Role of fibre in rabbit diets. A review

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Review

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Abstract — The effect of fibre on rate of passage, control of gut flora, caecal fermentation, and performance of rabbits has been reviewed. Both physical and chemical characteristics of fibre affect these variables. An increase of the proportion of fine particles (< 0.315 mm) increases NDF digestibility, acidity and weight of caecal contents, fermentation time and microbial protein recycled through caecotrophy, but decreases rate of passage and intake. A minimal proportion of large particles (> 1.25 mm) is also required to allow an adequate turnover rate of caecal contents, and then to maximise microbial efficiency. The fraction of pectin components (arabinose, galactose and uronic acids) of cell walls accounts for most of the total fibre digestibility. An increase in the dietary concentration of these constituents leads to an increase of acidity of caecal contents and microbial protein recycled through caecotrophy. Dietary lignin content is negatively related to energy digestibility and also to the accumulation of digesta in the caecum. Both excessive and insufficient dietary fibre levels lead to an impairment of rabbit's performance. Practical recommendations on optimal fibre concentrations and minimal proportion of large particles are given for breeding does, fattening rabbits and mixed diets.

fibre / rabbit / digestion / performance

Résumé — Rôle des fibres dans l'alimentation du lapin : revue. Cette revue concerne les effets des constituants pariétaux sur le transit digestif, le contrôle de la flore intestinale, la fermentation cæcale et les performances des lapins. Les caractéristiques, tant physiques que chimiques, des constituants pariétaux interviennent sur ces variables. Un accroissement de la proportion des particules de petite taille (< 0,315 mm) augmente la digestibilité des constituants pariétaux, l'acidité et le poids du contenu cæcal, ainsi que la durée de fermentation et le recyclage des protéines microbiennes via la cæcotrophie, mais, en revanche, produit une diminution du transit digestif et de l'ingestion. Une proportion minimale de particules de grande taille (> 1,25 mm) est nécessaire pour obtenir un taux de renouvellement du contenu cæcal convenable et augmenter, ainsi, l'efficacité de la synthèse microbienne. La digestibilité totale des parois cellulaires résulte en grande partie de celle des substances pectiques (arabinose, galactose et acides uroniques). Un accroissement de la teneur de ces constituants dans l'alimentation augmente l'acidité du contenu cæcal et le recyclage des protéines microbiennes

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via la cæcotrophie. La teneur en lignine du régime est négativement liée à l'énergie digestible et à la réplétion du cæcum. Les niveaux tant excédentaires que déficitaires de constituants pariétaux dans le régime donnent lieu à une diminution des performances des lapins. Des recommandations pratiques pour les teneurs optimales en constituants pariétaux et la proportion minimale de particules de grande taille sont donnés pour les lapines allaitantes, les jeunes en croissance et les rations mixtes.

fibre / lapin / digestion / performance

1. INTRODUCTION

Fibre is one of the main constituents of commercial diets for intensively reared rabbits, which typically include around one-third of forages and fibrous by-products. The role of fibre in rabbit nutrition is not limited to nutrient supply. Fibre also plays a major role in the regulation of rate of passage of digesta, the control of gut flora and the maintenance of intestinal mucose integrity. Chemical composition and physical structure of plant cell walls vary widely among fibre sources, so that both type and level of fibre have important effects on rabbit digestion.

The aim of this paper was to review recent works on the feeding value of fibre in rabbits.

2. FIBRE DIGESTION

As in other animal species, fibre constituents can only be digested in rabbits through microbial fermentation. The main fermentative area is the caecum, which accounts, including its contents, for about 7 % of the whole body weight. Caecal microorganisms (10^{10}–10^{12}/g of caecal contents) ferment preferentially the fraction of digesta longer retained in the caecum: the shortest sized (< 0.3 mm) particles of digesta, the soluble fibre and some endogenous materials [1, 24]. As caecal contents are emptied daily to produce soft faeces, caecal retention time is limited to around 10 h [26]. Because of this short fermentation time, the caecal cellulolytic activity is quite low [29] (*figure 1*). However, the microflora resident in the caecum is able to degrade significant amounts of the more soluble non-

