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Do goats have a salivary constitutive response to tannins?

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ABSTRACT

The effect of tannin-rich fodder (TRF) consumption on the saliva response of Criollo goats without previous browsing experience was determined. Eighteen kids were allocated into three treatments (n = 6 each): control group (CG), short-term tannin stimulus (TS) and long-term tannin stimulus (TL). Three experimental periods were used: adaptation (two weeks) in which the three treatment groups were fed *Pennisetum purpureum* grass and supplemented with a balanced feed. In period 1 (five weeks), TS and TL treatments were fed TRF (*Lysiloma latisiliquum*) with 55.5 g/kg DM condensed tannins (CT), grass and balanced feed. In period 2 (three weeks), *L. latisiliquum* fodder was withdrawn from the TS group. Thus, both the TS and the CG kids were only offered grass and balanced feed, while TL kids continued to receive TRF. In each period, saliva samples were collected to measure the tannin–protein interaction, salivary protein and protein turbidity index (PTI). The salivary protein was similar in all treatments and periods ($P > .10$). The goats' saliva reacted similarly when mixed with either tannic acid or *L. latisiliquum* water-acetone extract. Although the PTI tended to increase in the TL group compared to CG and TS with time, such difference was not significant. Thus, TRF intake failed to further increase the salivary response or PTI. Therefore, the saliva of goats from Yucatan, without previous browsing experience do have a constitutive response as it can block tannins irrespective of TRF stimulus.

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Goats; tannins; salivary protein; saliva turbidity

Introduction

In México, rangelands have been used for goat production due to the availability of plants which, depending on the predominant vegetation, can have low-to-moderate crude protein (CP) such as in the Baja California Peninsul (Ramirez-Orduña et al. 2008) or with high protein content such as in the North of Mexico, (Ramírez et al. 1991) or the Yucatan Peninsula (Torres-Acosta et al. 2008). Thus, in the south east of Mexico, the predominant areas used for range goats are deciduous tropical forest the vegetation and nutritive value of which has been briefly described by Gonzalez-Pech et al. (2014) Ortega-Reyes (1985) and Rios and Riley (1985). Most plants in those rangelands contain secondary compounds such as condensed tannins (CT). The ingestion of these compounds can have both positive effects such as better utilization of dietary protein, faster growth rates of liveweight or wool, higher milk yields, increased fertility, and improved animal welfare and health through prevention of bloat and lower worm burdens, and negative effects such as lower feed intake, protein and dry matter digestibilities, liveweight gains, milk yield and wool growth (Mueller-Harvey 2006). To cope with this kind of compounds, ruminants have developed different behavioral and physiological mechanisms (Estell 2010) amongst which are the tannin-binding salivary proteins (TBSP). Shimada (2006) classified the TBSP into two groups: those that contain proline-rich proteins (PRP) or those which contain histatins. The TBSP proteins have been identified in non-ruminants such as the wood mouse (Shimada 2006), rhinoceros (Clauss et al. 2005) and humans (Bennick 2002). In ruminants, proline-rich TBSP have been identified in deer but not in cattle and sheep saliva proteins (Austin et al. 1989). In goats, only a few studies have investigated the TBSP. Lamy et al. (2008) found major differences in saliva protein within the range of 25–35 kDa and hypothesized their relation with differences on feeding behaviour comparatively to sheep. No PRPs were found either in sheep or in goats maintained on a regular tannin-free diet (Lamy et al. 2009). Also, Hanovice-Ziony et al. (2010) did not find this type of salivary proteins in Mediterranean goats. However, further studies (Lamy et al. 2011) observed changes in the saliva composition of both species when these were subjected to a CT-enriched diets. In addition, recent evidence obtained from goats with browsing experience in a tannin-rich vegetation of Yucatan, Mexico, suggested the existence of TBSP or at least the ability of their saliva to block tannins: (a) the use of polyethylene glycol, a tannin blocking agent, failed to increase the goats' consumption of tannin-rich fodders (TRFs) (Hernández-Orduño et al. 2012); (b) the saliva turbidity (TU) was increased in the presence of tannic acid in a dose-dependent manner (Alonso-Díaz et al. 2012). Furthermore, the saliva of those same goats had up to 30% of histidine, an amino acid found in TBSP (histatins). However, it is unknown whether this salivary response is a constitutive response or is a consequence of the stimulus arising from the consumption of a tannin-rich diet. Therefore, the objective was to determine the effect of TRF consumption on the saliva turbidity of Criollo goats without previous browsing experience.

