Role of dietary fibre in rabbit nutrition and in digestive troubles prevention.

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Summary

This paper review recent studies dealing with the nutritional role of dietary fibre, and on their impact on digestive health of the rabbit. Results show clearly that a minimum dietary fibre supply is essential to prevent digestive troubles in the growing rabbit. The most recent fibre recommendations have implicated several classes of fibre, including low-digested fibre (lignocellulose) and digestible fibre (hemicelluloses and pectins). The present review focuses also on the nutritional role of the digestible fibre for the rabbit that was less studied. To allow the formulation of complete feeds with adequate fibre levels, a synthetic table summarising the levels of several fibre classes (including digestible fibre and pectins) in some raw materials classically used in rabbit feeding is given. A brief overview of some characteristics of dietary fibre and of some routine methods to estimate fibre fractions in animal feed ingredients is first presented.

1. Introduction

The rabbit is a monogastric herbivorous animal, and its digestive physiology is well adapted to high intake of plant cell walls. Therefore dietary fibres are the main constituent of a rabbit complete feed (even in intensive production) and depending of the analytical technique range from 15 till 50% (Table 1). The digestion of fibre by the rabbit has been recently reviewed (De Blas et al., 1999; Gidenne et al., 1998a), and the favourable role of low-digested fibre (mainly lignin and cellulose) on the incidence of digestive disorders in the rabbit was confirmed (see section 4, and Lebas et al., 1998). More recently, further studies have highlighted the favourable effect of digestible fibre, such hemicelluloses and pectins (Perez et al., 2000; Gidenne et al., 2001b) on rabbit digestive health.

Consequently, dietary fibre recommendations for the growing rabbit have sharply evolved since 5 years. First the level **and** quality of lignocellulose (ADF), e.g. the ratio lignin to cellulose, is implicated. Secondly, recommendations in digestible fibre "DgF" defined as the sum of hemicelluloses (NDF-ADF) and pectin (water-insoluble) have been highlighted (Gidenne, 2000). In addition, by-products of the agroindustry, such brans and pulps of fruits rich in DgF, are extensively used in the rabbit feed industry. Therefore hemicelluloses and pectins are a major part of the polysaccharides present in rabbit diets. However, presently there is no method to analyse the DgF in animal feed, and that could be available in a routine laboratory. Nevertheless, because of the importance of this fibre fraction in rabbit nutrition, particularly for preventing digestive troubles (see section 4), it is essential to evaluate them as precisely as possible in feed ingredients to formulate complete feed.

Table 1: Current levels of fibre in a complete feed for the growing rabbit, according to the analytical method.

Fibre determination criteria (1)	**%DM**
Crude fibre	14 - 18
Acid Detergent Fibre (ADF)	16 - 21
Neutral Detergent Fibre (NDF)	27 - 42
Water insoluble cell-wall (WICW)	28 - 47
Total dietary fibre (TDF)	32 - 51
Other feed constituents	
Starch	10 - 20
Crude protein	13 - 18

(1) : see the definition of the section 2.2

Thus the present review will remember briefly some characteristics of dietary fibre and of some routine methods to estimate fibre fractions in animal feed ingredients. We then consider the nutritional role of fibre in rabbit digestion, and more particularly that of Digestible fibre (DgF). Finally, values of DgF and pectins obtained from a literature survey are presented for the most frequent raw material used in rabbit feed industry.

2. Brief overview of some characteristics of dietary fibre and of some methods to estimate fibre fractions in animal feed ingredients

2.1- Dietary fibre definition and some main characteristics

Initially dietary fibre was defined as the skeletal remains of plant cell in the diet, which are resistant to hydrolysis by the digestive enzymes of the man (Trowell, 1978). Other authors prefer a definition more close to the plant physiology, and thus fibre would address only the polysaccharides and lignin belonging to the cell wall. Despite numerous research over the last years no universal agreement has been yen obtained (De Vries et al., 1999). In fact, this lack of uniformity in defining the fibre in an animal (or human) feed seems to be mainly attributable to the very complex structure of the cell wall. In addition cell wall polymer are frequently linked to other fractions of the cell, such protein (Carpita and Gibeaut, 1993). Moreover, the chemical structure as well the organisation of the polysaccharides in the wall differ widely according to the botanical origin of the plant (e.g. grasses vs leguminous...).

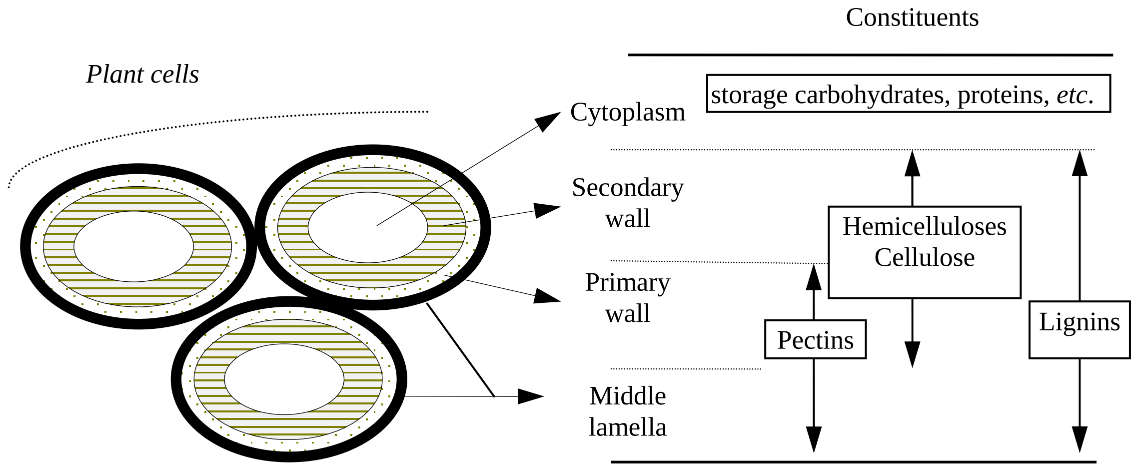


Figure 1: Schematic representation of plant cell walls, and their main constituents

