Effect of a Daily Supplementation of Polyethylene Glycol on Intake and Digestion of Tannin-Containing Leaves (*Quercus calliprinos, Pistacia lentiscus,* and *Ceratonia siliqua*) by Goats

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Intake and digestion of leaves of *Quercus calliprinos*, *Pistacia lentiscus*, and *Ceratonia siliqua*, with and without supplementation of various amounts of polyethylene glycol (PEG), were examined. The tannin contents in these species exerted a substantial negative effect on feed intake and digestion. The effects were species specific and related to tannin content. Once-daily Supplementation with PEG efficiently neutralized the negative effects of tannins. The amount of PEG needed to produce a maximal increase in feed intake was lower than the amount required to produce a maximal increase in digestibility. The intake of digestible crude protein and metabolizable energy was raised in PEG-supplemented animals from a submaintenance level to levels considerably exceeding the maintenance requirement of goats. The response was related to the tannin content of the plant.

Keywords: *Goats; tannins; polyethylene glycol; foliage digestibility*

INTRODUCTION

Trees and shrubs are an important fodder source for livestock in tropical and dry environments (Topps, 1992). Recently, there has been a growing interest in the grazing of livestock, especially goats, on woody rangelands in an attempt to reduce the vegetative biomass in areas prone to fire or shrub encroachment (Sverson and Debano, 1991). However, the use of browse sources by herbivores is restricted, in many cases, by defensive or deterrent mechanisms related to high tannin content in woody plants (Provenza, 1995). The inverse relationship between high tannin level in the forage and palatability, voluntary intake, digestibility, and nitrogen (N) retention in mammalian herbivores has been well established (Robbins et al., 1987; Silanikove et al., 1994). Thus, any attempt to improve performance and bush clearing capacity of livestock on woody rangelands must first overcome the problems posed by high contents of tannins in the forage.

The PEG−tannins complex is irreversible over a wide range of pH, and its presence reduces the formation of a protein−tannin complex (Jones and Mangan, 1977). Application of PEG by spraying of tannin-rich green bushes, mixing with harvested leaves, infusion into the rumen, and drenching the animals has been reported to increase feed intake, digestibility, and wool growth in sheep (Kumar and Vaithiyanatan, 1990; Pritchard et al., 1992; Terril et al., 1992). However, these methods are either uneconomical or impracticable. Recently, a new direction that is practical for field application has been proposed; that is, effective administration of PEG to sheep and goats by a once-daily supplemental provision under both stall feeding conditions (Silanikove et al., 1994) and under natural grazing conditions (Silanikove et al., 1992) results in increases in digestible energy intake, weight gain, birth weight of lambs and kids, and milk yield of goats. These results suggest that this method of administering PEG is highly profitable.

Quercus calliprinos (the common oak, or simply oak) is the dominant wild woody species in the eastern Mediterranean ecosystem and is the predominant browse in the diet of goats (Perevolotsky et al., 1993). *Pistacia lentiscus* (pistacia) is the predominant wild tree in open, disturbed Mediterranean areas because of its aggressive regrowth after disturbance and because the leaves of this tree are scarcely grazed by wild herbivores or domesticated livestock, most likely because of their high tannin content (Dafni, 1991). The pods and leaves of the *Ceratonia siliqua* (carob) are an important uncultivated domestic browse in countries bordering the Mediterranean Sea (Zohary, 1966). Previous research indicated that the intake of oak and carob leaves is limited by the presence of condensed tannins (Perevolotsky et al., 1993; Silanikove et al., 1994).

The purposes of the present experiment were (i) to determine the composition of oak, pistacia, and carob and their nutritional value for goats; (ii) to examine whether PEG, given to goats once daily, is effective in neutralizing negative effects of tannin; and (iii) to determine the amount of PEG required for maximal voluntary feed intake and digestion.

MATERIALS AND METHODS

Animals. The experiments were carried out with four non-lactating and non-pregnant Mamber goats (a breed indigenous to the Mediterranean woodland) weighing 35 kg (SD, ±5 kg). The animals were stall-fed individually in a yard protected from rain and wind and equipped with troughs that facilitated quantitative measurement of feed intake.