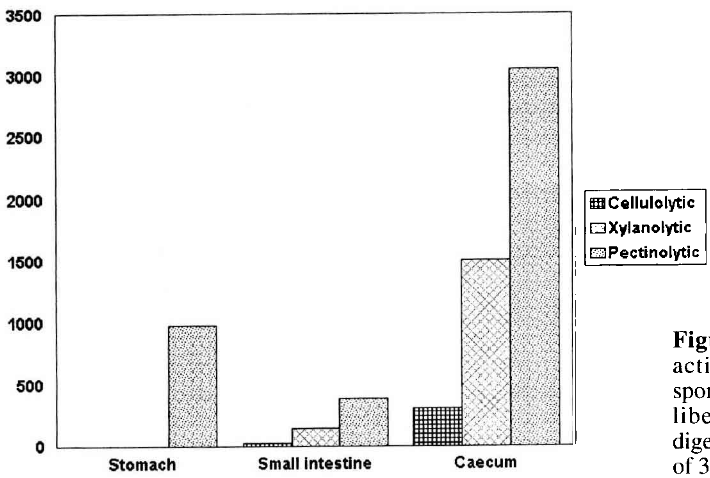

Figure 1. Total enzymatic activity (as mg of corresponding monomeric sugars liberated/h) in differents digestive segments in rabbits of 3 months [29].

Table I. Ileal and faecal digestion (%) of pectin components of different feedstuffs (unpublished observations).

Ingredient	Paprika meal	Alfalfa hay	Soybean hulls	S.E.
Fine particles[a]	94.9	78.6	67.0	–
Uronic acids				
Ileal	47.9	43.6	33.7	6.0
Faecal	85.4	72.3	60.6	1.4
Arabinose				
Ileal	27.5	41.7	23.8	7.0
Faecal	73.9	70.2	53.9	1.1
Galactose				
Ileal	19.7	18.3	34.3	6.0
Faecal	75.5	62.6	74.8	1.0

[a] Proportion of particles shorter than 0.315 mm.

starch polysaccharides (pectins, pentosans, β-glucans, oligosaccharides) [29]. Some enzymatic activity on these soluble constituents has also been observed in the small intestine and in the stomach. The latter has been related to the presence of intact soft faeces at the fundic area during several hours after meal [4, 13, 22].

Recent determinations of ileal and faecal digestion of pectin components (uronic acids, arabinose and galactose) of different feeds are presented in *table I*. According to these results, average faecal digestibility of pectin components (estimated as the sum of uronic acids, arabinose and galactose) was 72 %, ranging among feeds from 61 to 84 %. This variation was related to its proportion of fine particles, rather than to the chemical composition of the cell walls. The effect might be explained by differences in time of fermentation among the ingredients studied. In this way, García [17] using several fibrous sources observed a highly significant ($P < 0.001$) positive correlation ($r = 0.89$) between fermentation time and proportion of fine particles (< 0.315 mm). Data in *table I* also showed that at least half of digestion of the main pectin components occurred before digesta reached the caecum, as observed previously by Gidenne [23] with dehydrated alfalfa.

Concentration of pectin components of these ingredients was 43 % (as % NSP) on average, but accounted for 68 % of the total non-starch polysaccharides (NSP) digested. Non-starch polysaccharides digestibility of fibrous feedstuffs is then mainly related to their content of pectin components, and also to their proportion of fine particles ($r = 0.82$; unpublished observations). However, dietary level of fibre has little effect on fibre digestibility [26].

3. CONTRIBUTION OF CAECOTROPHY TO PROTEIN AND AMINO ACID INTAKE

Caecotrophy allows rabbits to utilise microbial cells contained in the soft faeces. The main nutrient recycled is protein, which accounts for around 16 % of total daily intake [4–6, 13, 32]. Average contribution of soft faeces is slightly higher for some essential amino acids as threonine, lysine and methionine (25.4, 19.2 and 22.5 %, respectively) [40]. These results agree with recent data observed in our laboratory.

Fibre constituents are a main energy source for caecal microorganisms, so that an effect both of level and type of dietary fibre on the amount of microbial protein recycled daily throughout soft faeces, might be expected.

