Feeding ground and pelleted hay rather than chopped hay to ponies
2. Consequences on fibre degradation in the cecum and the colon

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Abstract

This study was designed to evaluate the effect of the physical form of a hay diet on (1) in situ DM and NDF degradation rate and (2) postprandial evolution of pH and VFA concentrations, in the cecum and the right ventral colon of ponies. Four gelded ponies, fitted with cannulae in the cecum and the right ventral colon, were kept on wood shavings and fed twice daily a maintenance diet composed of equal parts of Lucerne and Cocksfoot hay. The hay, either chopped (CH) or ground (1.5 mm screen) and pelleted (GPH), was offered to the ponies at the same level of DM intake in a crossover design. The in situ disappearance of hay DM and NDF was measured during a 48 h incubation period in the cecum and the colon. Cecal and colonic VFA concentrations, and pH were measured before the morning feed, then every hour until 8 h post-feeding.

Grinding and pelleting the hay caused a significant decrease in both the rate and the extent of in situ fibre degradation. However, they did not alter significantly the apparent digestibility of fibre (Drogoul et al., 2000), in spite of a significant increase in mean retention time (MRT) of both the liquid and particulate phases of digesta. This phenomenon may result from a decrease of the cellulolytic activity. These results suggest that, as in ruminants, fibre digestion in the hindgut of ponies is a function of both the time available for digestion and the microbial degradation rate. The rates of disappearance of DM and fibre from bags in the cecum and the right ventral colon were similar. Because the MRTs of both particles and solutes were much higher in the colon than in the cecum (Drogoul et al., 2000), our results showed the more significant role of the colon relative to the cecum in fibre digestion in the ponies. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Pony; Hay processing; Fibre digestion; Equine hindgut; In sacco degradation; VFA production

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1. Introduction

Grinding forages greatly increases structural cell wall area exposed to fibrolytic microorganisms. However, in situ fibre degradation, assessed using the in sacco technique, is significantly reduced in ruminants fed pelleted forages (Journet and Demarquilly, 1967; Shaver et al., 1986; Udén, 1988). In ruminants, this effect is often associated with adverse physicochemical conditions in the rumen, which can influence the microbial population (number of species and amount of each of them, and attachment to particles). To our knowledge, this effect has never been tested in horses.

Feeding ground and pelleted hay (GPH) instead of chopped hay (CH) at the same feed intake (1.7 kg DM/100 kg live weight) did not significantly alter apparent digestibility of fibre in the pony, whereas it did significantly increase retention time, especially in the colon, compared to CH (Drogoul et al., 2000). These results suggest that the expected increase in digestibility as a result of an increase in both particle MRT and particle area in contact with enzymes may have been offset by a decrease in the rate of the cell wall degradation in the hindgut. In order to test this hypothesis, the present study examined the effect of hay physical form on (1) in situ fibre degradation rate and (2) postprandial physicochemical parameters such as pH and volatile fatty acids (VFA) concentrations, in the cecum and the colon of ponies.

2. Material and methods

2.1. Experimental conditions

Experimental conditions were described in Part 1 of this study (Drogoul et al., 2000). Briefly, four crossbred gelded ponies (230 ± 50 kg average bodyweight) fitted with cannulae in the cecum and the right ventral colon were used. The CH diet was fed as two equal meals each day (08:00 h, 16:00 h) according to French recommendations (0.038-UFC/MBW, i.e. 540 kJ of ME/kg MBW, Martin-Rosset et al., 1994). The GPH diet was offered at the same dry matter intake as the CH diet.

The ponies were used in a crossover design (two diets × two periods × two animals/diet). All animals were assigned randomly to their diet. Each experimental period consisted of 3 weeks for diet adaptation in individual boxes, 5 weeks for in situ measurements, 1 week to measure postprandial variation in pH and VFA concentrations and 9 days for rate of passage measurements (reported in Drogoul et al., 2000).

