Effect of polyethylene glycol on rumen volume and retention time of liquid and particulate matter along the digestive tract in goats fed tannin-rich carob leaves (*Ceratonia siliqua*)

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Abstract

The present work studied the effects of tannins in carob leaves (CL) on rumen volume and kinetics, and on the retention time of fluid and particulate components of the digesta along the gastrointestinal tract (GIT) in goats. The experimental design was a two factor crossover experiment, i.e. in phase 1, two goats were fed CL and 2 CL and polyethylene glycol (PEG) and in phase 2, the treatments were switched. The main effects of tannins were depression of the rumen fluid and particulate content of the rumen, acceleration of the passage of liquid from the abomasum, and delay of the passage of digesta in the intestine. The overall effect was a delay in the passage of fluid and particulate matter throughout the entire GIT. It is hypothesised that these responses are largely the consequence of the interaction of tannins with digestive enzymes and the epithelium lining of the digestive tract.

Keywords: Condensed tannins; Rumen volume; Mean retention time; Digestibility

1. Introduction

Condensed tannins (CD) are complex phenolic compounds which are found in a variety of browse sources (Kumar and Vaithiyathan, 1990), including carob leaves (CL) (Silanikove et al., 1994) and pods (Silanikove et al., 1996c). We have shown recently that the CD in CL reduced food intake, protein and structural carbohydrates’ digestibility, and reduced ruminal and intestinal enzymes’ activities in sheep and goats (Silanikove et al., 1994, 1996a). The possibility that some of the negative effects of CD in CL were due to induction of systemic toxic effects was overruled (Silanikove et al., 1996b). However, it is possible that some of the effects of CD in tannin-rich browse on feed intake and intake pattern are a consequence of nausea caused by irritation of the digestive tract epithelium (Silanikove et al., 1997b).

Polyethylene glycol (PEG), a tannin-binding agent (Jones and Mangan, 1977), was shown to be a powerful tool for isolating the effect of tannins on various digestive functions (Barry et al., 1986; Kumar and Vaithiyathan, 1990; Makkar et al., 1995; Silanikove et al., 2000). Once-daily provision of PEG (molecular weight = 4000) increased markedly the intake and digestion of tannin-containing leaves offered to sheep and goats (Silanikove et al., 1994, 1996a).

The retention time and the content of digesta in the various sections of the GIT are among the important factors that determine the efficiency of digestion (Van...
Soest, 1982). However, reports on the effects of CD on these aspects are few and inconsistent. Nunez-Hernandez et al. (1991) found, in sheep fed up to 50% mountain mahogany leaves, that animals given PEG had a greater ruminal fluid volume than those not fed PEG, but both groups had similar fluid dilution rates and outflow rates. On the other hand, Waghorn et al. (1994) found, in sheep fed *Lotus pedunculatus*, that rumen digesta pool was similar in the PEG and no-PEG groups, but that the dilution rate was higher in the PEG-fed sheep than in those not fed PEG.

In the present study, we took advantage of the dramatic response of goats fed CL to PEG supplementation (Silanikove et al., 1996a, 1997a) to study the effects of CD on rumen volume and kinetics, and on the retention time of fluid and particulate components of the digesta along the GIT.

2. Materials and methods

The experiment was carried out with four non-lactating and non-pregnant 2–3-year-old female Mamerber goats (a breed indigenous to the east Mediterranean woodland) weighing 35 (S.D. ± 5) kg. Two months prior to the start of the experiment the animals were equipped with a cannula in their rumen (i.d. 7.5 cm) and with a fistula in the abomasum (i.d. 3 cm). These procedures were carried out under general anaesthesia. The animals were stall-fed individually in a protected yard that was equipped with troughs, which enabled quantitative measurement of feed intake.

Carob leaves attached to small branches (2–3 mm in diameter) were harvested and kept as described before (Silanikove et al., 1994). Water was available ad libitum at all times. Feed and feed residuals were analyzed as described by Silanikove et al. (1996c). The leaves had 54% dry matter (DM) and contained on a DM basis 972 organic matter, 79 protein, and 575 g/kg NDF, 0.7% condensed tannins, and were able to bind (73 g PEG/kg DM). PEG binding to plant level in vitro was developed as a measure for tannins and their biological effects (Silanikove et al., 1996c).

The goats were adapted for 3 weeks to consume CL as described before (Silanikove et al., 1994). Digestibility was determined as described by Silanikove et al. (1994). Rumen volume and mean retention time of particulate matter and fluid in the rumen, foregut and the intestine was determined as described by Silanikove et al. (1993).