Feeds. Oak, pistacia, and carob leaves attached to small edible branches (2−3 mm wide) were harvested once weekly early in the morning and stored at −20 °C. The daily allocation was removed from the freezer, thawed, and fed once daily *ad libitum* at 8 a.m. Water was always available. The PEG

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Table 1. Experimental Design

expt	basal food	treatment order: PEG, g/day							
1	carob	0	10	20	0	5	40	0	5
2	oak	0	5	10	20	10	0	30	–
3	pistacia	40	30	20	10	0	–	–	–
4	wheat straw	0	10	0	10	–	–	–	–

used had molecular weight of 4000 and was of pharmacological grade (Degussa, Germany).

Experiments. The animals were adapted for 2 weeks to consume one of the plant sources by gradual replacement of their previous diet (wheat straw *ad libitum* + 100 g concentrates/day) until they were fed only oak, pistacia, or carob for 1 week. The intake and digestibility of wheat straw was also tested when it was given alone and with PEG at 10 g/day. Each treatment (level of PEG) lasted 2 weeks, and the reported values for feed intake and digestibility trials were carried out during the second week. The order of treatments within each experiment is described in Table 1.

Digestibility Trials. PEG, mixed with a small amount (3−5 g) of concentrates (16% protein in a mash form), was given to each animal separately in the morning (8 a.m.), before the leaves were provided. Wheat hay cell-wall-Cr mordant, prepared as described by Uden et al. (1980) to yield a Cr concentration of 5.1%, was used as an external marker. Each morning, starting 1 week before the digestibility trial, 10 g of the marker were given along with PEG supplementation. Daily subsamples from the fresh feed offered and from total feed refusals were stored at −20 °C for further analysis. Fecal grab samples were taken every 6 h over a period of 4 days and stored at −20 °C. Digestibility of organic matter, protein (N × 6.25), and cell wall (neutral detergent fiber, NDF) was determined by measuring their concentrations and the concentrations of external marker in the feed and fecal samples. The animals were weighed routinely every 2 days at 10 a.m. on electronic scales. After the termination of each set of treatments, the animals returned to eat wheat straw and concentrates (100 g/day) for 2−3 weeks. If the animals failed to reach their original weight, they were replaced with other goats before the commencement of the next set of treatments.

At the end of each experimental period, rumen samples were taken with a stomach tube, before the feed was provided (7:30 a.m.) and three times at 2-h intervals thereafter.

Chemical and Statistical Analyses. Feed, feed refusals, and fecal samples were dried at 40 °C to constant weight to minimize changes in tannin content and activity (Hagerman, 1988; Makkar and Singh, 1991), and then ground to pass through a 1-mm screen. Dry matter (DM), organic matter, N (Kjeldahl), and cell wall (NDF) were determined as described by Silanikove et al. (1994). Concentrations of Cr in feed and feces were determined according to Uden et al. (1980).

Tannins were extracted from feeds offered and feed refusals with 70% aqueous acetone and with 1% HCl in methanol (Hagerman, 1988). Total phenolic compound contents were measured by the Folin−Denis method (Swain and Hillis, 1959), and the values were expressed as tannic acid (BDH) equivalent. Condensed tannin was measured by the butanol/HCl method (Porter et al., 1986) using quebracho (Trask Chemical Corp., Georgia) condensed tannin as the standard, after purification on Shephadex LH-20 (Pharmacia) according to Asquith and Butler (1985).

Trypsin and amylase activities were determined in non-dried fecal samples taken from goats fed carob, alone or supplemented with PEG at 10 g/day, as described by Silanikove et al. (1994). The pH of rumen fluid was measured with a pH meter soon after sampling. Concentrations of volatile fatty acids (VFA; acetic, propionic, butyric, and valeric acids) were determined by gas−liquid chromatography (GLC) as described by Tagari et al. (1977), and ammonia was determined according to the method of Krom (1980).