Basically, the plant cell wall is composed of microfibrils of cellulose forming a strong framework that gives rigidity to the plant. These microfibrils are embedded in a matrix composed of a lignin network (phenylpropane units) which cements other matrix polysaccharides (plus some glycoproteins), such as hemicelluloses (arabinoxylans, xyloglucans...) and pectins (Carpita, 1996). These polymers have different proportions according to the structure of the wall (figure 1). For instance, as the plant is ageing the lignin network is enlarging from secondary to primary wall, and is laid down incrusting the microfibrils leading to a lower accessibility for wall polysaccharides to be hydrolysed by bacterial enzymes.

Among the numerous types of cell wall polymers (Chesson, 1995), it is convenient to select five major classes of fibre, according to their chemical structure and to their properties (figure 2): 4 classes of water insoluble polymers (lignins, cellulose, hemicelluloses, pectic substances), and one class of various water soluble non starch polysaccharides and oligosaccharides.

Lignins are the only non-saccharidic polymer of the cell wall. They can be described as very branched and complex three-dimensional networks (high molecular weight), built up from three phenylpropane units (conyferilic, coumarilic and sinapyilic acid). Lignin networks tend to fix the other polymers in place, excludes water and makes the cell wall more rigid and resistant against various agents, such as bacterial enzymes. Most concentrate feeds and young forages contain less than 5% of lignin. With ageing, plant cell wall is lignifiying reaching 12% in forages.

Cellulose is the major structural polysaccharide of the plant cell wall, and the more widespread polymer on the earth. It is an homopolymer (contrary to hemicelluloses and pectins), formed from linear chains of ß-(1→4) linked D-glucopyranosyl units (whereas starch is formed of α-(1→4) linked D-glucopyranosyl chains). The degree of polymerisation is usually around 8000 to 10000. Individual glucan chains aggregate (hydrogen bonding) to form microfibrils, and could serve as the backbone of the plant. Thus, cellulose is only soluble in and partially hydrolysed in strong acid solutions (i.e. 72% sulphuric acid). Quantitatively, cellulose represents 40 to 50% of DM in hulls of legume and oilseeds, 10 to 30% in forages and beet pulps, 3 to 15 % in oilseeds or legume seeds. Most cereal grains contain small quantities of cellulose (1 to 5 % DM) except in oats (10%).

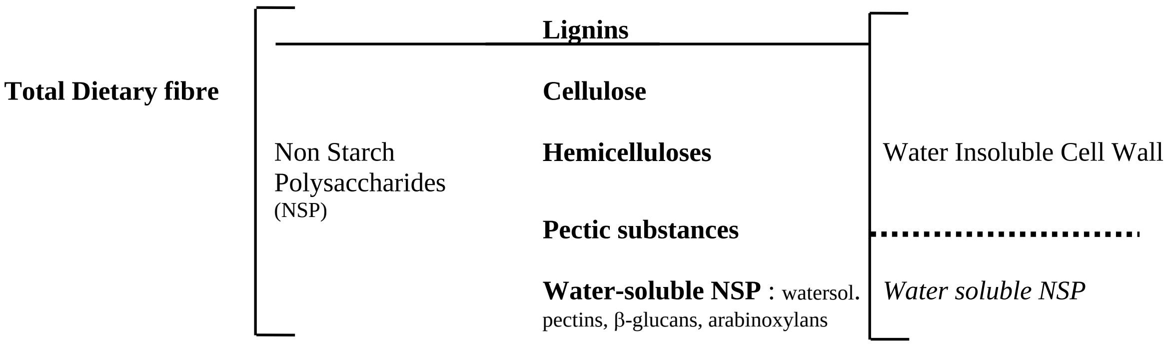


Figure 2 : Global classification of dietary fibre.

The hemicelluloses are a group of several polysaccharides, with lower degree of polymerisation than cellulose. They have a β1→4 linked backbone of xylose, mannose or glucose residues that can form extensive hydrogen bonds with cellulose. Xyloglucans is the major hemicellulose of primary cell wall in dicotyledonous plants (in vegetables, in seeds), whereas mixed linkage glucans (β1→3,4) and arabinoxylans are the predominant hemicelluloses in cereals seeds (the two latter include partly water-insoluble and water-soluble polymers, cited above). Hemicelluloses include other branched heteropolymers (units linked in β1→3, β1→6, α1→4, α1→3) such as highly branched arabinogalactans (in soya bean), galactomannans (seeds of legumes), or glucomannans. Polymers formed of linear chains of pentose (linked in β1→4) such as xylans (in secondary walls), or hexose such as mannans (in palm kernel meal) are also classed as hemicelluloses. Hexosans such as mannans, glucomannans or galactans can only be solved in strong basic solutions (17-24%). Pentosans such as xylans and arabinoxylans are soluble in weak basic solutions (5-10%), or in hot dilute acids (5% sulphuric acid). They consist of a linear β1→4 linked xylan backbone to which alpha -L-arabinofuranose units are attached as side residues via α1→3 and/or α1→2 linkages. Cereal arabinoxylans exhibit a great deal of structural heterogeneity with respect to ratio of arabinofuranose/xylopyranose, substitution pattern of urbanises, content of feruloyl groups and molecular size (Izydorczyk and Biliaderris, 1995). They exhibit various conformation and physicochemical properties (viscosity, gelation potential, intermolecular association) in aqueous solutions that lead to specific nutritional action in the digestive tract. Quantitatively, hemicelluloses constitute among 10 to 25% of the dry matter (DM) in forages and agro-industrial by-products (brans, oilseeds and legume seeds, hulls and pulps) and about 2 to 12% DM of grains and roots. In rabbit complete feed, hemicellulose fraction originates mainly from cell walls of cereals (mainly arabinoxylans), or from beet pulp where they are predominantly xylans (Marry et al. 2000) They are also provided by soyabean cell wall where they correspond mainly to xyloglucans (Huisman et al., 2000),

