OM. However, there are also direct and indirect effects on the digestibility of protein. As illustrated in Figure 8.9, fibres in the cell walls encapsulate potentially available nutrients (mostly protein) and thereby withhold them from digestion by the endogenous enzymes in the small intestine [27]. A further contributing factor for the negative effect of fibre on the digestibility of protein may be the increased viscosity and water-binding capacity of high-fibre diets that enhance the secretion of endogenous protein [28]. The relationships between the concentration of fibre and the ileal digestibility of OM and protein in diets with a diverse chemical composition can be expressed as:

$$\text{Ileal digestibility of OM} = 95.1 - 0.135 \times \text{fibre}, \; R^2 = 0.77 \quad (2)$$

$$\text{Ileal digestibility of protein} = 88.0 - 0.095 \times \text{fibre}, \; R^2 = 0.28 \quad (3)$$

Irrespective that some NSP already are degraded during passage in the stomach and small intestine, the large intestine is the main site for NSP degradation. The rate and degree of degradation of NSP in the large intestine are influenced by the chemical composition, the solubility and the degree of lignification [8]. This is illustrated in Figure 8.10 that shows the degradation of lignified and nonlignified cell wall NSP. NSP from non-lignified cell walls, which typically have high content of soluble NSP, are easily fermentable and are degraded almost exclusively in the caecum and

proximal colon, whereas the NSP in lignified cell walls with a high content of insoluble NSP are degraded more slowly and at more distal locations.

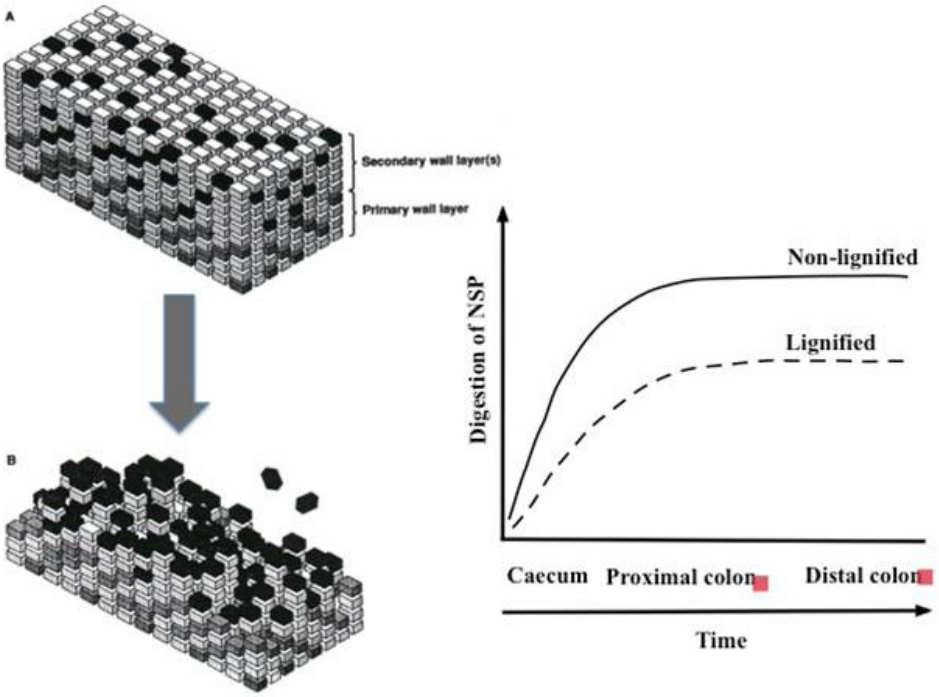


Figure 8.10. Exemplification of the degradation of non-starch polysaccharides in non-lignified and lignified cell walls. In non-lignified cell walls, the degradation is rapid and almost complete, whereas in the lignified cell walls the degradation is incomplete because the lignin cross-link the cell wall polysaccharides. At a certain stage, the lignin makes further degradation impossible because non-degradable lignin hinders the access for the microorganisms to cell NSP.

