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Original article

Replacement of digestible fibre by starch in the diet of the growing rabbit. I. Effects on digestion, rate of passage and retention of nutrients

Thierry GIDENNE*, Jean-Marc PEREZ

INRA, Station de Recherches Cunicoles, Centre de Recherches de Toulouse,
BP 27, 31326 Castanet-Tolosan Cedex, France

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Abstract — The effects of digestible fibre replacement (25 to 15%) by starch (12 to 23%), were studied on rabbit digestion with four diets (A12 to A24) having a similar level of lignocellulose (ADF, 18%). Faecal digestibility, retention of nutrients and rate of passage were measured on four groups of 12 young rabbits fed the four diets ad libitum from weaning to slaughter (72 d). Intake, weight gain, and feed conversion were not significantly different among the 4 treatments (mean 102.4 $g \cdot d^{-1}$, 34.0 $g \cdot d^{-1}$, 3.02 respectively). Despite a 100% increase in the starch level between A12 and A24, the digestibility of organic matter and energy were similar (mean 65.5 and 63.7% respectively). Energy or protein retention were not significantly affected by treatments (mean 28.4 and 13.6% respectively). With a reduction of the supply in digestible fibre, overall fibre digestibility (NDF) was logically reduced (–10 units), particularly for the uronic acid fractions (71 to 44% respectively for A12 and A24). Consequently the quantity of degraded NDF (period 28–72 d) decreased from 13.7 to 8.1 $g \cdot d^{-1}$ for the A12 to A24 diets, while it doubled for starch (12.5 vs. 23.1 $g \cdot d^{-1}$). Whole tract mean retention time for the particulate phase increased by 2 h ($P = 0.06$) for the A12 to A24 diets, while it increased by 4 h ($P < 0.01$) for the liquid phase. Caecal retention time of fine particles was more affected (+6 h) than that of large particles (+2 h). In conclusion, digestible fibre replacement by starch did not change the digestive efficiency of the rabbit, but slowered the passage rate.

rabbit / digestion / passage rate / dietary fibre / starch / retention

Résumé — Apports d'amidon en remplacement de fibres digestibles dans l'alimentation du lapin en croissance. I. Conséquences sur la digestion, le transit et la rétention des nutriments. En raison de ses conséquences importantes sur la digestion et la pathologie digestive du lapin, la lignocellulose (ADF) est un critère souvent utilisé pour recommander un apport de fibres. Cependant, les interactions entre l'amidon et les fibres « digestibles » (hémicelluloses et pectines) non prises en compte par le critère ADF ont été très peu étudiées. Les effets d'un remplacement croissant de

* Correspondence and reprints
Tel.: 33 (0)5 61 28 51 03; fax: 33 (0)5 61 28 53 19; e-mail: gidenne@toulouse.inra.fr

fibres digestibles (25 à 15 %) par de l'amidon (12 à 23 %) ont été analysés sur les paramètres de la digestion, du transit et sur la rétention, à l'aide d'une gamme de 4 aliments (A12 à A24) à taux voisin d'ADF (18 %), distribués de 28 à 72 jours d'âge à 4 groupes de 12 lapereaux. L'ingestion, le gain de poids et l'indice de consommation (entre 28 et 72 j) ne diffèrent pas significativement entre les 4 traitements (respectivement 102,4 $g \cdot j^{-1}$; 34,0 $g \cdot j^{-1}$; 3,02 en moyenne). Bien que le taux d'amidon double entre les régimes extrêmes (A12 vs. A24), la digestibilité de la matière organique et de l'énergie est similaire (en moyenne 65,5 et 63,7 % resp.). De même, la rétention de l'énergie ou des protéines ne diffère pas entre les traitements (28,4 et 13,6 % resp.). Parallèlement, la digestion des fibres est logiquement abaissée avec la réduction de l'apport de fibres digestibles (–10 points), en particulier pour les acides uroniques (71 et 44 % resp. pour A12 et A24). La quantité de NDF digérée passe de 13,7 à 8,1 $g \cdot j^{-1}$ entre A12 et A24 (période 28–72 j), alors que la quantité d'amidon digéré double (12,5 vs. 23,1 $g \cdot j^{-1}$). En parallèle, le transit digestif est plus lent (+2 h pour les particules, +4 h pour la phase liquide) surtout dans le cas du transit caecal des particules fines (+6 h). En conclusion, la substitution de l'amidon à des fibres digestibles n'entraîne pas de variation majeure de l'efficacité digestive chez le lapin, mais ralentit le transit digestif.