Pectins are composed of polygalacturonic acid linear backbone always branched with neutral sugars (mainly arabinose and galactose). From place to place, the linear backbone is interrupted by L-rhamnose unit, leading to deviation of the chain axe (Colonna et al., 1995). Pectic substances correspond to several classes of polymers, including pectins (rhamno galacturonans backbone and side chains of arabinose and galactose) and neutral polysaccharides (arabinans, galactans, arabinogalactans) frequently associated to pectins. Pectic substances are a group of polysaccharides present in the middle lamellae and closely associated to the primary cell wall, especially in the primary cell wall (young tissues) of dicotyledonous plants. Pectins of the middle lamellae serve in plant tissue as the "glue", cementing plant cells together. Pectins are found in relatively high level in leguminous plant and in cell wall of fruits. One of the major source of pectins in animal feeds is pulp from sugarbeet or citrus pulp. Sugar beet pulp contains 25% pectin, leguminous plant 5-10% (e.g. alfalfa). More precisely, Oosterveld et al. (2000) showed that pectic polysaccharides extracted from sugar beet pulp are homogalacturonans, rhamnogalacturonans, arabinans and relatively small amounts of glucomannans and xyloglucans. Marry et al. (2000) indicate that pectins from sugarbeet pulp are in fact composed of several types polygalacturonic acids with heterogeneity in molecular weight and neutral sugar composition, and with variations in their methyl esterification or feruloylation or acetylation. In cotyledons of legume seeds, total pectins (soluble and insoluble) reach 4 to 14% of DM, such as in soybean, pea, faba bean, white lupins.

Water soluble polysaccharides and oligosaccharides include several classes molecules with a degree of polymerisation ranging from about 15 to more 2000 (β-glucans). Most of them are insoluble in ethanol:water 80:20. They are generally in a low level in animal feed ingredients. We can mentioned, soluble hemicelluloses such as arabinoxylans (in wheat, oat and barley ≈2 to 4% of DM) and β-glucans (in barley or oat ≈1 to 3% of

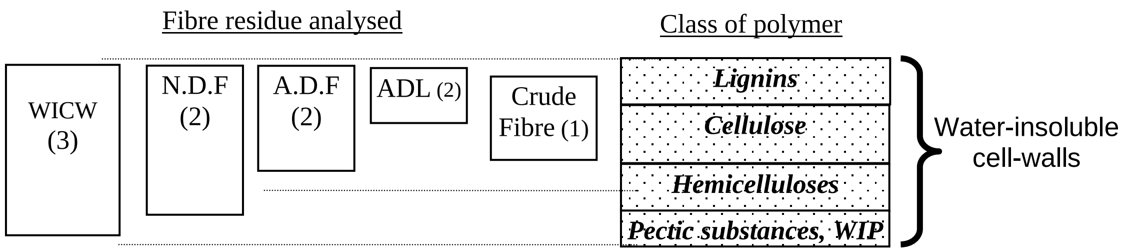
DM), oligosaccharides such as α-galactosides (in lupine, pea or soya seeds 5 to 8% of DM), and soluble pectic substances (pulps of fruits or beets, up to 10% of DM).

2.2- Current methods to estimate fibre fractions in complete feed and feedstuffs

For feed industry, the interest for a fibre criteria is not to obtain a precise biochemical analyses. First, it must have a nutritional significance for the animal feeding or must have an impact in nutritive value evaluation or prediction (e.g. for digestible energy value). Second, a fibre criteria must be performed in a routine laboratory with high reproducibility (and low cost) in order to follow the quality of raw materials batches, and thus informs the formulation matrix that adjust the final ingredient composition of the feed (hypothesising that additivity law is respected).

For rabbit feeding, estimating the dietary fibre covers another primary interest, because a deficiency in the fibre supply leads to serious digestive problems, diarrhoea and mortality in the growing animals (Bennegadi et al. 2001). Consequently, it is of first importance to evaluate the concentration in the different classes of fibres and their effects on the digestive processes (Gidenne, 1997; Gidenne et al., 2000).

Methods have been developed to extract fibre fractions in animal feeds, but none is biochemically precise. Detailed reviews have been published on this subject (Asp et Johansson, 1984; Carré, 1991; Giger-Reverdin, 1995; Bach Knudsen, 2001). So we here remind only the two procedures routinely used in rabbit feeding: the Weende method (Crude fibre) and the sequential procedure of Van-Soest (figure 3). These methods have been recently standardised in the frame of rabbit nutrition studies (EGRAN, 2001).



(1) : according to Weende technique (Henneberg and Stohmann, 1864).
(2) : Sequential procedure of Van-Soest: NDF = neutral detergent fibre; ADF = acid detergent fibre; ADL = acid detergent lignin (Van-Soest *et al.*, 1991, AFNOR, 1997).
(3) : WICW = water insoluble cell-wall (Carré et Brillouet, 1989) ; WIP: water_insoluble pectins.

Figure 3 : Gravimetric methods for the determination of dietary fibre in animal feeds.

