# NUTRITIONAL AND ONTOGENIC FACTORS AFFECTING RABBIT CAECO-COLIC DIGESTIVE PHYSIOLOGY

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**Abstract** - The caecum is the largest compartment of the rabbit digestive tract (40% of digestive mass). It plays a key role in the digestive physiology as the major site of fibre degradation and fermentation. Disorders in caecal microbial activity (CMA) are supposed to be at the origin of the digestive troubles observed in the growing rabbit fed low fibre/high starch diets. First, the main traits of caecal digestive physiology and recent advances are presented. Ontogenic factors and then nutritional factors affecting CMA are reviewed. Finally, caeco-colic digestive disturbances arising from inadequate nutrient supply are described, including the related hypothesis explaining the occurrence of enteritis.

## INTRODUCTION

The caecum of the rabbit can only partially be compared with that of other monogastric animals, such as the pig, the horse or the rat, as it has several specific structural characteristics including a secreting appendix and a spiral fold. In addition, the caecotrophy practice leads to a diurnal rhythm of caecal filling and emptying. Consequently, the knowledge of caecal physiology obtained from other monogastric animals can not be easily transferred to knowledge of the rabbit caecum. In addition, rabbit caecal physiology exhibits specific problems of digestive pathology related to nutrition. At present, one of the main objectives for research on rabbit caecal metabolism is to understand and influence the microbial activity that is supposed to play an important role in the occurrence of digestive disturbances originating from an inadequate nutritional balance. On the other hand, the caecum participates in the digestion of the nutrient and is the major site of fibre degradation and fermentation. For instance, in adult rabbits, VFA absorption could represent 30% of the basal metabolism (PARKER, 1976; MARTY and VERNAY, 1984). Consequently, mid-term research might focus on the improvement of the caecal digestive process for a better utilisation of the nutrients. Research already performed on other monogastric animals would then be of interest.

Our review will be limited to the first objective cited previously. In evidence, the caecal microbial activity (CMA) plays a key role in the nutrition and health of the rabbit. A change in the diet could modify the nature of the digesta to be fermented in the caecum, and consequently could modify the microflora and its activity. Thus, nutritional factors affecting CMA will be examined thereafter. However, ontogenic factors will also be considered, because digestive problems occur mainly in the growing rabbit and more particularly around the weaning period. It is thus of importance to describe how the CMA is developing and interacting with nutritional factors from around three weeks of age (beginning of the feed intake) to the end of the growth period.

First of all, a brief review of some traits of caecal digestive physiology and of recent advances will be presented.

### 1) Some characteristics of caeco-colic digestive physiology and related studying methods

The caecum (Figure 1) is the largest digestive compartment of the rabbit (40% of the digestive tract). Proportionally the rabbit caecum is 5 to 6 times larger than that of the horse. Its volume changes according to a diurnal rhythm under the control of caecotrophy. Low caecal content (<20%) has been observed before or during caecotrophy, as measured by the marker dilution method (LENG and HÖRNICKE, 1976) or by the slaughter technique (FRAGA *et al.*, 1984; GIDENNE and LEBAS, 1984).

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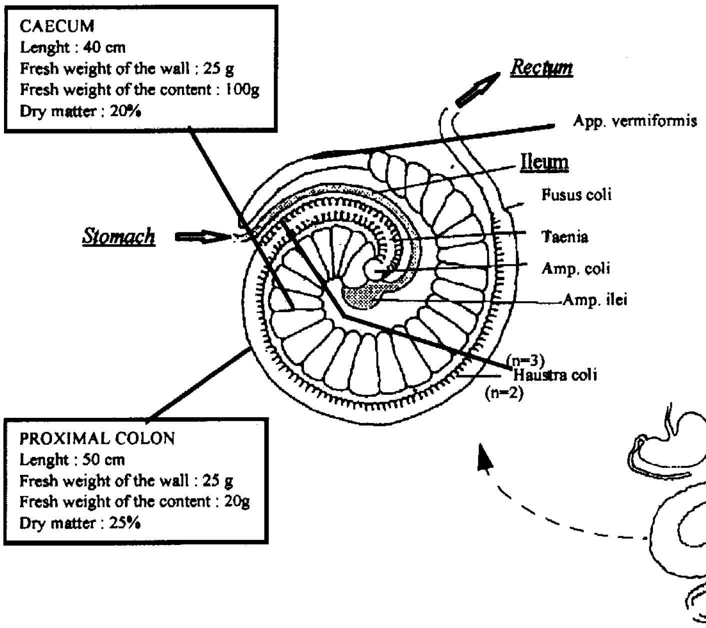
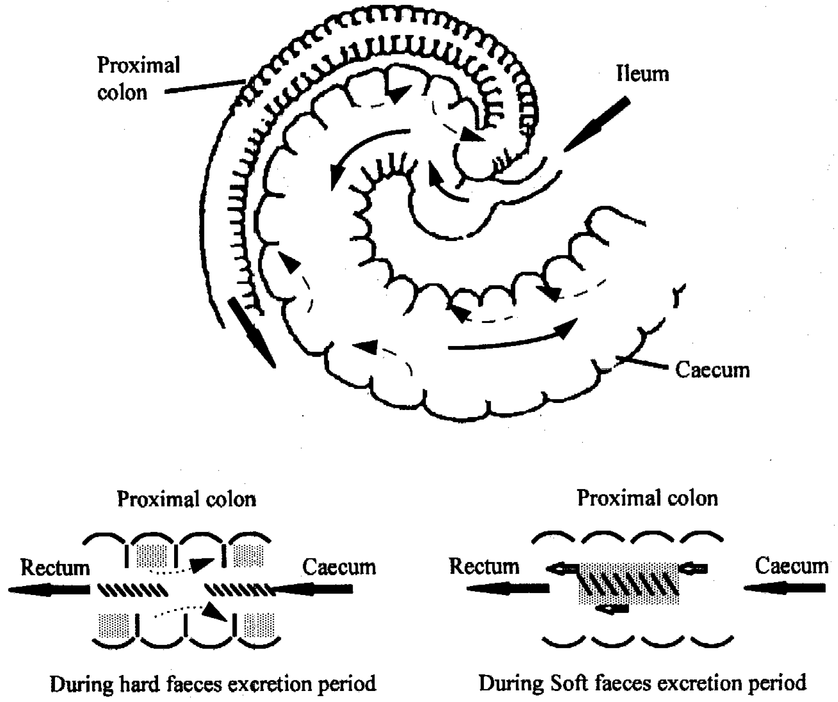
Figure 1 : Diagram of the ileo-caeco-colic segment
of the rabbit digestive tract (12 wk old).



Caecal motility should not be considered alone, because the ileo-caecal region, the caecum and the proximal colon form a functional unit. It must be remembered that outside the caecotrophy period, the motor processes of this unit allow amounts of large (over 300 mm) size particles (mainly fibre material) to pass through the hind-gut (Figure 2), while retaining only the fine particles for bacterial degradation in the caecum (BJÖRNHAG, 1981; JILGE, 1980). During caecotrophy, the caecal digesta pass through the gut without great changes (except water and mineral exchange) and are incorporated in soft faeces. The function of the ileo-caeco-colic region was reviewed by LAPLACE (1978) and more recently results of the effects of caecotrophy were obtained by EHRLEIN *et al.* (1983). However, to have a comprehensive view of caecal transit, studies of function should be coupled with studies of digesta passage time. Unfortunately, this was never done in the same experiment, probably because of the difficulty to perform simultaneously motility (e.g. electromyography) and rate of passage measurements (e.g. feed labelling techniques). In addition, measurement of caecal digesta rate of passage would require implantation of a cannula or catheter in the ileum and the proximal colon, which is very difficult.

Figure 2 :Movement of digesta in the ileo-caeco-colic segment



▨ : liquids and fine particles (<300µm)

\\\\\\\\\\ : large particles (>300µm)

Consequently, literature reports only ileo-rectal or caeco-rectal mean retention time, ranging between 7 and 16 h for particulate phase and between 16 and 42 h for liquid phase (Table 1). To overcome these methodological difficulties a new procedure, based on mathematical modelling of the faecal marker excretion curves (adapted from ruminants), was assayed for rabbit by GIDENNE (1994b). Caecal rate of passage could be thus calculated without fitting rabbits with cannula. However the validity of this modelling technique should be confirmed.

**Table 1 : Digesta mean retention time (MRT) in the rabbit caeco-colic segment**

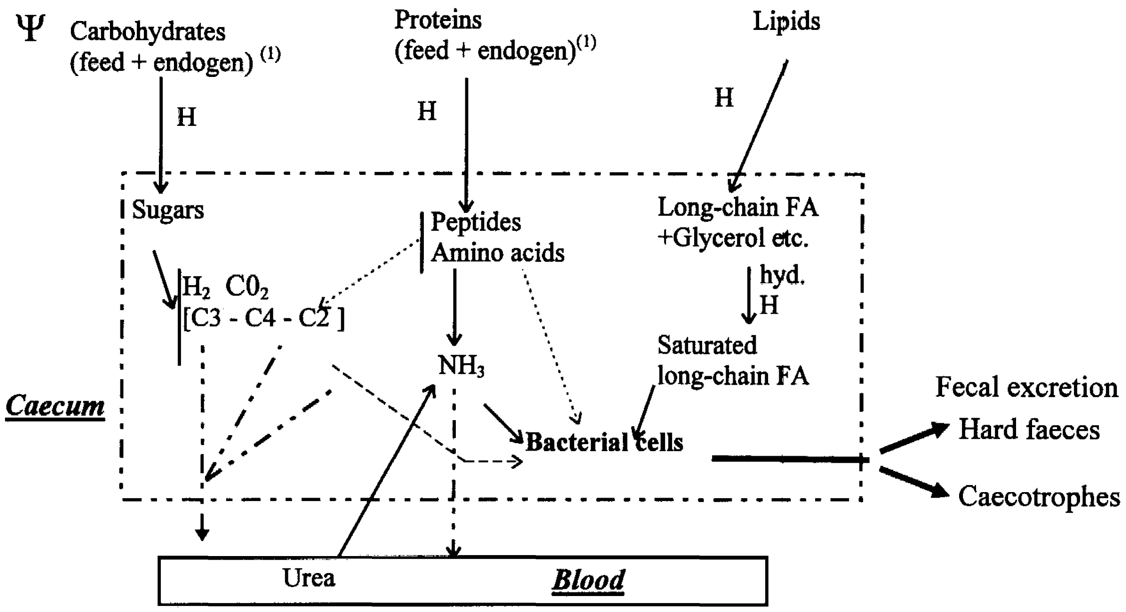
| | MRT of particulate phase (hours) | | | | |
|---|---|---|---|---|---|
| Animal (LW; nb) | ileo-rectal | caeco-rectal | caecal | *Method* | *References* |
| Adult | | 12.0 | | $Cr_2O_3$ infusion + NI | LENG *et al.*,1977. |
| (5.1kg; n=2) | | 10.8 | | Mordanced Cr.+ NI | UDEN *et al*, 1982. |
| Adult (1.3kg; n=2) | | 7.8 | | Mordanced Cr.+ NI | UDEN *et al*, 1982. |
| Grower (1.1kg; n=5) | | 9.6 | | $^{141}$Ce + NI | BELLIER, 1994 |
| Grower (1.5kg; n=10) | | 7.1 | | $^{141}$Ce + NI | GIDENNE & JEHL, 1996 |
| Adult (3kg; n=3) | 9.6 | | | Mordanced Cr. + NI | GIDENNE & RUCKEBUSCH, 1989 |
| Adult (3kg; n=7) | 12.1 | | | $^{169}$Yb + NI | GIDENNE *et al.*, 1991 |
| Adult (3.3kg; n=4) | 16.5 | | | $^{141}$Ce + NI | GIDENNE & PEREZ, 1993 |
| Grower (1.2kg; n=27) | | | 11.1 | $^{141}$Ce + modelling | GIDENNE & PEREZ, 1994 |
| Adult (4kg; n=4) | | | 14.1 | $^{169}$Yb + modelling | GIDENNE, 1994$^b$ |
| Adult (4kg; n=4) | 16,6 | | | $^{141}$Ce + NI | GIDENNE, 1994$^b$ |
| | MRT of liquid phase (hours) | | | | |
| Animal | ileo-rectal | caeco-rectal | caecal | *Method* | *References* |
| Adult | | 16.4 | | C$^{14}$ -PEG + NI | LENG *et al.*,1977. |
| Grower (1.1kg; n=5) | | 42.4 | | $^{51}$Cr- EDTA + NI | BELLIER, 1994 |
| Grower (1.5kg; n=10) | | 30.7 | | $^{51}$Cr- EDTA + NI | GIDENNE & JEHL, 1996 |

