Chapter 17
Polymers of the Plant Cell Wall or “Fiber”
Their Analysis in Animal Feeding and Their Role in Rabbit Nutrition and Health
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17.1 Introduction

Dietary fiber concepts historically differ in animal feeding as compared to human nutrition and health. For the latter, this is a rather modern concept, mainly developed in the 1960s (Hipsley 1953) to deal with several pathologies (colorectal cancer, etc.), regularly revisited (Trowell 1978, De Vries 1999, Elleuch et al. 2011), and often restricted to the polysaccharides of the plant cell wall of the fruit and legumes. In contrast, animal nutritionists deal with other “less refined” fiber sources, often from whole plants (forages, by-products of seeds processing, etc.), and recover a larger range of chemical components, including other polymers, such as polyphenolic (lignins, tannins) or polylipidic compounds (cutins) and so on. Thus, two centuries ago, Heinrich Einhof developed the so-called Weende method (which in fact was setup at Möglin in 1806, Germany, and not at the Weende agronomy station) to isolate a “crude fiber” residue (Van Soest and Mc Queen 1973) to assess the nutritional value of ruminant feeds (forages and grasses). Over the years, many systems of analysis have been proposed for the replacement of crude fiber, but none have been successful in dislodging Weende procedure as the official method, and it is still used in animal feeding, for example, for quality checking of fiber sources.

Now, these two concepts are converging, and dietary fiber is generally defined as the polysaccharides and associated substances resistant to mammal enzyme digestion and absorption that can be partially or totally fermented in the gut. Champ et al. (2003) provide a concise synopsis of various views regarding the classification of dietary fibers. The overall tendency is toward an extension of the definition by including resistant starches as well as nondigestible oligosaccharides, and it was recently revisited by De Vries (2010) to reach an official enzymatic-gravimetric method that recovers total dietary fiber (TDF) in feeds. However, today, this topic is still subjected to very active research because of the complexity of the physical structure and chemical composition of the plant cell walls, and in the wide and different physiological effects of the different constituents.

The importance of dietary fiber in animal feeding is due to its influence on the passage rate and mucosa functionality, and its role as a substrate for gut microbiota that relates to performances and digestive health (Montagne et al. 2003). Our review will consider briefly the definition and structure of the different classes of fiber and cell wall constituents, followed by a description of some analytical methods employed for animal feeds. In addition, as an example, the nutritional role and impact of fiber intake on digestive health will be described for the growing rabbit, since, as a monogastric herbivore, this animal is a very pertinent research model and is of interest to meat production in Western Mediterranean, Eastern Europe, and Asian countries (China, Vietnam, etc.).
17.2 Plant Cell Wall Polymers in Feeds for Monogastric Animals: Definition, Analysis, and Physicochemical Properties

17.2.1 Definition in Animal Feeding: Dietary Fiber Concept Is Evolving

Briefly recall that the terms “cell wall” and “dietary fiber” refer to a common plant structure, and are often imprecisely used in various contexts. The term “plant cell walls” should be employed when describing the structure of the plant cell, which is extremely complex, and not uniform: the type, size, and shape of the wall are closely linked to the function of the cell within the plant (skeletal tissue, seeds, etc.). The plant cell walls consist of a series of polymers often associated and/or substituted with glycoproteins (extensin), phenolic compounds, and acetic acid, together with, in some cells, the phenolic polymer lignin. Cutin and silica are also found in the walls and/or in the middle lamella. A growing plant cell is gradually enveloped by a primary wall that contains few cellulosic microfibrils and some noncellulosic components, such as pectic substances. During plant ageing, some cells develop a thick secondary cell wall consisting of cellulose embedded in a polysaccharide + lignin matrix (Mc Dougall et al. 1996). Globally, the wall is formed of cellulose microfibrils (the backbone) embedded in a matrix of lignins, hemicelluloses, pectins, and proteins (Figure 17.1).

The concept of dietary fiber is larger than the cell wall botanical definition, since, in animal nutrition, it includes not only the polysaccharides (cellulose, hemicelluloses, pectic substances, etc.) but also oligosaccharides, gums, resistant starch, and inulin. According to their botanical origin, they may be associated with lignins and other noncarbohydrate components (e.g., polyphenols, waxes, saponins, cutin, phytates, and resistant protein). Dietary fiber is often defined by nutritionists as the feed components resistant to mammal enzyme digestion and absorption, and that can be partially or totally fermented in the gut. This “catch-all” definition

![Figure 17.1 Schematic representation of plant cell walls and their main constituents.](image-url)
Polysaccharides thus includes resistant starch, oligosaccharides, fructans, protein linked to the cell wall, and so on (De Vries and Rader 2005). Another approximation is the dietary fiber for polygastric animals defined by Mertens (2003) as the indigestible or slowly digesting organic matter of feeds that occupies space in the gastrointestinal tract, mainly insoluble fiber. It excludes rapidly fermenting and soluble carbohydrates (oligosaccharides, fructans, etc.), and thus seems unsuitable for monogastric animals. Accordingly, depending on the feeds classically used for one animal species or feeding system, the dietary fiber concept differs largely. An even broader definition may include synthetic nondigestible oligosaccharides (DP > 3, fructo-oligosaccharides, polydextrose, etc.). Each definition is convenient for its own paradigm sourcing from the botanical origin of fibers that differed totally according to the final target for their physiological effects: human (legumes, cereals, fruits, etc.), ruminant (forages, straws, etc.), or monogastric animal (brans or by-products of cereals or seeds). For the latter, we will detail the biochemical characteristics of the main sources of dietary fiber in the following section.

### 17.2.2 Biochemical Characteristics of Dietary Fiber

The biochemical features of dietary fiber are highly variable, depending on many factors such as molecular weight, nature of monomers, and type of linkages. Accordingly, the biochemical features of fiber are one of the main factors responsible for variations in their physiological effects, and thus it is of importance to describe them. With the exception of lignin, the cell wall constituents are predominantly polysaccharides composed of neutral and/or acidic sugars.

There are two main groups of dietary fiber components according to their location, chemical structure, and properties (Figures 17.1 and 17.2):

- **Cell wall components**
  - Water-soluble nonstarch polysaccharides (part of β-glucans, arabinoxylans, pectic substances, etc.)
  - Water-insoluble polymers: lignins, cellulose, hemicelluloses, and pectic substances
- **Cytoplasm components**
  - Oligosaccharides, fructans, inulin, resistant starch, and mannans

Water-soluble polysaccharides and oligosaccharides include several classes of molecules with a degree of polymerization ranging from about 15 to more than 2000 (β-glucans). Most of them are insoluble in ethanol (80% v/v). Examples include soluble hemicelluloses such as arabinoxylans (in wheat, oat, and barley ≈ 20–40 g kg$^{-1}$ DM) and β-glucans (in barley or oat ≈ 10–30 g kg$^{-1}$ DM), oligosaccharides such as α-galactosides (in lupin, pea, or soya seeds, 50–80 g kg$^{-1}$ DM), and soluble pectic substances (pulps of fruits or beets, from 100 to 400 g kg$^{-1}$ DM). Because of their highly variable structure,
no satisfactory method is at present available to determine precisely these compounds in animal feeds.