lapin / digestion / transit / fibres alimentaires / amidon / rétention

1. INTRODUCTION

The favourable role of lignocellulose (ADF) on mortality by digestive disorders in the growing rabbit was highlighted by Maître et al. [27] then confirmed by Blas et al. [5]. Moreover, other studies specified the respective effects of cellulose and lignins on digestion, transit, performances and digestive pathology [19–21, 33, 35]. However, before to propose fibre recommendations based on a single criterion (the ADF), it is advisable to control the absence of any interaction between starch and the other fibrous fraction not accounted for in the ADF fraction. Thus for a constant lignocellulose supply, one must check that the increase in the dietary starch supply by substituting the fibre such as hemicellulose or pectin, has no negative effects on digestion and zootechnical performances.

On this point, a preliminary work has shown, using a simplified dietary model, that the rabbit highly utilises the hemicellulose and pectin fractions (when replacing starch), and without a detrimental effect on digestive transit [18].

Thus, a concerted study was performed in order to specify, using a complex dietary model (close to commercial feeds), the effects of the replacement of digestible fibres by starch, on digestion, transit and retention of nutrients (present study), and on zootechnical performances and mortality using a high number of animals (second part of the study [36]).

2. MATERIALS AND METHODS

2.1. Feeding and animals

The dietary model consisted of a partial replacement of the most quickly fermentable fraction of the fibres (hemicelluloses and pectins) by starch, and without variation of the less digestible fibrous fractions (cellulose and lignins Van Soest) or of the protein supply. Four diets were manufactured and pelleted at one time (Sanders, Sourches), using the same batches of raw materials (Tab. I). The diets corresponded to a linear increase in starch level (12 to 23%) and to a linear decrease in digestible fibre, whereas the level of lignocellulose (ADF = 18%) was conform to recommendations [11, 26].

Thus the ADF/starch ratio decreased from 1.5 to 0.75 for the A12 to A24 diets (Tab. II). Alfalfa and wheat straw constituted the main supply in lignocellulose,

while the more digestible fibres were mainly provided by beet pulp and wheat bran (Tab. I). Moreover, the diets had a common starchy basis (wheat and barley), and had a similar DP/DE (digestible proteins/digestible energy) ratio. The diets did not contain any drug supplementation (antibiotic or coccidiostatic).

Table I. Ingredients of the experimental diets.

Ingredients (%)	Diets			
	A12	A16	A20	A24
Barley	4.30	9.80	15.30	20.80
Wheat	4.30	9.80	15.30	20.80
Soya bean meal (cake)	7.90	9.10	10.30	11.50
Sunflower meal (cake)	5.40	5.93	6.46	7.00
Dehydrated alfalfa	15.00	15.00	15.00	15.00
Wheat straw	8.00	8.00	8.00	8.00
Wheat bran	27.00	18.00	9.00	0.00
Beet pulp	20.00	13.33	6.68	0.00
Soya bean hulls	0.00	2.33	4.67	7.00
Grape seeds meal	1.00	1.50	2.00	2.50
Beet molasses	5.00	5.00	5.00	5.00
Mineral & vitamins*	2.10	2.21	2.29	2.40

* Contained: ($g \cdot kg^{-1}$, respectively for the A12, A16, A20, A24 diets) bicalcium phosphate (20, 40, 60, 80), DL methionine 15% (9.0, 7.7, 6.3, 5.0), salt (5.0, 5.4, 5.6, 6.0); and 5.0 $g \cdot kg^{-1}$ diet of vitamin premix (without antibiotics or coccidiostatics).