Statistical comparisons among treatments were made by two-way analysis of variance, with goats and treatments as independent terms in the model. Within each experiment (type of food), the statistical significance between pairs of treatments was assessed by the Duncan's test following a significant main effect using SAS (1982) procedures. No time effects were found in the case of repeated samplings for rumen and plasma metbolites, or with repeated PEG treatment within a specific diet, and therefore these results were pooled.

RESULTS

Composition of Oak, Pistacia, and Carob Leaves and Wheat Straw (Table 2). The composition of feed refusals was not significantly different (by *t* test analysis) from the composition of the feed offered. The DM content was highest in wheat straw (91%), lowest in carob (54%), and intermediate in pistacia and oak (67 and 60%, respectively). Water-soluble materials contents were similar (20−23.9%) in all plant samples. Crude protein content was the highest in carob, and NDF content was the lowest in pistacia. The highest amount of condensed tannin was obtained by extraction with aqueous acetone in the case of carob (Silanikove et al., 1994) and with acidic methanol in the cases of oak and pistacia. Contents of soluble phenolics and condensed tannins were lowest in carob (1.84 and 5%, respectively), intermediate in oak (4 and 9.54%, respectively), and highest in pistacia (7.1 and 20.5%, respectively). Wheat straw contained negligible amounts of soluble phenolics and condensed tannins. Most of the soluble phenols (93−96%) in the foilage could be percipitated by PEG, suggesting that they were composed of tanniferous material. Oak species are known to contain hydrolyzable tannins (Kumar and Vaithiyanathan, 1990), so it is possible that some of the soluble phenolics were composed of hydrolyzable tannins and exerted antinutritional effects. However, these compounds were not measured in the present experiment.

Intake (Figure 1). When the goats were fed solely on leaves, DM intake ranked carob (799 g/day) > oak (664 g/day) > pistacia (465 g/day). Maximal intake of DM was obtained after PEG supplementation at 10 g/day to goats fed carob and oak, and at 20 g/day to goats fed pistacia. Maximal DM intake ranked carob (1261 g/day) > oak (890 g/day) > pistacia (820 g/day). The DM intake of wheat straw was 800 g/day (SD = 33) and did not respond to PEG supplementation.

Body Weight (Figure 1). When the goats were fed solely on carob, oak, or pistacia, they were not able to sustain their body weight and lost 39, 275, and 375 g/day, respectively. The goats maintained body weight when PEG was added to carob and oak at 5 g/day and to pistacia at 20 g/day. Maximal weight gain (38 and 70 g/day, respectively) was obtained after PEG supplementation at 10 g/day to carob and oak leaves, and at 20 g/day to pistacia (27 g/day weight gain).

Organic Matter (OM) Digestibility (Figure 2). The OM digestibility in goats fed solely on carob was almost double that of those fed on oak and pistacia (46.9% versus 25.8 and 24.5%, respectively). Supplementation of PEG at 5 g/day elevated the OM digestibility of oak to 45.1%, a level recorded for goats fed carob with no PEG. Maximal OM digestibility was obtained with PEG at 20 g/day in goats fed carob (65%) and pistacia (52%); PEG at only 10 g/day was required for goats fed oak (60%). The OM digestibility of wheat straw was 40.6% (SD = 3.6%) and was not affected by PEG supplementation.

Crude Protein (CP) Digestibility (Figure 2). In goats fed solely on pistacia, CP excretion in feces considerably exceeded CP intake, resulting in negative digestibilities (−72.3%). Supplementing pistacia with

Table 2. Chemical Composition of the Leaves of *Q. calliprinos* (Oak), *P. lentiscus* (Pistacia), *C. siliqua* (Carob) and Wheat Straw during the Feeding Trials (Percent of Dry Matter)[a]