Pectic substances are a group of polysaccharides present in the middle lamellae and closely associated with the primary cell wall, especially in the primary cells (young tissues) of dicotyledonous plants, such as in legume seeds (40–140 g kg$^{-1}$ DM in soybean, pea, faba bean, white lupin), and also in fruits and pulps. Pectic substances correspond to several classes of polymers, including pectins (rhamnogalacturonan backbone and side chains of arabinose and galactose or xylose) and neutral polysaccharides (arabinans, galactans, arabinogalactans) frequently associated with pectins. Their extraction requires the use of a chelating agent such as ammonium oxalate or ethylene diamine tetraacetic acid (EDTA) (present in the solution for determining neutral detergent fiber (NDF), so they are not completely recovered in NDF analysis as described below). Pectins of the middle lamellae serve as an adhesive in plant tissue, cementing plant cells together.

In the cell wall, the cellulose is the major structural polysaccharide and the most widespread polymer on earth. It is a homopolymer (in contrast to hemicelluloses and pectins), formed from linear chains of β[1 → 4]-linked d-glucopyranosyl units (whereas starch is formed of α[1 → 4]-linked d-glucopyranosyl...
The degree of polymerization is usually around 8000–10,000. Individual glucan chains aggregate (hydrogen bonding) to form microfibrils, and could serve as the backbone of the plant. Thus, cellulose is only soluble in a strong acid solution (i.e., 72% sulfuric acid) where it is hydrolyzed. Quantitatively, cellulose represents 400–500 g kg\(^{-1}\) DM in the hulls of legumes and oilseeds, 100–300 g kg\(^{-1}\) DM in forages and beet pulps, and 30–150 g kg\(^{-1}\) DM in oilseeds or legume seeds. Most cereal grains contain small quantities of cellulose (10–50 g kg\(^{-1}\) DM) except in oats (100 g kg\(^{-1}\) DM).

The hemicelluloses are a group of several polysaccharides, with a lower degree of polymerization than cellulose. They have a \(\beta[1 \to 4]\)-linked backbone of xylose, mannose, or glucose residues that can form extensive hydrogen bonds with cellulose. Xyloglucans are the major hemicelluloses of the primary cell wall in dicotyledonous plants (in vegetables, in seeds), whereas mixed linked glucans (\(\beta[1 \to 3,4]\)) and arabinoxylans are the predominant hemicelluloses in cereal seeds (the latter two include partly water-soluble and water-insoluble polymers, described above). Hemicelluloses include other branched heteropolymers (units linked \(\beta[1 \to 3]\), \(\beta[1 \to 6]\), \(\alpha[1 \to 4]\), \(\alpha[1 \to 3]\)) such as highly branched arabinogalactans (in soybean), galactomannans (seeds of legumes), or glucomannans. Polymers formed of linear chains of pentose (linked \(\beta[1 \to 4]\)) such as xylans (in secondary walls), or hexose such as mannans (in palm kernel meal) are also considered as hemicelluloses. Pentosans such as xylans and arabinoxylans are soluble in weak basic solutions (5–10%), or in hot dilute acids (5% sulfuric acid). Hexosans such as mannans, glucomannans, or galactans can only be dissolved in strong basic solutions (17–24%). Quantitatively, hemicelluloses constitute 100–250 g kg\(^{-1}\) of the DM in forages and agro-industrial byproducts (brans, oilseeds, and legume seeds, hulls, and pulps) and about 20–120 g kg\(^{-1}\) DM of grains and roots.

Lignins are polyphenolic compounds of the cell wall. They can be described as highly branched and complex three-dimensional network (high molecular weight), built up from three phenylpropane units (conyferilic, coumarilic, and sinapylic acids). A lignin network tends to fix the other polymers in place, exclude water and make the cell wall more rigid and resistant to various agents, such as bacterial enzymes. Most concentrate feeds and young forages contain less than 50 g lignin kg\(^{-1}\). The degree of lignifications of the plant cell wall may reach 120 g kg\(^{-1}\) with ageing in forages, or up to 590 g kg\(^{-1}\) in grape seed meal.

Other constituents are also present in cell walls, but frequently in smaller quantities. Minerals, such as silica, are essentially in graminaceous leaves. Phenolic acids are chemically linked to hemicelluloses and lignin in graminaceous plants. Some proteins are linked to cell walls through intermolecular bonds from amino acids such as tyrosine, and thus resist standard extractions. In addition, plant epidermal cells may be covered by a complex lipid (cutin for aerial parts, suberin for underground structures), which could encrust and embed the cell walls, making them impermeable to water. Other
phenolic compounds can also be mentioned, that is, condensed tannins, which may exist in higher plants. They form cross-linkages with protein and other molecules. They could be included in the sum of indigestible polysaccharides + lignin. However, condensed tannins, lignins, and indigestible proteins are closely related because indigestible complexes of these substances are common in plants (Van Soest 1994).

17.2.3 Methods for Fractionating and Estimating Dietary Fiber Fractions in Animal Feeds

Because of the wide diversity of plant cell types, and of cell walls accordingly, that constitutes the different plant tissues, it implies that the quantitative analysis of the different fiber fractions could be only approached by a combination of methods. The fractionation methods are thus varied and were developed according to the material tested. There is no global method used, and the choice of the method to investigate the fiber depends on the composition of each particular dietary fiber fraction. Detailed reviews have been published on this subject (De Vries and Rader 2005, Hall 2003, Mertens 2003). The methods mentioned here (Figure 17.2) describe the techniques of fractionation that are sufficiently precise and pertinent in a “routine” laboratory in charge of controlling the quality of the feed sources and give chemical parameters for implementing the databases for feed formulation.

17.2.3.1 Crude Fiber and Dietary Fiber Fractionation with Van Soest Procedures

The crude fiber method (AOAC 962.10) must be mentioned because it is highly reproducible, quick, simple, cheap, and frequently used all over the world. This technique extracts a fibrous residue after an acidic hydrolysis followed by a basic hydrolysis. The main drawback of crude fiber lies in the high variability in the chemical composition of its residue, as depending on the feed, it can dissolve up to 60% cellulose, 80% pentosans, and 95% lignin. For these reasons, this criterion is not able to explain the physiological effects exerted by most of the fiber sources on the animal digestive physiology. Since the crude fiber criterion is cheap and precise, it is commonly used to verify the lignocellulose concentration of a raw material to be compared with values in tables of feed composition.