Table II. Chemical composition of experimental diets (% air dry basis).

		Diets			
	n	A12	A16	A20	A24
Dry matter	*6*	88.5	89.4	88.8	88.4
Ash	*6*	7.8	7.5	7.2	6.9
Crude Fat	*4*	1.9	1.9	1.6	1.5
Crude protein (N × 6,25)	*6*	15.8	16.0	16.4	16.5
Starch	*5*	12.0	16.0	19.8	23.3
Total sugars	*1*	8.0	8.0	7.9	7.1
Crude fibre	*6*	15.3	15.0	14.7	14.5
NDF	*6*	35.0	33.6	32.3	29.6
ADF	*6*	18.1	18.0	18.9	17.7
Lignins (ADL)	*5*	4.1	4.2	4.4	4.5
Hemicellulose (NDF-ADF)	*6*	16.0	14.7	13.5	11.6
Cellulose (ADF-ADL)	*5*	14.8	13.8	13.9	12.9
WICW[1]	*1*	39.6	35.5	32.4	30.4
Uronic acids	*1*	6.6	5.4	4.5	3.8
Pectins[2]		8.9	7.0	5.2	3.3

n = number of locations for analyse.
[1] WICW = Water insoluble cell wall [10].
[2] Water-insoluble pectins, calculated from tabulated data [23].

2.2. Digestibility and passage rate measurements

The four diets were allotted to four groups taking into account litter origin and weight at weaning. They were given ad libitum to 4 groups of 12 young rabbits (Neo-Zealand White, males and females), from weaning (28 days of age) to slaughter (72 days of age). The animals were maintained in metabolism cages throughout the experiments, in a closed and ventilated room (18 °C ± 2 °C) and with 12 h light (07.00–19.00). The live weight and feed intake were individually measured each week. After a phase of adaptation to the diets covering the period from 28 to 48 days of age, the measurement of faecal apparent digestibility was performed individually (for 9 rabbits out of 12) between 48 and 52 days of age according to the "European" reference method [34].

In parallel, measurements of digestive transit were carried out between 49 and 56 days of age, on 4 additional groups of 7 rabbits (3 successive experimental series), by analysing the kinetics of faecal excretion of 2 markers [17]: 51-Cr-EDTA and 141-Ce, associated respectively with the liquid and solid phase of the digesta. A dose of 0.5 mL of a solution of 51-Cr-EDTA was given at 9.00 am, using an oesophageal probe. It was followed 15 minutes later, by an oral administration of a dose (100 mg) of fibrous particles (NDF residue of each diet) labelled with 141-Cerium (2 kBq per dose). The labelled particles were obtained after a 24 h soaking in an acidic solution of 141-Ce, then filtered on a sieve of 50 µm. Faecal excretion was then fractionated (36 samples) over a 4 day period, using an automatic faecal sampler (API, Castanet, France). The quantity of the marker excreted in each faecal sample was then analysed by gamma spectrometry (Packard Instrument, Model 5 530, Downersgrove, IL, USA).

The mean retention time (MRT) of the solid or liquid phase of the digesta was calculated according to the general formula TSM = Mi·Ti, where Ti represents the time elapsed between T0 (administration of the marker) and the ist collect, and Mi the mass of marker excreted between Ti – 1 and Ti. The minimum transit time (TTm) is the delay time (average time between two collects) for the first appearance of the marker in the faeces, which is equivalent to the passage time in the small intestine and the distal colon of the rabbit [17]. Moreover, caecotrophy causes to inflect the decrease of the faecal concentration (Ct) of the marker of the solid phase [19], because of a recycling of labelled particles in soft faeces. We thus carried out a double adjustment of the decreasing part of the kinetics before and after caecotrophy, using a non-linear regression according to an exponential ($Ct = Co \cdot \exp -kt$). We defined two indices TCgp and TCpp, as the inverse of the two constants of time of the 2 equations, each one representing a residence time in the compartment "caecum-proximal colon". TCgp corresponds to the residence time of the large labelled particles (> 0.3 mm) quickly excreted in hard faeces. TCpp corresponds to the finer labelled particles, driven back to the caecum by the proximal colon during the period of hard faeces excretion, and which are thus potentially incorporated in the caecotrophe and consumed a second time.