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Material and methods

The study was carried at Facultad de Medicina Veterinaria y Zootecnia in Merida, Yucatan, Mexico, from October to November 2012. The climate of the region is tropical warm sub humid with rainfall in summer (AW_0). The annual precipitation is 940–1100 mm.

Animals

Eighteen weaned Criollo kids, male and females, approximately two months old (13 ± 2 kg live weight (LW)) were used. Animals had no previous experience with tannin-rich forage consumption. Kids were weighed at the beginning of the adaptation period and at weeks 0, 5 and 8. Animal management and handling during the experiment complied with local regulation on animal welfare.

The Faculty sheep and goat farm uses both grass paddocks and an adjacent area of tropical deciduous forest where animals are taken to browse. *Lysiloma latisiliquum* is a tannin-containing foliage which is commonly found and browsed within the vegetation. Thus, this plant was selected as a model to study the response of animals to tannin intake.

Adaptation period

Before the beginning of the experiment, kids were fed a grain-based tannin-free diet. At weaning, kids were allocated to individual metabolic cages. They were kept in those cages for two weeks (adaptation period). At this time, kids were fed 300 g fresh basis (FB) of *Pennisetum purpureum* grass for 3 h, then 400 g FB of a grain-based balanced feed, formulated and mixed on-station, was offered as powder (standard particle size for each feed) (Table 1). Animals had access to water at all times. Then, kids were distributed into three treatment groups (six kids per treatment) according to their initial weights (Table 2).

Period 1

This period lasted five weeks of the trial (week 1–5). At the beginning of this period, three groups of animals ($n = 6$) were formed:

a) CG: Fed 500 g FB of *P. purpureum* grass and a tannin-free balanced feed (430 g FB) (the same diet as the adaptation period).
b) Long-term tannin stimulus (TL): Fed grass (300 g FB), tannin-free balanced feed (430 g FB) and *L. latisiliquum* forage (330 g FB) containing tannins. This group was to be kept with *L. latisiliquum* forage for the whole experiment (8 weeks).
c) Short-term tannin stimulus (TS): Fed grass (300 g FB), tannin-free balanced feed (430g FB) and *L. latisiliquum* forage (330 g FB). This group was to be kept with *L. latisiliquum* forage only for five weeks (period 1).

Table 1. Chemical composition (means ± s.dev.) of feeds used in the experiment (g/kg DM except where stated).

	P. purpureum	*L. latisiliquum*	Balanced feed[a]
g DM/ kg FB	300.3	466.1	893.2
CP	49.6 ± 2	154.2 ± 14	164 ± 6
NDF	753.2 ± 19	527.3 ± 33	391.3 ± 17
ADF	490.2 ± 10	387.6 ± 22	199.8 ± 15
Lignin	90.8 ± 5	230.6 ± 12	n.a.
Ash	52.6 ± 5	53.93 ± 4	74.5 ± 3
CTs	0	55.5 ± 4	0

Notes: CP: crude protein, NDF: neutral detergent fibre, ADF: acid detergent fibre, n. a. not analysed.
CTs measured as per Vanillin method of Price et al., (1978).
[a]Feed formula based on maize grain, wheat bran, soybean meal and mineral premix.

Period 2

This period of the trial lasted three weeks (weeks 6–8). At the beginning of period 2, the amount of food offered to the animals was increased to ensure that diets allowed a small LW gain. The treatment groups, CG and TS, were fed only 500 g FB of grass and 500 g FB of tannin-free balanced feed. Meanwhile, TL treatment kids received 300 g FB of grass, 500 g FB tannin-free balanced feed and 500 g FB of *L. latisiliquum* forage.