The main alternative to crude fiber is the sequential procedure of Van Soest developed in 1967 and successively updated (Mertens 2003). The NDF method was designed to isolate insoluble dietary fiber (IDF) components in the plant cell walls by using a hot neutral detergent solution: cellulose, hemicelluloses, and lignins (Mertens et al. 2002), as pectin substances are partially solubilized. This method is criticized due to its variability among laboratories, especially when it is compared with the results obtained with other feed constituents. It is partially due to the different procedures that can be used to perform it (with heat-stable amylase and/or sodium sulfite or not, ash-free or not), but usually described with the same reference (Uden et al. 2005). The acid detergent fiber
Polysaccharides (ADF) (AOAC 973.18) method isolates cellulose and lignin, the worst digested fibrous fractions, by a hot acid detergent solution. For complex feeds (such as for monogastrics), it is designed to be done after NDF analysis, as if it is performed directly it also retain pectins. As crude fiber, it was used to predict dietary energy value for some species, such as pigs or rabbits (Wiseman et al. 1992). Final step is the isolation of the acid detergent lignin (ADL) residue by using a strong acid solution at room temperature (Robertson and Van Soest 1981) which correspond to the lignin fraction. The main advantages of this sequential methodology are that is possible to obtain an approximate estimation of lignin (ADL), cellulose (ADF-ADL), and hemicelluloses (NDF-ADF) content, and that it is relatively quick, simple, and economical, and has an acceptable reproducibility when used a standardized methodology (EGRAN, 2001) and improves the fractionation of the cell wall.

These methods have been complemented by the estimation of the fiber dissolved by the neutral detergent solution (NDSF: neutral detergent soluble fiber; Hall et al. 1997) that mainly includes fructans, galactans, β-glucans, and pectic substances. The NDSF is obtained gravimetrically as the difference between ethanol/water insoluble residue and starch and NDF after correction for protein and ash. Therefore, the NDSF measurement may be affected by the accumulation of errors in the measurement of the different components, as well as the error linked to the value used for protein correction (Hall 2003). Now, the determination of NDSF is not adapted for routine analysis in animal feeding.

17.2.3.2 Concepts of Water-Insoluble Cell Wall, Total Dietary Fiber, and Soluble Dietary Fiber Parallel to the difficulties to estimate the water-soluble polysaccharides, the concept of dietary fiber has emerged, first in human nutrition, and has now been extended to other mammals (De Vries 2010, Trowell 1978), and assayed in the feeding of monogastric animals, such as rabbits, because of the high dietary fiber content (>50%). For instance, in poultry feeding, the concept of water-insoluble cell wall (WICW) (Figure 17.2) was developed to simply and precisely predict the metabolizable energy content of a feed (Carré 1990). WICW is a criterion obtained through a simple enzymatic-gravimetric procedure. It corresponds to lignins and polysaccharides that are water-insoluble (Carré and Brillouet 1989) and not digested by poultry.

Currently, TDF is primarily analyzed by enzymatic-gravimetric methods based on AOAC procedures 985.29 and 991.43 that solubilize the different fiber fractions with enzymes and solvents and measure the weight of residues after these treatments (reviewed by Bach Knudsen 2001, De Vries 2010, Elleuch et al. 2011). Recently, these procedures (Figure 17.2) have been updated to include nondigestible oligosaccharides and resistant starch (Mc Cleary et al. 2010). IDF could be quantified by the above-mentioned AOAC method for TDF, by avoiding the recovery of water-soluble structural polysaccharides. IDF should correspond to polysaccharides that are slowly hydrolyzed and
fermented in the gut, that is, mostly lignins (indigestible), hemicelluloses, and cellulose. Conversely, IDF should not include “soluble” polysaccharides, which are rapidly fermented (e.g., pectins and β-glucans), and highly digested (at similar levels compared to starch or proteins).

When calculating the difference between the residual TDF and any measurement of “insoluble fiber” (NDF, WICW, etc.), you can estimate this “soluble” fiber fraction content (SDF). According to Van Soest et al. (1991), “soluble fiber” may be obtained by subtracting the content of NDF after correction for ash and protein from the TDF value, thus including nonstarch polysaccharides (NSP), that is, fructans, galactans, β-glucans, and pectins. One of the problems for calculating a difference between two methods (e.g., TDF and NDF) is that for some raw materials we obtained negative values (such as for sunflower meals, Table 17.1). Soluble fiber content may also be calculated by difference as organic matter–(protein + fat + soluble sugars + starch + NDF).

It is also possible to determine “directly” the soluble fiber content of a feed according to the AOAC Prosky enzymatic-gravimetric procedure (AOAC procedure 993.19, Megazyme 2005, Prosky et al. 1992); the carbohydrates are solubilized in phosphate buffer or MES (4-morpholine-ethanol sulfonic acid)/TRIS buffer; α-glucans are hydrolyzed by amyloglucosidase; insoluble fiber is separated by filtration; solubilized dietary fiber is precipitated with an ethanol solution from the solvent extract and measured gravimetrically after correction for protein and ash contents. Inaccuracies in the SDF determination may arise from the partial degradation of carbohydrates, the incomplete extraction and/or precipitation with the addition of ethanol, the interference by other substances, and differences in the nature of the analyzed feed (Hall et al. 1997, Theander et al. 1994).

Besides, let us recall that for a biochemist the solubility of polysaccharide is related to its structure; they can be set regularly (insoluble) or irregularly (soluble) on the backbone or as side chains. For example, the presence of a substitution group such as COOH increases solubility. But since the soluble and insoluble nature of dietary fibers involves differences in their technological functionality and physiological effects, the term “soluble” is frequently indifferently used for biochemical or physiological properties, and this provides some confusion for nonadvertised readers.

17.2.3.3 Other Approaches for Cell Wall Polysaccharide Analysis

Another approach is to estimate dietary fiber from the sum “NSP + lignin.” There are several methods available to estimate total, soluble, and insoluble NSP (Bach Knudsen 2001, De Vries and Rader 2005), where the nonfibrous components are extracted by solubilization, by enzymatic hydrolysis, or by combining both procedures. Once isolated, the fiber residue can be quantified gravimetrically (weighing the residue) or chemically (hydrolyzing the residue and determining its single constituents: sugars and lignin). According to these procedures, there are three types of methodologies: chemical-gravimetric,
• Polysaccharides

By this way, TDF can be quantified (NSP and lignin) and separated into insoluble and soluble fiber (in aqueous solution), and its monosaccharide composition is obtained. The combination of the monosaccharide composition of fiber with additional chemical information may allow describing better fiber structure that influences its physicochemical properties, and accordingly, the effect exerted in the animal on the digestive physiology and digestibility. However, these methodologies are complex, expensive, with a relatively low reproducibility (especially for monomers determination), and are difficult to implement as routine analysis.