2.3. Energetic and proteic balance, using body composition analysis

The rabbits were sacrificed at 72 days of age by elongation and bleeding. The skin was separated from the head and the body at the level of the third caudal vertebra and distal epiphyses of the *radius-ulna* and tibia bones, in agreement with WRSA recommendations [6]. The following slaughtering parameters were measured: weight of the skin, empty gastrointestinal tract, chilled carcass (after 24 h chilling in a ventilated cold room at 0–4 °C), liver and carcass

of reference (chilled carcass without head, fore and hind legs, liver, lungs, thymus, trachea) but with kidneys [6]). The nutritional balance was established from the chemical analysis of the carcass of reference, homogenised in a screw mincer. An aliquot was ground at low temperature (–196 °C) using a ball-grinder (Dangoumau). The analyses (water, ash, nitrogen, energy) were carried out on the freeze-dried fine powder. The protein and energy retention during growth were calculated from the difference between the amounts of nitrogen and energy measured on the reference carcass of rabbits at the end of the experiment (72 days of age), and the amounts of nitrogen and energy in the body of the same rabbits at weaning estimated by regression starting from the analysis of a standard batch at weaning. Therefore, an additional group of 31 young rabbits with a large range of live weight (348 to 630 g) and with the same genotype (NZW, INRA 1077), was sacrificed at weaning (28 days old) and was analysed under the same conditions as previously, in order to establish prediction models of their body chemical composition from their initial live weight.

2.4. Chemical analyses of feed and faeces

The following chemical analyses were carried out: dry matter (24 h at 103 °C), ash (5 h at 550 °C), total nitrogen (method Dumas, Leco, N*6,25), crude energy (adiabatic calorimeter PARR), fibres (NDF, ADF and ADL) according to the sequential method of Van Soest et al. [40] with an amylolytic pre-treatment (adopted by AFNOR [1]). The non-nitrogenous cellular content (NNCC), which includes starch and also the major part of pectins, was estimated by difference according to the relation: NNCC (%) = OM (%) – CP(%) – NDF (%).

The water insoluble cell walls were analysed in feed according to the method of Carré and Brillouet [10]. After extraction of the soluble sugars (ethanol 40%, under shaking at ambient temperature), the starch was enzymologically measured in feed and faeces (quantitative hydrolysis by glucoamylase, after gelatinisation and autoclaving); the released glucose was then measured using the hexokinase system (EC2.7.1.1)-glucose-6-phosphate dehydrogenase (NAD, EC1.1.1.49) (Boëhringer Mannheim).

The uronic acids were analysed on feed and faeces, according to the following procedure: after an alcoholic extraction (ethanol 80%) followed by an ultra-grinding of the residue, the samples were pre-hydrolysed in concentrated acid (H_2S0_4, 26N), then hydrolysed in diluted acid (H_2S0_4, 2N); the uronic acids were thens analysed by colorimetry according to the *m*-phenylphenol method [7].

2.5. Statistical analyses

Animals showing abnormal feed intake or faecal excretion were not included in the statistical analysis. Measurements of digestibility and transit were subjected to a monofactorial variance analysis (diet effect), according to the GLM procedure of SAS [39]. Multiple comparison of means were treated using the Scheffe test. The adjustments of the decreasing phase of the marker level curves (solid phase) were calculated by non-linear regression according to the NLIN procedure.

