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Original article

Flow and passage rate studies at the ileal level in the rabbit

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Summary — Six female rabbits fitted with a simple glass cannula in terminal ileum and a further 6 non-cannulated rabbits were used to perform digesta flow and transit measurements. The animals received *ad libitum* a diet based mainly on lucerne meal. Flow and transit measurements were carried out using two particulate markers : ytterbium (Yb) fixed on lucerne meal cell-walls by soaking, and chromium (Cr) fixed by mordancing. Both markers were incorporated in the same diet before pelleting.

The digestibility coefficient or total mean retention time (MRTt) in the whole tract was not affected by cannulation. MRT values between cecum and rectum could be obtained in cannulated rabbits : 9.6 h. The MRTt values estimated with Yb were higher than those obtained with Cr because the size of particles labelled with Cr was probably greater and thus the particles were excreted more rapidly in hard feces. Flow measurements were not affected by the choice of marker, confirming indirectly the validity of ileal digesta samples.

These first ileal flow measures obtained on cannulated rabbits indicate that about half (49 %) of the digestible organic matter and two-thirds of the digestible crude protein apparently disappeared before the cecum. Cell-walls (CW), determined as NDF fraction, were totally recovered at the terminal ileum, although hemicellulose (NDF—ADF) digestion could occur in both the small intestine and the cecocolic parts. These results are discussed in relation to the specificity of the Van Soest method for digesta cell-wall analysis.

digesta flow — passage rate — rabbit — marker

Résumé — Mesures de flux et de transit au niveau iléal chez le lapin. *Douze lapines adultes dont la moitié portent une canule à l'iléon terminal ont reçu* ad libitum *un aliment constitué à 40 % de luzerne déshydratée. Les mesures de flux et de transit ont été réalisées en utilisant deux marqueurs de la phase particulaire : l'ytterbium (Yb) fixé par trempage sur les parois de la luzerne et le chrome (Cr) fixé par mordançage. Les deux marqueurs ont été incorporés dans le même aliment, avant la granulation.*

La canulation n'affecte pas les mesures de digestibilité et de temps de séjour moyen (Tableau II). Cette technique permet la mesure de temps de séjour moyen entre le caecum et le rectum : 9,6 h. Les valeurs de temps de séjour totaux mesurées avec l'Yb (20,0 h ± 1,7, n = 8) sont supérieures à celles mesurées avec le chrome mordancé (17,9 ± 1,4 h, n = 8). En effet, la taille des particules marquées au Cr serait plus grande; elles seraient donc excrétées plus rapidement dans les fèces. Par contre, les mesures de flux ne sont pas affectées par le choix du marqueur, confirmant indirectement la représentativité des échantillons de contenus d'iléon collectés au moyen d'une canule.

Environ la moitié (49 %) de la matière organique digestible et les 2/3 des protéines brutes digestibles sont digérés avant le caecum. Les fibres (résidu NDF) sont retrouvées en totalité à l'iléon terminal. Toutefois, une part des hémicelluloses (NDF-ADF) serait apparemment dégradée dans l'intestin grêle. La fiabilité de l'analyse des fibres dans les digesta par la technique de Van Soest est discutée, en relation avec les mesures de flux à l'iléon terminal.

flux digestif — transit — lapin — marqueur

INTRODUCTION

Digestibility of food in the rabbit is usually obtained from total fecal collections. A major drawback of this method is that the role of different portions of the digestive tract in the digestion of a diet cannot be clearly defined. Digesta flow measurements have not yet been performed satisfactorily in the rabbit because of two major problems : the obtention of representative samples of digesta, and the precise and correct chemical evaluation of digestive content. An attempt was made to measure the passage of digesta along the digestive tract after slaughter (Wolter *et al.,* 1980) or after slaughter with prevention of caecotrophy (Gidenne and Poncet, 1985; Gidenne, 1987), but the results were not consistent with the theoretical model. In order to resolve the first problem, sampling of digesta contents by ileal cannulation was carried out (Gidenne *et al.,* 1988). This offered the possibility of determining the apparent digestibility of a diet before its fermentation in the large intestine, where the mean retention time of digesta is 4—6 times longer than that recorded for the small intestine.