Feeding schedule

The concentrate feed and grass were offered to ensure that all animals would meet their metabolizable energy and protein requirements to obtain at least 100 g/d LW gain. The increment in the amount of feed during period 2 was the direct result of animal growth and to keep the same growth rate as in Period 1. Early in the morning (approximately at 08:00 h), the balanced feed ration was offered. Animals consumed all the feed within the first hour. Approximately at 12:00 h, the TS and TL groups received the *L. latisiliqum* forage, while the CG received half of the *P. purpureum* grass ration. After 4 h, any *L. latisiliquum* leftover was collected from the individual feed trough. The remaining portion of grass was offered to all three groups. Grass leftovers were collected the next day before balanced feed was offered.

Period 2. The feeding management was maintained without change for groups TL and CG. Meanwhile, the TS group started to be managed in the same manner as the CG.

Grass and fodder material

The grass and the *L. latisiliquum* foliage were harvested daily. Grass was chopped before being offered to the animals. The foliage was manually harvested from tree branches. Feed intake was measured daily as the differences between the amount offered and amount left in the respective feeders. Feed samples (200 g FB of each feed) were taken weekly for chemical analysis.

Saliva collection

Individual saliva samples (approximately 40 ml) were collected at the end of the adaptation period (week 0), and on weeks 5 and 8. The samples from week 0 were taken as baseline for the saliva characterization. Samples from week 5 were taken to assess a possible change in saliva turbidity (TU) due to the stimulus caused by the ingestion of a foliage containing tannins. The samples from week 8 were taken to measure changes in saliva TU when withdrawing the tannin stimulus

Table 2. Dry matter intake of Criollo goats in the experimental period (g DM/day).

	Period 1 (week 5)				Period 2 (week 8)			
Intake	CG	TS	TL	SE	CG	TS	TL	SE
LW (Kg)	15.5	17.1	17.9	–	17.7	18.9	20.2	–
Total (g DM/d)	475[b]	558[a]	562[a]	11.1	562[a]	532[a]	716[b]	21.6
Total (g DM /Kg LW $^{0.75}$)	61.0[a]	66.7[b]	65.1[ab]	1.1	65.3[a]	58.7[c]	75.8[b]	2.3
L. latisilliquum (g DM/d)	–	140.6[a]	137.8[a]	4.1	–	–	226.5	–
L. latisiliquum (g DM/Kg LW$^{0.75}$)	–	8.3[a]	7.3[a]	0.5	–	–	11.4	–

Notes: CG = control treatment, TS = treatment short-term tannin stimulus, TL = treatment with long-term tannin stimulus, SE = standard error.
Different letters in row are significantly different $p < .05$.

(treatment TS) or when maintaining the tannin stimulus (treatment TL). The CG treatment was the control for normal physiological changes of saliva in all the periods.

Saliva samples were collected with a plastic pipe (1/4 inches Ø) directly from the kids' mouths. The hose was connected to a low vacuum pump (MSL1J, WEG, Mexico) and a 500 ml Erlenmeyer plastic flask trap to collect saliva while preventing its flux to the vacuum pump. Saliva collected was transferred into sterile polypropylene tubes (50 ml). Saliva tubes were kept inside a cool box with ice during collection and transportation to the lab. As the saliva collection time for each animal was 20 min approximately, and to reduce perturbation of feeding time schedule, only six kids were sampled on each day (two from each treatment). Thus, three consecutive days were employed to sample all six animal per treatment. All saliva samples were collected in the morning before feeding the kids to reduce sample contamination and kept in an insulated box with ice. The samples of saliva were divided in two portions, one for a turbidity test (TU) and the other to measure its CP content.

Laboratory analysis

Feed samples: The weekly samples of *P. purpureum, L. latysiliquum* and balanced feed were oven dried 60 °C for 48 h (DM), milled (1 mm screen) and analysed for CP, Ash (A), Lignin (L) (AOAC 1980). Analysis of neutral detergent fibre (NDF), acid detergent fibre (ADF) was elaborated with ANKOM^{200} method 10–21–05. Additionally, total tannins (TT), total phenols (PT) (Folin-Ciocalteu method, Makkar 2003) and CT were estimated (Vanillin method, Price et al. 1978).