3. RESULTS

3.1. Diet compositions (Tab. II)

In agreement with the objectives of the formulation, the analysis of diets (repeated in 6 locations) indicated a linear increase in the contents of starch, and a proportional decrease of the hemicellulose and pectin supplies (25 to 15%). Since the rate of lignocellulose (ADF) remained constant, the

ADF/starch ratio evolved from 1.5 (diet A12) to 0.75 (diet A24). In addition, the supplies in lignin (ADL), cellulose (ADF-ADL) and proteins remained similar for the different diets.

3.2. Digestibility (Tab. III)

The overall feed digestibility (OM or energy) and that of crude proteins remained similar for the different diets; thus the DP/DE ratio remained constant, in accordance with the objectives of the formulation. The digestion of the glucidic fractions (starch or NNCC) were almost complete (> 90%), and increased slightly with the starch supply ($P < 0.05$). The digestibility of the fibrous fractions was strongly and linearly reduced (–10 units for NDF and ADF, $P < 0.01$) when digestible fibres were replaced by starch. This was particularly clear for uronic acid digestibility that declined from 71 to 44%. Consequently, over the period 28–72 days of age, the daily quantity of degraded fibre (NDF) was reduced by 40% (13.7 vs. 8.1 g·d^{-1}), while that of starch almost doubled (12.5 vs. 23.1 g·d^{-1}).

3.3. Rate of passage (Tab. IV)

The mean retention time "MRT" of solid phase (marker = 141-Ce) in the whole tract was 8.3 h and tended to increase linearly ($P = 0.03$) between the A12 and A24 diets. This effect appeared to be clearer for the caecal transit of the fine particles excreted after the first phase of caecotrophy (TCpp), which rose sharply (+5 h) between A12 and A24 (linear effect $P = 0.007$). The caecal

Table III. Faecal digestibility coefficients (%) and nutritive value of experimental diets.

Diets	A12 *(n = 9)*	A16 *(n = 9)*	A20 *(n = 8)*	A24 *(n = 9)*	SEM[1]	Effect of diet	Linear effect
Feed intake (g·d^{-1})[2]	104.2	106.1	109.4	105.6	4.2	0.85	
Digestibility (%)							
Organic matter	65.2	65.2	65.0	66.5	0.79	0.52	0.30
Energy	63.2	63.3	63.3	64.9	0.80	0.40	0.16
Crude protein	73.1	74.7	72.6	73.0	1.1	0.59	0.67
Starch	98.4	nd	nd	98.9	0.14	0.036	nd
NNCC[3]	90.8^{bc}	91.8^{bc}	94.6^{ab}	95.4^{a}	0.83	< 0.01	< 0.01
NDF	37.0^{a}	32.5^{ab}	29.3^{b}	27.3^{b}	1.6	< 0.01	< 0.01
ADF	26.6^{a}	20.9^{ab}	20.9^{ab}	17.7^{b}	1.7	< 0.01	< 0.01
ADL	13.3	9.2	1.7	8.7	2.1	0.34	0.21
Hemicellulose[4]	49.2^{a}	47.4^{ab}	40.7^{b}	41.1^{b}	1.8	< 0.01	< 0.01
Cellulose[5]	30.7^{a}	24.6^{ab}	24.0^{ab}	20.9^{b}	1.8	< 0.01	< 0.01
Uronic acids	71.1	nd	nd	44.1	2.8	< 0.01	nd
Nutritive value (air dry basis)							
DP[6] (g·kg^{-1})	121	123	122	121			
DE[7] (MJ·kg^{-1})	10.10	10.15	10.10	10.40			
DP/DE (g·MJ^{-1})	12.0	12.1	12.0	11.6			

[1] SEM = standard error of the mean; [2] mean feed intake during digestibility measurements (4 days); [3] NNCC (non nitrogenous cellular content) = OM-CP-NDF; [4] NDF-ADF; [5] ADF-ADL; [6] DP = digestible crude protein. [7] DE = digestible energy; [a,b] means having a common superscript are not different at the level $P = 0.05$; nd: not determined.

retention time of the coarser particles (TCgp) was slightly lowered. The MRT of the liquid phase (marker = 51-Cr-EDTA), double that of the solid phase (particles), increased by 4 hours (+30%, $P < 0.01$) between the A12 and A24 diets. The minimal transit time (TTm) was not affected by the diet, either for the liquid or solid phase.