	DM		ash		CP		NDF		WSM		SP		CD	
feed	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
oak	60[c]	1	5.4[a]	0.4	6.5[b]	0.4	48[b]	5	20.9	1.2	4.0[c]	0.6	9.5[c]	1.7
pistacia	67[b]	1	5.5[a]	0.4	6.4[b]	0.6	44[b]	3	21.9	1.1	7.1[d]	0.9	20.5[d]	3.4
carob	54[a]	2	6.3[a]	0.5	9.0[a]	0.4	50[b]	6	20.0	1.3	1.8[b]	0.3	5.0[b]	0.3
wheat straw	91[a]	2	3.2[b]	0.3	4.8[c]	0.2	80[a]	9	23.9	1.5	0.1[a]	0.0	0.04[a]	0.0

[a] Values followed by different superscript letters are significantly different ($p < 0.05$). DM, dry matter; CP, crude protein; NDF, cell wall; WSM, water soluble material; SP, soluble phenolics as tannic acid equivalent; CD, condensed tannins as purified quebracho condensed tannin equivalent.

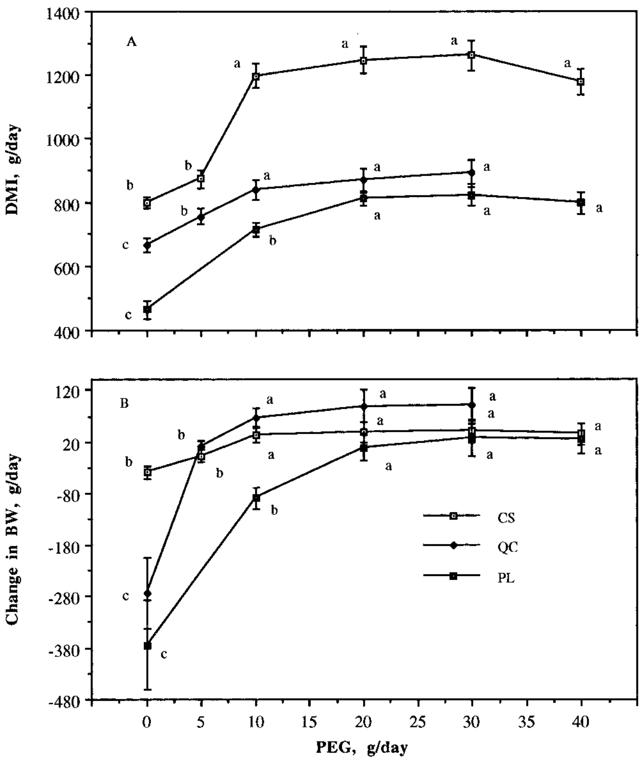

Figure 1. Effect of once-daily supplementation with PEG-4000 on (A) voluntary dry matter intake (DMI) and (**B**) changes in body weight of goats fed *Q. calliprinos* (oak); QC, ◆), *P. lentiscus* (pistacia) PL, ■) and *C. siliqua* (carob) CS, ⊡) leaves. Mean values for four goats with SD. Values marked with different letters differ significantly ($p < 0.05$) within foods.

PEG at 10 g/day improved ($p < 0.05$) CP digestibility but it was still negative (−21.8%). Administration of PEG at 20 g/day brought CP digestibility to a positive value (4.6%, $p < 0.05$). Supplementation with PEG at 30 and 40 g/day resulted in improvement ($p < 0.05$) of CP digestibility (30.2 and 45.2%, respectively). In goats fed solely with carob or oak, CP digestibility was positive but low (7.8 and 11.3%, respectively). Each increase of 5 or 10 g/day in PEG was followed by an improvement ($p < 0.05$) in CP digestibility (except for the increase in PEG from 10 to 20 g/day in goats fed carob). Maximal CP digestibilities were 66.5 and 69.9% in goats fed carob and oak and supplemented with PEG at 40 or 30 g/day, respectively.

Cell Wall (NDF) Digestibility (Figure 2). In goats fed solely on pistacia, NDF digestibility was −15.4%. The NDF digestibilities for oak and carob were 28.7 and 35.4%, respectively. PEG supplementation significantly improved the NDF digestibilities of all three types of leaves. Maximal NDF digestibilities were 74.8, 65.3, and 38.7%, in goats fed carob, oak, and pistacia, respectively (these values were obtained following supplementation with PEG at 40 g/day to carob and pistacia diets, and with PEG at 30 g/day to oak leaves).