Saliva samples: the CP of saliva was measured (Lowry et al. 1951) using bovine serum albumin (22%, Sigma Co.) as standard.

A turbidity test was used to determine the interaction of tannins–protein (Horne et al. 2002). Immediately after the collection of saliva, the samples were centrifuged at 2200 g ×10 min to remove any feed contamination in saliva. Then, 4 ml of saliva was mixed in a vortex, with 4 ml of water solution containing tannic acid (Sigma Co.) or *L. latisiliquum* tannin-rich extract (Alonso-Diaz et al. 2008a) both at 1% w/v. Immediately after mixing, haze development was measured at 0 and 90 min with UV/VIS spectrophotometer (Lambda 25, Perkin Elmer, Beaconsfield, UK) at 610 nm of transmittance.

The 0 min value was taken as baseline to assess any change of saliva transmittance (Δ%) after 90 min of saliva being mixed with tannic acid or *L. latisiliquum* extract. A positive value represents an increase in turbidity and a negative value is a decrease in turbidity. Also, a portion of the saliva was left without adding any type of tannins and this was used as a reference value to quantify the change of turbidity (Δ%).

A PTI was used to measure the changes in saliva turbidity adjusted by the amount of CP in the saliva. The PTI was obtained as follows:

PTI = (Δ% haze development)/(salivary protein (mg)).

Statistical analysis

Results were analysed as a completely randomized design. DM Intake in periods 1 and 2 and saliva CP content in weeks 0, 5 and 8 were analysed with one-way ANOVA. Turbidity test results (Δ %) and PTI on weeks 0, 5 and 8 were analysed with repeated-measures ANOVA (SAS 2002) with the following model (Kaps and Lamberson 2004):

$$y_{ijk} = \mu + \tau_i + \delta_{ij} + t_k + (\tau * t)_{ik} + \varepsilon_{ijk},$$

where:

y_{ijk} is the response of the kid j with treatment i in the period k, μ is the global mean, τ_i is effect of treatment i, δ_{ij} random error of kid j with treatment i, t_k effect in period k, $(\tau * t)_{ik}$ interaction effect of treatment i with period k, ε_{ijk} random error of kid j with treatment i in period k.

Results

Chemical composition of the feeds

Chemical composition of the feeds is presented in Table 1. The foliage of *L. latisiliquum* contained 55 g CT/kg DM. Meanwhile, the balanced feed and the grass were confirmed without CT. Grass was low in CP (6.6 g/kg DM) and high in NDF (753 g/kg DM); the *L. latisiliquum* forage had a CP content close to the amount of the balanced feed (154 vs. 164 g CP/kg DM, respectively).

Feed intake

During Period 1, animals in treatments TL and TS had similar DM feed intake and both were higher than that of animals in the CG ($P < .0001$). During period 2, the animals fed *L. latisiliquum* (TL) had a higher intake than animals in CG and TS (75.8 vs. 65.3 vs. 58.7 g DM/Kg LW$^{0.75}$, respectively) ($P < .0001$) (Table 2).

Saliva protein content

The amount of CP in the saliva of Criollo goats was the same in all treatments at the three sample points measured (weeks 0, 5 and 8). No change in saliva protein content was observed as a

Table 3. Saliva CP content (µg CP/ml saliva) in Criollo goats during experimental periods.

Week	CG (SE)	TL (SE)	TS(S.E)	SE
0	58.1 (±8)	71.9 (±9)	84.2 (±10)	5.6
5	52.5 (±4)	51.9 (±6)	52.2 (5)	2.7
8	67.7 (±14)	43.2 (±8)	73.1 (±7)	6.1

Note: CG = control treatment, TL = treatment with long-term tannin stimulus, TS = treatment short-term tannin stimulus, SE = standard error.

response to the intake of a foliage containing tannins (*L. latisiliquum*) during a short (TS) or long (TL) terms (Table 3).