NI : calculation of the MRT by numerical integration of the quantitiy of marker excreted in faeces (method of reference).

The caecal flora present two main characteristics: a slow implantation (almost no flora till 3 d old), and a relatively simple composition (mainly gram negative non sporulated bacilli, *bacteroides*) (GOUET and FONTY 1973). However, various caecal bacterial activities have been found: cellulolytic, pectinolytic or xylanolytic (BOULAHROUF *et al.*, 1991); ureolytic (SALSES *et al.*, 1976; HILL, 1983; CROCIANI *et al.* 1984; FORSYTHE and PARKER, 1985b); proteolytic (EMALDI *et al.*, 1979); and amylolytic (PADILHA *et al.* 1995). The metabolic activity of the flora leads to the production of volatile fatty acids (VFA) and ammonia ($NH_3$) respectively after fermentation of simple sugars and amino acids (Figure 3). The caecal VFA profile is specific to the rabbit, with a predominance of acetate (C2 = 60 to 80 mmol/100mol) followed by butyrate (C4 = 8 to 20) and then by propionate (C3 = 3 to 10). Moreover, ADJIRI *et al.* (1992) showed *in vitro* (using a semi-continuous flow fermentor) that this VFA pattern was specific to the caecal flora and not to the composition of the substrate fermented. The fermentative activity of the bacteria varies according to a diurnal rhythm, including a low concentration of VFA (<25%) during the caecotrophy period compared to high VFA level found during the hard faeces excretion phase (GIDENNE, 1986). More recently, these results were confirmed *in vivo*, but diurnal changes of the fermentation pattern differed between 6 wk old and adult rabbits (BELLIER *et al.*, 1995), thus suggesting that results obtained on the adult could not be extrapolated to the young rabbit. This diurnal pattern of the caecal fermentative activity coincides with a similar rhythm of VFA absorption and metabolisation (VERNAY *et al.*, 1984; VERNAY, 1986; VERNAY, 1989). The caeco-colic metabolism of water and electrolytes is likewise under caecotrophy control, as described by HÖRNICKE (1984).

On the other hand, studies on caecal fermentative activity are usually restricted to ammonia and VFA measurements, and almost no results are available on gas production (hydrogen, methane) associated with fermentation. For instance, using an *in vitro* approach (batch incubation technique of caecal contents), PIATTONI *et al.* (1996) evaluates that methanogenic activity was around zero until weaning, and only begins to rise after 36 d of age.

**Figure 3 : Caecal metabolism of the main nutrients**



Ψ : primary substrates, escaping absorption in the small intestine, available for microorganisms

(1) : feed = starch, fibre *etc.*; endogen = mucous polysaccharides, epithelial-cell protein, enzymes

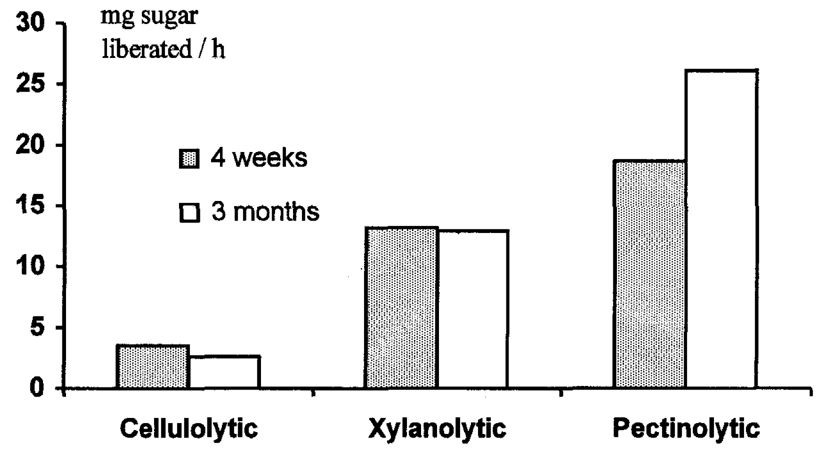
H = hydrolysis of polymers

hyd. : hydrogenation of unsaturated long-chain fatty acids (FA)

At present, more knowledge is needed to assess the variations of CMA according to age or nutrient intake. But the techniques used for bacterial enumeration are time consuming and offer relatively low precision. On the other hand, the measurement of the fermentation end-products levels is more of a qualitative indicator of CMA than a quantitative one and is insufficient to give an appreciation of the relationship between the flora and the nutritional status of the animal (BELLIER, 1994). Thus, some recent studies have dealt with new approaches for evaluating CMA. For instance, the measurement of the ATP caecal level as an indicator of the energetic metabolism of the bacteria, validated in pigs (BACH KNUDSEN *et al.*, 1991), showed too-high inter-individual variability to be of interest for studies in the rabbit (BELLIER and GIDENNE, 1996). The evaluation of the microbial biomass using DAPA (diaminopimelic acid) as an internal marker of bacteria was initially developed for ruminants. While recent application of this method in the rabbit indicated a good relationship between biomass formed and fibre intake (JEHL and GIDENNE, 1996), further studies are required to confirm the validity of this approach. Another way to assess the floral activity in response to variations of the substrate consists of measuring the enzymatic activity of the bacteria. The evaluation of the bacterial cellulolytic activity in the caecum was first performed by COOLS and JEUNIAUX (1961). More complete caecal enzymatic profiles were then reported, including enzyme activities specific to bacteria (urease, cellulase) and other non-specific activities from the host and/or from bacteria (amylase, lipase, proteinase, dehydrogenase) (CROCIANI *et al.* 1986; MAKKAR and SINGH, 1987). Compared to the rumen, caecal fibrolytic activity was lower, while amylolytic and proteolytic activities were logically higher because of the contribution of the host. JEHL *et al.* (1995) also indicated that attempts to fractionate the caecal flora into liquid- and solid- associated bacteria, as done for rumen flora, are not justified, due to the high homogeneity of the caecal content. Recently, MAROUNEK *et al.* (1995) described more precisely the caecal fibrolytic activities, and mentioned high pectinolytic activities followed by xylanasic and then by cellulasic ones (Figure 4). This hierarchy corresponds to that of cell wall constituent's digestibility in the rabbit (pectins > hemicelluloses > cellulose) and corresponds also to the fermentability level of the fibre fraction as demonstrated *in vivo* by BENSON and PARKER (1980) for the rabbit caecum (figure 5). It must also be pointed out that these fibrolytic enzymes are also found in soft faeces, and pectinolytic activities were found at a relatively high level in the stomach of rabbits (MAROUNEK *et al.*, 1995), while xylanasic and cellulasic activities were negligible. This recycling of pectinolytic enzymes causes us to inquire about the ability of pectinolytic enzymes to be active during their passage through the stomach and small intestine. This recycling could explain (at least in part) that positive ileal digestibility was found for uronic acids (from 20 to 38%) GIDENNE (1992). However, further investigations into fibre digestion in the pre-ileal tract (stomach, small intestine) are necessary to elucidate this *phenomenon* which is specific to the rabbit (unique in mammals).

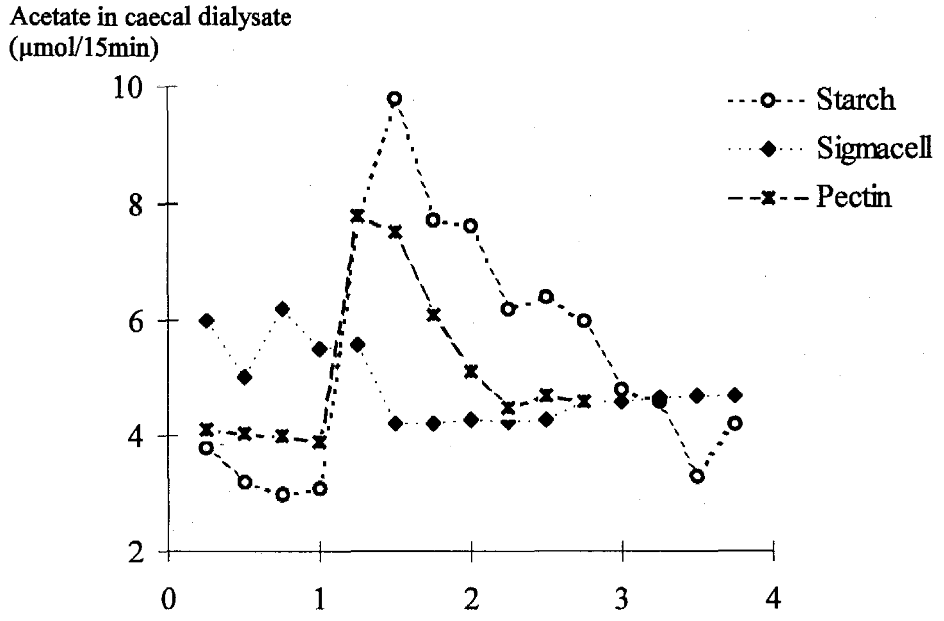
The CMA can also be addressed through its contribution to the supply of nutrient via the ingestion of soft faeces. PIATTONI *et al.* (1995) evaluates that around 50% of the caecal nitrogen was of bacterial origin, using a new indicator based on RNA/crude protein ratio. The nitrogen produced by the flora and recycled in soft faeces was evaluated recently using a method based on the measurements of the purine/bacterial nitrogen ratio (GARCIA *et al.*, 1995) or on the measurements of DAPA levels (JEHL and GIDENNE, 1996), in isolated caecal bacterial preparation. According to this technique, the bacterial contribution to the total nitrogen intake ranged between 12 and 24%.