The Weende method (Henneberg and Stohmann, 1859) must be reminds because it is quick, simple, low-cost, and frequently used all over the world. This technique extracts a fibre residue "the crude fibre" (after an acid followed by a basic hydrolysis) that corresponds partly to a mixture of cellulose, lignins, cutin, suberin. The main limitations of this method are that crude fibre is a too global criteria. The Weende residue contains various amount of several fibre classes (depending of the raw material analysed) : 30 to 100% of cellulose, 14 to 20% of pentosans, 16 to 90% of lignin (e.g. 30% for a wheat straw). Thus it is not a sufficiently precise criteria for fibre recommendations in rabbit.

The technique of Van Soest and Wine aims to fractionate the cell wall, and to obtain fibre residue without contaminant such as proteins, through the combinative activity of detergents (in neutral and then acidic). The method developed initially for forages, has been then modified by several authors in order to be used for "concentrates" (raw materials and compound feeds used in monogastric feeding, such as cereals and various by-products) (Van Soest *et al.*, 1991), through the use of pre-extraction steps with proteolytic and amylolytic enzymes. The main advantage of this method is to obtain three fibre residues (see Figure 3), from which it is possible to evaluate the lignins (ADL), the cellulose (ADF-ADL) and the hemicelluloses (NDF-ADF). Limitations of this method are that the crude protein content of the NDF fibre could be highly variable (1 to 20% for concentrates, NDF could also contain starch or residual pectins), the pectic substances and the water soluble non starch polysaccharides are lost in the NDF procedure, the pre-treatment with enzymes is not totally standardised, and some hemicelluloses may be left in the ADF fraction. Nevertheless, the Van Soest procedure is very widely used for animal feeds, because it gives a lignocellulose residue without main contamination such as found for crude fibre, and because this technique is relatively quick and simple and improves noticeably the fractionation of the CW.

Besides, Carré and Brillouet (1989) develop an enzymatic-gravimetric procedure that extract the water insoluble cell wall (including pectins) "WICW". It is routinely used in poultry feed and provides a simple fibre criteria that is included in prediction equation of metabolisable energy (Carré, 1991).

The Neutral detergent soluble fibre procedure of Hall and al. (1997) should also be mentioned because it addressed the problem of analysing the pectin and "NDF" soluble fibre fraction in animal feed ingredients. However, this procedure is presently too complex to be routinely used in feed industry.

Similarly, other fibre methods has been developed for measuring total dietary fibre "TDF", that corresponds to soluble and insoluble NSP (including pectins and ßglucans) + lignins (Lee *et al.*, 1992; Li, 1995). However, the method has presently only be assayed for human foods and remains to be validated for animal feeds. Therefore, because of the highly variable structure of water-insoluble pectins and water soluble non-starch polysaccharides no satisfactory method is presently available to determine precisely these compounds in animal feeds.

3. Digestion of insoluble dietary fibre by the rabbit

As a consequence of the lack of precise methods for analysing fibre in animal feed, the nutritionnist is obliged to use the available fibre criteria, that could be really usable in a feed company. Therefore, we present here mainly the nutritional effect of fibre analysed through the Van-Soest fibre criteria, although it does not consider the soluble fibre and the pectins.

While dietary fibre recommendations in human nutrition used a global fibre criteria (including soluble and insoluble fibre), in rabbit feeding we need to evaluate the levels of low and highly digested cell-wall because they have a specific role in preventing the digestive troubles. In addition, the ingredients used for animal feeding contains very low level of water-soluble polysaccharides (contrary to human foods). Thus soluble fibre are presently not considered, since they could not have an essential role in rabbit nutrition.

The cellulosic microfibrils are highly ordered and they are slowly hydrolysed by the enzymes of host ecosystem, mainly composed of bacteria and protozoa according to animal species. Conversely, the amorphous region of the wall, mainly hemicellulosic and pectic fractions, is less ordered and is generally more rapidly hydrolysed and fermented. Besides, the lignins remain largely undigested because of its polyphenolic structure that is not hydrolysed by bacteria heberged in stomach or caeco-colic segment of domestic animals. These general facts are also proved in rabbit, since whole tract digestion of cellulose remain inferior to that of hemicelluloses (table 2).

Table 2: Whole tract digestibility coefficient of fibre fractions (%) in the growing rabbit.

Class of dietary fibre	Mean	Range
Lignins (ADL)	10-15	-13 to +50
Cellulose (ADF-ADL)	15-18	4 to 37
Hemicellulose (NDF-ADF)	25-35	11 to 60
Pectins (total uronic acids)	70 to 76	30 to 85

NDF, ADF, ADL = sequential procedure of Van-Soest (Van-Soest et al., 1991; AFNOR, 1997, EGRAN, 2001).

The whole tract digestibility of uronic acids (main part of the pectin) is generally over 70%, except for some specific fibre source given at a high level (>60% of the diet) such as olives leaves or sunflower hulls (Skrivanova et al., 1996; Garcia et al., 1999). At the ileal level, the uronic acids are already highly digested (25 to 50%, Gidenne, 1992; Carabaño et al., 2001). This particular fact could originate in an important pectinase activity in the stomach (Marounek et al., 1995), probably provided by the soft faeces remaining at least 5 to 6 hours in this segment. In addition, the fibrolytic activity of caecal bacteria is the highest for pectic substrates followed by hemicellulose and then by cellulose (Gidenne et al., 2000). This corresponds also to a higher colonisation of pectinolytic flora (10^8 to 10^9 CFU/g) compared to celluloytic one (10^6 to 10^7 CFU/g) (Forsythe and Parker, 1985; Boulharouf et al., 1991, Sirotek et al., 2001). Uronic acids also are an important factor that modulate the fermentative activity in the caecum (Garcia et al., 2000) and the caecal pH as demonstrated in a collaborative study (Garcia et al., 2002).