Table 17.1  Cell Wall Constituents (% DM) According to Several Methods of Analysis in Some Raw Materials Used in Rabbit Feeds

<table>
<thead>
<tr>
<th>Ingredients</th>
<th>Wheat Straw</th>
<th>Wheat Bran</th>
<th>Dehydrated</th>
<th>Sugar</th>
<th>Sunflower Meal</th>
<th>Soybean Hulls</th>
<th>Grape Pomace</th>
</tr>
</thead>
<tbody>
<tr>
<td>aNDFom(^a)</td>
<td>80</td>
<td>45</td>
<td>45</td>
<td>46</td>
<td>42</td>
<td>62</td>
<td>64</td>
</tr>
<tr>
<td>ADFom(^b)</td>
<td>54</td>
<td>11</td>
<td>34</td>
<td>22</td>
<td>31</td>
<td>44</td>
<td>54</td>
</tr>
<tr>
<td>ADL(^c)</td>
<td>16</td>
<td>3</td>
<td>8</td>
<td>2</td>
<td>10</td>
<td>2</td>
<td>34</td>
</tr>
<tr>
<td>NDSF(^d)</td>
<td>—</td>
<td>3</td>
<td>18</td>
<td>30</td>
<td>22</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Crude fiber(^e)</td>
<td>40</td>
<td>10</td>
<td>27</td>
<td>19</td>
<td>26</td>
<td>36</td>
<td>26</td>
</tr>
<tr>
<td>WICW(^f)</td>
<td>84</td>
<td>45</td>
<td>47</td>
<td>58</td>
<td>39</td>
<td>72</td>
<td>69</td>
</tr>
<tr>
<td>TDF(^g)</td>
<td>85</td>
<td>46</td>
<td>48</td>
<td>68</td>
<td>41</td>
<td>—</td>
<td>72</td>
</tr>
<tr>
<td>IDF(^h)</td>
<td>82</td>
<td>45</td>
<td>42</td>
<td>55</td>
<td>37</td>
<td>—</td>
<td>68</td>
</tr>
<tr>
<td>INSP(^i)</td>
<td>55</td>
<td>36</td>
<td>33</td>
<td>64</td>
<td>26</td>
<td>55</td>
<td>36</td>
</tr>
<tr>
<td>Rhamnose</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>11</td>
<td>&lt;1</td>
<td>11</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Arabinose</td>
<td>2</td>
<td>8</td>
<td>2</td>
<td>18</td>
<td>3</td>
<td>4</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Xylose</td>
<td>18</td>
<td>16</td>
<td>6</td>
<td>2</td>
<td>5</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td>Mannose</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>1</td>
<td>1</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>Galactose</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Glucose</td>
<td>33</td>
<td>9</td>
<td>19</td>
<td>19</td>
<td>11</td>
<td>29</td>
<td>19</td>
</tr>
<tr>
<td>Uronic acids</td>
<td>2</td>
<td>2</td>
<td>7</td>
<td>18</td>
<td>5</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>SNSP(^j)</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>10</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Crude protein</td>
<td>3</td>
<td>15</td>
<td>16</td>
<td>9</td>
<td>34</td>
<td>11</td>
<td>13</td>
</tr>
</tbody>
</table>

\(^a\) Neutral detergent fiber assayed with a heat-stable amylase and expressed free of ash.
\(^b\) Acid detergent fiber expressed free of ash.
\(^c\) Acid detergent lignin (Van Soest et al. 1991).
\(^d\) NDSF, neutral detergent soluble fiber (Hall et al. 1997, Hall 2003).
\(^e\) According to the Weende method (AOAC procedure 993.19: official method 962.10).
\(^f\) Water-insoluble cell wall, including lignin (Carré and Brillouet 1989).
\(^g\) Mc Cleary et al. (2010).
\(^h\) Insoluble nonstarch polysaccharides, not including lignin, determined by direct monomeric analysis of cell wall polysaccharides (Englyst 1989, Barry et al. 1990).
\(^i\) Water-soluble nonstarch polysaccharides (Brillouet et al. 1988, Englyst 1989).
17.2.3.4 Conclusions about Methods for Fiber Analysis  The determination of the fiber content of a compound feed or a raw material is highly variable, depending on the analytical method of estimation. The choice of which definition should be used by the nutritionist thus depends on the type of information required (to relate to digestive processes, to predict the nutritive value).

They can be determined using sophisticated extraction techniques, and examples of their concentration in some feedstuffs are given in Table 17.1.

Finally, the enzymatic-gravimetric determination using the Van Soest procedures is still (NDF, ADF, ADL) the most simple, low-cost, rapid, and reproducible method, for analyzing the fiber fractions that are slowly digested in the gut. Now, to examine the effects of the highly digested fractions of the dietary fiber (water-insoluble pectins, β-glucanes, water-soluble pectins, oligosaccharides, etc.), new criteria are assayed. One approach is to estimate this “soluble” fraction by difference, from TDF and another criterion for insoluble fiber (NDF, etc.). Although these “soluble” fiber fractions remain hard to analyze in the feed, their effects on the digestive physiology of the animal are presently subjected to much research, and the results are summarized for the rabbit in the following section.

17.3 Nutritional Role of Dietary Fiber for Growing Rabbit

Plant polymers are the major fraction in rabbit diets and account classically for at least 40–50% (Table 17.2). The importance of fiber is due to its influence on intake, rate of passage, and its role as a substrate for microbiota. But, for the growing rabbit, one of the main challenges is to provide fiber recommendations for the prevention of digestive troubles without too large an impairment in performance (growth, feed efficiency).

The concepts of dietary fiber, fiber quantification, and characterization of the different fractions have thus been largely discussed, and have promoted changes in fiber recommendations for the growing rabbit.

17.3.1 Fiber Level in the Feed and Intake Regulation

One of the main dietary components implicated in feed intake regulation, after weaning, is the digestible energy (DE) concentration. The domestic rabbit (fed a pelleted balanced diet) is able to regulate its DE intake (and thus its growth) when the dietary DE concentration is between 9 and 11.5 MJ kg⁻¹ (Figure 17.3). But a higher correlation is obtained with the lignocellulose level of the diet, when the dietary fiber level is between 10% and 25% ADF. However, the incorporation of fat into the diet, while maintaining the dietary fiber level, increases the dietary DE level, but leads to a slight reduction in the intake.

Finally, the voluntary feed intake is more related to the dietary ADF level because of the low digestion of this fraction, and probably because the ADF level also corresponds to a “ballast” value that limits the intake. For
### Table 17.2  Fiber Levels and Other Main Constituents in Commercial Pelleted Feeds Used for the Growing Rabbit in Conventional Breeding

<table>
<thead>
<tr>
<th>Chemical Criteria (g kg⁻¹ as Fed)</th>
<th>Mean Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total dietary fiber (TDF)</td>
<td>450–600</td>
</tr>
<tr>
<td>Neutral detergent fiber (aNDFom)</td>
<td>280–460</td>
</tr>
<tr>
<td>Acid detergent fiber (ADFom)</td>
<td>150–230</td>
</tr>
<tr>
<td>Acid detergent lignin (ADL)</td>
<td>35–65</td>
</tr>
<tr>
<td>Crude fiber</td>
<td>120–180</td>
</tr>
<tr>
<td>Soluble fiber⁺</td>
<td>35–120</td>
</tr>
</tbody>
</table>

**Other Constituents**

<table>
<thead>
<tr>
<th>Other Constituents</th>
<th>Mean Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Starch</td>
<td>80–130</td>
</tr>
<tr>
<td>Sugars</td>
<td>30–60</td>
</tr>
<tr>
<td>Crude protein</td>
<td>140–190</td>
</tr>
<tr>
<td>Ether extract</td>
<td>20–40</td>
</tr>
</tbody>
</table>


⁺ McCleary et al. (2010).

⁻ Calculated as OM-CP-EE-aNDFom-starch-sugars.