3. Results

The goats fed CL alone lost ~600 g of BW (significantly different from 0, \( P < 0.05 \)) during the 3 weeks of measurement (~30 g per day), whereas those that received supplemental PEG gained 300 g of BW (NS). PEG supplementation increased dramatically (\( P < 0.001 \)) feed intake (from ~800 to ~1200 g per day of DM), and the digestibility of organic matter (from ~450 to 600 g/kg), protein (from ~100 to ~400 g/kg), and NDF (from ~350 to ~550 g/kg).

Rumen volume increased by 33% (\( P < 0.05 \)) from 3.85 (110 g/kg BW) to 5.111 (145 g/kg BW). The DM content in the rumen increased by 31% (\( P < 0.05 \)) from 1.16 (33 g/kg BW) to 1.52 kg (43.5 g/kg BW) (Table 1). This increase in the content of digesta in the rumen was easily visible because in the control animals the height of the digesta was below the cannula position, whereas in the PEG treatment it was well above the cannula position.

The ruminal MRT of the liquid (~23 h) and particulate phase (~32.5 h) was similar in both treatments.

### Table 1

<p>| Rumen volume and dry matter content <em>a</em> in goats fed carob leaves with, or without PEG supplementation |
|----------------------------------|-------------------|-------------------|-----------|</p>
<table>
<thead>
<tr>
<th></th>
<th>Without PEG</th>
<th>With PEG</th>
<th>S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rumen volume Absolute (l)</td>
<td>3.85 <em>b</em></td>
<td>5.11 <em>b</em></td>
<td>0.123</td>
</tr>
<tr>
<td>Rumen volume Fraction of BW (g/kg)</td>
<td>110.1 <em>b</em></td>
<td>145.1 <em>b</em></td>
<td>4.42</td>
</tr>
<tr>
<td>Rumen volume Fraction of intake (g/kg)</td>
<td>4.78</td>
<td>4.25</td>
<td>0.331</td>
</tr>
<tr>
<td>Rumen DM content Absolute (kg)</td>
<td>1.16 <em>b</em></td>
<td>1.52 <em>b</em></td>
<td>0.085</td>
</tr>
<tr>
<td>Rumen DM content Fraction of BW (g/kg)</td>
<td>33.0 <em>b</em></td>
<td>43.5 <em>b</em></td>
<td>1.22</td>
</tr>
<tr>
<td>Rumen DM content Fraction of intake (g/kg)</td>
<td>1.44</td>
<td>1.26</td>
<td>0.217</td>
</tr>
</tbody>
</table>

*a* The DM content of the rumen was calculated by multiplying rumen volume by the fraction of DM content (300 g/kg ± 50 (S.D.) in the rumen samples. This seems to be justified based on the following evidence: (i) the rumen content appears homogenous without any sign of the typical stratification seen when goats are fed high-fibre foods; (ii) the DM percentage of the rumen samples was similar in both treatments; and (iii) the increase or decrease in BW (~1.6 kg) 24 h after adding, or omitting, the PEG supplementation, was consistent with the total changes in rumen content. 

*b* The values are significant at \( P < 0.01 \).
(Table 2). The omasal + abomasal MRT of the particulate phase (~11.7 h) was similar in both treatments. However, PEG treatment increased ($P < 0.01$) the omasal + abomasal MRT of the liquid phase from 2.7 to 9.2 h. Consequently, the MRT of the particulate phase in the foregut was similar (~44 h) in both treatments, whereas the MRT of the liquid phase was longer (30.9 versus 27.6 h; $P < 0.05$) in the PEG treatment (Table 2). PEG treatment reduced ($P < 0.01$) the intestinal MRT of either the particulate (from 16.9 to 10.4 h) or liquid (from 19.4 to 6.1 h) phases. PEG treatment reduced significantly ($P < 0.05$) the whole GI tract MRT of either the particulate (from 61.7 to 53.1 h) or liquid (from 47.2 to 35.1 h) phases (Table 2).

### 4. Discussion

PEG binding to plant samples is a measure of the total amount of tannins in the sample, and their ability to negatively affect the in situ degradation in the rumen (Silanikove et al., 1996c, 2000). The amount of PEG bound to the leaves used in the present experiment reflects a capacity of the condensed tannins in these leaves to reduce the organic matter in situ degradation in the rumen by 141 g/kg (from 645 to 502 g/kg; Silanikove et al., 1996c). This suggest that tannins in carob leaves have the potential to affect substantially the digestibility of the organic and protein matter in these leaves, which is consistent with the in vivo results.