In a recent study, García [17] compared semisynthetic diets, containing six sources of fibre varying widely in chemical composition of cell walls and physical characteristics. Type of fibre affected significantly ($P < 0.001$) recycling of microbial protein (MPr), which varied among sources from 2.1 to 5.2 g/d. A stepwise regression analysis on these data, selected dietary concentration of pectin components (PC, %) and proportion of fine particles (< 0.315 mm, FP) as the best independent variables in the predictive model. As described above, these are also the variables that better explain the extension of NSP digestion. In a third step the model included a positive effect ($P = 0.026$) of the proportion of large particles (> 1.25 mm, LP). A balance between fine and large particles increases caecal motility and would lead to an adequate turnover rate of caecal contents and therefore to a higher microbial efficiency.

$$\text{MPr (g/d)} = -\,1.02\ (\pm 0.29) + 0.016\ (\pm 0.0025)\ \text{FP}$$
$$P = 0.00 \qquad P < 0.001$$

$$+\ 0.032\ (0.013)\ \text{PC} + 0.035\ (\pm 0.015)\ \text{LP}$$
$$P = 0.015 \qquad P = 0.026$$

$$R^2 = 0.446;\ n = 60$$

Furthermore, an increase of dietary fibre level in balanced diets leads to an increase of feed intake and soft faeces production [4]. However, both protein and amino acid concentrations in soft faeces decrease parallely (unpublished observations), so that the amount of crude protein and amino acids daily recycled does not vary. As reviewed by Gidenne et al. [26], caecal retention time decreases when level of fibre in balanced diets increases, which would impair rate of microbial protein synthesis.

4. CAECAL pH

Acidity of caecal contents is frequently determined in digestion studies. Both a high caecal pH and low VFA concentrations have been related in in vitro studies to a higher proliferation of *E. coli* [39, 43].

A general relationship among caecal pH, basic buffering capacity of caecal contents (BBC, μeq) and caecal VFA and ammonia ($N\text{-}NH_3$) concentrations (mmol/L), has been established by García [20] using semisynthetic diets containing six different sources of fibre:

$$\text{pH} = 7.15\ (\pm 0.36) - 0.007\ (\pm 0.002)\ \text{BBC} - 0.012$$
$$P < 0.001 \qquad P = 0.007$$

$$(\pm 0.0039)\ \text{VFA} + 0.009\ (\pm 0.006)\ \text{N-NH}_3$$
$$P = 0.005 \qquad P = 0.149$$

$$R^2 = 0.491;\ n = 24$$

Volatile fatty acids are a main product of microbial fibre fermentation. According to the review of Gidenne et al. [26], caecal VFA concentration averages 57.2 mmol/L ranging from 31.8 to 88.5. As could be expected, the lowest values have been obtained using highly lignified sources of fibre (e.g., grape byproducts, sunflower hulls), whereas the highest correspond to feeds with a higher pectin content (e.g., beet and citrus pulps, alfalfa hay). The same authors indicate that fermentation of endogenous materials and other dietary components might contribute significantly to VFA production. Some authors [21, 41] have related an increase of hindgut VFA production to an improvement of mucosal integrity in human and other non-ruminant species. This effect might be explained since VFA, preferentially butyric acid, are used by the colonocytes as the main energy source [42]. According to this, the inclusion of purified lignin in rabbit diets compared to cellulose or pectins, produced a reduction in both caecal VFA concentration and muscle layer thickness of caecum and colon [7].

Ammonia concentration is slight positively related to caecal pH. This concentration increases when dietary protein is in excess, but also when using both highly lignified byproducts (wheat straw, sunflower hulls) [19] and pectin enriched byproducts (beet and citrus pulps) [13.]

The relation between caecal pH and dietary fibre characteristics has been established by García [17] using stepwise regression analysis. The model included again as independent variables the proportions of pectin components and fine particles (< 0.315 mm).

$$pH = 7.04 (\pm 0.17) - 0.056 (\pm 0.0094) \quad P < 0.001 \quad P < 0.001$$

$$PC - 0.0090 (\pm 0.0020) FP \quad P < 0.001$$

$$R^2 = 0.51; n = 58$$

The effect of dietary level of fibre on caecal pH can be analysed from the results presented in *figure 2*, obtained using a common methodology. As a whole, dietary NDF content had no effect on this trait, which agrees with the above mentioned lack of influence on fibre digestion. However, caecal pH decreased in those works where the increase of fibre was associated to a parallel increase of sugar-beet pulp content [6, 15, 16]. The contrary occurred when fibre was mainly supplied with wheat straw [9].