The aim of this study was to assess on the same animal the flow of digesta (organic matter, cell-walls) at the ileal level and to perform transit measurements in the whole tract and between ileum and rectum. Furthermore, two types of marker (ytterbium, yb : Ellis and Huston, 1968; and mordanced chromium, cr : Uden *et al.,* 1980), differing in their labelling method, were compared for transit and also for flow measurements. Such data are requisite for the development of an experimental model for *in vivo* study of the digestion (digestion and transit) of diet constituents before and after the fermentation step, especially cell-wall constituents.

MATERIALS AND METHODS

Experimental procedures

Six adult femal rabbits (New Zealand White x Californian) weighing 2.5—3.5 kg were fitted with a single T glass-cannula in the terminal ileum (group F) as previously described

(Gidenne *et al.*, 1988). Six female rabbits without a cannula were used as controls (group N) for conventional digestibility and transit measurements in the total tract. The animals were kept in individual metabolism cages under a 12:12 light—dark schedule. Feeding was *ad libitum* with a pelleted diet containing dehydrated lucerne meal (40 %), barley (30 %), oats (10%), soya bean meal and minerals (5 %) (for chemical composition, see Table I). Two particulate markers were bound on lucerne meal cell-walls, according to the technique of Uden *et al.* (1980) for mordanced chronium, and according to Ellis and Beever (1985) for ytterbium (cell-walls were labelled after 24 h of soaking in a Yb solution, then chelated with citric acid). Then, the two batches (Yb + Cr) of labelled lucerne cell-walls were incorporated in the diet before pelleting, at a rate of 69 mg/kg DM for Yb and 46 mg/kg DM for Cr.

Apparent digestibility coefficient in the whole tract was calculated from daily fecal collection during two 4-day periods (Colin and Lebas, 1976) for F + N group. The feces were pooled individually in a plastic bag and stored at −18 °C for further analysis. Soft feces were obtained from rabbits wearing a plastic collar for 24 h (Gidenne and Lebas, 1987), and an individual mean sample was constituted from two separate collection periods for each rabbit.

Digesta were collected from the ileal cannula after a 2—3 week period of recovery after surgery. Eight collections, each lasting 1 h, were made for each animal throughout a period of 24 h, *i.e.* at 09.00, 12.00, 15.00, 18.00, 21.00, 24.00, 3.00 and 6.00 h. Collections were made over a period of 5 days in order to prevent too much stress on the animals. Then a mean sample was prepared for each rabbit.

After the digestibility and flow measurements, mean retention time in the total tract (MRTt) was calculated (groups F and N) from a collection of feces starting after the replacement of the labelled diet by the same diet without markers, at 9.30 a.m. (TO). Collections were made every second hour until 14 h, every fourth hour until 38 h and every eighth hour until 54 h. The feces were dried for 24 h at 104 °C, then weighed and analyzed for Cr and Yb.

Mean retention time between terminal ileum and rectum (MRTp) was measured in 3 rabbits of the F group fed with the non-labelled diet. A single dose of chromium (100 mg of mordanced dietary cell-walls containing 5 mg of Cr) was administered in the ileum by means of the cannula at 11.00 p.m. (TO), and the feces were collected as described above.

Table I. Chemical composition of the diet, the ileal content, hard and soft feces.