**Figure 4 : Activity of bacterial fibrolytic enzymes in the caecum, according to the age of the rabbit**



Data from MAROUNEK et al., 1995

**Figure 5 : Hydrolysis of polysaccharides in the caecum**



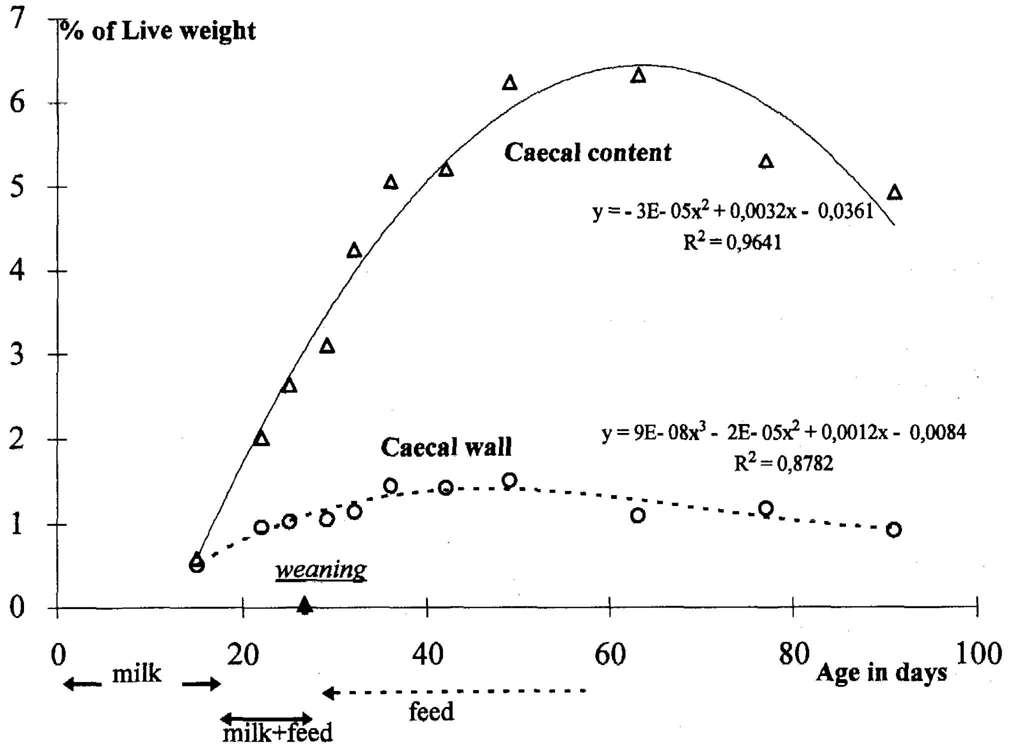
Adapted from Benson and Parker, 1980

## 2) Ontogenic factors affecting caecal microbial activity

The growth of the caecum (wall and content) is relatively slow from birth until 10 d of age (ALUS and EDWARDS, 1977). But from 15 d to 40 d rapid growth produced a 10 times weight increase (0.5 to 5% of the live-weight) (Figure 6), in parallel to the increase of the dry feed intake, while the growth rates of stomach and small intestine appeared linear from 0 to 30 d of age.

The implantation of the cellulolytic flora begins only when the intake of feed starts (around 3 wk old) and reaches $10^4$ to $10^7$ bact./g between 7 and 9 weeks old, while at 15 d of age the amylolytic and total anaerobic flora is already installed (respectively $10^{10}$ and $10^{11}$ bact./g fresh caecal content, figure 7) (PADILHA *et al.*, 1995). The age-dependant variations of the caecal flora were more fully analysed by FONTY (1974) and PADILHA (1995). Relationships between microflora and caecal fermentation were recently addressed by PADILHA *et al.* (1995). From 15 to 30 d of age, the VFA level increased from 8 to 35 mmol/L, the C3:C4 ratio reversed and the ammonia level decreased sharply (-50%) at weaning. This was associated with the development of the cellulolytic flora.

**Figure 6 : Relative development of the caecum (wall and content) according to the age of the rabbit**

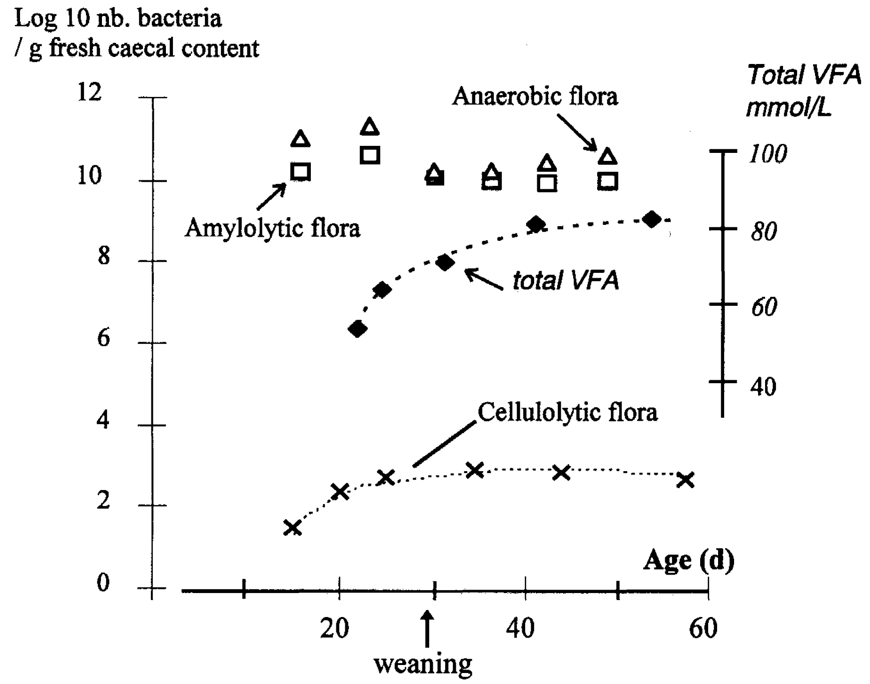


Data from : LEBAS and LAPLACE, 1972 ; CANDAU *et al.*, 1978; PADILHA *et al.*,1995.

The VFA level would also be dependant on the physiological status of the animal. For instance, PADILHA (1995) reported VFA levels for SPF (specified pathogen free) rabbits that are 50% lower than those registered on conventional rabbits (50 to 80 mM, Figure 6) by PIATTONI *et al.* (1995). PADILHA (1995) also indicated higher counts of cellulolytic bacteria ($10^4$ and $10^5$ bact./g fresh caecal content at 2 wk of age) in rabbits reared in "farm conditions" (without concentrated feeds etc.) associated with a higher level of VFA compared to that of SPF rabbits.

The implantation of the cellulolytic flora seems to be achieved at five weeks of age (Figure 7), while the VFA level continues to increase. Enumeration of the bacteria may thus not reflect their metabolic activity. The fermentation level may also depend on the activity of the different strains of fibrolytic bacteria that seem to have different establishments with age. For instance, MAROUNEK *et al.* (1995) reported that activity of cellulolytic bacterial enzymes remained low between 4 wk and 3 months of age (figure 4), while xylanolytic and pectinolytic activities increased sharply. It would thus be of interest to develop an approach based on the measurement of the bacterial enzymatic activity (especially fibrolytic) and of the fermentation pattern, to analyse more precisely the establishment of the CMA in the growing rabbit.

**Figure 7 : Kinetics of establishment of the caecal flora and of volatile fatty acids (VFA)**



Data from : BOULAHROUF *et al.*, 1991; PIATTONI *et al.*,1995; PADILHA *et al.*, 1995.

In order to separate the effect of age from that of nutrient intake, PADILHA *et al.* (1996) have extended the milking period (as sole source of feed) until 6 weeks old. Caecal pH then remains at a high level (6.9), and volatile fatty acids concentration did not increase whereas the ammonia increased from 10 to 17 mM/L. In addition, the cellulolytic flora did not implant, whereas the establishment of the *coli* flora was unaffected. This underlined the impact of the nutritional factors on CMA, and also suggested that there was no relationship between *Escherichia coli* flora development and VFA or pH level, contrary to *in vitro* results obtained by PROHASZKA (1980).

The effects of nutritional factors on CMA have been generally studied in finishing growing rabbits (part 3), without assessing possible interactions with age. However, changes in the development of caecal fermentative activity according to the supply of dietary fibre have been noticed by CANDAU *et al.* (1978) and BELLIER (1994), and results indicate that changes in CMA took place before 7 weeks of age. This is in agreement with previous considerations indicating that the greatest changes in fibrolytic activity take place between 3 and 7 weeks of age (Figure 7).

### 3) Nutritional factors affecting caecal microbial activity

Nutritional factors could act at least at two levels: supplying appropriate quantity and quality of nutrients to the flora, and ensuring a correct caecal motility and digesta transit. Obviously, CMA depends closely upon the nutrient supply, as only a few hours of starvation leads to a sharp decrease in caecal VFA level and to a reversed C3:C4 ratio (VERNAY and RAYNAUD 1975, PROHASZKA and SZEMERIDI, 1984; GIDENNE and BELLIER, 1992).

Studies concerning the dietary effect on caecal digestive physiology are often restricted to measuring the fibre digestibility with sometimes a description of the fermentation pattern and/or fibre rate-of-passage measurements. For example, a correct assessment of the ileal flow of nutrients, which is of first importance in evaluating the dietary effect on caecal metabolism, remains very difficult and time-consuming, and is rarely performed. Thus it should be kept in mind that the results listed in the following review present an important lack of precision in obtaining a comprehensive view of the impact of nutritional factors. Effects of nutritional factors upon CMA will be presented for major nutrients, as almost no studies concern the interaction between nutrients.