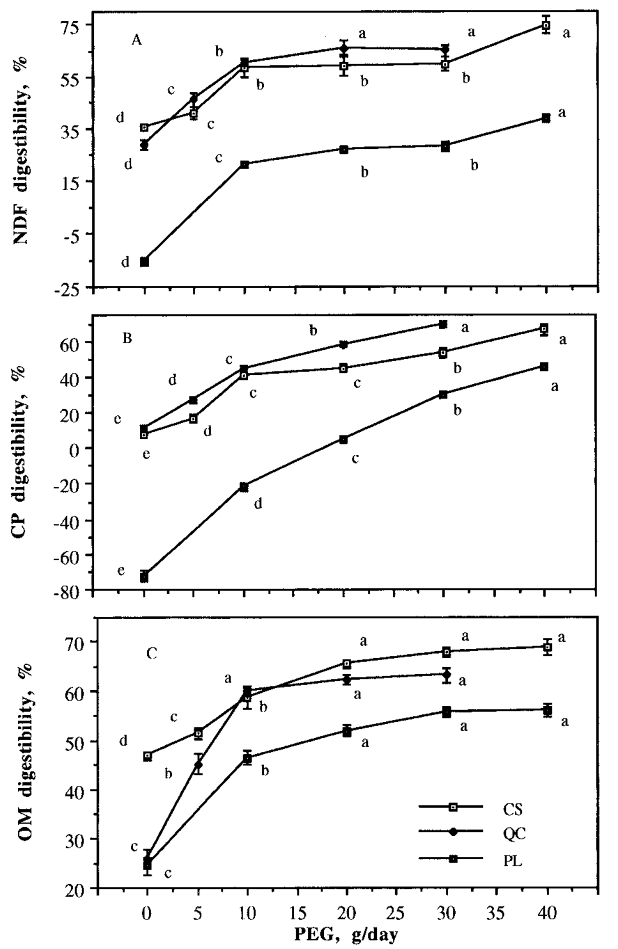

Figure 2. Effect of once-daily supplementation with PEG-4000 on (A) cell wall (NDF), (B) crude protein (CP), and (C) organic matter (OM) digestibilities for goats fed *Q. calliprinos* (oak), *P. lentiscus* (pistacia), and *C. siliqua* (carob) leaves. Mean values for four goats with SD. Values marked with different letters differ significantly ($p < 0.05$) within foods. Symbols are the same as in Figure 1.

pH, Ammonia, and Volatile Fatty Acids (VFA) in Rumen Liquor (Figure 3). Rumen liquor pH ranged from 6.92 to 7.01 with the three diets and was not influenced by PEG. Ammonia concentration in the rumen fluid was not affected by supplementation of PEG at 10 g/day. Each further PEG addition of 10 g/day linearly increased the ammonia concentration by 4.4% with oak (not significant, NS), 3.5% with pistacia ($p < 0.04$), and 11.6% with carob ($p < 0.001$). The differences between the slope of the oak line and those of carob and pistacia lines were significant ($p < 0.005$). There was no response to PEG supplementation in goats fed wheat straw (data not shown).