The degree of lignification has a very strong influence on the total tract digestibility of the NSP. Lignin cannot be degraded by the microflora in the large intestine, and the cross-link between the lignin and the polysaccharides makes the whole polysaccharide-lignin complex highly insoluble and difficult to degrade [4], [34]. It has been shown that cellulose located in lignified materials (hulls or bran of cereals) is much more resistant to degradation than cellulose present in non-lignified materials (e.g. sugar beet pulp). It is therefore not surprising that fibre is the dietary component that has the largest negative impact on the total tract digestibility of OM and protein. The relationships can be expressed as:

$$\text{Total tract digestibility of OM} = 101.0 - 0.09 \times \text{fibre}, R^2 = 0.70 \quad (4)$$

$$\text{Total tract digestibility of protein} = 97.0 - 0.094 \times \text{fibre}, R^2 = 0.61 \quad (5)$$

Fibrous components are for several reasons more extensively degraded in sows and adult animals compared to piglets and growing pigs. Adult animals will usually have a lower feed intake per unit of body weight, a slower passage rate of digesta through the gut, a greater intestinal volume and a higher activity of cellulytic bacteria. These factors are the main reasons why the digestibility of fibre and of metabolizable energy is higher in sows than in growing pigs [8].

7. Factors influencing digestion and absorption of carbohydrates

This section will cover four common feeding aspects that may influence the digestion of carbohydrates and other macronutrients in different ways and with different mechanisms, thereby influencing production parameters in pigs. The influence of particle size, thermal treatment, exogenous enzymes and fermentation on the quantitative digestion and absorption of carbohydrates will also be described, and the effects are summarised in Table 8.4. As primarily the digestibility in the small intestine is influenced, the table only covers these aspects.

Table 8.4. Effects of particle size, thermal treatment, xylanase and fermentation on the ileal digestibility (% of intake) of nutrients and ileal viscosity.

		Digestibility, %					Viscosity
	N	OM	Starch	NSP	Protein	Fat	mPa·s
Reference	78	76	96	21	75	69	-
Particle size							
Wheat - fine, 24% > 1 mm		76	96	8	83	70	-
Wheat - coarse, 38% > 1 mm		75	96	6	84	70	-
Barley - fine, 16% > 1 mm		74	97	18	83	75	-
Barley - coarse, 52% > 1 mm		60	92	-7	76	60	-
Thermal treatment							
Raw - type A		79	93	28	81	-	-
Extruded - type A		81	99	13	89	-	-
Raw -type C		65	79	6	73	-	-
Extruded - type C		68	92	8	82	-	-
Exogenous enzymes							
Control		49	98	6	61	66	1.6
+ xylanase 1		50	98	20	65	70	1.4
+ xylanase 2		55	98	23	66	70	1.4
Control		85	98	24	81	-	2.4
+ xylanase	2	84	99	39	81	-	1.5
Fermentation							
Wheat, non-ferm.		76	95	36	80	60	-
Wheat, ferm.		77	98	30	77	59	-
Barley, non-ferm.		65	84	43	72	55	-
Barley, ferm.		69	90	36	75	55	-

OM = organic matter; NSP = non-starch polysaccharides

7.1. Particle size

For nutrients to be efficiently digested, it is necessary to reduce the size of the dietary particles exposed to the digestive enzymes in the gastrointestinal tract. Grinding is a physical process that reduces the size of the particles and thereby increases the surface area. This can be illustrated by the following example: A cube measuring 1 cm on each side will have a total surface area of 6 cm^2. If the cube is divided into cubes each measuring 0.1 cm, the surface area of the divided cube will increase to 60 cm^2 - a ten-fold increase.

In growing pigs, starch in coarsely ground cereals is not digested as well as starch in finely ground cereals (Table 8.4). Some data indicate that the digestibility of starch in barley is more sensitive to variations in the particle size than is the digestibility of starch in wheat. A reduction in the digestibility of starch in the small intestine by e.g. 5 percentage units will move a substantial amount of starch from digestion in the small intestine to digestion in the large intestine. Provided

that the net energy value of SCFA is only half of the energy obtained from carbohydrates absorbed as glucose in the small intestine, the reduction in the energy value can be estimated to be approx. 1%. This is, however, less than actually found in performance studies where feeding of coarsely ground cereals may reduce the growth rate and feed conversion ratio by 4-5% [24]. Since the total tract digestibility is only marginally affected as long as the cereal particles are not too coarse (recommendations say less than 40% over 1 mm), a lower digestibility of other nutrients, e.g. protein and fat, and extra energy costs of handling coarsely ground materials in the gastrointestinal tract may be factors contributing to the lower energy utilisation.