(g/kg DM)	*OM*	*CP*	*Starch*	*Total sugars*	*NNCC*	*GE (mj/kg DM)*	*NDF*	*ADF*	*ADL*
Diet	899	175	207	35	352	17.89	372	230	50
Ileum	834	155	13	25	224	17.35	455	307	73
(*n* = 6)	(6)	(6)	(2)	(3)	(19)	(0.67)	(20)	(20)	(5)
Hard feces	875	138	< 10	< 10	21	18.02	713	476	122
(*n* = 12)	(7)	(12)			(14)	(0.10)	(17)	(7)	(8)
Soft feces	881	317	< 10	—	151	19.05	412	259	75
(*n* = 6)	(12)	(35)			(42)	(0.22)	(53)	(28)	(6)

Mean values with standard deviation in parentheses, for rabbit of group F (*n* = 6) or for rabbit of group F + N (*n* = 12).
OM: organic matter; *CP* = crude protein; *NNCC* = *OM—CP—NDF*;
GE = gross energy; *NDF* = neutral detergent fiber; *ADF* = acid detergent fiber; *ADL* = acid detergent lignin.

Analytical procedures

Analyses were performed on duplicate freeze-dried samples (feed, digesta, soft and hard feces) and data were expressed on a dry matter basis. Organic matter (OM) was determined by ashing at 550 °C for 5 h. Nitrogen was measured by a Kjeldhal procedure and converted to crude protein (CP) using the factor 6.25. Starch was enzymically hydrolysed (Thivend *et al.*, 1965) and glucose from starch was measured by using the hexokinase/glucose-6-phosphate deshydrogenase/NADP system (Boehringer Mannheim, cat. No. 716251). Soluble carbohydrates were extracted using alcohol 80 % v/v, and total sugars were analyzed by colorimetry (Tollier and Robin, 1979). Gross energy was measured by an adiabatic bomb calorimeter. Cell-wall constituents were determined according to the method of Van Soest and Wine (1967), modified by Giger *et al.* (1979). The non-nitrogenous cellular content (NNCC) was defined as OM—CP—NDF. Ytterbium and chromium were determined by atomic absorption spectrometry.

Calculation and statistics

Flow calculation

The fecal recovery rate of the markers was calculated on a total fecal collection of 2 x 4 days. To express the nutritive value of the diet only, and to compare IADC to digestibility in the whole tract (DI—feces/DI), the quantity of constituents which desappeared between mouth and ileum (TI—IF) was expressed in percent of the diet intake (DI). Then, ileal apparent digestibility coefficient (IADC) was calculated by the formula :

IADC = (TI—IF)/DI, with TI (total intake) calculated as the sum of DI and soft feces intake; IF (ileal flow) was calculated using Yb and Cr separately (single marker method), from the ratio of the nutrient in the ileal digesta to the corresponding ratio in the diet.

Transit calculation

MRT values were calculated from the equation : $MRTt = T1 + \Sigma Ai (Ti + 1 - Ti)$ according to Faichney (1975) and $MRTp = \Sigma Ti \cdot Mi$ according to Blaxter *et al.*, (1956) for total and partial retention time respectively. T1 was the time elapsed between the end of feeding the labelled diet (TO) and the defaecation for which A first became less than unity; Ai was the marker concentration in the ith defaecation as a fraction of the equilibrium concentration, and Ti was the time elapsed between TO and ith defaecation. Mi was the marker excreted in the ith defaecation as a fraction of the total amount excreted.

An index of transit, E24h was defined for rabbit as the quantity of marker excreted (expressed in percent of total quantity of marker excreted) before the next period of caecotrophy (approximately 24 h), which corresponded to an absence of hard feces excretion in the morning. This index required only one analysis and corresponded to the quantity of marker excreted before the recycling of particles by caecotrophy.

Statistics

To determine the effect of cannulation or/and effect of marker, analysis of variance was carried out using the GLM SAS procedure (1985).

RESULTS

Methodology

The apparent digestibility in the whole tract (Table II) was not significantly different between rabbits of group F and those of group N for any constituent of the diet. Mean digestibility coefficients of fistulated rabbits had a higher SD than those of the controls (group N). This result was probably in relation with the greater variations in diet intake for group F (35.6 ± 11.8 g DM/kg live weight) than for group N (40.8 ± 6.8).

Table II. Effect of the ileal cannulation on the digestibility (%) of organic matter (OM) and its main components, in the whole tract.