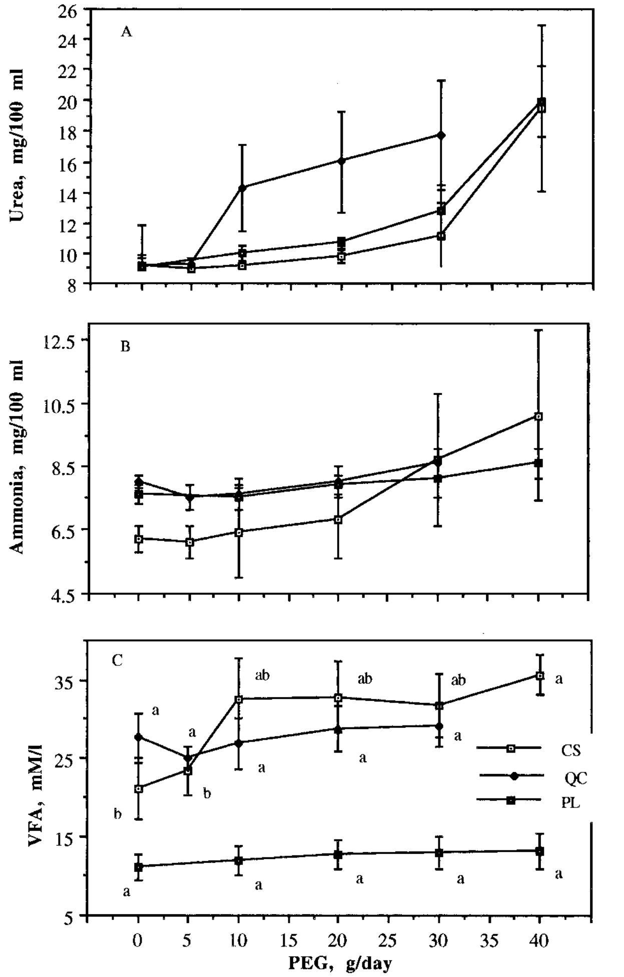

Figure 3. Effect of once-daily supplementation with PEG-4000 on urea concentration in blood serum, (B) ammonia concentration in rumen fluid, and (C) volatile fatty acids (VFA) in rumen fluid of goats fed *Q. calliprinos* (oak), *P. lentiscus* (pistacia), and *C. siliqua* (carob) leaves. Mean values for four goats with SD. Values marked with different letters differ significantly ($p < 0.05$) within foods. Symbols are the same as in Figure 1.

The VFA concentrations in goats fed carob, oak, and pistacia were 21.1, 27.5, and 11.1 mM/L, respectively. Each 10-g/day increase in PEG increased the VFA concentration by 5% with pistacia (NS), by 10% with oak ($p < 0.1$), and by 31.5% with carob ($p < 0.001$). Again, the differences between the oak slope and those of carob and pistacia were significant ($p < 0.005$).

Enzymatic Activity. In goats fed solely with carob, amylase and trypsin activities in fecal samples were 0.42 (SD = 0.2) and 1.35 (SD = 0.4) units/g DM, respectively. Supplementation with PEG at 10 g/day was followed by an increase ($p < 0.05$) in amylase and trypsin activities to 0.78 (SD = 0.3) and 2.60 (SD = 0.5) units/g DM, respectively.

DISCUSSION

Effect on Digestion. The high pH of rumen fluid, which did not drop following intake of fresh food, and the low level of rumen VFA (4−5 times lower than that with a typical roughage diet; Silanikove et al., 1993), which did not change following eating, indicate that fermentation was considerably depressed in comparison with the fermentation of typical, medium-quality, roughage diets. This result is consistent with the finding thatVFA production during in vitro fermentation was greatly reduced (five times or more) when the substrate contained >6% condensed tannin (Van Hoven and Furstenburg, 1992). The depression in the fermentation process could be a result of (i) direct interaction between tannins and bacterial cell wall or protozoal membranes (Henis et al., 1964; Jones et al., 1994), (ii) the effect of tannin on ruminal microorganism enzymes (Tagari et al., 1965; Bae et al., 1993), or (iii) the effect of small tannins or non-tannin phenolics on the metabolism of ruminal microorganisms (Akin et al., 1988).

The increase in OM digestibility following PEG intake was much greater than the increase in VFA concentration. Silanikove et al. (unpublished results) found in goats fed carobs that PEG supplementation increased the fluid DM and the water contents of the rumen by 30% in comparison to non-supplemented goats. Such a response, although it would increase the production of VFA, was not reflected by a proportional increase in the concentration of VFA in the rumen fluid. A second possibility is that a considerable increase in digestibility occurred in the intestine (Silanikove et al., 1994). The most impressive effect of tannins was the depression of CP digestibility. The antinutritional effect of tannins is exerted through the reduction of food protein availability and depression of digestive tract enzyme activities (Kumar and Singh, 1984; Robbins et al., 1987; Jones et al., 1994). In monogastric mammals (Ahmed et al., 1991; Jansman et al., 1993; Longstaff and McNab, 1991) and in goats (present study) and sheep (Silanikove et al., 1994), one of the main adverse effects of tannins on nutrient utilization is caused by a depression in pancreatic enzyme activities.