2.2. Kinetics of in situ disappearance of hay DM and NDF in the cecum and the colon

The effect of the physical form of hay on the kinetics of the diet hay DM and neutral detergent fibre (NDF) degradation in the cecum and the colon, was assessed using the Nylon bag technique (Michalet-Doreau et al., 1987). Bags (Blutex T120, 3.5 × 11 cm² size, pores of 46 μm, 32% exchange area) containing approximately 0.8 g of ground hay (1 mm screen) were incubated simultaneously in both compartments for 2, 4, 8, 12, 24 or 48 h. Just before the morning meal, four bags were introduced in each compartment for
the 2, 4, 8 and 24 h incubation time points (1 bag per incubation time). Four other bags were introduced 48 h later and incubated for 12 h (1 bag), 24 h (1 bag) and 48 h (2 bags). This in sacco procedure was repeated five times in order to have enough residue for NDF analysis (5 bags per animal and per incubation time except for the 24 and 48 h incubation points where 10 bags were needed). Immediately after removal from the gut, the bags were rinsed under cold tap water, hand-squeezed and deep frozen at $-18^\circ C$. At the end of the trial, all bags were thawed and gently washed in cold tap water (three or four times for 5 min using a small washing machine) until rinsing were clear. The remaining DM was determined after drying (48 h at 65°C). Twelve bags, not incubated, were soaked in warm water (39°C) for 2 h and then washed with the others to estimate disappearance of DM due to both solubility and loss of DM during the washing procedure. For each compartment and incubation time, dried residual contents of the incubated bags were pooled separately for each pony. NDF analyses were carried out in triplicate using the procedure of Van Soest and Wine (1967) and reported as dry residue. The data for in situ DM and NDF disappearance rates ($D_t$) with time were obtained for each pony in each compartment. They were fitted to the following equation (Ørskov and McDonald, 1979):

$$D_t = A + B(1 - e^{-ct})$$

where $D_t$ is the fraction of the hay component lost from the bag during incubation to time $t$, $A$ the rapidly degradable fraction of the component, $B$ the slowly degradable fraction of the component and $c$ the fractional disappearance rate (h$^{-1}$) of the component.

2.3. Postprandial pH and VFA concentrations

Samples of the liquid phase of digesta were taken simultaneously from both compartments. Samples were taken just before the morning feed (T0) and then every hour for 8 h (T1–T8). Liquid samples were obtained by suction using a 250 ml syringe with a plastic tube (1 cm internal diameter) attached. The extremity of the tube was drilled with holes (1 mm) on 25 cm and covered with Nylon (Blutex™ T120, pores 46 μm) to exclude particles (see Fig. 1). One tube (80 cm long) was inserted into the cecum and another one (40 cm long) in the right ventral colon of each pony just before the first sample was taken. Tubes were maintained, closed by a clamp, all daylong in the cannula (see Fig. 1). In order to collect a representative sample, approximately 100 ml of fluid were drawn out and pushed back three times before taking a 25 ml sample. Five replications for each diet and compartment were made at intervals of at least 48 h.

Immediately after sampling, pH was measured. For each sample, 2 ml duplicate subsamples, stabilised by addition of 400 μl of $H_2PO_4 + HgCl_2$ solution (1% (w/v)) were stored at $-40^\circ C$ in Eppendorf™ tubes. VFA analysis was performed in duplicate by gas chromatography (gas chromatograph with a glass spire column filled with Chromosorb VAW plus 2% $H_3PO_4$, 80–100 mesh and a flame ionisation detector, Packard 437A, Jouany, 1982).

2.4. Data treatments and statistical analysis

All data treatments and statistical analysis were performed using the statistical analysis system (SAS) (SAS/STAT, 1998). In situ data were fitted to the model using the
multivariate sequential non-linear iterative (N.LIN) procedure. In situ data were analysed according to the general linear model (procGLM) of SAS where classification variables were animal (four levels), diet (two levels), compartment (two levels) and incubation time (six levels), and considering the animal variable as a random effect. pH and VFA concentration values were analysed using the same model (procGLM) where classification variables were animal (four levels), diet (two levels), compartment (two levels) and sampling time (nine levels). The animal variable was considered as a random effect. Means were compared using the Student’s t-test.

3. Results

3.1. Diet characteristics and feed intake

Diet chemical composition, particle size distribution and DM intake for the two diets were as reported in a previous companion paper (Drogoul et al., 2000).