5. RATE OF PASSAGE TIME OF FEED

Retention time of digesta in the digestive tract is an important characteristic of feeds, as it is related to voluntary intake. This trait has been measured in a few works with rabbits [20, 23], which showed that it can vary from 16 to 54 h depending on the dietary source of fibre, averaging 18 h for normal diets [12, 25]. According to Gidenne [25] and García et al. [20] caecal retention time accounts for more than 60 % of the total retention time, so that a negative correlation exists between rate of passage of digesta and weight of caecal contents (r = – 0.56, $P < 0.001$; $n = 40$) [20]. The latter is much easier to determine, and there is a large number of studies where it has been related to type of diet. As it depends on sampling time, results presented in *figure 3* are

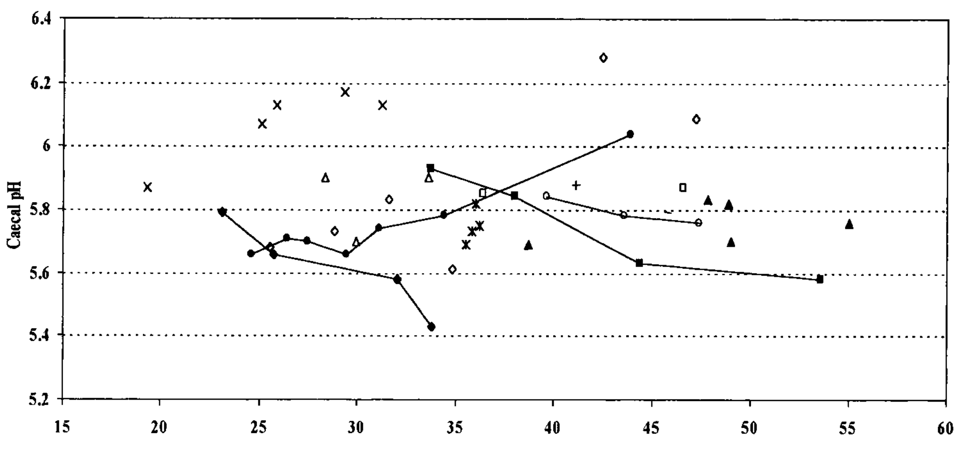

Figure 2. Effect of dietary neutral detergent fibre (NDF) on caecal pH. — ● — [9]; — ○ — [15]; — ▲ — [18]; — + — [3]; — ■ — [16]; — ◇ — [19]; — □ — [5]; — △ — [32]; — ⁎ — [33]; — × — [13]; — ◆ — [6].

restricted to those using the same methodology. From a stepwise regression analysis, the following equation was derived:

$$CC = 18.0\ (\pm 2.1) - 0.64\ (\pm 0.12)\ NDF + 0.0081$$
$$P < 0.001 \qquad P = 0.06$$

$$(\pm 0.0015)\ NDF^2 - 0.028\ (\pm 0.013)\ ADL_{NDF}$$
$$P < 0.001 \qquad P = 0.04$$

$$R^2 = 0.52;\ n = 40$$

where CC is the weight of caecal contents (% body weight), NDF is on dry matter basis, and ADL_{NDF} is the degree of lignification of NDF (%).

From this equation it can be calculated that CC takes a minimal value for a 39.5 % of dietary NDF content on DM. An increase of the weight of digestive tract contents with high levels of fibre is common to other animal species. However, accumulation of digesta in the caecum in low fibre diets is characteristic of rabbits and it is related to the positive effect of fibre on ileocaecal motility [25]. Furthermore, the regression analysis shows a negative influence of lignin concentration on CC at a given dietary fibre level.

Recently, an effect of both particle size and lignin concentration on CC has also been reported by Nicodemus et al. [33, 35]. Accumulation of digesta in the caecum of fattening rabbits increased significantly in the first study when the proportion of fine particles (< 0.315 mm) increased above 78 %, and in the second for dietary ADL concentrations lower than 4.1 % DM.

6. ENERGY EFFICIENCY

As reviewed above, rabbits do not ferment the largest feed particles, and time of fermentation of the shortest is restricted because of the daily caecum emptying. As a consequence, rate of passage of digesta is faster than in other species, as ruminants, pigs or horses [44], and extension of fibre digestion is lower.