### *3.1) Fibre and starch*

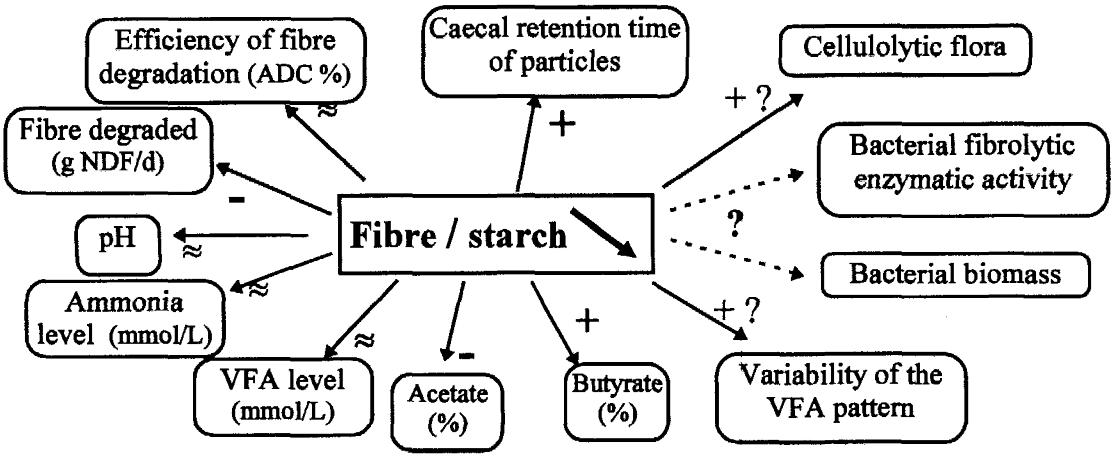
Many experiments aimed to evaluate the effect of fibre/starch level on caecal metabolism, because it is acknowledged that a fibre deficiency greatly affects the caecal metabolism and the health of the rabbit (see part 4). However, few studies have been able to separate strictly the effect of dietary fibre content from that of the effect of the type of cell wall constituents. This could be attributed to the use of complex dietary models associated with a too-global analysis of fibre (often restricted to "crude fibre"). Moreover, the dietary starch level is generally inversely correlated to the fibre level, but in some experiments the starch level has not been completely controlled, thus inducing confounding effects with fibre.

We will first deal with effects on caecal digestion of a change in the fibre/starch ratio that induces variations in fibre intake (part 3.1.1), secondly with effects attributed to the type of cell wall constituents (3.1.2) and then with effects of variations in the starch intake (3.1.3). Effects of fibre and starch intake on rabbit digestion have also been reviewed recently (GIDENNE, 1996).

#### *3.1.1) Effect of the fibre/starch ratio*

A lower dietary fibre level, without major changes in the proportions of the cell wall constituents (hemicelluloses or lignins etc.), did not greatly affect the weight of the caecal content but altered its composition. The level of fibre in the caecum decreased (CARABAÑO *et al.*, 1988), as did crude protein level, while the starch concentration remains low (around 1.5%, FRAGA *et al.*, 1984). Most of the authors report no significant changes in the concentration of the fermentation end-products (ammonia, VFA) and caecal pH (Figure 8), in response to a decrease in fibre intake (HOOVER and HEITMANN, 1972; CHAMPE and MAURICE, 1983; CARABAÑO *et al.*, 1988; STRUCKLEC, 1990; GARCIA *et al.*, 1995; BELLIER and GIDENNE, 1996). However, the VFA molar proportion is affected by the fibre level. For instance, the proportion of butyrate generally rose significantly when the fibre/starch ratio decreased. Fibre digestibility is not greatly affected by the level of fibre, while the quantity of fibre degraded decreased (combination of a lower feed intake and of a lower dietary fibre level). In fact, we can suppose that the quantity of fibre entering the caecum is not a limiting factor for the fermentation processes, probably because the digesta retention time in the caecum is relatively short allowing the degradation of mainly the easily digestible fibre fractions such as pectins or hemicelluloses (Figure 5). Moreover, the retention time in the caecum increased proportionally to the reduction of the fibre intake (GIDENNE, 1994b), and could then compensate for an eventual limitation of the quantity of fibre entering the caecum. However, for very low fibre level (ADF lower than 10%) some increase in the efficiency of fibre degradation was noticed (DE BLAS *et al.*, 1986; BELLIER and GIDENNE, 1996) and may be attributed to a prolonged fibre retention in the caeco-colic segment. Besides, the level of fibre seemed to not influence the energetic supply from caecal fermentation (GIDENNE, 1994a), however these results were obtained for adult rabbits fed semi-purified diets and must be confirmed.

**Figure 8 : Effect of lowering the dietary fibre/starch ratio on several caecal digestive criteria in the growing healthy rabbit**



? : need of further studies ; ≈ : not significant effect

*3.1.2) Effect of the type of cell wall constituents.*

The effect of the type of fibre on caecal metabolism was addressed either by using various sources (purified or not) of cell-wall (*e.g.* pectins from apple, beet pulp etc.), or by using complex diets (numerous raw materials) in order to obtain a variation for one cell-wall constituent (*i.e.* lignins) without changes for others (cellulose, pectins etc.). The lignin fraction of the plant cell wall is theoretically non digestible by bacteria, although faecal digestibility of lignins appeared frequently positive (20 to 50%) in rabbits. The inhibitory effect of lignins on ruminal fermentations is well acknowledged. For rabbits, studies on the effect of lignins have often used agro-industrial by-products (grape marc, etc.) which are not well defined from a chemical point of view (associations with tannin and cutins). Thus, contrasting results were reported indicating either lower caecal VFA and ammonia levels (MOTTA FERREIRA, 1990; CHIOU *et al.*, 1994) or no major impairment of the fermentation pattern (GIDENNE, 1986; FALCAO E CUNHA, 1988; PEREZ DE AYALA, 1989). An increase of the dietary lignin level leads to a lower fibre digestibility and to a shorter retention time (PEREZ DE AYALA, 1989; GIDENNE and PEREZ, 1994) and appeared efficient in reducing the mortality rate in the growing rabbit (PEREZ *et al.*, 1994). The effects of purified lignins on the histology of the caecal wall seemed similar to those obtained with pectins or lucerne, while inclusion of purified cellulose in the diet would reduce the depth of the crypt in the caecum (CHIOU *et al.*, 1994).

Although few studies concerned the effect of dietary cellulose content (analysed by difference between ADF and ADL residue) on rabbit digestion, the effect of cellulose incorporation on fibre digestion and caecal rate of passage seemed lower than those observed for lignins (FALCAO E CUNHA, 1988; GIDENNE and PEREZ, 1996). Nevertheless, cellulose appeared as efficient as lignins in reducing the mortality rate during fattening (PEREZ *et al.*, 1996).

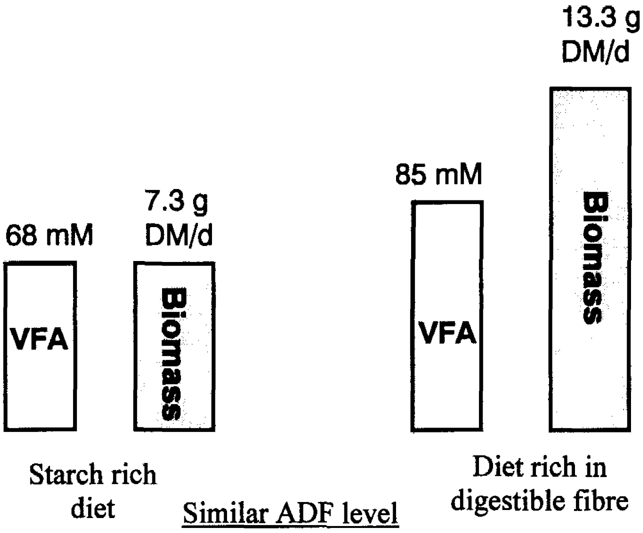
The effects of more easily digestible fibres (hemicelluloses or pectins) such as beet or citrus pulp were more extensively studied. Compared to less digestible fibre source (i.e. lucerne) the incorporation of beet pulp induced higher caecal content and was associated with higher VFA levels and lower pH (CANDAU *et al.*, 1978; BELLIER, 1994). The rate of passage in the total digestive tract (FRAGA *et al.*, 1991) or between caecum and rectum (BELLIER, 1994) was not affected, while the efficiency of the fibre degradation was improved. A supply of digestible fibre could thus stimulate the CMA and favour its establishment in the growing rabbit. This assumption is supported by the results of CANDAU *et al.* (1978) who reported an earlier stabilisation (at 5 wk of age) of the caecal fermentation for rabbits fed a diet based on beet pulp compared to a lucerne-based diet (at 7 wk). Interactions between the establishment of the caecal fermentation pattern and dietary fibre supply were also reported by BELLIER (1994).

*3.1.3) Effect of starch intake*

Starch not completely hydrolysed in the small intestine is then quickly fermented by the caecal flora (Figure 5). The proportion of starch degraded by the flora is emphasised in the weanling rabbit, because the pancreatic amylase is not well established before 6 wk of age. BLAS *et al.*(1994) reported, in 6 wk old rabbits, that when the dietary starch level increased (16 to 25%), the ileal starch content doubled while the caecal level of starch could reach 6%. Thus, dietary starch could play a substantial role, in interaction with fibre, to control digestion in the caeco-colic segment of the tract. For instance, GIDENNE and PEREZ (1993) indicated, in restricted-fed adult rabbits, that an increased ileal flow of starch (without change in fibre intake) was associated with a higher fibre degradation and with a longer retention time. An interaction between starch and fibre could also be noticed in the study of MOTTA FERREIRA (1990) who registered significant changes in caecal VFA level with incorporation of beet pulp, contrary to the literature (part 3). This could be explained by a parallel increase of the dietary starch and beet pulp level (without feed intake variation) which thus may impair the CMA.

In order to separate the effect of starch from that of fibre, the caecal fermentative activity and daily bacterial biomass production were recently compared in growing rabbits (JEHL and GIDENNE, 1996) fed a diet rich in starch "S" (starch = 26.6 g/kg DM) or a diet rich in digestible fibre "DF" (hemicellulose + pectin = 27.1 g/kg DM), but containing a similar ADF content (20.5 g/kg DM) adequate according to the current recommendations. Caecal VFA concentrations, measured *in vivo* in healthy rabbits fed DF diet were higher (Figure 9) associated with a higher total bacterial biomass production (excreted in hard and soft faeces). However the biomass recycled in soft faeces (13% of the feed intake) was not affected by the diet as was also found by GARCIA *et al.* (1995) using rabbits fed lucerne hays, with hays varying in NDF content.