7.2. Thermal treatment

Thermal treatment alters the physical form of the starch from a crystalline structure to a gel structure. This enlarges the surface area and ensures an efficient entry of digestive enzymes into the polar solution. A negative effect of hydrothermal treatment, however, can be the formation of retrograded starch that cannot be degraded by α-amylase. However, the water content in the type of processes normally applied for feed processing (pelleting, expanding, extrusion cooking) does not lead to the formation of any significant quantities of retrograded starch.

The effect of thermal treatment depends on the type of starch (A, B or C) and the digestibility of the raw starch [9]. For instance, for cereal starches (type A) the increase in the ileal starch digestibility is in the order of +2-6 percentage units; for legume starches (type C) the effect of thermal treatment is in the order of +10-12 percentage units; whereas for potato starch (type B) the digestibility can increase by as much as +50-60 percentage units by hydrothermal treatment [37]. The positive effect of thermal treatment on the energy value is estimated to be 1-3% for cereal-based diets and approx. 5-6% for legume-based diets.

7.3. Exogenous enzymes

Exogenous enzymes are used in diets for pigs with the primary aim of degrading the feed structures that cannot be degraded by the endogenous digestive enzymes in the small intestine. Enzymes targeting different carbohydrate structures such as oligosaccharides, starch and NSP are commercially available, but only xylanases are commonly used in Denmark. In the future, xylanases can be expected to be of even greater importance because more fibre containing co-products from the biofuel industry will become available. The mode of action of the xylanases may vary; some xylanases will solubilise insoluble arabinoxylans, whereas others will depolymerize soluble arabinoxylans thereby reducing the viscosity. In both cases, xylanases will help give access to the cell content for endogenous digestive enzymes in the small intestine.

The effects of xylanase on the ileal digestibility of macronutrients obtained in two series of experiments with weaners and growing pigs, respectively, are shown in Table 8.4. In both cases, the supplementation with xylanases had no effect on the digestibility of starch, whereas the digestibility of NSP, protein and fat improved. The improved digestibility of protein and fat is likely to be associated with the degradation of the fibre matrix that enables access for proteases and lipases to encapsulated nutrients. In addition, the xylanases reduce the digesta viscosity that improves the efficiency of the proteases and lipases.

7.4. Fermentation

A high proportion of growing pigs in Denmark are raised on liquid feed. The original purpose of using fermented liquid feeding was to enable the use of cheap liquid co-products from the food and brewing industry, but liquid feeding systems are now also commonly used when handling raw dry feed materials and ingredients. The effect of fermentation on animal performance varies, which may be a reflection of variable diet palatability and efficiency of the fermentation processes to influence the nutritive value of the feed [13], [14]. The fermentation process leads to degradation and conversion of sugars, oligosaccharides and a small part of soluble NSP into organic acids, whereas the impact of fermentation on insoluble NSP and starch is very limited [36]. Fermentation resulted in improvement of the ileal digestibility of starch. It should be noted, however, that the

improvement in the abovementioned experiment was primarily seen for the barley diet, which had a low initial starch digestibility, whereas the effect was much smaller for the wheat diet [36]. Most likely, the prolonged fermentation process had softened the coarse particles thereby easing the penetration of the endogenous enzymes into the particles.

8. Quantitative aspects of carbohydrate digestion and absorption

In this section, the quantitative aspects of digestion and absorption of carbohydrates will be introduced. Data are based on compilations of results from studies with ileal[2] cannulated pigs (Table 8.5) and portal vein catheterised[3] pigs (Figures 8.11 and 8.12). In addition to data obtained on growing pigs, the section also includes the quantitative aspects of carbohydrate digestion and absorption in piglets and sows.

Table 8.5. Daily intake and recovery of nutrients (g/day) in ileum and faeces, and the effects of fibre on the recovery of nutrients in the ileum and faeces.