Saliva turbidity (TU)

The TU results in all treatments were similar when using tannic acid or *L. latisiliquum* extract to induce the haze development ($P > .05$) (Table 4). The saliva used as reference (saliva without added tannins) did not develop turbidity. When the change in turbidity was compared in the saliva exposed to two tannin sources (tannic acid or *L. latisiliquum* extract), the response was clearer with tannic acid because all values were positives (increased turbidity). Meanwhile, when the saliva was placed in contact with the *L. latisiliquum* extract, some negative values were evident (Table 5). However, when the saliva without added tannins was used as reference value, all the differences in turbidity were positive when exposed to *L. latisiliquum* extract in period 1 (CG: 1.20, TL: 0.19 and TS: 1.36) and period 2 (CG: 2.67, TL: 1.24 and TS: 3.26).

Protein turbidity index

When Criollo goats consumed *L. latisiliquum* foliage for eight weeks, the PTI was higher in TL than in TS (when exposed to tannic acid). No differences with CG were observed in different periods.

Discussion

Intake

During the whole experiment, the average total DM intake for all treatments (range 58–76 g DM/kg $LW^{0.75}$) was between the expected values for goats (AFRC 1998). Although *L. latysiliquum* contained tannins, no apparent negative effect due to its intake of was observed, as animals in TL had higher total DM intakes ($P < .05$) during the time this foliage was offered (Table 2). During the first five weeks, TS and TL had similar foliage intake (7.3 and 8.3 g DM/Kg $LW^{0.75}$, respectively). The foliage intake was lower than that in a previous report from Alonso-Diaz et al. (2008b) who reported a *L. latisiliquum* intake of 10.3 g DM/Kg $LW^{0.75}$ in adult goats. However, at week 8, animals in the TL had an intake of 11.4 g DM/Kg $LW^{0.75}$, which is slightly higher than the previous report. It is possible that the animal experience with this foliage has a role in achieving its potential foliage DM intake (Provenza et al. 2003). Thus, it is noteworthy that Criollo kids were able to reach almost their potential foliage intake from an early age. Also, these animals showed a total DM intake, which is similar to that of animals not ingesting foliage containing tannins.

Table 4. Change of turbidity (Δ%) in saliva of Criollo goats during experimental periods.

		Tannic acid		
Week	CG	TL	TS	SE
0	3.52	2.33	3.57	0.45
5	5.16	4.20	4.36	0.28
8	2.78	2.93	2.77	0.43
	L. latisiliquum extract			
Week	CG	TL	TS	SE
0	0.46	0.49	−1.08	0.74
5	−0.19	−1.24	−1.45	0.55
8	0.21	0.01	0.04	0.25

Notes: CG = control treatment, TL = treatment with long-term tannin stimulus, TS = treatment short-term tannin stimulus, SE = standard error.
Effects treatment $P = .2382$, time $P = .0225$, treatment*time $P = .8411$ with tannic acid.
Effects treatment $P = .0995$, time $P = .0019$, treatment*time $P = .7783$ with *L. latisiliquum* extract.

Table 5. PTI in saliva of Criollo goats during experimental periods.

		Tannic acid		
Week	CG	TL	TS	SE
0	1047.9[a]	607.1[a]	782.6[a]	142.2
5	1721.0[a]	1460.6[a]	1582.4[a]	131.4
8	1106.5[ab]	1299.3[a]	636.6[b]	153.5
		L. latisiliquum extract		
Week	CG	TL	TS	SE
0	136.8[a]	77.0[a]	−162.9[a]	151.1
5	−102.2[a]	−448.1[a]	−530.5[a]	126.3
8	139.4[a]	167.4[a]	−160.0[a]	78.0

Notes: Different letters in row are significantly different $p < .05$.
CG = control treatment, TL = treatment with long-term tannin stimulus, TS = treatment short-term tannin stimulus, SE = standard error.
Effects treatment $P = .2952$, time $P = .0012$, treatment*time $P = .3526$ with tannic acid.
Effects treatment $P = .2048$, time $P = .03$, treatment*time $P = .9020$ with *L. latisiliquum* extract.