**Figure 9 : Caecal VFA level and bacterial biomass production, in the growing rabbit fed diets having a high-starch of high-digestible fibre level, but with similar ADF content**



Adapted from JEHL and GIDENNE (1996)

### *3.2) Proteins and lipids*

The flow of crude protein entering the caecum, composed of undigested dietary and endogenous protein (cell desquamation, enzymes secretions etc.), was evaluated in adult rabbit (fed a diet containing a purified protein source) to one third of the NDF ileal flow in adult (GIDENNE, 1992). However, the flow of crude protein could vary according to the dietary fibre sources (MERINO and CARABAÑO, 1992). Proteins are then fermented by the caecal flora and converted to ammonia that represents the main nitrogen source for the microbial protein synthesis (figure 3). The caecal ammonia level range is generally between 4 and 18 mM/L, although some authors have reported ammonia levels reaching 25 to 30 mM/L (GIDENNE, 1986; MORISSE *et al.*, 1985). However, other metabolic pathways contribute to the supply of ammonia to the caecum. About 25% of the caecal ammonia pool originates from the catabolism of blood urea absorbed by the caecal wall (FORSYTHE and PARKER, 1985a) and then converted to ammonia by ureolytic flora (EMALDI *et al.*, 1979; CROCIANI *et al.*, 1984; FORSYTHE and PARKER, 1985b). In addition, some urea (15% of the urea degradation rate) was provided through the ileal digesta. As judged from rumen levels, CARABAÑO *et al.* (1988) estimated that caecal ammonia level is not a limiting factor for the microbial protein synthesis. It could be of interest to replace dietary protein by non-proteic nitrogen sources. But numerous studies have demonstrated that urea supply is useless, because 90% of the urea is hydrolysed and absorbed before reaching the caecum (CANDAU *et al.*, 1980). Urea is only efficiently utilised if directly infused into the caecum (SALSES *et al.*, 1977). However, MAKKAR *et al.* (1990) reported that the enzymatic cellulolytic activity should be higher for a diet supplemented with urea, and ROBINSON (1986) showed that urea in feed should be partially utilised by the growing rabbit for amino acid synthesis. More recently, CROCIANI *et al.* (1991) pointed out that biuret could be efficiently utilised by the growing rabbit, and showed the presence in the caecum of an aerobic facultative biureolytic flora.

Very few studies were performed to assess CMA according to the dietary supply of protein. FRAGA *et al.* (1984) indicated that increasing the dietary crude protein level from 12.8 to 16% (without major change in ADF level) led to a similar rise in caecal nitrogen concentration and to an increase (5.82 to 6.48) of the caecal pH. An excess of dietary protein could also favour the proliferation of *Clostridia* in the adult rabbit and could also slightly increase the prevalence of *E. coli* (CORTEZ *et al.*, 1992).

Unsaturated fat escaping digestion in the small intestine of the monogastric is subjected to hydrogenation (increase of the degree of saturation) by the caeco-colic flora (Figure 3). However, as the fat level is generally low in rabbit feed (1 to 4%), fat hydrogenation by the caecal flora may be presumed to be of relatively low importance. Information is lacking about the effect of dietary fat addition on CMA. Only two studies mentioned that the addition of vegetable fat, in contrast to animal fat, tended to improve the crude fibre digestibility, and particularly for low energy feeds (SANTOMA *et al.*, 1987; FEKETE *et al.*, 1989).

### *3.3) Feed additives*

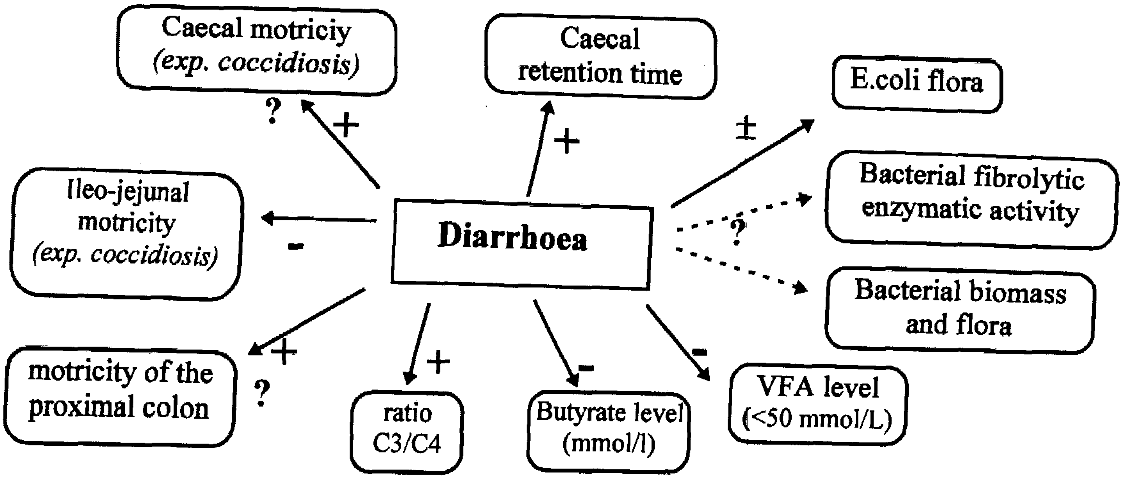
Various "feed additives" aiming to modify the composition of the caecal content and/or the CMA have been experimented with, including chemical compounds, enzymes, buffers, acidifiers, and live micro-organisms. At first, studies aimed to control the pH of the caecal content, in order to impair proliferation of detrimental flora. A relatively slight acidification of the caecal content was obtained with acetate, but acidification was not significant with lactate or lactulose (MORISSE *et al.*, 1979), although lactulose seemed to reduce enteritis. Evidence that lowering caecal pH could prevent enteritis was thus not provided.
Several experiments have dealt with the effect of "synthetic" oligosaccharides (*e.g.* from *in vitro* bacterial fermentation processes). These compounds are undigested in the small intestine, but they are rapidly fermented by caecal flora, and may thus modify the CMA and consequently may improve the growth performance and/or the health status of the animal. However, the effect of oligosaccharides on rabbit caecal fermentation is not clear. Increased levels of caecal VFA were obtained with galacto-oligosaccharides (PEETERS *et al.*, 1992) and fructo-oligosaccharides (FOS) (MORISSE *et al.*, 1990), whereas in other studies the addition of FOS or gluco-oligosaccharides (GOS) did not affect caecal fermentation (LUICK *et al.*, 1992 ; LEBAS 1993; GIDENNE, 1995). Concerning the rabbit's health status, GIDENNE (1995) has registered a significant negative effect of GOS supplementation. The effect of oligosaccharides on rabbit mortality and morbidity has not been reported previously, although some protective effect of FOS was recorded for animals experimentally infected with entero-pathogenic *E. Coli* (PEETERS *et al.*, 1992; MORISSE *et al.*, 1993).

Attempts to reduce the caecal ammonia level with glycocomponents extracted from the yucca plant failed, although a reduction of mortality rate was registered (CHMITELIN, 1992). Similarly, addition of probiotics (yeast or *lactobacilli*) seemed to not greatly modify the caecal fermentation as measured *in vivo* by KERMAUNER *et al.* (1994) or *in vitro* by ADERIBIGBE and CHEEKE (1993), nevertheless some improvement in growth performance and mortality were mentioned (HOLLISTER *et al.*, 1990).

## 4) Caeco-colic digestive disturbances resulting from inadequate nutrient supply

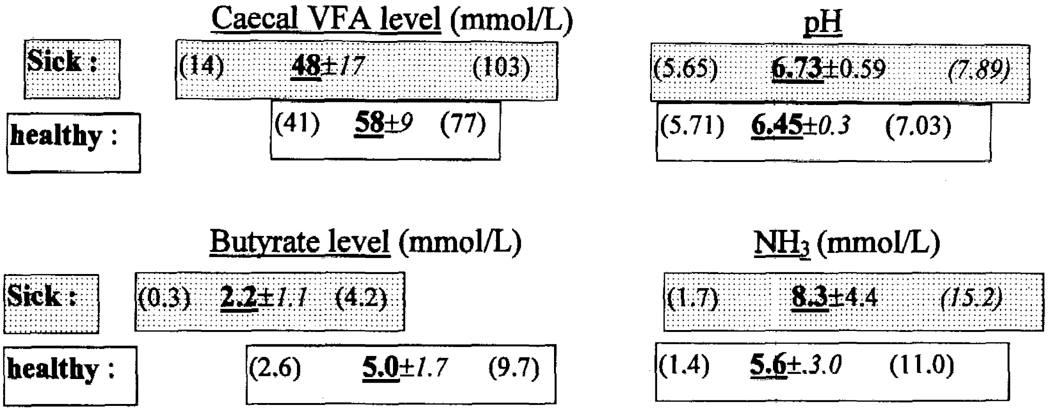
Diarrhoea and caecal impaction are the two main symptoms associated with digestive disturbances of the caeco-colic segment. However, no evidence of a relationship between caecal impaction and nutritional factors has yet been provided, and thus we will not develop this point. In contrast, several studies have reported an increase in occurrence of digestive disturbances when the fibre/starch ratio in the diet is too low (HECKMANN and MEHNER, 1970; FRANCK and COULMIN 1978; BLAS *et al.*, 1994; PEREZ *et al.*, 1994). The antagonism between feed efficiency (often improved through a reduction of the fibre/starch ratio) and the health status of the animal constitutes one of the main problems encountered in the nutrition of the growing rabbit. The composition of the caecal content as well as caecal function and CMA are deeply affected in case of enteritis (Figure 10), but no studies have gathered results on these different aspects of the caecal physiology to obtain a comprehensive view of the caeco-colic dysfunction. Motility of the caecum was stimulated whereas that of ileum and jejunum were inhibited in experimentally induced diarrhoea with *coccidia* (FIORAMONTI *et al.*, 1981). On the other hand, HODGSON (1974) observed, in rabbits fed a low fibre diet, an increased motility of the proximal colon that appeared contracted and thickened, and a higher retention of digesta in the total tract. This probably reflects a higher antiperistaltic activity of the proximal colon induced by the high proportion of fine particles in a low fibre diet. Consequently, the caecal retention time increased, as described previously (part 3.1.1). It is thus difficult to postulate that rabbit diarrhoea is characterised by an hypomotility of the caeco-colic segment. In parallel, the caecal fermentative activity is disturbed (Figure 11). For a 6 wk old rabbit, the caecal VFA concentration falls to under 50 mM/L, and particularly the butyrate (leading to a C3/C4 quotient in the range between 1.5 and up to 8), and an increase of the ammonia and pH (+0.5) could also be observed (CHMITELIN *et al.*, 1992; BELLIER, 1994; JEHL and GIDENNE 1996). In addition, BELLIER and GIDENNE (1996) noticed that the variability of the caecal fermentation profile was increased for a low fibre diet. The caeco-colic flora could also be affected in composition, but results are not consistent showing sometimes a decrease or an increase in *E. coli* and/or *Clostridia* (MORISSE *et al.*, 1979; MORISSE, 1982; MORISSE *et al.*, 1985; CORTEZ *et al.*, 1992).

Figure 10 : Caecal changes occuring in case of digestive troubles (diarrhea) in the growing rabbit



? : need of further studies ; ± : not consistent results

**Figure 11 : In-vivo⁽¹⁾ caecal fermentation pattern of healthy and sick⁽²⁾ growing rabbits (means of 80 and 21 rabbits respectively for healthy and sick animals)**



figures in parenthesis are minimum and maximum values observed

(1): cannulated rabbits, between 7 and 11 weeks of age ; (2) : rabbits having punctual digestive troubles, or abnormally low intake.