Therefore it is not surprising that ingredients rich in pectins and hemicelluloses are particularly well digested by the rabbit. 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 utilisation for growth of these fibre 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 do not affect the feed efficiency in the growing rabbit (Gidenne and Perez, 2000). In addition, because the retention time in the caeco-colic segment is relatively short (8-12h, Gidenne, 1997), the rapidly fermentable cell-wall polysaccharides can play a key role either for the rabbit digestive processes than for digestive health and sanitary status.

Besides, the botanical origin of fibres can influence digestion and cæcal microbial activity, independently of the quantity or the nature of fibres. Thus, supplying **fibre from a single botanical origin** (e.g. wheat: straw + bran) does not favour caecal fermentations nor the health status (Gidenne *et al.*, 1998c). This situation is however unusual in rational breeding, where the rabbits received pelleted feeds containing plants of diversified origin.

4. Role of fibre in preventing the digestive troubles in the growing rabbit

The need of fibre is more particularly expressed during the post-weaning period. Low fibre intake, without variations of fibre nature or origin, involves lower growth rate during the 2 weeks after weaning (Gidenne and Jehl, 1999; Pinheiro and Gidenne, 1999) that are associated with an increased incidence of intake troubles or digestive disorders (Bennegadi et al., 2001). Moreover, the favourable effect of fibres with respect to resistance to pathogenic agents was clearly shown recently (Licois and Gidenne, 1999).

In return, supplying fibre in the feed leads to an energy dilution of the diet. The rabbit thus attempts to increase its voluntary feed intake to satisfy energetic needs, and the feed conversion is reduced. When the dietary fibre 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.

Therefore, if we want to reduce digestive troubles in the growing rabbit and also to preserve its growth performance, we must supply adequate concentrations of fibre fractions. Furthermore, we also must take into account the nature of fibres and the interactions with starch. So, to reach adequate fibre recommendations for the rabbit, we propose to respect four points (see table 3):

1. the minimum quantity of lignocellulose (ADF).
2. the quality of lignocellulose, i.e. the lignins ratio / cellulose.
3. the quantity of digestible fibres (DgF = hemicelluloses and pectins) compared to lignocellulose (low digestible fibres), by calculating the ratio " DgF/ADF ".
4. the quantity and the nature of the starch (particularly during the period around weaning).

Table 3: Requirements in fibre and starch for the rabbit.

	(1) Unit	**Fattening rabbits**		**Does**	
		Post weaning (till 45d of age)	**End of fattening**	**Young does**	**Breeding does**
Lignocellulose "ADF"	g	≥190	≥170	*> 200*	*>140*
Lignins "ADL"	g	≥55	≥50	*?*	*?*
Cellulose (ADF-ADL)	g	≥130	≥110	*?*	*?*
Ratio Lignins/ Cellulose		>0.40	>0.40	*?*	*>0.30*
Hemicelluloses (NDF-ADF)	g	>120	>100		
DgF/ADF		≤1.3	≤1.3	*?*	*?*
Starch	*g*	*<140*	*≤180*	*?*	*?*

1: as concentration per kg^{-1} of raw feed, corrected to a dry matter content of 900 g/kg^{-1}.
Note: fibre requirements are established mainly for preventing digestive troubles of the growing rabbit, and also for improving performances of does.
NDF: Neutral detergent fibre; ADF: Acid Detergent Fibre; ADL: Acid Detergent Lignin (sequential procedure of Van-Soest *et al.*, 1991 ; AFNOR, 1997; EGRAN, 2001). DgF : digestible fibres (pectins + hemicelluloses). Hemicelluloses= NDF-ADF.

Most of the recent studies dealing with interactions between fibre and health of the rabbit have been performed on large groups of rabbits (n>40 per treatment) from european New Zealand White hybrid strain, having a feed intake of 90 to 120 g/d in post-weaning period, and 120 to 160 g/d in finishing period (and fed ad libitum a complete pelleted feed). The analysis of the health status of the animals was performed by a daily control of the mortality, associated with autopsies to try to determine the origin of the death. In 99% of the cases the death originated from a profuse diarrhoea, without any clinical symptoms indicating a known pathology (such coccidiose or colibaccilosis or clostridiose). Consequently, digestive troubles that affect the animal was defined as a non-specific enteropathy. In addition to control of mortality, we measure **the morbidity rate** that corresponded to animals still alive but showing transitory diarrhoea or very low intake or a very low growth rate (values above 2.5 SD from the mean). We thus calculated a global **sanitary risk index** (SR, %) that corresponds to mortality + morbidity rate.

4.1- Requirements of lignocellulose (ADF) : impact of quantity and quality of ADF.

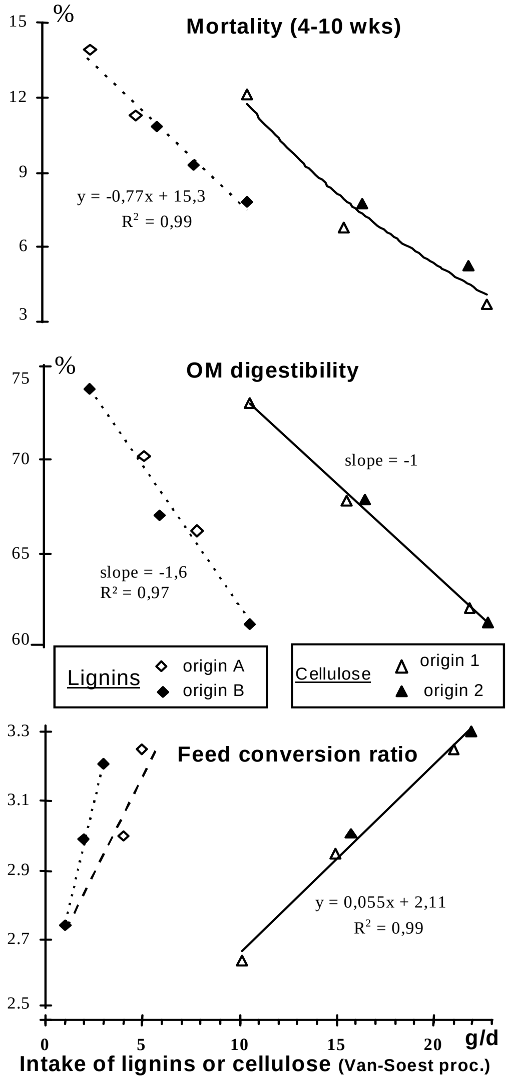


Figure 4 : Nutritional role of lignins and cellulose in the growing rabbit.