---

**Figure 17.3**  Voluntary feed intake of the rabbit, after weaning, according to the ADF or the digestible energy content of a pelleted feed. DFI: daily feed intake measured between weaning (4 weeks) and 11 weeks of age.

\[
y = -0.029x + 186.6 \\
R^2 = 0.65
\]

\[
y = -0.079x^2 + 5.05x + 49.0 \\
R^2 = 0.92
\]
instance, the replacement of starch with digestible fiber fractions (hemi-celluloses or pectins), without changing the ADF level, did not greatly affect the intake (Gidenne et al. 2004, Perez et al. 2000). Further research is required to assay the effects of other fiber fractions, such as the most “soluble” ones.

In return, when the dietary fiber level is very high (>25% ADF), the animal cannot increase its intake sufficiently to meet its energetic needs, thus leading to a lower growth rate, but without digestive problems.

17.3.2 Fiber Digestion in Rabbit: A Main Source of Energy through Microbial Activity

It is acknowledged that polysaccharides of the cell wall are hydrolyzed and then fermented only by bacterial enzymes. Accordingly, in monogastric mammals, fiber became an energy source only from the activity of the microbiota, which takes place mainly in the large intestine: the cecum and proximal colon for the rabbit. However, the extent of the fiber digestion is rather different according to the fraction, ranging from 10% for cellulose to 90% for soluble fiber (TDF-NDF). Obviously, the digestion of fiber is lower than that of protein or starch, and increasing the dietary fiber level led to a reduction in the digestive efficiency.

For the adult rabbit that is fed a high-fiber diet, the energy provided by the cecal volatile fatty acid (VFA) absorption could represent up to 50% of the maintenance energy (Gidenne 1994, Marty and Vernay 1984). But increasing the fiber intake (and lowering that of starch) either increases or has no effect on the fibrolytic activity and cecal VFA concentration (ranging from 80 to 100 mM), while a lower butyrate molar proportion is generally registered. Since the fiber digestibility is frequently not affected by the dietary fiber concentration, it may be assumed that the quantity of fiber entering the cecum is not a limiting factor for the fermentation processes, as the digesta retention time in the cecum is relatively short, allowing, predominantly, degradation of the more easily digestible fiber fractions such as pectins or hemicelluloses. The quality of fiber, particularly their fermentability, is able to modulate the microbial activity. For instance, increasing the levels of pectins through the incorporation of beet pulps in a diet increases the VFA concentration in the cecum. In a collaborative study, García et al. (2002) reported that the cecal VFA level decreased with the degree of lignification of NDF, and that the dietary uronic acids concentration (provided mainly by pulps) is positively correlated to the cecal VFA and pH. In association with changes in microbial activity, it is suspected that the dietary fiber supply would be able to modulate the microbial population balance, as suggested by Combes et al. (2013).

Though, the extent of fiber degradation is ultimately determined by the time necessary for the microbiota to hydrolyze and ferment polysaccharides. Because the retention time in the ceco-colic segment of the rabbit is
relatively short (8–12 h, Gidenne 1997), only the most rapidly fermentable cell wall polysaccharides are highly digested (pectins, soluble fiber fractions, etc.), whereas lignocellulose is degraded only to a small extent. For instance, when wheat bran and beet pulp replace starch (with constant level of ADF), the whole tract digestibility of the diet was not reduced (Gidenne and Bellier 2000, Gidenne and Perez 2000). The utilization for the growth of this fiber fraction is particularly high and comparable to that of starch, since the replacement in a complete diet of 10 points of starch by hemicelluloses (NDF-ADF) and pectins does not affect the feed efficiency in the growing rabbit (Gidenne and Perez 2000).

However, it must be stated that for some diets, the level of digestible cellulose is higher than that of digestible hemicelluloses. Lignins and cutin are considered almost totally nondegradable, although positive values for lignin digestibility have been obtained, which might indicate a solubilization rather than digestion. In rabbit feeding, the two main raw materials that increase the digestible hemicelluloses level in the diet are sugar beet pulp (low lignified and with a high hemicelluloses/cellulose ratio, 1.1 compared to alfalfa, 0.4) and wheat bran (with the highest hemicelluloses/cellulose ratio, 3.2). Uronic acids, an important constituent of pectins (and depending on the source of fiber also of hemicelluloses) and more soluble than other cell wall components, are the substrates that are more easily fermented. It would suggest that other components of soluble fiber (pentosans, mannans, galactans, etc.) might have a similar or even higher degradability than uronic acids.

While the fibers are mainly degraded in the large intestine, there are some evidences that some components of structural carbohydrates are degraded prior to entering the cecum of rabbits. This has also been observed in other nonruminant species such as pigs and poultry. The extent of prececal fiber digestion in rabbits varies from 5% to 43% for NDF (Gidenne and Ruckebusch 1989, Merino and Carabaño 1992) and from 0% to 37% for NSP (Carabaño et al. 2001, Gidenne 1992). It must be pointed out that the values obtained using NDF with respect to those obtained with NSP might be overestimated due to solubilization and filtration of cell wall components, which would be considered digested. When NSP were analyzed, it was found that arabinose and uronic acids, typical monomers of pectic substances, were largely digested before the ileum (from 0.2 to 0.5). On the contrary, glucose and xylose, the major monomers in most fiber sources, showed a much lower ileal digestibility (0–0.2). These results imply that around 0.4 (from 0.2 to 0.8) of total digestible fiber (including water-soluble NSP) is degraded before the cecum, which is similar to that observed in pigs (Bach Knudsen 2001). It could be explained from the cecotrophy practice of the rabbit: soft feces very rich in live microbiota are ingested daily and thus would provide fibrolytic enzymes that have been observed in the stomach and the small intestine (Marounek et al. 1995).
17.3.3 Role of Dietary Fiber in the Rabbit Cecal Ecosystem

Most of the effects exerted by fiber on the rabbit digestive physiology depend on their hydrolysis and fermentation by the digestive microbiota. However, it is difficult to study the influence of any dietary component on the microbiota, as the traditional cultivation techniques allow to work with around one-fourth of the intestinal microbiota. For this reason, other indirect techniques have been used as the volatile fatty acid concentration, the microbial nitrogen synthesized, or the fibrolytic activity. The cecal microbial population secretes enzymes capable of hydrolyzing the main components of the dietary fiber. Greater enzymatic activity for degrading pectins and hemicelluloses than for degrading cellulose has been detected in several studies (Jehl and Gidenne 1996, Marounek et al. 1995). These results are parallel to the fecal digestibility of the corresponding dietary fiber constituents in rabbits (Table 17.3), and are also consistent with the smaller counts of cellulolytic bacteria in the rabbit cecum as compared to xylanolytic or pectinolytic bacteria (Boulahrouf et al. 1991).

The cecal VFA profile is specific to the rabbit, with a predominance of acetate (77 mmol 100 mL\(^{-1}\) as average, and ranging from 65 to 87) followed by butyrate (17 mmol 100 mL\(^{-1}\) as average, and ranging from 6 to 28) and then by propionate (6 mmol 100 mL\(^{-1}\) as average, and ranging from 3 to 11). These molar proportions are affected by the fiber level. For instance, the proportion of acetate increases and that of butyrate generally decreases significantly when the fiber level increases, whereas propionic acid proportion was only positively correlated to dietary uronic acid concentration (García et al. 2002).