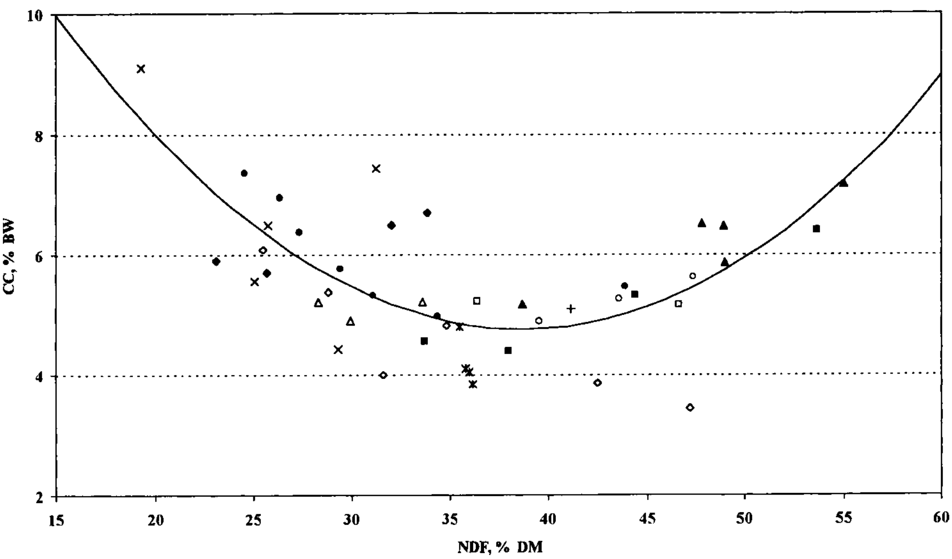

Figure 3. Effect of dietary neutral detergent fibre (NDF) on weight of caecal contents (CC, as percentage of body weight). — ● — [9]; — ○ — [15]; — ▲ — [18]; — + — [3]; — ■ — [16]; — ◇ — [19]; — □ — [5]; — △ — [32]; — ⋇ — [33]; — × — [13]; — ◆ — [6].

The effect of dietary fibre content on energy digestibility (Ed) is shown in *figure 4*. The regression equation was [10]:

$$Ed = 0.863\ (\pm 0.010) - 0.0012\ (\pm 0.0001)\ ADF\ (g/kg\ DM)$$

$$P < 0.001 \quad R^2 = 0.88; \quad n = 66 \quad RSD = 0.022$$

This equation underestimated Ed of diets containing low-lignified sources of fibre, where an increase of total mean retention and fermentation time would be expected [13] and dietary fibre was potentially more degradable. On the other hand, the equation overestimated diets with a high proportion of large sized particles, as those containing wheat straw. These diets would lead to a faster rate of passage, and therefore to a decrease of the digestibility of other dietary components.

An increase of dietary fibre content also decreased the efficiency of retention of digestible energy in growing animals (*figure 5*). This effect is explained by a parallel increase of fermentation losses (methane and heat of fermentation). Results presented in *figure 5* also showed that this efficiency decreased more when dietary fibre was supplied by enriched pectin feeds (as beet pulp), than when using less digestible sources of fibre (as a mixture of wheat straw and alfalfa hay).

7. INTAKE AND PERFORMANCE

According to previous paragraphs, both excessive and insufficient dietary fibre levels might affect rabbit's performance. High concentration of dietary fibre is associated to a low energy efficiency and net energy intake. On the other hand, diets with low fibre level are associated with higher total mean retention time, and then lower intake capability and higher risk of digestive disorders. Furthermore, diets with low digestible fibre level lead to a lower VFA concentration and to a higher caecal pH, so that mucosal integrity and control of hindgut

