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Effects of supplemental dietary tannic acid on digestion in plateau zokors (*Eospalax baileyi*)

Gong-Hua Lin[1], Jiu-Xiang Xie[1,2], Xue-Feng Cui[1,2], Eviatar Nevo[3], Jian-Ping Su[1] & Tong-Zuo Zhang[1,*]

[1)] *Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008, China (*corresponding author's e-mail: nwipb@hotmail.com)*
[2)] *Graduate University of the Chinese Academy of Sciences, Beijing 100049, China*
[3)] *Institute of Evolution, University of Haifa, Mount Carmel, Haifa 31905, Israel*

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We examined the effects of tannins on food digestion in the plateau zokor (*Eospalax baileyi*), a rodent that lives primarily underground. Our results indicate that (1) all experimental groups maintained their body weight; (2) food intake and food assimilation increased, while food digestibility decreased with an increasing tannin concentration in the diet; (3) protein digestibility, but not protein assimilation, decreased significantly with an increasing tannin concentration in the diet; (4) mean dry weights of the small intestine of the zokors fed with feed containing 3% and 6% tannic acid were 67% and 87%, respectively, greater than that of the control. Therefore, tannins in the diet affected negatively food and protein digestibility in zokors. The animals counteracted these effects and maintained their body weight and nutrient assimilation by increasing food intake as well as widening the lumen of their small intestine.

Introduction

In order to improve their survival and reproduction, plants have evolved many mechanical (thorns, spines, and trichomes) and chemical (various plant secondary metabolites, PSMs) weapons against herbivores (Carmona *et al*. 2011, Weinhold *et al*. 2011). In contrast, herbivores have also evolved various offensive traits to increase their evolutionary fitness (Karban & Agrawal 2002).

Tannins, which are widely distributed in various parts of plants, and are one of the most commonly used deterrent PSMs (Foley *et al*. 1999). Tannins may cause various adverse effects in mammalian herbivores after ingestion, such as reduction in digestibility, damage to the gastrointestinal mucosa and epithelium, and kidney or liver failure (Shimada 2006). However, different animals with different foraging strategies may have different responses to tannins (Bernays *et al*. 1989, Robbins *et al*. 1991). Among rodents, for example, acorns with high tannin concentrations had strong negative effects on the wood mouse *Apodemus speciosus*, causing obvious reduction in body weight and survival rate (Shimada & Saitoh 2003); while in *Octodon degas*, the analogous effects were rather moderate (Bozinovic *et al*. 1997).

Subterranean rodents are a widely distributed group of species highly adapted to a stressful subterranean environment (solid soil, darkness, low productivity, hypercapnia, hypoxia, and high infectivity) (Nevo 1999, Lacey *et al*. 2000, Nevo 2007). Digging for food and shelter is an energetically demanding process that can result in energy expenditure more than 300 times higher than that required to move the same distance across the soil surface (Vleck 1979). The high energy cost of digging underground, on the one hand, restricts movements of subterranean rodents in search for food resources and, on the other hand, makes these animals have larger energy demands. Hence, subterranean rodents tend to be generalists, foraging on diverse plant species (Heth *et al*. 1989). As a result, they must deal with PSMs in their habitats. Hence, the subterranean rodent species could become good candidates for the study of how vertebrates respond to various PSMs.

Because live trapping and lab keeping of subterranean rodents are not easy, studies of how these species deal with PSMs are rare (but *see* Zhang *et al*. 2000). The plateau zokor (*Eospalax baileyi*) is a typical subterranean rodent species, which uses various vegetation types in the meadows. The *Potentilla* spp. (Rosaceae), which has high concentrations of both condensed tannins and hydrolysable tannins (Li *et al*. 2008), form the main part of this animal's diet (Wang *et al*. 2000). In this study, we analyze the effects of dietary tannins on the nutritional ecology of the plateau zokor. We aim to test whether there are negative effects of tannins on plateau zokors, and also how the animals mitigate to these effects.

Material and methods

Animals

Zokors were captured during the spring 2011 in Datong County (37°7´29´´N, 101°48´41´´E, 2950 m a.s.l.), Qinghai, China, using live traps. The animals were maintained individually in plastic cages (35 × 25 × 20 cm) in a constant environment (at 25 ± 1 °C, day length 14 hrs). The plastic cages were made from polypropylene boxes, by replacing the base with iron mesh to maintain the food pellets while allowing the feces to drop down to the plastic trays beneath the boxes.

Diets and feeding protocol

After capture, we initially fed the animals with *Brassica oleracea* (Brassicaceae) and offered water in a drink bottle, to which zokors adapted well, although in nature they obtain water only from food. We then gradually introduced them to artificial feed, which was then the only food offered. We prepared the artificial feed (control diet) as dry pellets made with a pellet machine (Longfa Ltd., Xingyang, China). The pellets consisted (% dry matter): corn meal (35), wheat bran (20), wheat flour (30), soybean powder (5), fish meal (5), alfalfa meal (2.5), yeast powder (0.75), varied trace elements (0.75), varied vitamins (0.5), and NaCl (0.5). In order to avoid overheating while preparing pellets, the feed meal was moistened with 10% of water prior to preparing pellets.