Data from BELLIER (1994)

It could be assumed that nutritional factors, such as the fibre/starch ratio, act as permissive agents that increase the frequency of digestive disturbances. For example, a diet containing less than 3% of crude fibre did not induce diarrhoea in controlled experimental conditions (COLIN *et al.*, 1976; LICOIS *et al.*, 1980). Nevertheless, if some other unfavourable factors (pathogenic agents, stress, breeding conditions etc.) are also present, digestive troubles may occur. Further studies are thus necessary to analyse the function of the ileo-caeco-colic segment and the related CMA for rabbits having diarrhoea caused by an inadequate nutrient supply. But this remains difficult because no experimental model is presently available to reproduce such digestive troubles in the growing rabbit. However, several hypotheses have been drawn to explain how the dietary supply of starch and fibre affects the caecal digestive physiology, but none was completely validated by experimental results.

For instance, PROHASZKA (1980) put forward the antibacterial effect of caecal VFA, particularly in the case of *E. coli* infection. But numerous studies have not observed a close relationship between the concentration of caecal VFA and the pH or between *E. coli* flora and caecal pH (MORISSE *et al.*, 1979; MORISSE, 1982; MORISSE *et al.*, 1990; BELLIER 1994; PADILHA *et al.*, 1996). In addition, PADILHA *et al.* (1995) showed that between 29 and 49 d of age, the caecal pH is decreasing whereas *E. coli* flora remains steady.

The favourable effect of low-digestibility fibre (lignocellulose) could correspond to a control of the digesta rate of passage, particularly through the caeco-colic segment (part 3.1.2.). Moreover, most of the results indicate that all the factors contributing to an increase in retention time (lowering the fibre level, reducing the particle size of the feed, feed restriction) contribute to destabilising the CMA (LAPLACE, 1978) and favour enteritis. In fact, it could be supposed that a low caecal turnover would lead to an insufficient supply of substrates available for the fibrolytic flora.

Besides, MORISSE *et al.* (1985) suggested that a high fibre/low starch diet could impair the caecal fermentation, because of a too-low caecal input of fermentable sugars. In contrast, CHEEKE and PATTON (1980) postulated that a carbohydrate overload in the caecum could induce digestive troubles. More specifically, caecal input of glucose (originating from starch degradation) seemed to favour pathogenic species such as *Clostridium spiroforme* (BORIELLO and CARMAN, 1983). Nevertheless, the rabbit reduces its feed intake when the fibre level decreases, consequently the starch intake remains similar whereas the fibre intake is reduced sharply (Table 2). In these conditions, the ileal flow of starch between a low and a high-fibre diet should be similar, and could not be a primary factor of disturbances of the caecal function. However, in the pre-weaned rabbit we could suppose that the feed intake regulation is not completely established and neither is the pancreatic enzymatic activity. The combination of these two factors could lead to high flow of starch into the caecum which could then favour digestive disturbances. In addition, it can not be excluded that if the ileal starch flow increased for a similar intake of fibre (for example if using low-digestible starch), it could then become an important factor in destabilisation of the caecal flora. For instance, for rabbits fed a diet containing more than 20% of crude potato starch, HECKMANN (1972) noticed a higher water content in the faeces, and suggested that this could be the first stage of diarrhoea. GIDENNE (1995) also observed a higher incidence of diarrhoea for rabbits fed a diet containing a gluco-oligosaccharide that provides glucose after hydrolysis by caecal bacteria.

**Table 2 : Effect of the ratio fibre/starch on the nutrient intake**

| | Feed composition (g/kg DM) | | *INTAKE (g/d)* | | |
|---|---|---|---|---|---|
| **Feed** | *NDF* | Starch | *D.M.* | *N.D.F* | *Starch* |
| High Fibre/ low starch | 396 | 230 | *145* | *57,4* | *33,3* |
| Low fibre/ high starch | 304 | 342 | *114* | *34,6* | *39,0* |

Data from BELLIER & GIDENNE (1996)

On the other hand, JEHL and GIDENNE (1996) examined the CFA (caecal fermentative activity) of growing rabbits having a low or a high starch intake in substitution for digestible fibre (DF), but having a similar ADF intake. Animals fed the high-starch/low-DF diet showed a higher incidence of digestive disorders (diarrhoea) compared to those fed low starch/high DF diet. Digestible fibres entering the caecum were pectins (mainly from beet pulp) and hemicelluloses (mainly from wheat bran), that are fermented respectively into galacturonic acids and pentoses. This induced a higher CFA and biomass production (Figure 9). The better health status of these rabbits could be the result of a barrier effect from the fibrolytic symbiotic caecal flora against pathogenic species. On the other hand, the level of glucose entering the caecum would be lower than for starchy diets, and this could also impair the development of pathogenic bacteria. Moreover, no changes of caeco-rectal rate of passage were registered for these two diets (GIDENNE and JEHL, 1996), meaning that in these conditions of a similar ADF intake the caecal turnover rate was not an important factor in the control of CMA.

Thus, dietary recommendations of lignocellulose appear to be insufficient to prevent digestive disturbances in the growing rabbit. The starch level must be also considered, besides the ADF level, in the formulation of a feed for the growing rabbit. Interactions between caecal pathology and the establishment of the CMA must also be considered. For example, susceptibility of the rabbit to enteropathogenic strains of *E. coli* (O103) is low after 42 d of age (LICOIS *et al.*, 1992). Previous results (part 2) have shown that CMA changed greatly between 3 and 5 wk of age. Consequently, treatments (nutrient intake, additives etc.) aiming to control the CMA should be applied as soon as the feed intake begins (i.e. around three weeks of age).

## CONCLUSION

Several new methods were recently developed to analyse the caecal microbial activity. Now further studies are needed to confirm their validity, and particularly their ability to provide new criteria having a nutritional significance for the rabbit.

The CMA could be affected differently by fibres according to their degradability and interactions with dietary starch should also be considered especially in the young rabbit. However, the effect of protein and its potential interactions with fibre needs to be evaluated.

Further research on the caecal digestive physiology of the young rabbit is also necessary to define more precisely the relationship between nutrients entering the caecum, activity of the flora and digestive disturbances. Particularly, it would be beneficial to explore how CMA establishes under various nutritional conditions, as soon as the young rabbit begins to eat dry feed. Furthermore, it would be of interest to deal with the possible interactions between CMA establishment in the pre-weaned rabbit and the impact of pathogenic factors.

## REFERENCES

ADERIBIGBE A.O., CHEEKE P.R., 1993. Comparison of in vitro digestion of feed ingredients by rabbit caecal and bovine rumen fluids. *Anim. Feed Sci. Technol.*, **41**, 329-339.

ADJIRI D., BOUILLIER-OUDOT M., LEBAS F., CANDAU M., 1992. Simulation *in vitro* des fermentations caecales du lapin en fermenteur à flux semi-continu. 2) Effet de la nature de l'inoculum. *Repr. Nutr. Develop.*, **32**, 361-364 ,

ALUS G., EDWARDS N.A., 1977. Development of the digestive tract of the rabbit from birth to weaning. *Proc. Nutr. Soc.*, **36**, 3A.

BACH KNUDSEN K.E., BORG JENSEN B., ANDERSEN J.O., HANSEN I., 1991. Gastrointestinal implications in pigs of wheat and oat fractions. 2. Microbial activity in the gastrointestinal tract. *Br. J. Nutr.*, **65**, 233-248.

BELLIER R., 1994. Contrôle nutritionnel de l'activité fermentaire caecale chez le lapin. *Thèse de Doctorat.* Ecole Nationale Supérieure Agronomique, Institut National polytechnique de Toulouse. 117p.

BELLIER R., GIDENNE T., 1996. Conséquences of reduced fibre intake on digestion, rate of passage and caecal microbial activity in the young rabbit. *Br. J. Nutr.*, **vol. 75**, 353-363.

BELLIER R., GIDENNE T., VERNAY M., COLIN M., 1995. In vivo study of circadian variations of the caecal fermentation pattern in postweaned and adult rabbits. *J. Anim. Sci.*, **73**, 128-135.

BENSON M., PARKER D.S., 1980. Substrates for fermentation in the rabbit caecum. *IId World Rabbit Congress*, 15-18 april, Barcelona, Spain. (Round table on physiology of the rabbit large intestine in connection with caecotrophy).

BJÖRNHAG G., 1981. The retrograde transport of fluid in the proximal colon of rabbits. *Swedish J. Agric. Res.*, **11**, 63-69.

BLAS E., CERVERA C., FERNANDEZ-CARMONA J., 1994. Effect of two diets with varied starch and fibre levels on the performances of 4-7 weeks old rabbits. *World Rabbit Sci.*, **2**, 117-121.

BORIELLO S.P., CARMAN R.J., 1983. Association of iota-like toxin and *Clostridium spiroforme* with both spontaneous and antibiotic-associated diarrhea and colitis in rabbits. *J. Clin. Microbiol.*, **17**, 414-418.

BOULAHROUF A., FONTY G., GOUET P., 1991. Establishment, counts and identification of the fibrolytic bacteria in the digestive tract of rabbit. Influence of feed cellulose content. *Current Microb.*, **22**, 1-25.

CANDAU M., DELPON G., FIORAMONTI J., 1978. Influence de la nature des glucides membranaires sur le développement anatomofonctionnel du tractus digestif du lapin. *2èmes Journées de la Recherche Cunicole*, 4-5 avril, Toulouse, INRA ed., Toulouse, 1.1-1.4.

CANDAU M., FIORAMONTI J., TOUITOU M., 1980. Sites de dégradation de l'urée dans le tube digestif du lapin. *Proc 2nd Congr. of World Rabbit Sci. Assoc.*, 16-18 April, Barcelona, Spain. WRSA ed., **Vol 1**, 81-89.

CARABAÑO R., FRAGA M.J., SANTOMA G., DE BLAS J.C., 1988. Effect of diet on composition of caecal contents and on excretion and composition of soft and hard feces of rabbits. *J. Anim. Sci.*, **66**, 901-910.

CHAMPE K.A., MAURICE D.V., 1983. Response of early weaned rabbits to source and level of dietary fiber. *J. Anim. Sci.*, **56**, 1105-1114.

CHEEKE P.R., PATTON N.M., 1980. Carbohydrate overload of the hindgut. A probable cause of enteritis. *J. Appl. Rabbit Res.*, **3**, 20-23.

CHIOU P.W.S., YU B., LIN C., 1994. Effect of different components of dietary fiber on the intestinal morphology of domestic rabbits. *Comp. Biochem. Physiol.* **[A] 108**, 629-638.