3.2. In situ disappearance of the hay in the cecum and the colon

The chemical composition of the hay that was placed in the bags (1 mm screen ground CH diet hay) was similar to that of GPH (589 g NDF/kg DM). For each pony and diet, the mean DM disappearance from the bags incubated for 24 h with the first series (2, 4, 8 and 24 h time points) was not significantly ($p > 0.1$) different from that of the bags incubated for 24 h with the second series (12, 24, 48 h time points). So, the data were grouped to compose the disappearance curves for incubation times from 2 to 48 h after feeding (Figs. 2a and b for DM and NDF, respectively).
Whatever the diet, the in situ disappearance of hay DM did not show any significant differences \( (p > 0.1) \) between cecum and colon at each sampling time, whereas the in situ disappearance of NDF showed significant differences between cecum and colon \( (p < 0.05) \) except at the 24 and 48 h time points. However, the cumulated percentages of DM (and NDF) that disappeared from bags during the first 12 h were always lower in the colon than in the cecum. Noteworthy are the periodic variations in the kinetics of substrate disappearance from bags incubated in both compartments, mainly with the GPH
diet. They appear at the beginning of the incubation period in the colon as a lag phase that created a gap between the cecum and the colon curves.

Whatever the compartment, feeding GPH rather than CH, significantly reduced the percentage of DM \( (p < 0.01) \) and NDF \( (p < 0.001) \) that had disappeared at each incubation time. This diet effect was no longer significant \( (p > 0.1) \) at the 48 h incubation point. Concerning DM disappearance, the difference between diets was quite constant (about 5% units) regardless of the incubation time (Fig. 2a). However, the diet differentially affected the pattern of NDF disappearance depending on the incubation site. In the cecum, the rate of NDF disappearance was lower with the GPH diet than with the CH diet, whereas, in the colon, there was a time lag of about 8 h with the GPH diet, followed by a degradation phase at a rate similar to that observed with the CH diet (Fig. 2b).

The values for the parameters of the model fitted to the disappearance data did not show any significant differences between compartments except for the slowly degradable fraction \( (B) \) of the NDF on diet GPH (Table 1). Estimates of the parameters \( A, B \) and \( c \) (Table 1) were consistent with point-to-point observations. There were some differences between the cecum and the colon. Thus, the slowly degradable fraction \( (B) \) of DM and NDF, was larger in the colon than in the cecum with both diets, and the fractional disappearance rate \( (c) \) of NDF was larger in the cecum than in the colon, with the GPH diet. Difficulties in fitting the model to the data (particularly for the colon on diet GPH) may explain some discrepancies between curves observations and curves modelling. For

Table 1
Parameter estimates for the exponential model \( y = A + B(1 - e^{-ct}) \) (Ørskov and McDonald, 1979) fitted to the in situ DM and NDF disappearance from bags incubated in the cecum and the right ventral colon of ponies fed either CH or GPH at maintenance level\(^a\)

<table>
<thead>
<tr>
<th>Compartment</th>
<th>Model parameter</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A (%)</td>
<td>B (%)</td>
<td>c (h(^{-1}))</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cecum</td>
<td>Colon</td>
<td>Cecum</td>
<td>Colon</td>
<td>Cecum</td>
</tr>
<tr>
<td>DM disappearance</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GPH</td>
<td>31.7 a</td>
<td>29.8 c</td>
<td>27.9**</td>
<td>36.1 c</td>
<td>0.047 a</td>
</tr>
<tr>
<td>SE</td>
<td>±2.5</td>
<td>±2.8</td>
<td>±2.1</td>
<td>±3.6</td>
<td>±0.031</td>
</tr>
<tr>
<td>CH</td>
<td>38.8 b</td>
<td>34.2 d</td>
<td>28.6</td>
<td>30.8 d</td>
<td>0.060 b</td>
</tr>
<tr>
<td>SE</td>
<td>±1.5</td>
<td>±2.7</td>
<td>±4.5</td>
<td>±0.7</td>
<td>±0.013</td>
</tr>
<tr>
<td>NDF disappearance</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GPH</td>
<td>3.52 a</td>
<td>3.00</td>
<td>31.91*</td>
<td>37.30</td>
<td>0.072 a*</td>
</tr>
<tr>
<td>SE</td>
<td>±0.8</td>
<td>±0.5</td>
<td>±4.4</td>
<td>±1.0</td>
<td>±0.013</td>
</tr>
<tr>
<td>CH</td>
<td>5.41 b</td>
<td>3.94*</td>
<td>32.60</td>
<td>35.03</td>
<td>0.109 b*</td>
</tr>
<tr>
<td>SE</td>
<td>±1.4</td>
<td>±0.8</td>
<td>±2.5</td>
<td>±4.0</td>
<td>±0.020</td>
</tr>
</tbody>
</table>