Table IV. Rate of passage measurements.

Diets	A12 *(n = 5)*	A16 *(n = 6)*	A20 *(n = 7)*	A24 *(n = 7)*	SEM[5]	Effect of diet	Linear effect
Feed intake ($g \cdot d^{-1}$)[1]	135.8	126.8	119.4	121.6	13.3	0.20	
Solid phase (141-Ce)							
MRT (h)[2]	6.9	7.7	9.7	8.9	1.8	0.06	0.031
TCgp (h)[3]	5.9	7.3	8.4	7.7	0.76	0.21	0.11
TCpp (h)[3]	11.9[b]	14.5[ab]	17.5[a]	17.6[a]	1.5	0.048	< 0.01
TTm (h)[4]	4.5	4.4	5.4	5.0	1.8	0.74	0.42
Liquid phase (51-Cr-EDTA)							
MRT (h)	14.6[b]	17.8[ab]	19.3[a]	18.6[a]	4.8	< 0.01	< 0.01
TTm (h)	4.8	4.7	5.4	5.3	1.6	0.81	0.41

[1] Mean feed intake during rate of passage measurements (4 days); [2] MRT: Mean retention time (Mi.Ti/Mi); [3] TCgp, TCpp resp.: Mean retention time in the caecum, for large particles (> 0.3 mm) and fine particles (< 0.3 mm); [4] TTm: Minimal transit time (first appearance of marker in faeces); [5] SEM = standard error of the mean; [a, b] (see Tab. III).

Table V. Performances on the whole fattening period (28–72 d), and body composition at slaughter.

Diets	A12 *(n = 11)*	A16 *(n = 12)*	A20 *(n = 11)*	A24 *(n = 10)*	SEM	Effect of diet
Weight at weaning (g)	505	501	509	512	17.1	0.97
Weight at slaughter (g)	2 039	1 990	2 003	1 981	41.7	0.78
Weight gain ($g \cdot d^{-1}$)	34.8	33.8	33.9	33.4	0.8	0.63
Intake						
($g \cdot d^{-1}$)	105.9	101.6	101.8	100.5	2.2	0.35
(MJ DE$\cdot d^{-1}$)	1.07	1.03	1.03	1.05	0.02	0.54
Feed conversion						
($kg \cdot kg^{-1}$ gain)	3.05	3.01	3.00	3.02	0.05	0.94
(MJ DE$\cdot kg^{-1}$ gain)	30.8	30.5	30.3	31.4	0.51	0.53
Body composition (72 d)						
Skin (g)	261	253	254	255	6.7	0.82
Empty gastrointestinal tract (g)	149	149	151	147	4.9	0.97
Chilled carcass weight[1] (g)	1 253	1 224	1 231	1 242	30.2	0.91
Dressing out percentage (%)	61.5	61.5	61.5	62.7	0.55	0.32

[1] Carcass with head and fore and hind legs, chilled 24 h at 0–4 °C [6].

3.4. Performances and slaughtering parameters (Tab. V)

From weaning (28 d) to slaughter (72 d old), the feed intake remained similar among the diets (P = 0.35) because of the low number of data (11 rabbits per diet). Nevertheless, we noticed a decline in the intake (–5%) between A12 and the three other diets. The daily gain and the feed conversion index were not different for the diets (mean 34 g and 3.02 respectively). In the same way, the digestible energy intake (1.04 MJ DE·d^{-1}) and the energy conversion index (30.7 MJ·kg^{-1} gain) remained similar for the different treatments. The slaughter yield and respective weights of the skin, empty digestive tract and organs (results not detailed here) were not significantly affected by the diet.