However, these indirect methods in many circumstances do not seem to reflect adequately the changes produced in the microbiota population. The development of new molecular tools to characterize intestinal microbiota is improving our knowledge about nutrition and digestive microbiota functions in relation to fiber intake. For instance, the cecal microbiota is able to adapt very quickly (within 1 week) to a change in the dietary fiber level (Michelland et al. 2011). Further studies are presently conducted using high-throughput sequencing of the 16S rDNA and would provide new data about the relationship between microbiota and dietary fiber (Combes et al. 2013).

<table>
<thead>
<tr>
<th>Dietary Fiber Criteria</th>
<th>Mean Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neutral detergent fiber (aNDFom)</td>
<td>10–50</td>
</tr>
<tr>
<td>Uronic acids</td>
<td>30–85</td>
</tr>
<tr>
<td>Soluble fiber (TDF-aNDFom)</td>
<td>70–90</td>
</tr>
<tr>
<td>Hemicelluloses (aNDFom-ADF)</td>
<td>15–60</td>
</tr>
<tr>
<td>Cellulose (ADFom-ADL)</td>
<td>5–25</td>
</tr>
<tr>
<td>Lignin (ADL)</td>
<td>−15–15</td>
</tr>
</tbody>
</table>
17.3.4 Role of Dietary Fiber in the Digestive Health of Young Rabbit

Among the various health troubles related to feeding, the intestinal pathology along with respiratory diseases are the predominant causes of morbidity and mortality in commercial rabbit husbandry. The first of the two mainly occurs in young rabbits, after weaning (4–10 weeks of age), while the second one preferentially affects the adults. In France, enteritis in the growing rabbit induced a mortality rate of 11–12%, even with antibiotherapy strategies. Moreover, digestive disorders are responsible for important morbidity characterized by growth depression and bad feed conversion, and constitute a priority problem to be solved. Till the 1980s, only the crude fiber criterion was used to define the fiber requirements for the growing rabbit, and the value ranges from 6% to 18% according to the authors. Consequently, the precise assessment of the fiber requirements with more “adequate” criteria is essential to reach a low risk of digestive troubles without a too large impairment of the growth and feed efficiency.

17.3.4.1 What Is Digestive Health and How to Measure It?  

The term “digestive health” thus covers all the parameters that enable the animal to maintain its intestinal balance, in response to various factors such as nutrient intake or exogenous microorganisms. If the digestive balance is not maintained, troubles could appear, such as diarrhea in the young mammal (piglet, rabbit around the weaning period), either because of gut colonization by an identified pathogen (e.g., \textit{E. coli}) or from a multifactorial origin.

However, within a group of young rabbits, animals differently developed the clinical symptoms (diarrhea, impaction) and not all the sick animals died. Several mechanisms of defense could explain the variability in the disease sensibility, such as the gut barrier function and the competitive exclusion between saprophyte and pathogen bacteria. Nutrition and feeding strategies also play an important role in digestive health, in supplying the adequate nutrient quantity and quality to improve (i) mucosa integrity and immune response (avoiding pathogen attachment and colonization) and (ii) the growth/stability of the commensal microbiota (barrier effect).

To develop accurate nutritional strategies, it is necessary to identify the specific nutrients or bioactive components in feeds (or milk) that enhance these mechanisms of defense. These nutritional strategies must be focused around the weaning period, since it is a critical phase for the sensibility to digestive diseases, probably linked to the processes of digestive maturation, including the development of microbiota and the immune system.

The traditional indicator to evaluate the impact of a disease in groups of young domestic mammals is the mortality rate. More recently, a morbidity indicator was developed to assess more precisely the incidence of the clinical symptoms for the growing rabbit (Gidenne 1997), and it could be combined with mortality to obtain the health risk index (“HRi” = morbidity + mortality rate). This approach allows a more precise assessment of the health status.
But these traits show large variations according to many factors. For instance, the mortality rate of rabbits fed the same diet could range from 0% up to 70% according to various factors, such as the litter effect, preventive medication, and age at weaning. Thus, it means that a large number of animals are required to detect a significant difference between two treatments in mortality. For instance, to detect a 5% deviation among two mortality rates, more than 300 animals are required in each group.

When the clinical symptoms (diarrhea, cecal impaction, stomachal borborigmus, etc.) are clear, the morbidity rate is relatively easy to measure but it depends on the frequency of the measurements within a time period. For instance, if the morbidity is checked daily, the measure is more precise and gives a higher value compared to a weekly control (Bennegadi et al. 2001). However, when only a reduction of the growth rate is detectable, a threshold must be defined to class the animal as morbid or not, such that the average minus $2 \times$ standard deviation (signifying the 2.5% of the animals with lower growth rate), or up to 3 SD. But it needs to use a large set of rabbits within a group to define precisely the mean and its range of variation. Moreover, it must be outlined that adequate statistical methods are necessary to treat discrete data (such as mortality or morbidity). For instance, when analyzing models with more than one factor or including more than two levels (within a factor) or to test the interaction between two factors, specific categorical analysis based on a weighted least square analysis must be used instead of a simple Chi square test.

17.3.4.2 Relevance of Fiber Intake Compared to Starch in the Prevention of Digestive Disease Many experiments have been performed to elicit the respective effects of fiber and starch on the incidence of diarrhea in the growing rabbit, but most of them compared variations of the fiber:starch ratio, since, in complete feed formulation, one nutrient is substituted for another one.

Consequently, when a study reported a positive effect of an increased dietary fiber intake on the digestive health, it was in fact difficult to exclude that there was also an effect of a reduced starch intake.

We thus have to deal with two opposite hypotheses: are digestive troubles linked to a carbohydrate overload in the cecum? Or linked to a fiber deficiency? (Or both?). Recently, this question was elicited by studying the ileal flow of starch and fiber in the growing rabbit (5–9 weeks old). With high-starch diets ($\geq 30\%$ starch mainly from wheat), the ileal starch digestibility was very high ($>97\%$), the flow of starch remained under 2 g day$^{-1}$ (intake $\approx 30$ g day$^{-1}$) at the ileum, while that of fiber was at least 10 times higher ($\approx 20$ g NDF day$^{-1}$) (Gidenne et al. 2000). Thus, an overload of starch appears very unlikely since starch digestion was very efficient already at 5 weeks old. Moreover, a large-scale study using a network of six experimental breeding units (GEC French group) demonstrated through a $2 \times 2$ factorial design
Polysaccharides

(two level of starch “12 vs. 19%” combined with two ADF levels “15 vs. 19%”) that only the fiber level plays a role in digestive trouble occurrence, and not the starch level (Gidenne et al. 2004). Furthermore, by comparing iso-fiber diets but with several starch sources varying in their intestinal digestion (maize, wheat, barley), Gidenne et al. (2005) observed no effect of starch ileal flow on diarrhea incidence in the weaned rabbit. Fiber intake thus plays a major role in determining digestive trouble in the classically weaned rabbit (28–35 days old).