The favourable effect of ADF supply on the frequency of the digestive disorders and mortality in fattening rabbits was shown by Maître *et al.* (1990) using an adequate experimental design (380 rab./diet, in 5 sites). More recently, and with a similar design, Gidenne *et al.* (1998b) showed that the sanitary risk (SR = mortality + morbidity) increased from 18 to 28% when the dietary ADF content decreased from 19 to 15%.

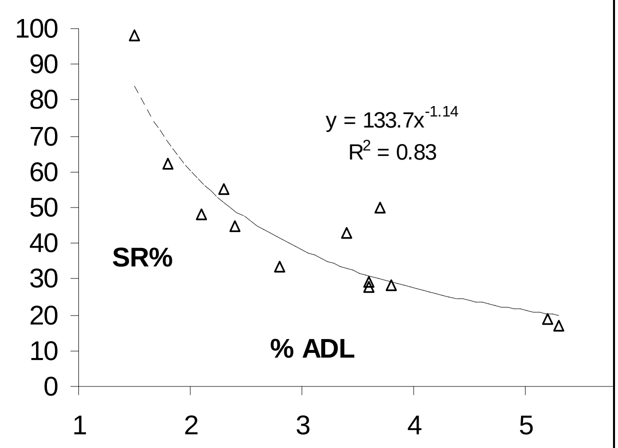
However, in a second step to improve fibre recommendations, the following question was examined : is a single criterion, such as the supply of lignocellulose, be sufficient enough to define the fibre contributions and the " level of security " of a feed for the growing rabbit ? Apart from the quantity of lignocellulose, other studies attempted to specify the effects of the quality of the ADF, i.e. the respective effects of lignins and cellulose (according to the Van-Soest procedure).

The nutritional role of the lignins was first addressed (Gidenne and Perez, 1994; Perez *et al.*, 1994). The intake of lignins (criterion ADL = Acid Detergent Lignin) involves a sharp reduction of the feed digestibility (see figure 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. On this last point, the botanical origin of lignins seems to modulate the effects observed. In parallel, a linear relationship (R^2=0.99; figure 4, n=5 feeds) between a chemical criterion of the plant cell wall (ADL) and mortality in fattening (by diarrhoea) were outlined for the first time (without major effect of the botanical origin of lignins). The favourable effect of the dietary ADL level on the SR was then confirmed with other experiments, as indicated in figure 5 (R^2=0.79; n=11 diets).

The effects of cellulose intake are less important than for ADL, regarding the decrease of the digestibility (see figure 4: slope = -1) or that of retention time (Gidenne and Perez, 1996; Perez *et al.*, 1996). The cellulose also favours the health status, but compared to lignins, the effects seems less important. These two components of lignocellulose exhibit similar effects for the prevention of the digestive disorders in rabbit. But, a major role is attributed to lignins, since the reduction of the ratio lignins/cellulose (L/C) involves a rise of the digestive disorders, as shown recently by Gidenne *et al.* (2001a). Furthermore, when the ratio L/C is lower than 0.4, a reduction of the growth rate (-5%) and a higher digesta retention time are observed. Similarly, for the doe, a recent study (Nicodemus *et al.*, 1999) showed a favourable effect of a linear rise of the ratio L/C (from 0.14 to 0.31) on the dairy production of the females and on the litter weight.

Globally, the **lignins requirement** (ADL) for the growing rabbit, can be assumed as to **5 to 7g/d**, and that out of cellulose (ADF-ADL) from approximately 11 to 12 g/d.

By comparing mixtures of fibre sources, we observed that the botanical origin of lignins (fig. 4) could affect the feed conversion, but would not



SR= Mortality + morbidity rate, measured from 28 to 70d old

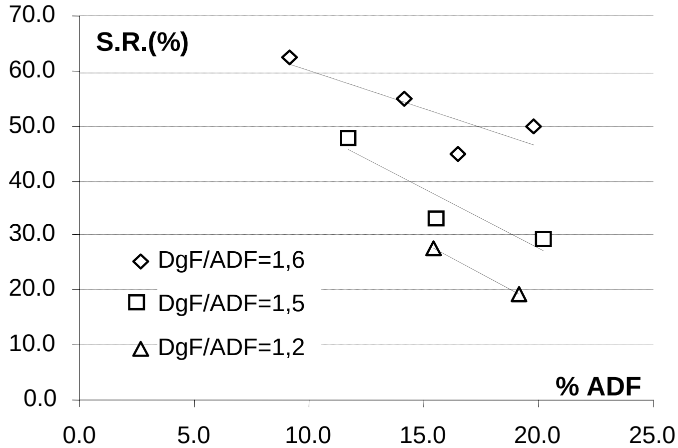
Figure 5 : Sanitary risk "SR" according to dietary lignin (ADL) level.

have a major effect on mortality by diarrhoea. 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 with such ingredients.

4.2- Effects of fibre fractions more digestible than lignocellulose.

A third step in evaluating the fibre requirements for 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 fibres, such as hemicelluloses and pectins?