	OM [1]	*CP*	*Energy*	*NNCC*	*NDF*	*ADF*	*ADL*
Group N ($n = 6$)	60.4 (1.0)	68.4 (1.9)	59.2 (1.0)	97.7 (2.0)	21.1 (1.4)	15.0 (2.6)	− 3.8 (7.5)
Group F ($n = 6$)	60.2 (2.7)	67.6 (4.5)	58.7 (3.0)	97.4 (1.4)	21.6 (4.3)	15.2 (5.2)	1.5 (4.2)
Résidual SD	2.2	3.5	2.2	1.7	3.2	4.1	6.1
Statistical significance	NS	NS	NS	NS	NS	NS	NS

Mean values with standard deviation (SD) in parentheses.
NS : Not significant
[1] : See analytical procedures

The fecal recovery rate for Yb and Cr respectively was : 100.4 ± 1.8 and 96.3 ± 1.8 in N group, 101.5 ± 2.6 and 100.6 ± 5.7 % in F group; it was not significantly affected by either the type of marker or the cannulation.

Mean dry matter flow at terminal ileum was 109.3 ± 39.0 g DM/d (969.0 ± 345.7 g of fresh matter) when calculated using Yb; it did not differ significantly from DM ileal flow calculated using Cr : 111.9 ± 38.2 g DM/d (992.1 ± 338.6 g of fresh matter). Therefore the flow of other constituents of the diet was calculated for each animal as the mean between flow calculated using Yb and that calculated using Cr (Table III).

Cannulation did not significantly affect MRTt or E24h, which were higher when calculated using ytterbium ($P < 0.01$) than using mordanced chromium (Table IV). Approximately 90 % of the marker intake was excreted before the next period of caecotrophy. The measure of this index (E24h) was easy (one fecal collection and thus one analysis of marker), but it was also less precise and had a lower discrimination capacity than MRT measure : values of Fischer—Snedecor parameter for marker effect were higher for MRT (10.96) than for E24h (8.77).

Digestibility and mean retention time in the whole tract and at the ileal level

The organic matter digestibility in the whole tract reached 60 % resulting in a digestible energy content of the diet of ≈ 10.58 MJ/kg DM. The NNCC and the starch fraction of the diet were totally digested by rabbits. Soft feces intake represented 21.5 % of the diet intake for crude protein, and only 13.3% for cell-wall fraction (NDF) (Table III). Cell-wall (NDF) digestibility reached 20 % (Table II) with a higher coefficient for hemicellulose NDF—ADF (30.8 %) than for cellulose ADF—ADL (20.0 %). The ADL fraction in

Table III. Intake (diet and soft feces) and flow measurements at terminal ileum (IF)

	OM	*CP*	*Energy*	*NNCC*	*NDF*	*ADF*	*ADL*
Intake (g/d)							
Diet	112.5 (39.7)	21.9 (7.7)	223.6 (78.8)	44.1 (15.5)	46.5 (16.4)	28.75 (10.14)	6.3 (2.2)
Soft feces	13.1 (6.2)	4.7 (2.2)	28.3 (13.2)	2.2 (0.9)	6.2 (3.1)	3.9 (1.9)	1.1 (0.5)
Ileal flow (IF) (Kj/d)							
(g/d)	92.2 (31.9)	17.1 (5.9)	192 (66)	24.4 (7.8)	50.6 (18.8)	34.4 (13.5)	8.2 (3.3)
% of total intake [1]	73.6 (1.8)	64.4 (4.4)	78.1 (1.7)	53.6 (4.8)	95.9 (1.5)	104.4 (4.3)	109.9 (6.6)
Ileal apparent digestibility [2]	29.4 (2.6)	43.3 (6.8)	24.8 (2.4)	48.7 (5.2)	4.6 (1.6)	− 5.1 (5.1)	− 11.5 (7.7)

Mean values with standard deviation in parentheses ($n = 6$)
[1] Total intake (TI) = diet + soft feces intake.
[2] [TI—IF/diet intake] x 100

this diet remained undigested. The high SD recorded for cell-wall digestibility originated mainly from the method of calculation. The use of the recovery rate to express the digestion of components with a low digestion rate seems more appropriate. Indeed, mean fecal recovery rate (both group F and N, $n = 12$) for ADL, cellulose, hemicellulose were respectively 101.1 ± 6.4; 79.9 ± 3.8; 69.2 ± 4.0 %.