Accordingly, several large-scale studies aimed to validate clearly the relationship between dietary fiber/starch levels and diarrhea incidence for the “classically” weaned rabbit, using an experimental design with a high number of animals per treatment. The relationship between low-fiber diets (<14% ADF) and a higher incidence of diarrhea was clearly established in two studies where the quality of fiber, for example, the proportions of fiber fractions as analyzed through the Van Soest procedure, has been controlled (Bennegadi et al. 2001, Blas et al. 1994). In France, the GEC group performed several large-scale studies (using at least 300 animals per treatment and five experimental sites) to determine the precise fiber recommendations for the prevention of digestive troubles in the growing rabbit. The relevance of Van Soest criteria was studied, since the crude fiber method was too imprecise for this purpose.

17.3.4.3 Primary Importance of Cellulose and Lignins Intake: Impact of Quantity and Quality of the Lignocellulose

The favorable effect of ADF supply on the frequency of the digestive disorders and mortality in fattening rabbits was first shown by Maître et al. (1990) using a large-scale design (380 rabbit/diet, in five sites). With a similar design, Gidenne et al. (2004) showed that the health risk index (HRi = mortality + morbidity) increased from 18% to 28% when the dietary ADF content decreased from 19% to 15%.

However, in a second step to improve fiber recommendations, the following question was examined: is a single criterion, such as the supply of lignocellulose, sufficient to define the fiber contributions and the “level of security” of a feed for the growing rabbit? Apart from the quantity of lignocellulose, other studies assessed if the quality of the ADF, that is, the respective effects of lignins and cellulose (according to the Van Soest procedure), had an impact on digestive health.

The nutritional role of lignins was first addressed (Gidenne and Perez 1994, Perez et al. 1994). The intake of lignins (criterion is ADL) involves a sharp reduction of the feed digestibility (Figure 17.4, slope = −1.6), associated with a reduction of the digesta retention time in the whole tract (−20%), and with a rise of the feed conversion ratio. For the latter, the botanical origin of lignins seems to modulate the effects observed. In parallel, a linear relationship ($R^2 = 0.99$; Figure 17.4, n = 5 feeds) between an ADL and mortality by diarrhea was outlined for the first time (without major effect of the botanical origin of lignins).
Figure 17.4 Nutritional role of lignins and cellulose in the growing rabbit.
The favorable relationship between the dietary ADL level and the HRi was then confirmed with other experiments, as shown in Figure 17.5. The effects of cellulose intake are less important than for ADL regarding the decrease of the digestibility (Figure 17.4, slope = −1) or that of retention time (Gidenne and Perez 1996, Perez et al. 1996). The cellulose (ADF-ADL) also favors digestive health. However, lignins play a specific role since an increase of the ratio lignins/cellulose (L/C) is associated with a lower HRi (Gidenne et al. 2001). Globally, the lignin requirement (ADL) for the growing rabbit can be assumed to be 5–7 g day$^{-1}$, and that of cellulose from ~11 to 12 g day$^{-1}$. However, to date, no correct and quick analytical method for lignins is available. Consequently, estimating the amount of lignins in a raw material remains difficult, particularly in tannin-rich ingredients (grape marc, etc.), and caution must be taken to fit requirements.

17.3.4.4 Effects of Fiber Fractions More Digestible than Lignocellulose

A third step in evaluating the fiber requirements for the growing rabbit was to test the following hypothesis: apart from quantity and quality of ADF, is it necessary to specify the effects of more digestible fibers, such as hemicelluloses and pectins or “soluble fiber” (Table 17.3)?

A first approach is to estimate the fiber fraction that is relatively digestible and in a relatively high proportion in feeds (to reduce the analytical error), then to measure the relationship with the digestive health. Digestible fiber “DgF” fraction could be estimated by the sum of the two fractions of hemicelluloses (NDF-ADF, according to the sequential procedure of Van Soest) and water-insoluble pectins. The procedure of the analysis of water-insoluble pectins remains complex; it is nevertheless possible to estimate their value in...
ingredients from the literature or tables (Bach Knudsen 1997, Maertens et al. 2002). Compared to lignocellulose, the DgF fraction is highly well digested by the rabbit (35–50%, Gidenne 1997).

Although the digestive health of the classically weaned rabbit depends on the level and quality of lignocellulose, it also varies greatly for the same ADF level (Figure 17.6) because the level of more digestible fiber fractions “DgF,” that is, [hemicelluloses (NDF-ADF) + water-insoluble pectins], could also vary independently of lignin and cellulose levels. For instance, the ratio DgF/ADF ranged from 0.9 to 1.7 in Figure 17.6. The DgF fraction would play a key role in digestive efficiency and for digestive health, since it is rapidly fermented (compared to ADF), in a delay compatible with the retention time of the ceco-colic segment (9–13 h, Gidenne 1997).

Without changes in ADF dietary level, digestive troubles are rather reduced when DgF replaces starch (Gidenne et al. 2004, Perez et al. 2000). This could originate from the favorable effect of DgF (compare to starch) on cecal fermentative activity (García et al. 2002), and possibly from their moderate effect on the rate of passage (Gidenne et al. 2004).

For the same set of diets as in Figure 17.6, but with an ADF level over 15%, we observed a very close relationship ($R^2 = 0.88$) between the ratio DgF/ADF and the HRi (Figure 17.7). A too high incorporation of DgF with respect to lignins and cellulose should be avoided to minimize the health risk index during fattening. It is thus recommended that the ratio DgF/ADF remain under 1.3 for diets having an ADF level over 15% (see Table 17.4). Therefore, a balanced supply of low- and high-digested fiber fractions is required to reduce the risk of digestive trouble for the rabbit after weaning.

**Figure 17.6** The risk of digestive trouble (HRi) in the growing rabbit is jointly dependent on low-digested “ADF” and digestible fiber “DgF.” ADF, lignocellulose (Van Soest sequential procedure, EGRAN 2001). DgF, digestible fiber = water-insoluble pectins + hemicelluloses (NDF-ADF); HRi, health risk index from digestive trouble = mortality + morbidity rate by diarrhea, measured from 28 to 70 days of age, on at least 40 rabbits/diet (one point = one diet, $n = 13$; for references, see Gidenne 2003).
When a sufficient supply of lignocellulose (at least 18%) is provided, it is advisable to replace some starch by digestible fiber fractions. The HRi is improved while the feed efficiency is little modified (Gidenne et al. 2004, Perez et al. 2000, Tazzoli et al. 2009, Trocino et al. 2011). Furthermore, a substitution of protein by DgF also led to a significant improvement in the digestive health status of the growing rabbit, without significant impairment in growth performances (Gidenne et al. 2013, Xiccato et al. 2011).

The favorable effect of supplying lignocellulose was also shown in the young during the weaning period (3–5 weeks old) by Fortun-Lamothe et al. (2005) with a large-scale study (six sites + three reproductive cycles). They reported a lower mortality rate for litters that were fed a diet rich in fiber or when fiber + lipids replaced starch.