Digestible fibres "DgF" fraction could be estimated by the sum of the two fractions hemicelluloses (NDF-ADF, according to the sequential procedure of Van-Soest) and water insoluble pectins. The procedure of analysis of pectins remains complex, it is nevertheless possible to estimate their value in ingredients from tables (IO7, 1993; Bach Knudsen, 1997). Compared to lignocellulose, the DgF fraction is highly digested by the rabbit (35 to 50%, Gidenne, 1997).

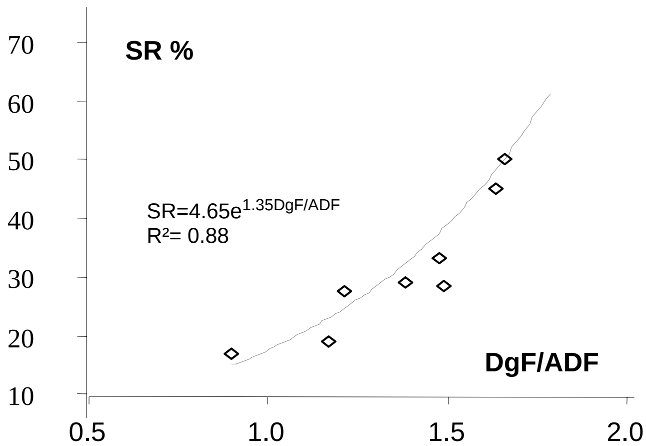


ADF= lignocellulose (Van-Soest sequential procedure); DgF: digestible fibre = pectins + hemicelluloses (NDF-ADF) ; S.R.= Sanitary risk from digestive trouble= Mortality + morbidity rate by diarrhoea (measured from 28 to 70d of age).

Figure 6: Sanitary risk in the growing rabbit, according to the dietary level of ADF.

As shown in figure 6, a large variation (20 to 50%) of the sanitary risk "SR" was observed according to the ratio DgF/ADF, and with a constant ADF level (± 20%). This confirmed that fibre requirement cannot be fulfilled only through requirement in lignocellulose.

On the other hand, for diets with a ADF level over 15%, we observed a very close relationship (R^2=0.88) between the rise in ratio DgF/ADF and the SR (figure 7). It would thus be advisable to maintain a ratio DgF/ADF lower than 1.3.



ADF, DgF, see figure 6. S.R.= Sanitary risk measured from 28 to 70d of age.

Figure 7: Sanitary risk "SR" according to the ratio DgF / ADF, and when ADF is over 15%

Besides, when starch is substituted by DgF, the growth performances (i.e. feed conversion, growth rate) are not greatly affected (Perez et al., 2000); illustrating that digestible fibres are efficiently utilised by the growing rabbit.

Further more, we also demonstrated that a substitution of protein by DgF also led to a significant improvement of the health status of the growing rabbit, without significant impairment in growth performances (Gidenne et al., 2001b).

4.3. Effects of starch supply ; interaction with fibre supply.

A fourth step in the evaluation of fibre needs, was to estimate if starch supply could interact or not with fibre supply (particularly ADF). For diets respecting the preceding constraints (> 18% ADF and DgF/ADF < 1,3), the starch substitution (24 to 12%) by digestible fibres " DgF " (ratio hemicelluloses / pectins = 75/25), led to a decrease in mortality after weaning (from 10.1 to 4.6%; Gidenne *et al.*, 1998b). This mortality associated to an excessive starch supply was higher during the post-weaning period. It would thus be advisable to respect in diets a starch level lower than 14% during this period. Recently, Gidenne *et al.* (2000) estimated that the starch ileal flow in finishing growing rabbit remained very weak (<2g/d), even for high starch level (30%). At the end of the fattening period, the starch supply would be thus only a secondary factor in the determinism of digestive disorders, the major factor remaining the fibre intake.

It has also been hypothesised that incorporating resistant starch in feeds would favour enteritis. However, when comparing iso-ADF feeds (16.5% ADF) having starch from maize or from wheat, only a slight reduction (P=0.25) in mortality was registered for "wheat" (5.6%, with 518 rabbit per diet) compared to "maize" diet (8.5%). Compared to the effects of the fibre supply, the nature of starch seemed not a primary factor in the determinism of digestive disturbances in the growing rabbit.

5. Contents in fibre fractions for some ingredients frequently used in rabbit feeding

To meet the previous fibre recommendations when formulating a complete pelleted feed for the rabbit, we must know the content of these fibre fractions for all ingredients used. Lignocellulose were already mentioned in previous tables of ingredients (Villamide and al., 1998). But DgF were never mentioned because there were no available method for a routine laboratory in a feed company. Nevertheless, as DgF are greatly implicated in digestive efficiency and health of the growing rabbits, feed industry asks for data on this fibre fraction in ingredients, to use this criteria in feed formulation and to respect the most recent fibre recommendations. Till now method to estimate pectins in a routine laboratory are not available, whereas hemicelluloses could be evaluated using the sequential system of Van-Soest. Consequently, it is necessary to dispose of informative tables for the most common ingredients used in rabbit feeds that mentioned the concentration in major fibre fractions (hemicelluloses, cellulose, lignins) and pectins.

Cellulose and lignins could be routinely analysed in raw material and feeds through the sequential procedure of Van-Soest, and values of NDF, ADF and ADL are reported in the table 4. Data are those already reported in the European table of ingredient composition and nutritive value for rabbit (Villamide and al., 1998).

Estimation of the DgF level (hemicelluloses and pectins) is more difficult. There is a particular problem for analysing hemicelluloses and pectic substances because some are water soluble, and a main part is water-insoluble (for ingredients of animal feeds). Therefore, hemicellulose fraction could be evaluated by difference between NDF and ADF residue, although this approach to estimate hemicellulose is not biochemically valid. However, it is the only available approach for a routine laboratory analysing feeds ingredients.