Table IV. Mean retention time and E24h index of lucerne meal cell-walls in the whole tract of the rabbit : effect of the marker used (Yb or Cr) and of the ileal cannulation.

	Group N (n = *5*)		*Group F* (n = *3*)		*Treatment significance*	
	Ytterbium	*Chromium*	*Ytterbium*	*Chromium*	*Marker*	*Cannulation*
Total MRT (h)	20.6 (1.3)	18.1 (1.2)	22.4 (1.8)	19.7 (1.8)	$P < 0.01$	NS
E24h (%)	89.1 (2.7)	94.3 (3.5)	84.6 (7.4)	92.6 (4.4)	$P < 0.05$	NS

NS : Not significant.

Cell-walls were quite undigestible in the stomach and small intestine (IRR = 95.9 %) but ADL ileal flow was slightly higher than ADL intake. The cellulosic fraction was entirely recovered (IRR = 100.6 ± 2.3), whereas IADC for hemicellulose fraction reached 16.9 %. Analysis of ileal contents revealed relatively high concentration for OM, NNCC, CP and energy. Mucous, bile and pancreatic enzymes undoubtely added OM, thereby lowering their digestibility coefficient before the cecum. The sum of starch and soluble carbohydrates in ileum content (Table I) did not exceed 4 % of OM. Then, approximately 20 % of the OM was constituted by non-nitrogenous products (muco-polysaccharides) and by cell-wall polysaccharides (such as pectic substances) soluble in neutral detergent solution. In feces, this fraction was < 1 %; thus it could be assumed that these components were entirely digested in the lower parts of the rabbit digestive tract. In soft feces the same components (NNCC—starch—soluble carbohydrates) represented 15 % of OM, whereas crude protein represented 36 % of OM.

Mean retention time (MRT) of labelled cell-walls of lucerne meal in the whole tract, reached 20 h. Between terminal ileum and rectum, MRT measured with Cr was 9.6 ± 0.5 h and compared with MRT in the whole tract (on the same animal); MRT between mouth and ileum was deduced by difference : 9.1 h.

DISCUSSION

The problems of digesta sampling are emphasized by the values of digesta flow found in samples from the different parts of the digestive tract obtained by slaughtering : a negative digestibility coefficient for nitrogen (–100 %) and a low digestibility for dry matter (20 %) at the end of the ileum (Wolter *et al.*, 1980). There are two reasons for this. Such measurements do not take into account : 1) soft feces production (total intake was not determined); and (2) circadian variations in digesta composition (Gidenne and Poncet, 1985). In addition, the high digestibilities obtained for the small intestine could be erroneous because of the low amounts of digesta sampled in this part of the tract at slaughter (Gidenne, 1987).

The representativity of the ileal sample collected by cannulation was verified in a previous work (Gidenne, 1988) by comparing the rate of Cr—EDTA (marker of the liquid phase) and Yb (particulate marker) in ileal samples obtained either by cannulation or after slaughter. In the present experiment, ileal flow of DM calculated using Yb or Cr remained similar, in spite of differences in the localization of the two markers. This result also shows indirectly that the particulate matter collected by cannulation was representative of that in the ileum.

Ileal cannulation was well supported by the rabbits for a minimum of 3 months (frequently 6 months or more), thus allowing flow measurements without significant disturbances in food intake, digestive or passage rate parameters. Between-animal variations in ileal flow were in the range of those observed by Braude *et al.* (1976) in pigs.