CHMITELIN F., 1992. Effect of protein level and De-odorase on performance and caecal fermentation of weanling rabbits. Proc. Fifth Congress of W. Rabbit Sci. Assoc., 25-30 July, Corvallis, USA. *J. Appl. Rabbit Res.*, **15**, 1113-1120.

COLIN M., MAIRE C., VAISSAIRE J., RENAULT L., 1976. Etude expérimentale du remplacement dans les aliments pour lapins de la cellulose par des lests minéraux : sable, vermiculite. *Rec. Méd. Vét.*, **152**, 457-465.

COOLS A., JEUNIAUX C., 1961. Fermentation de la cellulose et absorption des AGV au niveau du caecum du lapin. *Arch. Int. Physiol. Biochim.*, **69**, 1-8.

CORTEZ S., BRANDEBURGER H., GREUEL E., SUNDRUM A., 1992. Investigations of the relationships between feed and health status on the intestinal flora of rabbits. *Tierarztl. Umsch.*, **47**, 544-549.

CROCIANI F., BIAVATI B., CASTAGNOLI P., MATTEUZZI D., 1984. Anaerobic ureolytic bacteria from caecal content and soft faeces of rabbit. *J. Appl. Bact.*, **57**, 83-88.

CROCIANI F., MATTEUZZI D., MINARDI A., BRIGIDI P., GIOFFRE F., 1986. Urease activity in gastrointestinal tract of rabbit and electrophoretic behaviour of urease. *Ann. Inst. Pasteur Microbiol.*, **137A**, 287-294.

CROCIANI F., GIOFFRE F., PROTO V., ZANI G., MINARDI A., DI FRANCIA A., 1991. Dégradation microbienne du biuret et bilan azoté chez des lapins soumis à un régime alimentaire à base de biuret. *Cuni-Sci.*, **7**, 111-119.

DE BLAS J.C., SANTOMA G., CARABAÑO R., FRAGA M.J., 1986. Fiber and starch level in fattening rabbit diets. *J. Anim. Sci.*, **63**, 1897-1904.

EHRLEIN H.J., REICH H., SCHWINGER M., 1983. Colonic motility and transit of digesta during hard and soft faeces formation in rabbits. *J. Physiol.*, **338**, 75-86

EMALDI O., CROCIANI F., MATTEUZZI D., PROTO V., 1979. A note on the total viable counts and selective enumeration of anaerobic bacteria in the caecal content soft and hard feces of rabbit. *J. Appl. Bact.*, **46**, 169-172.

FALCAO E CUNHA L., 1988. Os constitutentes do parede celular no processo digestivo de coelho. *Thèse de docteur en agronomie.* Inst. Sup. Agronomia, Univ. Tecnica Lisbonne. 359p.

FEKETE S., HULLAR I., FEBEL H., 1989. Rabbit digestion and blood composition after fat or oil addition to the feed. *J. Appl. Rabbit Res.*, **12**, 233-238.

FIORAMONTI J., SORRAING J.M., LICOIS D., BUENO L., 1981. Intestinal motor and transit disturbances associated with experimental coccidiosis (*Eimeria magna*) in the rabbit. *Ann. Rech. Vét.*, **12**, 413-420.

FONTY G., 1974. Etude qualitative et quantitative de la microflore digestive du lapin holoxenique à différents niveaux du tube digestif et en fonction de l'âge. Effet de l'allaitement artificiel et du régime alimentaire. *Thèse 3eme cycle.* Univ. de Clermont-Ferrand. 91p.

FORSYTHE S.J., PARKER D.S., 1985a. Nitrogen metabolism by the microbial flora of the rabbit. *J. Appl. Bact.*, **58**, 363-369.

FORSYTHE S.J., PARKER D.S., 1985b. Urea turnover and transfer to the digestive tract in the rabbit. *Br. J. Nutr.*, **53**, 183-190.

FRAGA M.J., BARRENO C., CARABAÑO R., MENDEZ J., DE BLAS J.C., 1984. Effect of amounts of fibre and protein in the diet of growth and digestive traits of rabbits. *An. Inst. Nac. Invest. Agrar.*, Ganadera,, **21**, 91-110.

FRAGA M.J., PEREZ DE AYALA P., CARABAÑO R., 1991. Effect of type of fiber on the rate of passage and on the contribution of soft feces to the nutrient intake of finishing rabbits. *J. Anim. Sci.*, **69**, 1566-1574.

FRANCK Y., COULMIN J.P., 1978. Utilisation de la paille de blé broyée comme source de cellulose dans les aliments de lapins à l'engraissement; comparaison de deux taux de cellulose. *2ème Journée de la Recherche Cunicole*, 4-5 avril, Toulouse, INRA ed., Toulouse, comm. 10.

GARCIA J., DE BLAS J.C., CARABANO R., GARCIA P., 1995. Effect of type of lucerne hay on caecal fermentation and nitrogen contribution through caecotrophy in rabbits. *Reprod. Nutr. Dev.*, **35**, 267-275.

GIDENNE T., 1986. Evolution nycthémérale des produits de la fermentation bactérienne dans le tube digestif du lapin en croissance. Relations avec la teneur en lignines de la ration. *Ann. Zootech.*, **35**, 121-136.

GIDENNE T., 1992. Effect of fibre level, particle size and adaptation period on digestibility and rate of passage as measured at the ileum and in the faeces in the adult rabbit. *Br. J. Nutr.*, **67**, 133-146.

GIDENNE T., 1994a. Estimation de la production d'acides gras volatils et de leur apport energétique, chez le lapin : effets de la teneur en fibres du régime. *VIème Journées de la Recherche Cunicole*, 6 & 7 déc., La Rochelle (France), ITAVI ed., 2, 293-299.

GIDENNE T., 1994b. Effets d'une réduction de la teneur en fibres alimentaires sur le transit digestif du lapin. Comparaison et validation de modèles d'ajustement des cinétiques d'excrétion fécale des marqueurs. *Reprod. Nutr. Dev.*, **34**, 295-306.

GIDENNE T., 1995. Effect of fibre level reduction and gluco-oligosaccharides addition on the growth performance and caecal fermentation in the growing rabbit. *Anim. Feed Sci. Technol.*, **56**, 253-263.

GIDENNE T., 1996. Conséquences digestives de l'ingestion de fibres et d'amidon chez le lapin en croissance. Vers une meilleure définition des besoins. INRA, Prod. Anim., (in press).

GIDENNE T., LEBAS F., 1984. Evolution circadienne du contenu digestif chez le lapin en croissance. Relation avec la caecotrophie. *Proc. 3rd Congr. of the World Rabbit Sci. Assoc.*, 4-8 avril, Rome, WRSA ed., **2**, 494-501.

GIDENNE T., RUCKEBUSCH Y., 1989. Flow and rate of passage studies at the ileal level in the rabbit. *Reprod. Nutr. Dev.*, **29**, 403-412.

GIDENNE T., BELLIER R., 1992. Etude in vivo de l'activité fermentaire caecale chez le lapin. Mise au point et validation d'une nouvelle technique de canulation caecale. *Reprod. Nutr. Dev.*, **32**, 365-376.

GIDENNE T., PEREZ J.M., 1993. Effect of dietary starch origin on digestion in the rabbit. 2. Starch hydrolysis in the small intestine, cell wall degradation and rate of passage measurements. *Anim. Feed Sci. Technol.*, **42**, 249-257.

GIDENNE T., PEREZ J.M., 1994. Apports de lignines et alimentation du lapin en croissance. I. Conséquences sur la digestion et le transit. *Ann. Zootech.*, **43**, 313-322.

GIDENNE T., PEREZ J.M., 1996. Apports de cellulose dans l'alimentation du lapin en croissance. Conséquences sur la digestion et le transit. *Ann. Zootech.*, (in press)

GIDENNE T., JEHL N., 1996. Replacement of starch by digestible fibre in the feed for the growing rabbit. 1) Consequences on digestibility and on rate of passage. *Anim. Feed Sci. Technol.*, (in press).

GIDENNE T., CARRE B., SEGURA M., LAPANOUSE A., GOMEZ J., 1991. Fibre digestion and rate of passage in the rabbit: effect of particle size and level of lucerne meal. *Anim. Feed Sci. Technol.*, **32**, 215-221.

GOUET P., FONTY G., 1973. Evolution de la microflore digestive du lapin holoxénique de la naissance au sevrage. *Ann. Biol. Anim. Biochim. Biophys.*, **13**, 733-735.

HECKMANN F.W., 1972. Potatoe meal in complete feed of the fattening young rabbit. *Arch. Gefluegelk.*, **36**, 182-185.

HECKMANN F.W., MEHNER R.A., 1970. Protein and crude fiber contents of mixed feeds for fattening young rabbits. *Arch. Geflügelzucht Kleintierk.*, **19**, 29-43.

HILL R.R.H., 1983. Distribution of urease producing bacteria in the rabbit caecum. *S. Afr. J. Anim. Sci.*, **13**, 61-62.

HODGSON J., 1974. Diverticular disease. Possible correlation between low residue diet and raised intracolonic pressures in the rabbit model. *Am. J. Gastroenterol.*, **62**, 116-123.

HOLLISTER A.G., CHEEKE P.R., ROBINSON K.L., PATTON N.M., 1990. Effects of dietary probiotics and acidifiers on performance of weanling rabbits. *J. Appl. Rabbit Res.*, **13**, 6-9.

HOOVER W.H., HEITMANN R.N., 1972. Effects of dietary fiber levels on weight gain, caecal volume and volatile fatty acid production in rabbits. *J. Nutr.*, **102**, 375-379.

HÖRNICKE H., 1984. Neuere Ergebnisse zur physiologie des dickdarms beim kaninchen. I) Morphologie, Passagezeiten, Mikrobiologie, Wasser und Elektrolyte. *Übers Tierenächr.*, **12**, 215-250.

JEHL N., GIDENNE T., 1996. Replacement of starch by digestible fibre in the feed for the growing rabbit. 2) Consequences on microbial activity in the caecum and on incidence on digestive disorders. *Anim. Feed Sci. Technol.*, ( in press).

JEHL N., MARTIN C., NOZIERE P., GIDENNE T., MICHALET DOREAU B., 1995. Comparative fibrolytic activity of different microbial populations from rabbit caecum and bovine rumen. IVth International Symposium on the Nutrition of Herbivores, 11-15 sept., Clermont-Ferrand, France, INRA ed., *Ann. Zot.*, **44**, suppl., 186.

JILGE B., 1980. Selective cumulation of small-sized marker particles during hard feces excretion. *Proc. 2d Congr. of World Rabbit Sci. Assoc.*, 16-18 april, Barcelona, WRSA ed., 1.

KERMAUNER A., STRUCKLEC M., MARINSEK-LOGAR R., 1994. Influence of a probiotic added to different feed mixtures on the microbial metabolism in caecum of growing rabbits. *Znan. Prak. Poljopr. Tehnol.*, **24**, 120-127.