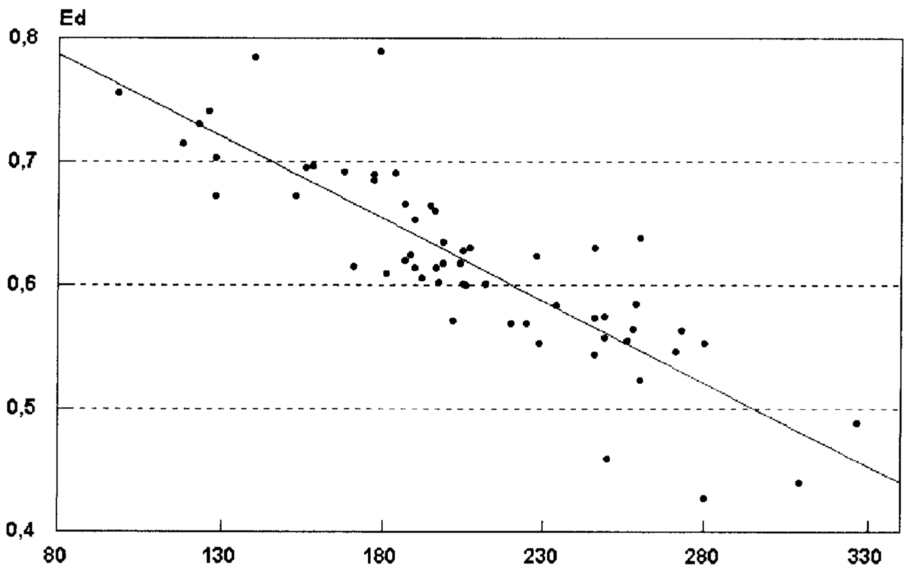

Figure 4. Effect of dietary acid detergent fibre (ADF) on energy digestibility (Ed) of diets [10].

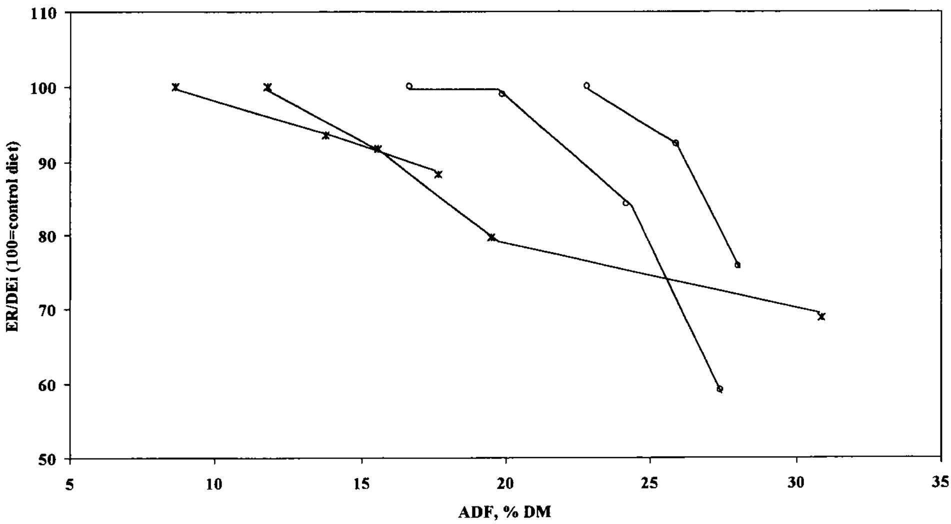

Figure 5. Effect of substitution of starch by different sources of fibre on efficiency of retention of digestible energy (ER/DEi) in growing rabbits [8, 14, 15, 37]. —○— Beet pulp; —★— Straw; —+— Alfalfa.

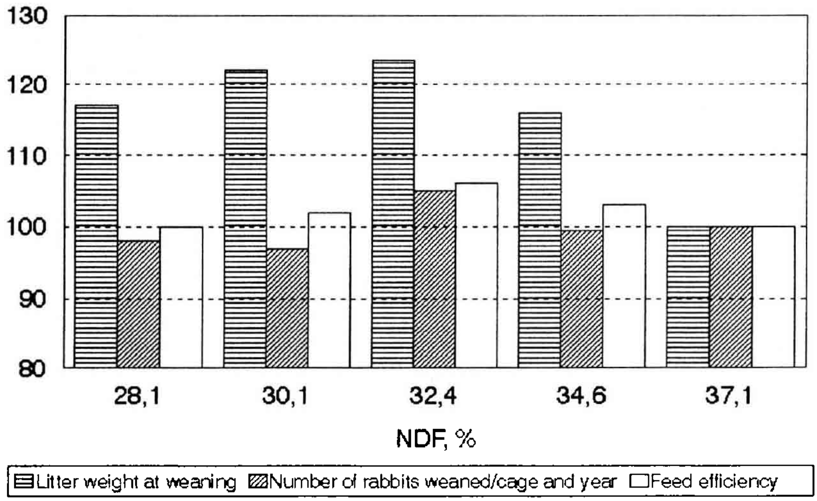

Figure 6. Effect of dietary neutral detergent fibre (NDF) on litter weight at weaning, number of rabbits weaned per cage and year and feed efficiency (base 100 = diet with 37 % NDF) [11].

pathogens would be decreased. Low levels of fibre could also imply a high concentration of dietary starch, which has been related to a higher diarrhoea incidence, especially in early weaned rabbits [2, 28].