The pattern of the relationship between PEG intake and increase in CP digestibility suggests that the potential for improving CP digestibility was not maximized in the present experiment. Although the relation between PEG intake and ME intake was asymptotic, that between PEG intake and digestible CP intake within the same range of PEG was linear (Figure 4). Intake of PEG at 1 g/day increased digestible CP intake by 1.17 g/day in goats fed oak and pistacia and by 1.73 g/day in goats fed carob ($p < 0.05$, Figure 4). It seems, therefore, that the tannin:PEG stoichiometry was different or that the tannin:protein stoichiometry was variable between carob and oak, or pistacia. The improvement in digestible CP intake was reflected in an increase in serum urea concentration, and the relationship was highly significant ($p < 0.01$).

The present results support findings that tannins may reduce cell-wall digestibility by binding bacterial enzymes and/or forming indigestible complexes with cell-wall carbohydrates (Barry and Manley, 1984; Barry et al., 1986; Reed, 1986). Tannin−protein complexes formed in the digestive tract were determined as fecal lignin (Reed, 1986), resulting in apparent negative digestibility of lignin in sheep fed carob (Silanikove et al., 1994) or negative NDF digestibility in goats fed pistacia (Figure 2). Improvement in NDF digestibility following PEG supplementation reflected (i) a decrease in the protein−tannin complex determined as NDF in feces and (ii) an enhanced rumen fermentation, indicated by an increase in VFA and ammonia concentration in the rumen fluid.

What Determines the Voluntary Intake of Tannin-Rich Fodder in Ruminants? Reduced palatability as a consequence of astringency, systemic tox-

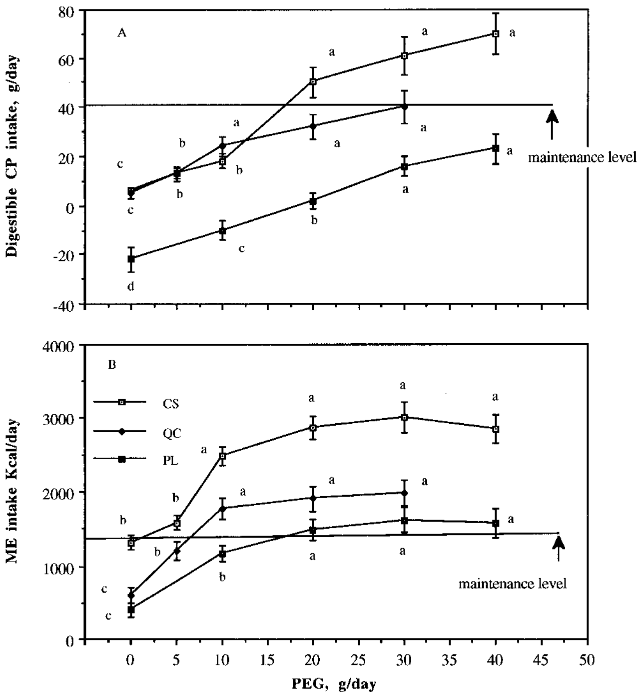

Figure 4. Effect of once-daily supplementation with PEG-4000 on (A) digestible crude protein (CP) intake and (B) metabolizable energy (ME) intake in goats fed *Q. calliprinos* (oak), *P. lentiscus* (pistacia), and *C. siliqua* (carob) leaves. Values marked with different letters differ significantly ($p < 0.05$) within diets. The ME intake was calculated from digestible energy intake with a conversion factor of 0.8. Symbols are the same as in Figure 1.