		Recovery	Effect of fibre			Recovery	Effect of fibre		
	Intake	Ileum	Intercept	Slope	R^2	Faeces	Intercept	Slope	R^2
	g/d	g/d				g/d			
Dry matter	2000	536	113	3.1	0.75	273	-25	2.2	0.79
Organic matter	1903	475	88	2.8	0.78	231	-38	2.0	0.80
Protein (N x 6.25)	351	88	39	0.4	0.29	56	10	0.34	0.65
Fat	130	36	25	0.1	0.06	35	21	0.1	0.15
- Carbohyd.	1327	227	-	-	-	82	-	-	-
- Sugars	99	5	-	-	-	0	-	-	-
- Starch	984	31	13	0.11	0.08	3	-1	<0.1	0.15
- NSP	244	191	5	1.3	0.76	79	-49	0.9	0.69
Klason ligning[1]	36	36[2]	-2	0.3	0.54	36[2]	-2	0.27	0.34
Residue	59	95	6	0.7	0.31	29	-16	0.3	0.21

The data in this table were compiled from 21 published and one unpublished papers representing 78 diets. The intake was calculated based on 2000 g of dry matter and converted to macronutrients from the reported chemical compositions. The recovery at ileum and in faeces was calculated based on the digestibility coefficients reported in the papers. The intercept, the recovery of nutrients in ileum and faeces, respectively, when no fibre were given, and the slope, the increase in recovery in ileum and faeces, respectively, when the dietary fibre level increases by one gram.
ND, not determined; NSP, non-starch polysaccharides.
1) Sugar residues in the ileum and faeces will be part of the residue fraction.
2) It is assumed that the lignin is not broken down during passage of the gut.

The data in Table 8.5 summarise the intake of nutrients and the recovery of nutrients at ileum and in faeces as influenced by the fibre concentration. These data are based on digestibility experiments with ileal cannulated pigs that are fed common feed and feedstuffs with variable macronutrient composition, i.e. the diets varied particularly in the concentration and types of starch and fibre.

2 In ileal cannulated pigs, a permanent cannula is installed in the terminal ileum, which allows sampling of digesta for separation of the digestion processes in the small and large intestine.

3 In portal vein catheterized pigs, two permanent catheters are placed in the portal vein and mesenteric artery and a flow probe is attached to the portal vein for measuring the blood flow. In this way, the total absorption of water soluble nutrients, i.e. glucose, LA and SCFA can be calculated

To make the data with ileal cannulated pigs comparable, the intake level was normalised to 2000 g/dry matter a day (approximately the feeding level for a 80 kg pig) and the calculations performed as:

$$\text{Intake of A} = cA_{diet} \times 2000 \quad (6)$$

$$\text{Ileal recovery of A} = \text{Intake of A} \times (1 - AID_A) \quad (7)$$

$$\text{Faecal recovery of A} = \text{Intake of A} \times (1 - TTAD_A) \quad (8)$$

where A is the specific nutrient in question (ash, OM, protein, fat, carbohydrates etc.), 2000 the feeding level in g dry matter a day, cA_{diet} the concentration of the specific nutrient, AID_A, the apparent ileal digestibility (as ratio) of nutrient A, and $TTAD_A$ the apparent total tract (faecal) digestibility of nutrient A.

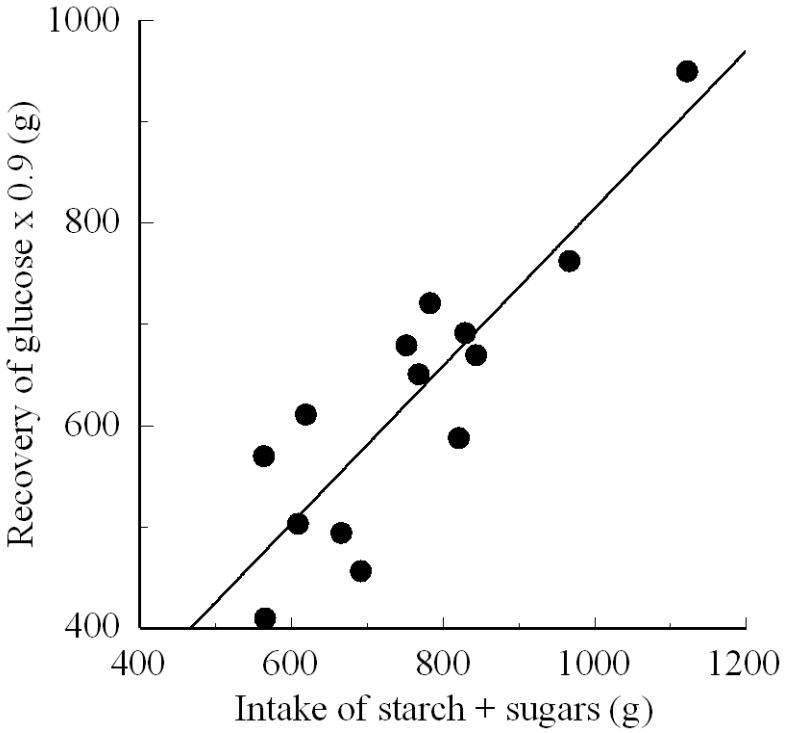


Figure 8.11. The relationship between the intake of starch and sugars (X, g) and the cumulated absorption of glucose expressed as polysaccharides (Y, g) in conscious portal vein catheterised pigs. The relationship can be expressed as: Y = 37 + 0.78 x X, R^2 = 0.77. Based on [9].