\(^a\) For the same component, different letters in the same column indicate significant difference between diets: a, b: \( p < 0.001; \) c, d: \( p < 0.01.\)

\(^*\) For the same component, different letters in the same row, indicate significant differences between compartments: \( p < 0.01.\)

\(^**\) For the same component, different letters in the same row, indicate significant differences between compartments: \( p < 0.001.\)
NDF disappearance, fitting the model of Dahnoa (1988) to the data for the colon, gave times lag of 1.44 and 3.73 h with diets CH or GPH, respectively, but had no significant effect on other parameters (A, B, and c).

Grinding and pelleting the hay significantly reduced the values for A and c for both DM and NDF, whereas the value for fraction B remained unchanged. NDF degradation appeared to plateau before DM degradation on diet CH. However, differences between in situ DM disappearance at 24 and 48 h incubation times were not significant ($p > 0.1$).

3.3. Postprandial pH and VFA concentrations

3.3.1. Postprandial pH in the cecum and the right ventral colon

In both compartments, pH values after the morning meal were in the physiological range for both diets (Fig. 3). With diet GPH, pH was higher in both compartments. During the first 2 h post-feeding, pH was higher in the cecum than in the colon and this difference disappeared thereafter. Also, differences existed in the pattern of post-feeding pH variation. On diet GPH, the pH was stable for the first hour after feeding, then decreased steadily with little variation. On CH, the pH in both compartments first increased, then decreased rapidly until 5 h after feeding, it then increased but had not reached the pre-feeding value, 8 h after feeding.

![Postprandial pH variation in the cecum and the right ventral colon of ponies fed the same hay either CH or GPH at maintenance level.](image)

For each time, diet effect in the same compartment is significant: A, B: $p<0.001$; a, b: $p<0.01$

For each time, compartment effect within same diet is significant ($p<0.05$) if one symbol empty
3.3.2. VFA concentrations in the cecum and the right ventral colon

Acetate (C2) was predominant in the VFA mixture in the cecum and the colon (Fig. 4) and range from 40 to 70 mM/l after the meal. This contrasted with the small variations in propionate (C3, mean 15 mM/l) and butyrate (C4, mean 5 mM/l) concentrations throughout the day and between diets and compartments. Thus, the pattern of variation of total VFA concentrations (results not shown) was determined by acetate concentrations.

Fig. 4. Postprandial variation in VFA concentrations (mM/l) in the cecum and the right ventral colon of ponies fed either CH or GPH at maintenance level.
Grinding and pelleting the hay decreased acetate concentrations and, to a lesser extent, propionate concentrations in both compartments. Although the differences were not always significant, acetate and propionate concentrations were always higher in the colon than in the cecum. Butyrate concentration, as well as isobutyrate, valerate and isovalerate concentrations (results not shown) did not differ \((p > 0.1)\) between compartments.

The postprandial changes in variations in acetate concentrations also differed between diets. As for pH, acetate concentrations tended to return to pre-feeding values before the evening meal on diet CH, whereas the values remained higher on GPH. It was partly the result of the uneven intervals between meals, and partly the lower rate of fermentation and digesta passage with GPH. As a consequence, the molar percentage of acetate in the VFA mixture (Fig. 5) was consistently higher on diet CH during the 5 h post-feeding. Differences between compartments were almost never statistically significant \((p < 0.05)\) with both diets. The percentage of propionate followed a reciprocal pattern and the diet effect was almost always significant \((p < 0.05)\).