3.5. Body chemical balance (Tabs. VI and VII)

The regression equations of the chemical characteristics on body weight, established on a standard group slaughtered at weaning, were of a satisfactory precision either to predict the contents of proteins (r = 0.94) or to predict the energy contents of the carcasses at 28 d of age (r = 0.92; Tab. VI). They were thus used for calculations of body chemical balance (Tab. VII).

The final body chemical composition (at 72 d of age) was not significantly affected by treatments. The "N intake/N retained" ratio and the retention coefficient for nitrogen (digestible N retained/N) were not dependant on the diet (an average 20.8 and 28.3% respectively), and likewise for energy (8.7% and 13.6% respectively; Tab. VII).

4. DISCUSSION

Nutrient intake evolved in parallel to their level in the diets since the voluntary feed intake showed weak changes among diets. Starch intake thus doubled between A12 and A24, whereas the digestible fibre intake (hemicelluloses and pectins) was reduced by half. Despite this sharp rise in starch consumption, growth remained unchanged, as well as feed conversion. The parameters of digestion confirmed this similarity of the nutritive value of the diets, and the high utilisation of digestible fibres by rabbits. Thus, about 50% of the dietary starch could be compensated by a digestible fibre supply, without significant variation in feed digestibility.

Although barley and wheat were not completely replaced by beet pulp and wheat bran, the similar dietary DE levels suggested that DE of the "bran + pulp" mixture would be rather close to that of the "wheat and barley" mixture, evaluated as 13.1 MJ·kg^{-1} by Villamide and De Blas [41]. This was in agreement with the DE values of these two by-products estimated as 12.55 MJ·kg^{-1} [12, 38, 41]. The slight rise in starch digestion (likewise for the NNCC fraction) parallel to the increase of the dietary starch level, was in agreement with the literature [4, 30].

Table VI. Prediction of the carcass composition (n = 31) for rabbits at weaning (28 d) from their live weight (x, expressed in grams).

Dependant variable	Regression equation	r	RSD (CV%)
Reference carcass (g)[1]	y = – 17.89 + 0.449 x	0.977	8.0 (4.0)
Proteins (g)	y = – 7.59 + 0.090 x	0.944	2.6 (7.1)
Energy (MJ)	y = – 0.253 + 0.00316 x	0.920	0.11 (8.6)

[1] Reference carcass = carcass without head and fore and hind legs, liver, thymus, lungs, trachea, but with kidneys [6].

Table VII. Body chemical composition (chilled carcass) at 72 d old, and efficiency of conversion for energy and crude protein, between weaning and slaughter.

Diets	A12 *(n = 11)*	A16 *(n = 12)*	A20 *(n = 11)*	A24 *(n = 10)*	SEM	Effect of diet
Reference carcass weight (g)[1]	981	958	887	961	42	0.42
Chemical composition (72 d)						
Dry matter (%)	31.9	32.4	32.2	32.1	0.45	0.91
Ash (% DM)	11.8	11.1	12.8	12.7	0.78	0.36
Crude protein (N × 6.25; % DM)	63.3	62.2	62.2	62.8	1.16	0.87
Gross energy (MJ·kg^{-1} DM)	13.99	14.25	13.84	13.93	0.36	0.53
Retention of protein (28–72 d)						
Proteins retained, PR (g)	160	155	152	155	5.26	0.73
PR/protein intake (%)[2]	20.8	21.0	20.2	21.1	0.53	0.59
CR (%)[2]	28.5	28.2	27.8	28.9	0.70	0.75
Retention of energy (28–72 d)						
Energy retained, ER (MJ)	6.34	6.42	6.14	6.17	0.29	0.88
ER/energy intake (%)[3]	8.5	8.9	8.5	8.7	0.27	0.59
CR (%)[3]	13.4	14.1	13.4	13.4	0.43	0.52

[1] Cf. Table VI.
[2] Crude proteins retained in the reference carcass, in percentage of crude protein intake, or in percentage of digestible protein intake (CR = coefficient of retention).
[3] Energy retained in the reference carcass, in percentage of gross energy intake, or in percentage of digestible energy intake (CR = coefficient of retention).