The reduction in ammonia and volatile fatty acids (VFA) concentration upon ingesting tannin-rich diets (Silanikove et al., 1994, 1996a, 1997a) is expected to suppress voluntary intake (Provenza et al., 2000; Villalba and Provenza, 1996, 1997). However, tannins also produce aversive postingestive effects that cannot be accounted for by digestion inhibition. This is primarily because they cause such rapid (i.e. few to 60 min) and dramatic decreases in food preference, eating activity (i.e. shortening meals, particularly the first meal), and total intake (Landau et al., 2000; Provenza et al., 1994; Silanikove et al., 1997b). These effects are best accounted for by astringency due to tannin binding to salivary proteins, or oral mucous, and due to lesions of gut mucosa and toxicity (Landau et al., 2000; Kumar and Singh, 1984; Provenza et al., 2000; Reed, 1995), which are likely to stimulate the emetic mechanisms in the central nervous system (Provenza, 1995). Recently, Dawson et al. (1999) provided direct evidence for incidence of ulceration and an increase in mucosal histiocytes along the GIT, particularly in the jejunum and ileum in CD-fed sheep. On the other hand, the possibility that the CD in carob leaves may cause systemic toxicity was annulled by the results of Silanikove et al. (1996b), leaving us with astringency and lesions of rumen or intestinal mucosa as the most probable explanation for the reduced intake. It is logical to assume that the distressing signals caused by such lesions are proportional to the area of the epithelium that is exposed to contact with the digesta. The presence of PEG in the digestive tract will attenuate these distressing responses due to its capacity to bind tannins. Consequently, the increase in the mass of rumen content in the PEG-treated goats may reflect the increased contact area that is required to produce distressing signal to stop voluntary food consumption. Tannin effects on voluntary intake are proportional to the concentration of tannins in food (Provenza et al., 2000; Robbins et al., 1987; Silanikove et al., 1994, Table 2).
fibrous matter because in the latter case it passes a much shorter than the MRT of less digestible organic matter is expected to be much shorter than in the control animals. The ratio, between rumen volume or mass and food intake was the same in the PEG treated and in the control goats (Table 1).

PEG supplementation increased two folds the digestible organic matter intake of the PEG goats (by 354 g/kg) in comparison with the control animals, in agreement with the results of Silanikove et al. (1996a). As suggested by Silanikove et al. (1996a, 1997a) part of the improved digestibility could be related to increased rumen fermentation and part to increased proportion and extends of feed digested in the intestine. The increase in digestibility of the digesta in the rumen and the intestine may be explained by release of tannin-bound proteins by the PEG treatment in the rumen (Aharoni et al., 1998), and by binding tannins by PEG in the intestine (Silanikove et al., 1994).

The short MRT of the liquid phase in the control group in the omasal + abomasal pools suggest that tannins induced copious secretion of abomasal juice. Such copious secretion may represent an effort to dilute and wash out the tannins from the abomasum, suggesting that the epithelium in this region is particularly sensitive to the effects of tannins. As tannins are widespread in the foods of humans, monogastric animals and ruminants, this novel observation deserves further research with a more direct approach.

Despite the larger outflow of particulate matter from the rumen in the PEG group, its MRT in the intestine was much shorter than in the control animals. The MRT of highly digestible organic matter is expected to be much shorter than the MRT of less digestible fibrous matter because in the latter case it passes a second cycle of rumen-like fermentation in the caecum. In the present analysis, the MRT in the caecum was part of the MRT in the intestine.

The protein–tannin complexes formed in the rumen may dissociate in the acidic environment of the abomasum (Jones and Mangan, 1977). We have presented evidence suggesting that the formation of tannin-endogenous enzyme complexes in the intestine inhibits digestion of microbial and dietary protein (Silanikove et al., 1994, 1996a). The reduction in pancreatic enzyme activity in the intestine may modify the secretion of GIT hormones, particularly cholecystokinin (Ahmed et al., 1991), which in turn may modify the digesta passage rate in the GIT (Grovum, 1981). The formation of ulceration and an increase in mucosal histiocytes in the jejunum and ileum in CD-fed animals (Dawson et al., 1999) may also affect the passage rate of digesta in the intestine.

**References**