The acetate/propionate ratio \((C2/C3; \text{Fig. 6})\) increased rapidly during the 3 h after feeding and then slowly decreased in ponies fed CH. This pattern was different on diet GPH in that the increase was slower, persisted during 6 h and was almost always significantly \((p < 0.05)\) lower on this diet. No compartment effect was noted except on diet CH from 6 to 8 h after the meal.

4. Discussion

Simultaneous measurements of digestive parameters in the cecum and the colon of horses are rare (Kern et al., 1974; Tisserand et al., 1980; Drogoul et al., 1994, 1995) and most of them report micro-flora concentrations (Alexander et al., 1952; Kern et al., 1974, 1973; Moore et al., 1993). Previous studies in our laboratory (Drogoul et al., 1994, 1995) showed that in situ fibre degradation rate was similar in the cecum and ventral colon of ponies fed CH. This was confirmed in the present study with two physical forms of hay, CH or finely GPH.

4.1. Effect of hay physical form on in situ degradation rate

Grinding the hay through a 1.5 mm screen gave a very fine product (Drogoul et al., 2000) probably at the extreme range of fineness in commercial pelleted feed given to horses. Such a large reduction of particle size increased the particle surface area exposed to fibrolytic micro-organisms. However, fibre degradation estimated using an in situ technique was significantly reduced in both the cecum and the colon when ponies were fed diet GPH compared to diet CH. These results are in agreement with earlier in vivo, in situ or in vitro studies on ruminants (Journet and Demarquilly, 1967; Shaver et al., 1986; Udén, 1988) where grinding forage caused a reduction in substrate fermentation rate and extent, and/or increased in the time lag before digestion began. Depressed DM and fibre digestion resulting from fine grinding of forage cannot reliably be related only to adverse conditions for fibre digestion in the cecum or the colon associated with low pH as
suggested for ruminant. Indeed, pH (Fig. 3) was significantly lower in both compartments in ponies fed CH compared to GPH and never fell below 6.75. With GPH, the drastic change in the consistency of digesta towards pasty contents (observed while placing the sampling tubes) may have impaired the circulation of bacteria and their adhesion to particles both by rendering exchange within the content and between the content and the sample in the bag more difficult (Weakley et al., 1983; Lindberg et al., 1984) and by destroying the fibre structure (Czerkawski, 1986; Faichney and Teleki, 1988). This may

Fig. 5. Postprandial variation in the molar percentage of acetate and propionate in the cecum and the right ventral colon of ponies fed either CH or GPH at maintenance level.
explain why the pH was higher, and VFA concentrations and rate of degradation were always lower on GPH. The diet effect observed in DM and NDF degradation curves was apparent at the first observation point (2 h post-feeding) and persisted (DM), or increased (NDF), thereafter. Degradation probably started more slowly, or with a time lag, on the GPH diet, whatever the compartment. In the colon, NDF degradation was very slow for 8 h and then became similar to that observed on the CH diet. A part of the diet effect may also be attributed to the differential transit time of the diet in the pre-cecal segment of the tract (Drogoul et al., 2000). Similarly, part of the gap between the cecum and colon curves was associated with the delay between feed residues arriving in the cecum and their passage into the right ventral colon. The rest of the difference between diets may be the result of differences in degradation efficiency of the microbial inoculum and of an artefact linked to the screening effect of the nylon bag. On the other hand, the lack of coarse fibrous material in the digesta may also contribute to the depressed DM disappearance from the nylon bags mediated by physical mechanisms (Weakley et al., 1983). The longer MRT of particle and solute markers observed in ponies fed GPH, compared to CH, in the first part of this study (Drogoul et al., 2000), could explain why the digestibility of dietary fibre components was not affected although the in situ fibre degradation rate was reduced on GPH. In order to estimate the quantitative role of the cecum and the colon, effective degradation (ED%) have been calculated using the following equation (Ørskov and McDonald, 1979): \[ ED = \frac{(A + Bc)}{(c + k)} \], at passage rates \((k)\) calculated as 1/MRT in the compartment for each pony (Drogoul et al., 2000).
This estimate supposes that the cecum and the colon are perfect mixing compartments, working in steady-state conditions, which is only partially true (Hume and Sakagushi, 1991). It supposes also that the in situ measurements in the right ventral colon are representative of the entire colon. Measurements with mobile bags would perhaps have been more representative. The ED values for DM and NDF and the total tract in vivo digestibility of DM (Drogoul et al., 2000) are presented in Table 2.