icity, and low rate of evacuation of digesta from the rumen (gut-fill effect; GFE) are factors that may explain the negative effects of tannins on feed intake in ruminants (Bryant et al., 1991; Kumar and Singh, 1984; Provenza, 1995). The effect of PEG starts from the rumen. Therefore, astringency could not be an important factor in suppressing voluntary feed intake in the present study. The possibility of systemic toxicity was ruled out by Gilboa et al. (1994), who showed that feeding goats with tannin-rich leaves had no effect on biochemical parameters in blood serum that are known to be associated with damage to the liver and kidneys. To the best of our knowledge, there is no evidence for tannin-related toxicosis in browsing goats in Israel or in other countries in the Mediterranean Basin. Native goats, such as the Mamber breed, have continuously inhabited woody areas in this part of the old world for the last seven millennia; therefore, lack of tannin-related toxicosis in these animals most likely reflects adaptation to tannin-containing forages.

According to the GFE theory, the control of intake of roughages with digestibility below 70% is mechanistic, and feed intake should respond linearly to any improvement in DM (or OM) digestibility (Conard et al., 1964; Campling, 1970). However, contrary to expectation, maximal feed intake preceded maximal OM digestibility. Similarly, Wilson (1977) and Perevolotsky et al. (1993) reported that there was no direct relationship between the intake of various woody species and their digestibility coefficients.

According to Provenza (1995), there is a fine line between satiety (positive postingestive feedback) and surfeit (negative postingestive feedback); hence, preferences and aversions to energy sources or specific nutrients are a compromise response. Consequently, neutralization of the negative effects of a fodder will accentuate its positive effects. In the present experiment, goats fed carob responded better to PEG than goats fed oak or pistacia because carob has a higher nutritional value than oak or pistacia and, consequently, greater potential for benefit from neutralization of the tannins.

Nutritional Implications. When goats were fed carob, oak, or pistacia alone, the voluntary consumption of calculated metabolizable energy (ME) was considerably below their maintenance requirements (1400 kcal/day; Figure 4). THe ME intake required to maintain constant body weight agreed with NRC (1981) recommendations. PEG supplementation increased ME intake of the animals to well above their maintenance requirements (Figure 4). These results are consistent with the positive responses to PEG supplementation of grazing goats and sheep (Silanikove et al., 1992) and of sheep under controlled conditions (Silanikove et al., 1994).

Comparisons. Feed intake and digestibility of oak in the present experiment were within the range found for the leaves of various oak species grazed by goats (Perevolotsky et al., 1993). However, in comparison with a previous study of Mamber goats fed oak (Perevolotsky et al., 1993), feed intake and digestibility of OM and CP were much lower in the present study, despite the fact that CP and cell-wall contents were very similar in both cases. The content of condensed tannins in the cited experiment was only half that in the present study, suggesting that differences in tannin contents were the main reason for the wide variability in the nutritional value of oak. The ecological factors governing the rather wide within- and between-species variability in tannin contents in trees constituting the east Mediteranean scrubland are not yet understood (Perevolotsky, 1994).

In comparison with sheep fed carob of similar composition (Silanikove et al., 1994), goats consumed greater amounts of leaf DM, on a metabolic basis, and responded better to PEG supplementation. In addition, the amount of PEG required to elicit maximal response in feed intake was much lower in goats than in sheep (10 versus 50 g/day). These differences are consistent with the notions that browsers are more efficient than grazers in utilizing tannin-rich plants in general (Robbins et al., 1991) and that goats are more efficient than sheep (Kumar and Vathiyanathan, 1990).

Conclusions. This study shows that the major negative effect of tannin on goats is depression of digestion, particularly of protein. However, depression of intake of tannin-rich fodder is driven not only by the effect of tannin on digestion, but also by an unknown post-ingestive effect of tannins, probably in the digestive tract. Once-daily supplementation with small amounts of PEG dramatically increased feed intake and digestion of tannin-rich fodder, even of leaves that normally are scarcely eaten by grazing ruminants. Therefore, this method of adminstering PEG opens a new possibility to reduce vegetative biomass in areas prone to fire and shrub encroachment and to increase the production of livestock on woodlands.

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