The effect of substitution of fibre for starch in rabbit doe diets has been studied by De Blas et al. [11]. Five diets were formulated with increasing levels of NDF (from 28 to 37 %, as fed) and decreasing levels of starch (from 24 to 12 %, as fed). Fat was added in parallel to fibre to obtain isoenergetic diets (10.6 MJ DE/kg). Results are presented in *figure 6*, which shows a curvilinear effect of dietary fibre level on several productive traits, as litter weight at weaning, number of rabbits weaned per cage and year and feed efficiency. Optimal values for these traits were reached for about 35.5 % NDF on DM (equivalent to 20 % of starch on DM), which is close to the level of dietary NDF that minimises weight of caecal contents. The impairment of performance observed for the high fibrous diets might be related to higher fermentation losses and to an insufficient uptake of glucose to meet pregnancy and lactation requirements. The negative effect of high starch diets was mainly related to an increase in diarrhoea incidence.

A curvilinear effect of substitution of fibre for starch on fattening performance has also been observed by De Blas et al. [9], Partridge et al. [38] and García et al. [15, 16]. Growth traits were optimised for a dietary fibre concentration slightly higher than for rabbit does (37.2 % NDF on DM). An increase of digestive disorders was observed below this level, whereas high fibre diets were related to a decrease of growth rate, feed efficiency and carcass yield.

Beside an optimal level of fibre, an adequate balance of digestible fibre and long sized particles is required to obtain a maximal performance. Recent work by Nicodemus et al. [34] has determined the effect of particle size on growth and lactation traits in isofibrous diets (36 % NDF on DM). According to this study, a minimal proportion of large sized particles (> 0.315 mm) of around 22 %, would be needed to get maximal weight gain, carcass yield, milk production, and litter weight at weaning. These effects were parallel to an increase of weight of caecal contents and a decrease of feed intake. A similar negative effect of an excess of short sized particles, has been reported by Laplace and Lebas [27] and Morisse [31] when reducing particle size by fine grinding. Another work [36] has measured the effect of a variation of ADL concentration (from 3.3 to 5.9 % on DM) on productive traits in isofibrous diets (43 % NDF on DM) containing a sufficient proportion of large particles. Results showed that a minimal ADL content of 4.1 % on DM would be needed in fattening rabbits to maximise feed intake and growth rate. This work also indicated that lignin requirement for maximal intake and performance of rabbit does might be higher (5.9 % ADL on DM) than in growing rabbits.

Table II. Fibre requirements (%, in diets 90 percent of dry matter) of intensively reared rabbits [30].

Nutrient	Breeding does	Fattening rabbits	Mixed feed
Neutral detergent fibre	31.5 (30.0–34.0)	33.5 (32.0–35.0)	33.0 (32.0–34.0)
Acid detergent fibre	16.5 (15.0–18.0)	17.5 (16.0–18.5)	17.0 (16.0–18.0)
Crude fibre	13.5 (12.5–14.5)	14.5 (13.5–15.0)	14.0 (13.5–14.5)
Acid detergent lignin	5.3	4.0	5.3
Proportion of large particles (> 0.315 mm)	25	25	25

8. PRACTICAL RECOMMENDATIONS

Optimal fibre concentrations for breeding does, fattening rabbits and mixed feeds are given in *table II*. Values in parentheses indicate the range of diets for which only a slight decrease with respect to the maximal performance can be expected. Acid detergent and crude fibre recommendations have been calculated from NDF levels, for diets containing common sources of fibre (alfalfa hay, wheat straw, wheat bran), and would not be adequate for highly lignified byproducts. Optimal fibre balance is ensured by establishing a minimal concentration of large particles and lignin. Both restrictions should be followed simultaneously, as some highly lignified byproducts (e.g., rice hulls or paprika meal) can have an insufficient content of large particles.

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