The ED of NDF in the colon was significantly \( p < 0.05 \) higher than in the cecum, and higher on CH compared to GPH. The diet effect was significant \( p < 0.05 \) in the cecum and the whole hindgut, but not in the colon. The calculated ED of NDF in the whole hindgut underestimated NDF degradation in comparison with NDF apparent digestibility estimated in vivo (Drogoul et al., 2000), especially for GPH diet (33% compared to 47%). It could possibly be due to differences in accessibility of particles in the bag to fibrolytic enzyme. Conversely, in situ ED of DM in the hindgut largely overestimated in vivo DM digestibility for unknown reasons. However, it is noteworthy that the EDs of NDF in the colon were similar on both diets in agreement with the in vivo results although they underestimated in vivo NDF digestibility. In ruminants, in situ estimates of degradation of NDF in ground (1 mm screen) forages is also known to underestimate (by about 10% units) rumen NDF degradation (Archimède, 1992). Estimation of the passage rate \( (k) \) in the cecum was less accurate than estimation of the passage rate in the colon (Drogoul et al., 2000). This may have affected the precision of the ED calculation in the cecum and, as a result, in the whole hindgut.

### 4.2. Effect of hay physical form on pH and VFA concentrations in the cecum and the colon

Our findings that VFA concentrations were consistently, although not always significantly, higher in the right ventral colon than in the cecum, whatever the diet, are

<table>
<thead>
<tr>
<th>Diet</th>
<th>ED in the cecum</th>
<th>ED in the colon</th>
<th>ED in the whole hindgut</th>
<th>Total tract in vivo digestibility(^c)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM (^a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GPH</td>
<td>35.5±4.8 a</td>
<td>53.0±1.05 c</td>
<td>69.7±2.6 d</td>
<td>53.8±2.2</td>
</tr>
<tr>
<td>CH</td>
<td>48.0±3.0 b</td>
<td>56.6±1.6 c</td>
<td>77.7±1.8 e</td>
<td>51.4±1.8</td>
</tr>
<tr>
<td>NDF</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GPH</td>
<td>6.7±0.7 a</td>
<td>28.9±2.1 b</td>
<td>32.7±1.7 d</td>
<td>47.0±3.7</td>
</tr>
<tr>
<td>CH</td>
<td>15.5±3.3 b</td>
<td>29.6±1.7 c</td>
<td>40.3±3.2 e</td>
<td>44.2±3.9</td>
</tr>
</tbody>
</table>

\(^a\) For the same component, different letters in the same column indicate significant difference between diets: \( p < 0.5 \). For the same component, different letters in the same row, indicate significant differences between compartments: \( p < 0.5 \).

\(^b\) The estimation has been done using the model of Ørskov and McDonald (1979) adapted to the prediction of ruminal degradabilities from in situ incubation measurement weighted according to rate of passage \( k \) (h\(^{-1}\)). \( k \) were determined using MRT (\( k = 1/\text{MRT} \)) measured with same diets and animals (Drogoul et al., 2000).

\(^c\) Drogoul et al. (2000).
in agreement with the results of Tisserand et al. (1977). As in situ degradation parameters were quite similar in both compartments, this difference was likely due to differences in cecal and colonic volumes, and digesta flow rates.

A fall in VFA concentrations in the gut of horses just after feeding has been reported by other authors (Willard et al., 1977; Wolter et al., 1978). It can be related to VFA dilution because copious amount of upper digestive tract secretions occur within less than 1 h of feeding when ponies are fed one or two large meals a day, resulting in a rapid transfer of fluid to the lumen of the gastrointestinal tract, regardless of the physical form of feed (Clarke et al., 1990).