The reduction in fibre digestion between the A12 and A24 diets could be logically related to an effect of the nature of the fibre, although the straw and alfalfa covered approximately half of the ADF supply, whatever the diet. Thus, the lignocellulose fraction was provided for about 40% by beet pulp and wheat bran in the A12 diet, whereas these ingredients were lacking in the A24 diet. The high accessibility of the pulp cellulose by bacteria has already been reported [3], thus explaining the highest digestion of the lignocellulose fraction. Similar results were obtained in other studies, but without a complete control of the lignocellulose supply [8, 28, 32]. In the same way, the highest digestibility of the quickly fermentable fibre fractions in the A12 diet, could also be explained by an effect of fibre origin, since 70% of pectins originated from pulp, while 70% were provided by the "alfalfa – sunflower meal – soya hulls" mixture in the A24 diet. In addition, Jehl and Gidenne [24] compared the A12 to A24 diets, and reported that this reduction of fibre digestion was associated to a reduction of the caecal fermentative activity and of the production of bacterial biomass.

Our measurements of energy and protein retention were based on the analysis of the "reference carcass" as defined by WRSA [6]. The retention coefficients thus correspond to the energy or protein efficiency mainly for the production of meat, as already reported by Ouhayoun and Cheriet [29]. The majority of the former studies on energy or proteic retention for growth were based on the analysis of the empty body. Obviously, higher values than those of the present study

have been reported. Theoretically, the increase in the dietary fibre loweres the coefficient of retention for energy [13, 31], because of losses due to caecal digestion (production of gases, heat of fermentation). However, when starch replaced digestible fibres (with constant ADF levels), we observed no changes in the protein or energy retention, even for a wide range of substitution. Similarly, in the absence of a variation of ADF level, Carabaño et al. [9] reported no variation of energy retention, when beet pulp replaced alfalfa. Conversely, substituting starch for fibre (beet pulps replaced by barley), but associated with a reduction of dietary ADF level, causes a strong reduction of energy and nitrogen retention [15, 16].

Compared to low digestible fibres (such as cellulose), pectins (for instance provided by beet pulp) are supposed to slow down the digestive transit in monogastric animals [22, 37]. In the rabbit, this effect has been mentioned for the liquid phase between the mouth and ileum [2]. Our results indicated on the contrary, a shorter caecal retention time (either for solid or liquid phase) when the level of pectins and hemicelluloses increased. This was in agreement with Gidenne and Bellier [18] as well as with the study of Fraga et al. [14]. The latter reported similar transit of the liquid phase for diets containing 1/3 alfalfa, 1/3 pulp or up to 50% citrus pulp.

The MRT of the solid phase (<10 h) appeared here to be relatively short compared to those usually mentioned in the literature (12 to 25 h). This could be explained by the high level of fibre intake (>35 g NDF·d^{-1}) observed in our study. In addition, the absence of a differential transit between the liquid and solid phase in the tubular segments (small intestine and distal colon) confirmed previous results [18, 24, 25].

In conclusion, the replacement of 10 points of starch by fibrous fractions that are quickly fermentable did not involve a significant reduction of the digestive efficiency of the rabbit. Improvements in fibre digestion were observed in spite of a shorter transit in the caeco-colic segment. This high utilisation of digestible fibres by the rabbit was also shown, by the absence of variation in energy retention, and more globally by the absence of a significant variation in feed conversion. Zootechnical performances and health status of the rabbit fed the same diets are reported in the second part of this study [36].

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