![Figure 17.7](image_url)

**Figure 17.7** The health risk index depends on a balance between low-digested (ADF) and high-digested (DgF) fiber fraction, and when ADF is over 15%. DgF, HRi: see Figure 17.6.

### Table 17.4 Fiber Requirements to Prevent the Digestive Troubles after Weaning, for the Rabbit Bred in Rational Breeding Systems

<table>
<thead>
<tr>
<th>Unit*</th>
<th>Post weaning (28–42 d old)</th>
<th>End of fattening (42–70 d old)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lignocellulose “ADFom”</td>
<td>≥190</td>
<td>≥170</td>
</tr>
<tr>
<td>Lignins “ADL”</td>
<td>≥55</td>
<td>≥50</td>
</tr>
<tr>
<td>DgF&lt;sub&gt;b&lt;/sub&gt;/ADF</td>
<td>≤1.3</td>
<td>≤1.3</td>
</tr>
<tr>
<td>Cellulose “ADF-ADL”</td>
<td>≥130</td>
<td>≥110</td>
</tr>
<tr>
<td>Ratio lignins/cellulose</td>
<td>&gt;0.40</td>
<td>&gt;0.40</td>
</tr>
<tr>
<td>Hemicelluloses “NDF-ADF”</td>
<td>&gt;120</td>
<td>&gt;100</td>
</tr>
<tr>
<td>SF (TDF-aNDFom)</td>
<td>&gt;7–10%</td>
<td>&gt;7–10%</td>
</tr>
</tbody>
</table>

*<sup>a</sup> g kg<sup>−1</sup> as fed basis, corrected to a dry matter content of 900 g kg<sup>−1</sup>.  
*<sup>b</sup> Digestible fiber fraction = [hemicelluloses (NDF-ADF) + water-insoluble pectins].
17.3.4.5 Impact of Quickly Fermentable Fiber on Digestive Physiology and Health of Growing Rabbit

Another way to analyze the role of cell wall polysaccharides that are rapidly fermented (and highly digested) is to determine the NDSF residue (Hall et al. 1997), which corresponds to the cell wall polysaccharides soluble in neutral detergent solution (= sum of water-soluble and water-insoluble pectins + β-glucans + fructans + oligosaccharides [DP > 15]). Although the level of NDSF is moderate in rabbit feeds, a reduction of its level (12% vs. 8%) could be unfavorable on the digestive health of the early-weaned rabbit (Gomez-Conde et al. 2009). Conversely, a higher level of NDSF improved the mucosal morphology and functionality and its immune response (Gomez-Conde et al. 2007). However, the NDSF criteria remain difficult to analyze, and precision is relatively low for complete feeds with low content of pectins or soluble fiber.

Accordingly, another approach is actually used to assess the content of the quickly fermentable fiber, or soluble fiber “SF” by the difference between the TDF and the aNDFom corrected for protein content. SF would thus be easier to handle in a routine laboratory for feed analysis. It would recover the part of TDF that comprises the nonstarch, non-NDF polysaccharides, including pectic substances, β-glucans, resistant starch, oligosaccharides, fructans, and gums.

But regardless of the advantages and disadvantages of the different methods and calculation procedures, the choice of the method to quantify SF will depend on the correlation with in vivo data collected in animals, and particularly the impact on the digestive health.

The soluble fiber level is generally increased in a complete feed by supplying raw materials rich in pectins, such as beet pulps, and thus most of the studies in fact relate “beet pulp level” to performances of physiological data. Accordingly, the SF dietary level is positively related to the fecal digestibility of insoluble fiber fractions (NDF and ADF). As a consequence, the soluble fiber level is likely to affect ileal and, especially, cecal microbiota (Gomez-Conde et al. 2007, 2009) by modifying the amount and type of substrate reaching the cecum. These changes in microbiota may also be related to the modified immune response observed in young rabbits that were fed soluble/insoluble fermentable fiber. The soluble fiber level favors the microbial activity (Trocino et al. 2010) with higher fermentation levels and lower pH, as shown in the meta-analysis of Trocino et al. (2013).

The relationship between mortality by digestive troubles and the SF dietary level is reported in Figure 17.8. To look more precisely at this effect, we selected six studies comparing diets having a similar level NDF, and we observed a very large variation of mortality for the same concentration of SF. Furthermore, for studies having a moderate mortality level (<15%), only two studies out of four relate SF to mortality, and a low number of animals were often used.
Accordingly, the criterion that quantifies the quickly fermentable fibers or soluble fibers seemed not to improve the mortality prediction. Thus, it remains very risky to recommend an SF concentration in rabbit feeds in order to reduce the risk of digestive troubles. Nevertheless, it seems that over an SF level of 7%, the mortality rate tended to be lower, and in fact this level is generally reached in feeds that follow the current recommendations for ADF and DgF (Table 17.4). Moreover, the criteria for quickly fermentable fibers correspond to a lower amount of fiber residue than for DgF criteria, and due to a higher analytical error, this could add further imprecision to recommendations.

More research is needed to elucidate the health response of rabbits to soluble fibers intake, with large-scale studies comparing the health of large groups of rabbits (over 100). In perspectives, the effects of the fiber fractions that are rapidly fermented should be precised. The main problem is to obtain a sufficiently robust analytical method (Xiccato et al. 2012) that could be used routinely in a feed control laboratory.

17.3.5 Dietary Fiber Recommendations to Reduce the Risk of Digestive Disorders in Weaned Rabbit

We propose a summary of fiber requirement (Table 17.4) for postweaned and growing rabbits. To reduce the risk of digestive troubles after weaning, for
the rabbit bred in rational breeding systems, one criterion is not sufficient for fiber recommendations.

Three key points must be taken into account:

The first criterion to be controlled is the level of ADF that should be over 19% in a complete pelleted feed (Table 17.4).
Second, the quality of lignocelluloses also plays a role in the digestive health, and the minimum level of lignins should be 5% in a feed.
Third, the balance between the low-digested “ADF” and high-digested fiber fraction should be respected; the ratio DgF/ADF should be under 1.3 to avoid too high an intake of highly fermentable polysaccharides (pectins, β-glucans, etc.).

In perspectives, the effects of fiber fractions that are rapidly fermented should be determined, particularly the impact of the “soluble” fiber. Recent studies report a global favorable effect of the soluble fiber, and the range for SF supply in a feed would be 7–10%. However, the concept of SF recovers more or less the same approach than DgF, although the polysaccharides implicated are not exactly the same. The main problem is to obtain a sufficiently robust analytical method (Xiccato et al. 2012) that could be used routinely in a feed control laboratory.

17.4 General Conclusions

The rabbit is a pertinent model to explore the relationships between fiber intake and digestive pathology. The favorable impact of quantity and quality of fiber fractions on the digestive health has been demonstrated. However, the analysis of the cell wall polysaccharides that are quickly fermented remains a challenge for the future. A criterion, such as TDF-aNDFom, needs to be validated in terms of reproducibility and repeatability for feed analyses. It should also be more precisely related to the digestive health of the young rabbit.

References