8.1. Small intestine

In growing pigs, approx. 88% of all carbohydrates are digested and absorbed in the small intestine (Table 8.5). This can be seen by subtracting the recovery of carbohydrates in ileum from the intake and compare it with the amount digested in the total tract (intake – recovery in faeces) and multiply the ratio by 100. The high enzymatic capacity ensures an almost complete digestion of sugars and starch. The regression analysis further tells us that the concentration of fibre had no influence on the digestibility of starch.

The monosaccharides released by the enzymatic hydrolysis of starch and sugars in the small intestine are absorbed very efficiently, and there is a direct relationship between the intake of starch and sugars and the amount of glucose recovered in the portal vein (Figure 8.11) [9]. The relationship can be expressed as:

$$Y = 37 + 0.78 \times X, R^2 = 0.77 \quad (9)$$

where Y denotes the recovery of glucose expressed as polysaccharides (glucose x 0.9) in the portal vein and X the intake of starch and sugars. The slope of 0.78 from the regression analysis showed that 78% of the ingested starch and sugars were recovered in the portal vein. From the appearance of glucose in the portal vein, it can also be seen that the absorption of glucose does not occur at a constant rate, but varies between the feedings (Figure 8.8). For instance, when the daily ration is divided into three equal meals, the rate of absorption during the first 2 hours after a meal will typically be in the order of 200-300 mmol/hour dropping to below 50 mmol/hour the last 2 hours before the next feeding. The rise in the glucose concentration in the portal vein after a meal triggers insulin secretion from the pancreas that ensures that glucose is taken up by the muscle cells for storage as glycogen and as energy that drives protein and fat synthesis in muscle and adipose tissues [3]. Along with the absorption of glucose after a meal, LA will also be absorbed. The absorption of this acid may reach 500-600 mmol/d and is the outcome of microbial fermentation in stomach and small intestine.

8.2. Large intestine

The amount of OM that reaches the large intestine is directly related to the dietary concentration of fibre (Table 8.5). This is primarily due to the indigestibility of NSP that represent the major part of the carbohydrates in OM and account for approx. 48% of the undigested residue, the remaining being protein, fat, lignin and a residue that cannot be accounted for by the methods currently used to analyse digesta materials. Mucus polysaccharides deriving from the epithelium of the small intestine and slaughter cells will most likely account for most of the residue.

Approximately half of the OM that reaches the large intestine is fermented in this compartment, but there are large differences between the carbohydrates; 59% of the NSP, 90% of the starch and 100% of the sugars disappear in the large intestine (Table 8.5). The amount of OM that is degraded in the large intestine increases with increasing fibre concentrations; i.e. the degradation is 170 g OM/d with a fibre level of 150 g/kg DM (approximately the level found when a wheat/soybean meal diet is fed) and 286 g OM/d with a fibre concentration of 200 g/kg dry matter (approximately the level found when a barley/soybean meal diet is fed).

The absorption of SCFA in the portal vein is directly linked to dietary levels of NDC (Figure 7.12) and expressed as:

$$SCFA = 452 + 3.5 \times NDC, R^2 = 0.69 \quad (10)$$

where the SCFA is expressed in mmol/d and the NDC in gram. While the diurnal fluctuation of glucose in the portal vein after a meal is substantial, the absorption of SCFA is much more constant and the portal concentration and hourly absorption reflect the intake of NDC [2]. The relative contribution of energy as SCFA can vary as much as 4-44% in growing pigs, but for diets typically used for growing pigs, the variation is somewhat lower in the order of 7-20% [3].