LAPLACE J.P., 1978. Le transit digestif chez les monogastriques 3) Comportement (prise de nourriture, caecotrophie), motricité et transit digestif et pathogénie des diarrhées chez le lapin. *Ann. Zootech.*, **27**, 225- 265.

LEBAS F., 1993. Effect of Profeed on nutritional efficiency in growing rabbits. *Cuniculture*, **20**, 19-173.

LEBAS F., LAPLACE J.P., 1972. Mensurations viscérales chez le lapin. 1) Croissance du foie, des reins et des divers segments intestinaux entre 3 et 11 semaines d'âge. *Ann. Zootech.*, **21**, 37-47.

LENG E., HÖRNICKE H., 1976. Diurnal variations in the rabbits caecal volume *in vivo* with C14-PEG. *Zbl. Vet. Med.*, **23**, 827-835.

LENG E., CLAUSS W., HÖRNICKE H., 1977. Colon passage time in rabbits in relation to the formation of caecotrophes. *Zbl. Vet. Med.*, **24**, 324-332.

LICOIS D., COUDERT P., COLIN M., 1980. Essai d'induction de la diarrhée chez le lapereau à l'aide d'aliments comportant différentes teneurs en cellulose. *Ann. Rech. Vét.*, **10**, 279-284.

LICOIS D., GUILLOT J.F., MOULINE C., REYNAUD A., 1992. Suceptibility of the rabbit to an enteropathogenic strain of *Escherichia coli* O103 : effect of animal's age. *Ann. Rech. Vét.*, **23**, 225-232.

LUICK B.R., EL-SAYAAD G.A.E., CHEEKE P.R., 1992. Effect of fructo-oligosaccharides and yeast culture on growth performance of rabbits. Proc. 5th Cong. of World Rabbit Sci. Assoc., Corvallis, USA, 27-30 July. *J. Appl. Rabbit Res.*, **15**, 1121-1128.

MAKKAR H.P.S., SINGH B., 1987. Comparative enzymatic profiles of rabbit caecum and bovine rumen content. *J. Appl. Rabbit Res.*, **10**, 172-174.

MAKKAR H.P.S., SINGH B., KRISHNA L., 1990. Effect of feeding urea on some hydrolytic and ammonia assimilation enzymes in rabbit caecum. *J. Appl. Rabbit Res.*, **13**, 35-38.

MAROUNEK M., VOVK S.J., SKRIVANOVA V., 1995. Distribution of activity of hydrolytic enzymes in the digestive tract of rabbits. *Br. J. Nutr.*, **73**, 463- 469.

MARTY J., VERNAY M., 1984. Absorption and metabolism of the volatile fatty acids in the hindgut of the rabbit. *Br. J. Nutr.*, **51**, 265-277.

MERINO J.M., CARABAÑO R., 1992. Effect of type of fibre on ileal and faecal digestibility. Proc 5th Congr. of World Rabbit Sci. Association, 25-30 July, Corvallis, USA. *J. Appl. Rabbit Res.*, **15**, 931-937.

MORISSE J.P., 1982. Taille des particules de l'aliment utilisé chez le lapin. Hypothèses de relation nutrition-pathologie digestive. *Revue Méd. Vét.*, **133**, 635-642.

MORISSE J.P., BODOLEC J.L., ANDRIEUX J., LE FLOCH B., 1979. Essais de prévention d'une entérite collibaccilaire chez le lapin par l'acétate le lactate ou le lactulose. *Rec. Méd. Vét.*, **155**, 943-954.

MORISSE J.P., BOILLETOT E., MAURICE R., 1985. Alimentation et modifications du milieu intestinal chez le lapin (AGV, NH3, pH, flore). *Rec. Méd. Vét.*, **161**, 443-449.

MORISSE J.P., LE GALL G., MAURICE R., COTTE J.P., BOILLETOT E., intestinaux et plasmatiques 1990. Action chez le lapereau d'un mélange de fructo-oligosaccharides sur certains paramètres. *5èmes J. Rech. Cunicoles*, 12-13 déc., Paris, ITAVI ed., vol. **1**, 53.1-53.8.

MORISSE J.P., MAURICE R., BOILLETOT E., COTTE J.P., 1993. Assessment of the activity of a fructo-oligosaccharide on different caecal parameters in rabbits experimentally infected with *E. coli* O103. *Ann. Zootech.*, **42**, 81-87.

MOTTA FERREIRA W., 1990. Effectos de la sustitucion partial de heno de alfalfa per orujo de uva o pulpa de remolacha, sobre la utilizacion de la dieta y los rendimientos en conejos en crecimiento. *Tesis Doctoral.* Univ. Politec. Madrid. 251p.

PADILHA M.T.S., 1995. Etude des relations entre la microflore et l'activité fermentaire caecale chez le lapereau, pendant la période péri-sevrage. *Thèse de doctorat.* Université F. Rabelais, Tours. 160p.

PADILHA M.T.S., LICOIS D., GIDENNE T., CARRE B., FONTY G., 1995. Relationships between microflora and caecal fermentation in rabbits before and after weaning. *Reprod. Nutr. Dev.*, **35**, 375-386.

PADILHA M.T.S., LICOIS D., GIDENNE T., CARRE B., COUDERT C., LEBAS F., 1996. Caecal microflora and fermentation pattern in exclusively milk-fed young rabbits. Proc. 6th Congress of the World Rabbit Sci. Assoc., 9-12 july, Toulouse, France.

PARKER D.S., 1976. The measurement of production rates of volatile fatty acids in the caecum of the conscious rabbit. *Br. J. Nutr.*, **36**, 61-70.

PEETERS J.E., MAERTENS L., GEEROMS R., 1992. Influence of galacto-oligosaccharides on zootechnical performances, caecal biochemistry and experimental collibacillosis O103/8+ in weanling rabbits. Proc. 5th Congress of the World Rabbit Sci. Assoc., 25-30 july, Corvallis, USA. *J. Appl. Rabbit Res.*, **15**, 1129-1136.

PEREZ J.M., GIDENNE T., LEBAS F., CAUDRON I., ARVEUX P., BOURDILLON A., DUPERRAY J., MESSAGER B., 1994. Apports de lignines et alimentation du lapin en croissance. II. Conséquences sur les performances de croissance et la mortalité. *Ann. Zootech.*, **43**, 323-332.

PEREZ, J.M., GIDENNE, T., BOUVAREL I., CAUDRON, I., ARVEUX, P., BOURDILLON, A., BRIENS C., LE NAOUR J., MESSAGER, B., MIRABITO L., 1996. Apports de cellulose dans l'alimentation du lapin en croissance. II. Conséquences sur les performances et la mortalité. *Ann Zootech.*, (in press)

PEREZ DE AYALA P.M., 1989. Utilizacion de distintos tipos de fibra por los conejos en cebo. *Tesis Doctoral.* Univ. Politec., ETSIA, Madrid. 115p.

PIATTONI F., DEMEYER D., MAERTENS L., 1996. In vitro study of the age dependant caecal fermentation pattern and methanogenesis in young rabbits. *Repr. Nutr. Develop.*, (in press)

PIATTONI F., MAERTENS L., DEMEYER D., 1995. Age dependent variation of caecal contents composition of young rabbits. *Arch. Anim. Nutr.*, **48**, 347-355.

PROHASZKA L., 1980. Antibacterial effect of volatile fatty acids in enteric E. coli infections of rabbits. *Zbl. Vet. Med. B.*, **27**, 631-639.

PROHASZKA L., SZEMEREDI G., 1984. Regulation of the metabolism of volatile fatty acids in the caecum of rabbits. *Zentralbl. Veterinärmed.*, **31**, 358-366.

ROBINSON K.L., CHEEKE P.R., MATHIUS I.W., 1986. Effect of age and caecotrophy on urea utilization by rabbits. *J. Appl. Rabbit Res.*, **9**, 76-79.

SALSES A., BEAUVILLE M., RAYNAUD P., 1976. Supplémentation d'un régime d'entretien par perfusion intra-caecale d'urée chez le lapin. *Proc. First World Rabbit Congress*, Dijon, France, comm. 53.

SALSES A., CRAMPES F., RAYNAUD P., 1977. Détermination de la valeur alimentaire de l'urée donnée en perfusion intra-caecale chez le lapin. *Ann. Biol. Anim. Bioch. Biophys.*, **17**, 559-565.

SANTOMA G., DE BLAS J.C., CARABAÑO R.M., FRAGA M.J., 1987. The effects of different fats and their inclusion levels in diets for growing rabbits. *Anim. Prod.*, **45**, 291-300.

STRUKLEC M., KERMAUNER A., MARINSEK LOGAR R., 1994. The effect of corn, barley or oats on digestion process and production parameters of growing rabbits. *Znan. Prak. Poljopr. Tehnol.*, **24**, 128-135.

UDEN P., ROUNSAVILLE T.R., WIGANS G.R., VAN SOEST P.J., 1982. The measurement of liquid and solid digesta retention in ruminants equines and rabbits given timothy hay (Phleum pratense). *Br. J. Nutr.*, **48**, 329-339.

VERNAY M., 1986. Influence de la caecotrophie sur la production, l'absorption et l'utilisation des acides organiques chez le lapin. *Repr. Nutr. Develop.*, **26**, 1137-1149.

VERNAY M., 1989. Incidence of the circadian rhythm of the excretion pattern on acetate absorption and metabolism in the rabbit hind-gut. *Repr. Nutr. Develop.*, **29**, 185-196.

VERNAY M., RAYNAUD P., 1975. Répartitions des acides gras volatils dans le tube digestif du lapin domestique. 2) Lapins soumis au jeûne. *Ann. Rech. Vét.*, **6**, 369-377.

VERNAY M., MARTY J., MOATTI J.P., 1984. Absorption of electrolytes and volatile fatty acids in the hind-gut of the rabbit. Circadian rhythm of hind- gut electrolytes and plasma aldosterone. *Br. J. Nutr.*, **52**, 419-428.

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**Physiologie digestive de l'ensemble caecum-côlon du lapin. Facteurs de variations nutritionnels et ontogéniques** - Le caecum est le compartiment le plus volumineux du tube digestif du lapin (40 % de la masse digestive totale). Il joue un rôle clé dans la physiologie digestive en tant que site principal de la dégradation des fibres et de leur fermentation. Un déséquilibre de l'activité microbienne caecale pourrait être à l'origine des troubles digestifs observés chez le lapin en croissance, nourri avec des aliments trop concentrés. Les principales caractéristiques de la physiologie digestive caecale, incluant les données récentes, seront donc tout d'abord présentées. Les facteurs ontogéniques puis les facteurs nutritionnels affectant l'activité microbienne caecale seront ensuite analysés. Enfin, les troubles digestifs caeco-coliques provenant d'un déséquilibre nutritionnel seront abordés ainsi que les hypothèses actuelles expliquant l'apparition des entérites chez le lapin en croissance.

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