Few passage rate studies have been performed in the rabbit using rare-earth (Laplace *et al.*, 1974; Gidenne *et al.*, 1987) or chromium mordanted fiber (Uden *et al.*, 1980; Ledin, 1984) as markers. These markers have never been used in the same experiment for comparison. The relevance of ytterbium and chromium as

markers lies in the fact that the complex Cr—fiber is indigestible and that rare-earth elements, like Yb, exhibit strong adsorptive properties in the particulate phase with less digestive unpairement. But the rare-earth ones like Yb are able to migrate from one particle to another during their transit through the rumen and other parts of the tract (Hartnell and Satter, 1979), more especially toward fine particles. Thus, the rate of comminution of particles is higher for Yb and the size of Yb-labelled particles is probably lower. This may explain results showing lower MRT values for Yb-labelled particles than for Cr in ruminants (Gonzalez *et al.*, 1987) or pigs (Pond *et al.*, 1986). Inversely, in the rabbit Cr gave lower MRTt values than those obtained with Yb for the same feedstuff. This result could be explained by the aboral movement of fine particles from the proximal colon to the cecum (Björnhag, 1972), these fine particles containing more Yb than Cr.

MRT values in the caecocolic segments (9.6 h for caecolic segments) observed in this study are in close agreement with those calculated by mathematical modelization of radio-cerium concentration in different segments of rabbit digestive tract (Jolivet *et al.*, 1975), or with that obtained by Uden *et al.* (1982) by introducing a dose of mordanced chromium through a caecal cannula.

Values of ileal flow obtained in cannulated rabbits are in agreement with the "theoretical model", as almost half (48 %) of the digestible OM and the two-thirds of digestible CP were apparently digested before the cecum. Similar ileal ADC was recorded in horses fed with a diet of similar composition (Hintz *et al.*, 1971). Furthermore, ileal flow of NDF gives the first experimental results in rabbit which show that cell-walls remain undigested before cecum fermentation.

Amounts of OM, CP and energy were overestimated in ileal content because they included endogenous products. Cell-wall analysis was not influenced by such products (without fiber). However, the mean recovery rate of ADL exceeded 100% at terminal ileum. In digesta, lignin residue obtained by Van Soest's method was probably contaminated by other products such as protein—lignin or polysaccharides—lignin complexes. This was also observed for human digesta by Holoway *et al.* (1978), who obtained negative digestibility coefficients (–70 %) for ADL in ileum. These lignin complexes probably contaminated the ADF fraction and contributed to an underestimated of the amount of hemicellulose (HC obtained by the difference : NDF—ADF) flowing at the ileum and thus to an overestimate of their digestibility. Our results indicate that half of the digestible HC disappeared in the small intestine. In pigs, similar values for HC digestibility before the cecum were found (Keys and Debarthe, 1974; Sambrook, 1979; Kass *et al.*, 1980). Gas chromatography analysis of cell-wall carbohydrates could overcome these contamination problems. Such results indicate that the part of xylose and arabinose of hemicellulose absorbed in ileostomized human could reached 30 % of that intake (Sandberg *et al.*, 1981). But in this case, a flora would develop in the terminal ileum, as shown in ileostomized pigs (Laplace, 1975).

CONCLUSION

Ileal-cannulated rabbit appears to be a convenient model for studying the relative importance of enzymic and fermentative digestion of a diet : the cannula, well

supported by adult rabbits, did not modify digestibility or transit rates, and provided representative samples of digesta. Furthermore, it is possible to associate total and partial digestibility measurements to total and partial transit measurements on the same animal. The choice of the marker for transit measurements (rare-earth or mordanced chromium) should be related to the digestibility of the labelled diet fraction.

These first measurements of ileal flow in rabbit are in agreement with the indigestibility of fiber in the small intestine. However, the relatively high ileal digestibility for HC suggests that chemical analysis of digesta remains a difficult task. Further experiments using ileal-cannulated rabbits and more specific analytical methods for structural carbohydrates are necessary to confirm these first results. Associated with the labelling of cell-walls, the nutritional role of dietary fiber will become clearer.

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