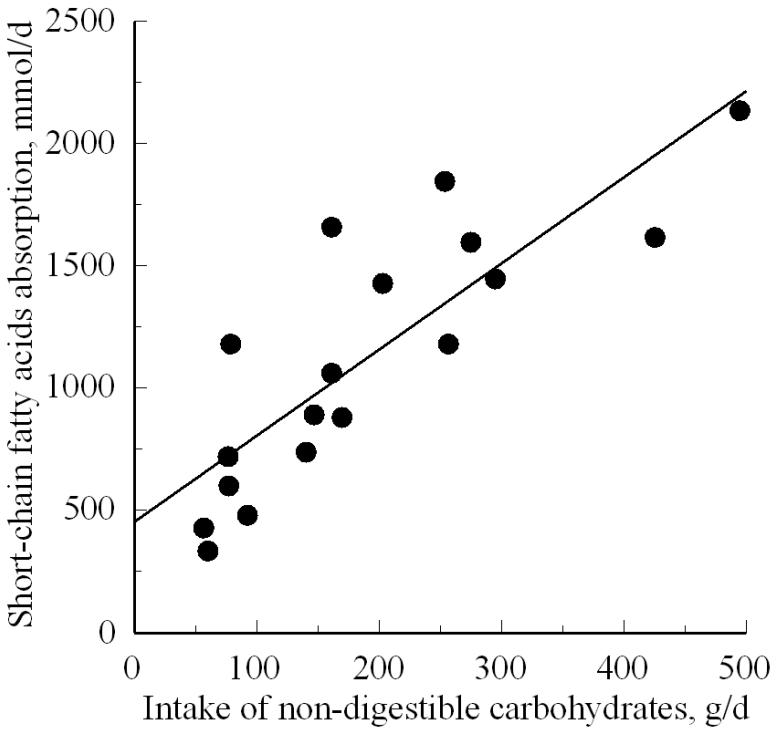


Figure 8.12. The relationship between the intake of non-digestible carbohydrates and the absorption of short-chain fatty acids in conscious portal vein catheterised pigs. The relationship can be expressed as: SCFA = 452 + 3.5 x NDC, R^2 = 0.69. NDC, non-digestible carbohydrates. Based on [2].

8.3. Special conditions for piglets and sows

In the immediate post-weaning period, weaners have a compromised capacity to digest starch. This has consequences for the quantitative flow and composition of nutrients flowing from the small intestine to the large intestine (Table 8.6), and starch is clearly the dominant substrate passing from the small to the large intestine during the first 10 days post-weaning. The high flow of readily digestible starch can be considered a risk factor for the development of diarrhoea and could potentially lead to an incomplete degradation of NSP in the large intestine.

Table 8.6. Model calculations of the amount of substrate passing from the small to the large intestine when feeding diets with diffrent levels of fibre in the periods 0-10 d and +10 d post-weaning.

Concentration	**Non-starch polysaccharides, g/kg DM**		
	7	80	120
Intake: 300 g/day			
Recovery, 0-10 d post-weaning			
Starch, g/d	52	46	42
Non-starch polysaccharides, g/d	2	24	36
Total carbohydrates, g/d	54	70	78
Intake: 600 g/d			
Recovery, > 10 d post-weaning			
Starch, g/d	15	13	12
Non-starch polysaccharides, g/d	4	43	65
Total carbohydrates, g/d	19	56	77

Studies performed with ileal cannulated sows demonstrated ileal digestibilities of starch in the same order as for growing pigs (Table 8.3). However, because of high gut fill gestating sows can handle much higher dietary fibre levels than growing pigs. In sows fed diets containing 429-455 g/kg DM of fibre, the digestion in the large intestine was as high as 350-500 g/day [35].

9. Carbohydrate composition and physiological energy

Since fibre represents the part of the feed that is not digested by endogenous enzymes in the small intestine and has a negative impact on the digestibility of other nutrients in the small and the total tract (Table 8.5), it is not surprising that fibre has the largest negative impact on the level of physiological energy in the feed (Figure 8.13).