Animals were fed the pellets *ad libitum* for four weeks before the start of the experiment, during which time we determine their baseline intakes by recording the daily amount eaten by each animal.

Two experimental diets were prepared by adding 3% and 6% tannic acid (Hengxing Ltd., Tianjin, China) to the artificial feed. The pellets were prepared as above, but to avoid the possibility for tannin–protein interactions (Chung-MacCoubrey *et al*. 1997), the feed meal was pre-wetted with 10% of water before tannic acid was added.

Three samples of each diet were randomly selected and air-dried on paper plates in an oven at 80 °C for 24 hours (based on our pre-experiment, the time is sufficient enough to dry them to a constant weight). The protein content of the three diets (totally nine samples) was measured with an automatic Kjeldahl apparatus (Xianjian Ltd., Shanghai, China).

Regardless of sex or age, individuals were randomly assigned to three groups: control (n = 6), 3% tannic-acid group (n = 8), and 6% tannic-acid group (n = 8). The initial body weights

(BW) of each zokor were recorded on day 0: the mean values (BW_0 ± SD) for the control, 3%, and 6% tannic-acid groups were 215.73 ± 37.22 g, 245.14 ± 51.35 g, and 232.45 ± 74.29 g, respectively. They were used as covariates in the statistical analysis (*see* below). Body weights of animals were also measured three days after the start of the experiment.

Diets were fed *ad libitum*: in the morning (09:00), 50 g of feed pellets were provided to each zokor, and the next morning, the remaining feed was replaced by another 50 g pellets. Although the gut-passage time was unknown, based on the data for *Microtus townsendii* (Hume *et al*. 1993), *Trichosurus vulpecula* (Williams *et al*. 2000) and *Cervus elaphus* (Clauss *et al*. 2009), we arbitrarily selected days 10, 15, and 20 as time points for data collection. The remaining feed and feces from these days were collected, air-dried on paper plates in an oven at 80 °C for 24 hours, and later separated to determine total feces output and total feed intake. In order to avoid inconsistency regarding water content between provided feed and remaining feed, we also air-dried (80 °C for 24 hours, *see* above) three samples of provided feed to calculate the dry matter intake. The protein content of dried feces of each individual was measured with an automatic Kjeldahl apparatus.

After the trial, the zokors were killed by cervical dislocation and the lengths of small intestines and large intestines were measured. The heart, liver, lungs, kidney, stomach, small intestines, large intestines, and caecum were emptied and washed with normal saline and air-dried on paper plates in an oven at 80 °C to constant weight and later weighed on an electronic analytical balance (Mettler Toledo Inc., accuracy 0.0001 g).

Statistical analyses

Using dry matter of provided feed (PF), remaining feed (RF), and feces output (FO), we calculated the following indices: food intake, FI = PF – RF; food assimilation, FA = FI – FO; food digestibility, FD = FA/FI × 100 (%). Consequently, using protein content of feed (P_1%) and feces (P_2%), we calculated the following indices: protein assimilation, $PA = FI \times P_1\% - FO \times P_2\%$; protein digestibility, $PD = PA/(FI \times P_1\%)$.

In order to improve the statistical reliability and also to exclude the effects of body weight, we used repeated-measures ANOVA to test the for the effect of tannins (tannic acid) on BW, FI, FA, FD, PA, and PD, with BW_0 as a covariate. At the same time, we performed pairwise comparisons of each variable between groups. We also used General Linear Model (univariate analysis) to test for the effect of tannins on the length of small intestine and large intestine as well as the weights of the nine visceral organs (heart, liver, lung, kidney, stomach, small intestines, large intestines and caecum), with BW_0 as a covariate. Significance of the differences in small intestine mean dry weights were tested with an independent-samples *t*-test. SPSS ver. 19.0 was used for calculations.

Results

We found no significant body weight differences among the groups (repeated-measures ANOVA indicated that; *see* Table 1).

The FD and FI of the 3% tannic-acid group were significantly lower and nearly significantly higher, respectively, than those of the control; while FA of the 3% tannic-acid group and that of the control did not differ significantly. The 6% tannic-acid group had significantly higher FI and FA but lower FD values than the control. The 6% tannic-acid group had significantly higher FI than the 3% tannic-acid group. However, no significant differences in FA and FD were found between the 3% and 6% tannic-acid groups. There are significant differences between groups in PD (0% > 3% > 6%), but not in PA (Table 1).