Similar trends in cecal acetate and propionate concentration values and variation patterns have been observed by various authors (Hintz et al., 1971; Willard et al., 1977; Wolter et al., 1978) for similar diets or feed physical forms (pelleted feeds). However, to our knowledge, no studies on the effect of the physical form of forage have been reported in horses. In ruminants, Shaver et al. (1986) reported that pH and acetate/propionate ratio (C2/C3) were reduced 0.55 and 1.2 units, respectively, in the rumen of cows fed GPH compare to CH. In our study, the C2/C3 ratio was also significantly ($p < 0.05$) reduced (0.78 unit in the cecum and 0.48 unit in the colon 3 h post-feeding) when ponies were fed GPH, as a consequence of a slower increase in acetate concentration in ponies fed CH. This earlier increase in VFA production with CH could be related to the decrease in digesta retention time before the cecum with this physical form of hay (Drogoul et al., 2000) and to higher fractional degradation rate with CH. It appears that grinding and pelleting hay reduced the extent of fermentation in the gut of ponies by reducing the rate of degradation of NDF (parameter $c$, Table 1). This reduction was reflected by the slow increase in VFA concentrations after feeding. Comparison of VFA concentrations data may be confounded by postprandial variations of gut fluid volume which were significant in the cecum with the CH diet (C. Drogoul, unpublished data). Therefore, we calculated pools of acetate, propionate and butyrate in the cecum of ponies fed either CH or GPH just before morning feeding, and 4 and 8 h later (Table 3). The differences between diets were highly significant ($p < 0.001$) for these VFA 4 h after feeding, and they were

| Table 3 |
| Postprandial variation in the VFA pool (g) in the cecum of ponies fed either CH or GPH at maintenance level |
|---|---|---|---|---|
| Diet | VFA$^a$ | | | |
| | Acetate | Propionate | Butyrate |
| | CH GPH | CH GPH | CH GPH |
| Before feeding | 14.0 a 16.4 a | 5.0 a 5.9 a | 1.6 a 2.3 a |
| 4 h after feeding | 38.1 b** 23.0 b | 10.9 b** 6.8 a | 4.6 b** 3.0 ab |
| 8 h after feeding | 24.4 c* 29.0 c | 7.3 c** 9.8 b | 2.9 c* 3.9 b |
| Mean values | 25.5 | 22.8 | 7.7 | 7.5 | 3.3 | 3.3 |

$^a$ For each VFA, different letters in the same column indicate significant differences between time post-feeding: $p < 0.001$.

$^*$ For each VFA, different letters in the same row indicate significant differences between diets: $p < 0.01$.

$**$ For each VFA, different letters in the same row indicate significant differences between diets: $p < 0.001$. 

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enhanced compared to those observed on the basis of concentration data. However, the average values over the whole period revealed no differences between diets, which is consistent with there being no difference in the digestibility of the two diets (Drogoul et al., 2000).

5. Conclusion

Prior to this study, we observed that feeding ground, pelleted hay instead of CH, at the same level of dry matter intake, did not significantly modify the apparent digestibility of fibre in the pony (Drogoul et al., 2000). However, the present paper shows that grinding and pelleting the hay caused a reduction of in situ degradation rate and extent, even though the microbial attack was favoured by an increase in the surface area exposed to enzymatic activity. This decrease in degradation rate was offset by the increase in MRT of both the liquid and particulate phase of digesta (Drogoul et al., 2000). Our observations agree with the results obtained in ruminants and reinforce the contribution of time available for digestion (MRT), which together with the rate of microbial digestion, determines the extent of fibre degradation in the gut of herbivores.

Rates of digestion in the cecum and the right ventral colon were similar. Because MRTs of both particle and solute markers were much higher in the colon than in the cecum (Drogoul et al., 2000), our results reflect the importance of the colonic ecosystem of horses in fibre digestion. However, the hay used in our work was finely ground and might have overemphasised the effects of grinding. For instance, gut motility may have been impaired. It is now necessary to confirm the responses of the horse digestive tract to different granulometry of forage and at ad libitum intake levels.

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