Determining the pectic substances in feed ingredients is more problematic. They could be determined partly by analysing the uronic acid content. But the procedure of Blumenkrantz and Ashboe-Hansen (1973) is relatively complex and costly, and could not be handled routinely in a feed industry laboratory. Therefore, the only way to estimate pectins is to refer to literature data reporting measurement of uronic acids and neutral sugar composition in fibrous ingredients. Indications about the monomer composition of some feedstuffs have been given in recent reviews (Brillouet et al., 1988; Colonna et al., 1995; Gidenne et al., 1998a). However, according to the botanical origin of the plant, the composition of pectins in neutral sugar (galactose, arabinose...) differ largely. Moreover, partition in water-soluble and insoluble needs to be more extensively studied, although some data are available for feed ingredients (Englyst et al., 1996; Bach Knudsen, 1997). So pectins could be estimated by adding the level of uronic acid and that of neutral sugars really implicated in the polysaccharide structure. But, only the level of water-insoluble pectins "WIP" is given in the table 4, because they were more data in literature and because soluble pectins are in very low quantity in animal feeds. Finally, the level of DgF is given as the sum of hemicellulose (NDF-ADF) and pectins (water-insoluble), in accordance with criteria used for fibre recommendations in growing rabbit (table 3).

Obviously, values given in the table 4 are proximate composition for "theoretical" ingredients. In practical conditions, the pectins should be calculated by using their ratio respect to lignocellulose content, within each ingredient, taking into account that for one same ingredient the proportions among the fibre fractions did not evolve significantly. However, this is not verified when comparing for example grasses at different age (first or second cut), but such ingredients are not frequently used in complete rabbit feed. The level of crude fibre and crude protein are also given in the table 4, to qualify more precisely the ingredient, avoiding thus any confusion among them.

6. Conclusion

In brief, the digestive health (morbidity as well mortality) of the weaned rabbit is dependant of the level and quality of lignocellulosic content of the diet, and a fibre deficiency impaired greatly the digestive health of the growing rabbit. But, digestive troubles are also rather reduced when DgF are included in a diet , in place of starch or protein. This could originate in favourable effect of the DgF (compare to starch or protein) on fermentative activity (Gidenne and Bellier, 2000) or on the rate of passage. However, a too high incorporation of pectins and hemicelluloses respect to lignins and cellulose (ratio DgF/ADF <1.3 with ADF >15%) should be avoided to minimise the sanitary risk (morbidity + mortality) during fattening.

Low-cost agro-industrial by-products, such brans and pulps, are highly used in rabbit feeding, thus supplying high level of hemicelluloses and pectins. But, this fraction is not analysed by the current routine method, although it have a specific nutritional role. Incorporating fibre sources rich in digestible fibre in the rabbit feeds covers a double interest. When they replaced sources of starch or protein, DgF are highly utilised for growth, and they improve the digestive health of the animal, if a correct supply in lignocellulose is respected. Because of their high digestibility, DgF may also have another nutritional role in stimulating the maturation of the caecal flora in the young. Further studies are thus necessary to precise the nutritional role of fibre for the young rabbit during the weaning period.

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Table 4 : Proximate fibre composition of some raw materials (90% DM) used in rabbit feeds, and with criteria used in fibre recommendations for the growing rabbit.

g/kg on as fed basis	**NDF**	**ADF**	**ADL**	**WIP**	**UAi**	**DgF**	***CF***	***CP***
Alfalfa meal 17	418	326	73	68	55	160	*261*	*153*
Grass meal	460	250	50	45	22	255	*225*	*144*
Wheat bran	428	128	35	30	14	330	*102*	*158*
Wheat straw	750	474	80	22	20	298	*395*	*36*
Sugarbeet pulp	428	212	18	250	190	466	*180*	*90*
Citrus pulp	220	155	16	120	80	185	*133*	*59*
Grape pomace	560	480	300	70	45	150	*280*	*117*
Soyabean husks	588	426	21	92	60	254	*355*	*122*
Sunflower husks	693	562	202	100	75	231	*468*	*54*
Cocoa husk	390	300	140	30	20	120	*183*	*164*
Grape seed meal	730	650	550	20	15	100	*441*	*99*
Rapeseed husk	563	400	190	125	79	288	*324*	*171*
Palm cake	520	317	90	30	10	233	*150*	*185*
Coconut cake	540	300	65	40	10	280	*160*	*215*
Soyabean meal 48	104	65	5	55	24	94	*50*	*468*
Sunflower meal 32	383	270	90	65	45	178	*225*	*306*
Rapeseed meal	277	189	86	100	50	188	*121*	*361*
Maize gluten feed	312	94	12	50	45	268	*78*	*215*
Whole seeds								
Soya	117	73	8	60	25	104	*56*	*369*
Pea (smooth, winter)	130	70	4	50	18	110	*57*	*220*
White lupins (smooth)	210	155	15	105	20	160	*128*	*326*
Faba bean	123	89	8	21	15	55	*77*	*257*
Oats	280	135	22	11	6	156	*111*	*106*
Barley	175	55	9	6	3	126	*46*	*108*
Wheat	105	31	9	5	3	79	*22*	*110*
Maize	100	25	5	7	5	82	*19*	*92*

NDF = neutral detergent fibre; ADF = acid detergent fibre; ADL = acid detergent lignin (Van-Soest *et al.*, 1991; AFNOR 1997; E.G.R.A.N., 2001). ; WIP : water insoluble pectins (see figure 3 and section 5) ;
DgF : digestible fibre = hemicelluloses (NDF-ADF) + WIP ; UAi: Water insoluble Uronic Acids ;
CF: Crude fibre, according to the method developed in the agricultural research centre of Weende (Henneberg and Stohman, 1859; E.G.R.A.N., 2001) ; CP : Crude protein (N x 6,25). Level of dry matter in ingredients = 900 g /Kg.