The lengths of the small and large intestines, as well as the dry weights of heart, liver, lungs, kidney, stomach, large intestines and caecum of the 3% and 6% tannic-acid groups did not differ significantly from those of the control (Table 2). The dry weights of the small intestine of the 3% and 6% tannic-acid groups were significantly larger than that of the control (independent-samples *t*-test $t_{12} = -3.888$, $p = 0.002$; and $t_{12} = -2.975$, $p = 0.012$; respectively), however, the difference between the 3% and 6% tannic-acid groups was not significant.

Table 1. Effects of tannin treatments on zokors as well repeated measures ANOVA and pairwise comparisons between them. Shown are means ± SDs. MD = mean difference between the groups. Results are considered significant at $p < 0.05$ (set in boldface).

	Tannin treatment			ANOVA (df = 2)		Pairwise comparisons					
	0%	3%	6%	*F*	*p*	3% *vs.* 0%		6% *vs.* 0%		6% *vs.* 3%	
						MD	*p*	MD	*p*	MD	*p*
Body weight (g)											
10 days	217.28 ± 40.80	247.29 ± 58.00	235.47 ± 61.98								
15 days	212.89 ± 40.96	246.40 ± 56.53	238.68 ± 70.56	0.763	0.481	5.739	0.368	7.365	0.244	1.626	0.777
20 days	213.34 ± 48.85	254.43 ± 58.61	241.12 ± 72.26								
Food Intake (g)											
10 days	12.18 ± 3.35	13.93 ± 4.41	15.53 ± 3.15								
15 days	10.31 ± 2.77	12.24 ± 3.28	14.94 ± 3.95	**8.375**	**0.003**	2.140	0.053	**4.152**	**0.001**	**2.012**	**0.046**
20 days	9.06 ± 4.53	15.65 ± 2.54	15.73 ± 2.32								
Food assimilation (g)											
10 days	8.53 ± 2.32	9.46 ± 3.07	10.22 ± 2.03								
15 days	7.36 ± 2.19	8.22 ± 2.47	9.97 ± 2.95	**5.846**	**0.011**	1.128	0.112	**2.260**	**0.003**	1.132	0.082
20 days	6.17 ± 2.97	10.60 ± 1.89	10.26 ± 1.81								
Food digestibility (%)											
10 days	70.05 ± 4.53	67.76 ± 1.44	65.97 ± 3.60								
15 days	70.97 ± 4.85	66.63 ± 5.93	66.45 ± 3.92	**6.467**	**0.008**	**–3.422**	**0.020**	**–4.698**	**0.002**	–1.276	0.311
20 days	69.87 ± 7.36	67.61 ± 1.78	65.17 ± 4.83								
Protein assimilation (g)											
10 days	1.65 ± 0.44	1.70 ± 0.56	1.65 ± 0.32								
15 days	1.45 ± 0.43	1.50 ± 0.49	1.68 ± 0.49	0.676	0.521	0.097	0.473	0.151	0.261	0.054	0.658
20 days	1.20 ± 0.59	1.90 ± 0.35	1.71 ± 0.33								
Protein digestibility (%)											
10 days	75.45 ± 3.14	70.05 ± 1.85	63.16 ± 4.47								
15 days	77.73 ± 3.74	69.20 ± 7.86	66.14 ± 5.74	**19.405**	**< 0.001**	**–6.96**	**0.002**	**–11.86**	**< 0.001**	**–4.90**	**0.012**
20 days	75.07 ± 6.77	69.42 ± 4.43	64.10 ± 6.08								

Discussion

Our results showed that both food and protein digestibility decreased with increasing tannin concentrations. Interestingly, however, the differences were smaller for FD than for PD. It has long been thought that tannins primarily act as protein-digestion inhibitors by binding dietary proteins and digestive enzymes (Bernays *et al*. 1989, Bozinovic *et al*. 1997, Foley *et al*. 1999). The tannin–protein complexes are stable when pH is between 3.5 and 8 (Frutos *et al*. 2004). pH values of the mouse and rat gastrointestinal tract are generally in this range (McConnell *et al*. 2008), thus detrimental effects of tannins (via binding both dietary proteins and enzymes for digestion of protein as well as other nutrient molecules such as sucrose) on nutrient digestibility (especially protein) will be inevitable. Moreover, recent studies revealed that ingested tannins also bind salivary proteins, which are stable across the whole pH range of the gastrointestinal tract, thus may reduce protein digestibility through endogenous nitrogen loss (Skopec *et al*. 2004). Therefore, reduced protein digestibility we found in this study is indicative of the negative effects of ingested tannins.