Saliva protein content

The CP content of saliva was similar during the whole experiment (weeks 0, 5 and 8) ranging from 43.2 to 84.2 µg CP/ml whole saliva. Those results were lower than previous reports from Hanovice-Ziony et al. (2010) and Lamy et al. (2009) who reported 173–316 µg CP/ml whole saliva (Damascus goats) and 100–200 µg CP/ml parotid saliva (Serpentina goats), respectively. The difference in the CP content of the saliva between our experimental animals and previous literature reports could be explained by: (i) differences in the body weight and age as the kids from the present experiment were lighter and younger than the Damascus and Serpentina goats from the literature reports (13 vs. 41 and 33.5 kg LW, respectively). Thus, differences in the LW and age might have an influence in saliva CP content. (ii) The experimental kids used in the present study had no previous browsing experience and those used in the other trials had several months of browsing experience and this might increase the saliva protein production. (iii) Differences related to methodological issues are also possible (collection, processing, chemical analysis, etc.) as well as source (whole vs. glandular saliva). Further studies are needed to fully address this difference in salivary protein. For example, Hanovice-Ziony et al. (2010) failed to find differences in CP content in the saliva of goats of different ages.

Saliva turbidity and PTI

The turbidity in the saliva from the kids in all treatments (CG, TS and TL) when put in contact with tannins was similar. There was no differential response attributable to the tannin stimulus (intake of *L. latisiliquum*). A clearer response was observed with the PTI, possibly due to the adjustment with the saliva protein content. It has been shown previously that salivary protein from this type of goats might have a differential response to different CT extracts (Alonso-Diaz et al. 2012). Comparing the turbidity found with saliva alone and that of the saliva in contact with *L. latisiliquum* extract could indicate that turbidity developed immediately after saliva was put in contact with the extract. Therefore, when the reading was taken at time 0, the turbidity had already developed and it was maintained or slowly disappeared during the 90-min period. As a result, the turbidity value obtained appeared to be negative. On the contrary, the saliva put in contact with tannic acid developed haze during the 90-min period.

Although the amount of *L. latisiquum* offered to the TL group increased from 300 g FB to 500 g FB per day from period 1 to period 2, resulting in a higher intake (from 7.3 to 11.4 g DM/kg $LW^{0.75}$), the TL group failed to show a higher saliva turbidity response compared to the results observed in week 5 in the same group. Therefore, it can be suggested that no further stimulus from either time (three additional weeks of *L. latisiliquum* consumption) or an increased amount of tannins consumed (from 7.6 to 12.5 g CT/d/animal) was observed. Thus, the results of the present experiment suggest that Criollo kids express a constitutive response in their saliva which is prepared to block tannins rather than a lack of response. The stimulus of TRF ingestion did not cause further increase in the response as has been observed in previous reports in browser animals such as rhinoceros (Clauss et al. 2005) and hair sheep (Vargas-Magaña et al. 2013). Those authors reported that both rhinoceros and hair sheep showed an induced response in their saliva after they were orally stimulated with tannin-rich materials. The rhinoceros were eating quebracho and tannic acid for six months and the hair sheep were fed *L. latisiliquum* fodder for three months. It has been previously suspected that goats might have TBSP in their saliva (Provenza and Malechek 1984; Vaithiyanathan et al. 2001), and the present results support earlier evidence of the TBSP presence in adult Criollo goats from the same region (Alonso-Díaz et al. 2012). Goats from tropical regions, such as South Mexico, have been in contact with tannin-rich materials for several generations. It is possible that they have maintained their constitutive expression of TBSP as a mechanism to survive in this environment. Given that in some areas, such as the Mediterranean, no major role has been given to TBSP to cope with dietary tannins (Hanovice et al. 2010), further studies are needed to confirm these results.

Conclusion

This work provides evidence indicating that the saliva of Criollo goats blocks tannins (tannic acid or a tannin-rich extract from *L. latisiliquum*) and this is a constitutive response. This feature seems to be an adaptation that may allow tropical goats to successfully harvest macronutrients from plants which contain tannins. This type of response helps to understand why goats are able to thrive in tropical rangelands where tannin-rich browse plants are a common source of nutrients.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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