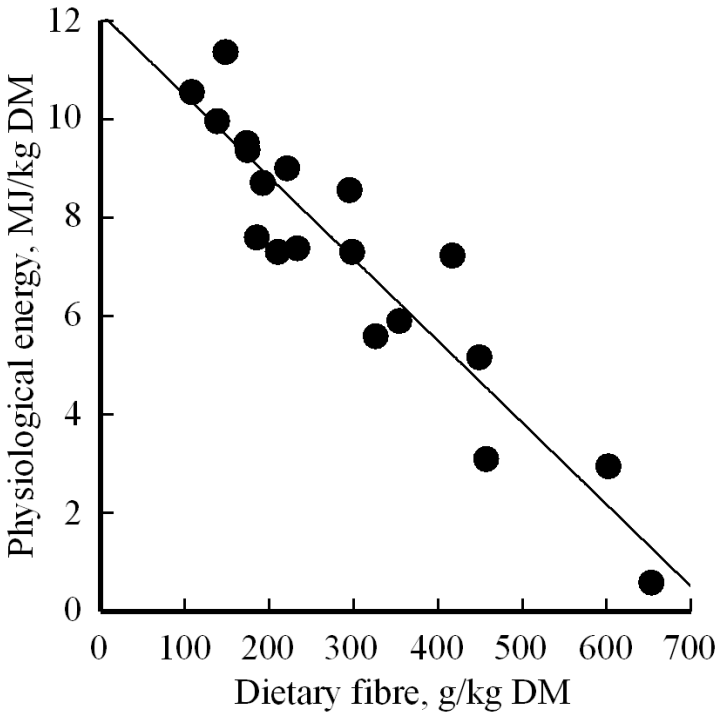


Figure 8.13. The relationship between the concentration of dietary fibre and the physiological energy in different feedstuffs. The relationship can be expressed as: Physiological energy = 12.1 – 0.017 x DF, R^2 = 0.87. DF, dietary fibre.

Not only will a higher fibre content decrease the overall digestibility, but the type of absorbed nutrients deriving from the carbohydrate assimilation will also change towards more SCFA with a lower energy utilisation than of glucose (Chapters 14, 20 and 21).

10. Quantitative digestion and absorption of carbohydrates in growing pigs and sows - a case study

In this section, we will discuss the digestion and absorption of carbohydrates in growing pigs and sows when fed low-fibre diets (LF1 and LF2) and high-fibre diets (HFI and HFS). The data are presented in Table 8.7 and serve as an illustration of how the dietary composition may influence the digestion and absorption of carbohydrates in the small and large intestine and the energy supply. The two low-fibre diets are those presented in Chapter 2 (“Finishers 30-100 kg with 200% phytase” and “Sow Unity U”), whereas the high-fibre diets are experimental diets that may potentially be used for growing pigs and sows.

The LF1 diet was composed of wheat, barley, wheat bran, soybean meal, rapeseed cake, sunflower seed, and molasses, and the HFI diet of barley, barley hulls, soybean meal and rapeseed cake as the main carbohydrate containing feed ingredients. The LF1 diet had a fibre concentration of 195 g/kg DM and the HFI diet of 260 g/kg DM. The feeding level of diet LF1 was set at 2 kg feed and the feeding level of diet HF1 was adjusted to the low concentration of physiological energy. The diets for sows were composed of wheat, barley, wheat cut, soybean meal and sunflower seed (LF2) and of wheat, barley, sugar beet pulp, potato pulp, pectin residue and soybean meal (HFS) as the main carbohydrate containing feed components (Table 8.7). The HFS diet also contained 5% vegetable fat. The two sow diets had a fibre concentration of 177 g/kg DM and 441 g/kg DM, respectively. As for growing pigs, the feeding level of diet LF2 was set at 2 kg feed and the feeding level of diet HFS 4% higher to compensate for the lower content of physiological energy.

Table 8.7. Intake (g/day) and digestion of carbohydrates in the small and large intestine and absorption (mmol/d) of carbohydrate-derived nutrients.

	Growing pigs						Sows					
	LF1			HFI			LF2			HFS		
	Intake	SI	LI	Intake	SI	LI	Intake	SI	LI	Intake	SI	LI
Feed	2000	-	-	2144	-	-	2000	-	-	2087	-	-
CHO	1166	893	177	1261	899	172	1207	958	162	1155	647	408
- Sugars	78	74	4	53	50	3	47	45	2	32	31	1
- Starch	766	743	23	772	749	23	865	831	35	401	365	36
- Oligos.	33	13	20	30	12	18	32	13	20	13	5	8
- Resistant starch	4	0	4	3		3	5	0	5	2	0	2
- NSP	286	63	126	404	89	125	258	70	101	707	191	360
Absorbed, mmol/d												
Glucose	-	4100	-	-	4008	-	-	4429	-	-	2124	-
Lactic acids	-	500	-	-	500	-	-	600	-	-	600	-
SCFA[1]	-	-	1581	-	-	1979	-	-	1483	-	-	2978
SCFA[2]	-	-	1655	-	-	1609	-	-	1517	-	-	3826
Absorbed energy, MJ/d												
Glucose	-	11.6	-	-	11.3	-	-	12.5	-	-	6.0	-
Lactic acids	-	0.7	-	-	0.7	-	-	0.8	-	-	0.8	-
SCFA[1]	-	-	2.0	-	-	2.4	-	-	1.8	-	-	3.7
SCFA[2]	-	-	2.3	-	-	2.3	-	-	2.1	-	-	5.4