Our results indicate that with a lower food digestibility, food assimilation of the 6% tannic-acid group was higher than that of the control. At the same time, protein digestibility in the test groups decreased with increasing tannin concentrations, protein assimilation was not significantly different. Moreover, all three groups maintained their body weights. This can be explained by increased intake of feed containing tannins (Table 1). Belovsky and Schmitz (1994) demonstrated by modeling that no type of plant defense (including toxic chemicals) can guarantee reduced consumption of plants by mammalian herbivores. In fact, although reduced intake of tannin-added diets is frequently reported (Glick & Joslyn 1970, Meyer & Richardson 1993, Burchfield *et al*. 2005), compensatory feeding, i.e. increasing intake of such diets, has also been observed (e.g. Bozinovic *et al*. 1997). Whether tannins result in an increase or decrease in food intake will depend on the availability of alternative food resources (Foley *et al*. 1999). For zokors, high energetic investment of finding food items underground by digging tunnels make it hard to turn to alternative food resources. As a result, zokors are inclined to consume higher amounts of tannin-reach food.

Zhang *et al*. (2000) first analyzed the effects of different amounts of terpene (another type of important PSMs) added to food on intake and digestion in plateau zokors. They found that, with increasing terpene concentrations the plateau zokors decreased food intake and defecation, while increasing food digestibility and, as a result, maintained their body weight. PSMs could be roughly grouped into two main categories: toxic chemicals and digestion-reducing chemicals (McArthur *et al*. 1993). Terpenes and tannins (both found in plants) are toxic and

Table 2. Characteristics (mean ± SD) of inner organs and Univariate comparison among groups. Results are considered significant at $p < 0.05$ (set in boldface).

Measure	Organ	Tannin treatment			Univariate analysis
		0%	3%	6%	
Dry weight (g)	heart	0.231 ± 0.062	0.250 ± 0.081	0.234 ± 0.048	$F = 0.061$, $p = 0.941$
	liver	2.786 ± 0.952	3.552 ± 1.180	3.344 ± 1.338	$F = 0.267$, $p = 0.768$
	lung	0.406 ± 0.092	0.420 ± 0.117	0.469 ± 0.130	$F = 0.877$, $p = 0.433$
	kidney	0.446 ± 0.106	0.505 ± 0.118	0.483 ± 0.096	$F = 0.141$, $p = 0.870$
	stomach	0.442 ± 0.273	0.379 ± 0.065	0.377 ± 0.076	$F = 0.992$, $p = 0.390$
	small intestines	**0.566 ± 0.274**	**1.045 ± 0.190**	**1.100 ± 0.369**	**$F = 10.123$, $p = 0.001$**
	large intestines	0.541 ± 0.288	0.568 ± 0.199	0.739 ± 0.314	$F = 2.165$, $p = 0.144$
	caecum	0.569 ± 0.362	0.559 ± 0.119	0.602 ± 0.154	$F = 0.178$, $p = 0.838$
Length (cm)	small intestines	103.58 ± 20.83	114.60 ± 16.37	120.38 ± 17.09	$F = 1.279$, $p = 0.302$
	large intestines	49.78 ± 4.29	55.99 ± 5.87	55.95 ± 8.42	$F = 1.402$, $p = 0.272$

digestion-reducing, respectively (Foley *et al*. 1999). When compering the result obtained by Zhang *et al*. (2000) with ours, it is clear that plateau zokors are able to cope with both terpenes and tannins. However, the responses are somewhat different or even totally reversed: toxic chemicals cause reduced food intake and defecation, while food digestibility increases; while digestion-reducing chemicals, with which food digestibility cannot be increased, cause increased food intake and defecation. Increased intake of tannin-enriched food also indicates that tannins have little toxic effects on zokors.

Several studies analyzed the effects of PSMs on internal organ size, including metabolism-related organs such as liver and kidney (He *et al*. 2010 and references therein), and digestive organs such as stomach and small intestine (Bozinovic *et al*. 1997). Lindroth and Batzli (1984) showed that relative liver sizes of prairie voles (*Microtus ochrogaster*) were not affected by the presence of tannic acid in the diet, but relative kidney sizes of voles fed 6% tannic acid at high and low levels of protein increased by 23% and 30%, respectively, as compared with those of the control. The results of Bozinovic *et al*. (1997) indicated that the *Octodon degus* responded to added tannic acid by increasing weight of the small intestine. Our study included eight main internal organs, covering both the digestive- and metabolism-related organs analyzed in the two above-mentioned studies. Our results show that the only organ which reacted to the added tannic acid was the small intestine. We arbitrarily corrected the dry weight of small intestine by dividing it by the animal body weight. Based on the corrected values (data not shown), we found that the mean dry weight of the small intestines of the 3% and 6% tannic-acid gropus were 67% and 87%, respectively, heavier than that of the control. The length of the small intestine, however, was not significantly changed, indicating the extreme tissue proliferation by probably widening the lumen of the small intestine to accommodate greater amount of food and prolonged digestion time (Bozinovic *et al*. 1997) could be an important physiological adaptation of zokors to tannins.

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