SI, small intestine; LI, large intestine; CHO, carbohydrates; LF1, low-fibre; HFI, high-fibre insoluble; LF2, low-fibre; HFS, high-fibre soluble; NSP, non-starch polysaccharides; SCFA, short-chain fatty acids.
1) Calculated from equation 10.
2) Calculated by the factorial approach: SCFA = degradation of carbohydrates in the large intestine x 0.75 x 17.7/1000.

In growing pigs, irrespective the diet composition, more than 80% of the carbohydrates were digested in the small intestine, whereas the digestion in sows ranged from 59 to 86% (Table 8.7). Based on equation no. 9, these amounts of carbohydrates digested in the small intestine result in absorption of around 4100 mmol/d of glucose, which equals 11.6 MJ/d[4] of energy in the diets for growing pigs. For sows, a larger variation in the absorption of glucose is seen; 2234 mmol/d for the HFS diet and 4429 mmol/d for the LF2 diet, which corresponds to 6.0 MJ/d and 12.5 MJ/d, respectively. Under the given feeding regimes, the absorption of LA will amount to 500-600 mmol/d in all diets corresponding to 0.7-0.8 MJ/d[5].

4 A factor of 2,817 kj per mol of glucose was used.
5 A factor of 1,370 kj per mol of LA was used.

The digestion of carbohydrates in the large intestine of growing pigs was estimated to approx. 175 g/d and in sows to 162 and 408 g/d for the low-fibre diet and the high-fibre diet, respectively. The absorption of SCFA was estimated in two ways; either by using equation no. 10 or by a factorial approach[6] that utilizes the equations for the conversion of carbohydrates into SCFA expressed in equation no. 1.

The data in Table 8.7 show that the results of the two approaches are reasonably similar for the two low-fibre diets (LF1 and LF2) and to some extent for diet HF1 with values in the order of 1600 mmol/d, 1500 mmol/d and 1800 mmol/d for diets LF1, LF2, and HFI, respectively. These absorption values corresponded to the absorption of 1.8-2.3 MJ/d[7] of energy as SCFA. The spread between the two SCFA absorption estimates, however, becomes significantly wider when applied to the HFS diet with values varying from 3213 to 4275 mmol/d (4.0 vs. 5.6 MJ/d). The most likely reason for this discrepancy at the high-fibre level is that equation no. 10 is developed on growing pigs based on a much more narrow variation in fibre concentration.

A certain fraction of the diet will not be digested. For the two diets for growing pigs, this amounts to 97 g/d of carbohydrates in diet LF1 and 190 g/d of carbohydrates in diet HFI, and for the two diets for sows to 87 and 170 g/d of carbohydrates for diets LF2 and HFS, respectively. Lignin is another dietary constituent that is not digested. For the diets for growing pigs, it amounts to 62 and 85 g/d, respectively, and in the two diets for sows to 54 and 135 g/d, respectively.

11. Concluding remarks

The intention with the present chapter was to provide the reader with an understanding of the diverse nature of carbohydrates present in common feedstuffs and to give an insight into how the different carbohydrates are digested and absorbed in pigs from weaning to maturity. The chapter span from the qualitative to the quantitative aspects of digestion and absorption ending with a case story of the quantitative aspects of digestion and absorption in common diets for growing pigs and sows. Factors that may influence digestion and absorption were also described and discussed. It is the hope of the authors that with the present key knowledge the reader should be able to judge the nutritional consequences for weaners, growing pigs and sows of diets varying in carbohydrate composition.

6 SCFA = degradation of carbohydrates in the large intestine x 0.75 x 17.7/1000.
7 A factor of 1,235 kj per mol of SCFA (65% acetate, 25% propionate, 15% butyrate) was used.

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