

Review

Potential mechanisms to increase shrub intake and performance of small ruminants in mediterranean shrubby ecosystems

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Received 26 January 2007; received in revised form 27 May 2007; accepted 19 July 2007

Available online 4 September 2007

Abstract

Shrubby vegetation types called “maquis” and “garrigue” are widespread throughout the Mediterranean Basin, including the Adriatic littoral of Croatia. In Croatia and elsewhere, these shrublands represent traditional grazing areas and are a significant source of forage for small ruminants, particularly during the dry summer. Utilization of these Mediterranean shrublands is often limited by secondary compounds that adversely affect forage intake and animal health. Likewise, shrubs containing substantial quantities of secondary compounds dominate arid and semiarid rangelands globally. These secondary compounds reduce livestock productivity, cause significant toxicity and abortion problems, and reduce efficiency of use of rangeland shrubs worldwide.

Feed additives (e.g., activated charcoal, polyethylene glycol, and calcium hydroxide) may be useful for enhancing shrub intake through decreased absorption and/or increased elimination of secondary compounds. The biological diversity of Mediterranean maquis vegetation may also positively influence shrub consumption by small ruminants. Consumption of combinations of shrubs containing varied classes of secondary compounds (e.g., tannins and saponins) may lead to complementary chemical interactions within the intestinal tract and/or post-absorption that reduces their toxic effects and/or increase efficiency of detoxification. Although goats consumed more total shrubs than sheep across experiments, both species responded similarly to supplemental charcoal, PEG, and calcium hydroxide.

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Keywords: Mediterranean shrubs; Small ruminants; Activated charcoal; Calcium hydroxide; Polyethylene glycol; Saponins; Tannins; Terpenes

1. Introduction

In resource limited arid ecosystems, significant herbivore pressure has favored plants that have evolved defensive physical and chemical mechanisms that reduce herbivory (Freeland, 1991). Mediterranean shrubby vegetation (maquis and garrigues) covers over one million

hectares in Mediterranean Croatia (Rogosic, 2000; Rogosic et al., 2006b) and about 100 million hectares in the entire Mediterranean basin (Le Houerou, 1980). These traditional grazing areas are a critical resource for animal forage in the Mediterranean region, particularly during the dry summer (Devendra, 1990; Rogosic, 2000). Vegetation of these plant communities usually consists of 20–25 shrub species in southern Croatia, but typically only six or seven species are dominant (*Quercus ilex*, *Erica multiflora*, *Arbutus unedo*, *Juniperus phoeniceae*, *Viburnum tinus*, *Pistacia lentiscus*, and *Hedera helix*) and represent the major dietary components of sheep and

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goats. The nutrient composition of these shrubs varies considerably (Rogosic et al., 2006b), ranging from low to intermediate diet quality. However, utilization of the Mediterranean shrubs is often limited by secondary compounds such as tannins, terpenes, and saponins (Perevolotsky et al., 1993; Silanikove et al., 1994; Rogosic et al., 2003, 2006b, 2007a,b). High concentrations of these components can adversely affect forage intake and animal health. The objective of this manuscript is to review the current knowledge regarding the secondary chemistry of this shrubby Mediterranean vegetation, mechanisms by which small ruminants cope with these compounds, and some of the management options available to counteract their negative effects.

Secondary compounds vary greatly in terms of structure and concentration both within and among compound class and plant species. Consequently, mechanisms by which secondary compounds affect browsing ruminants also differ greatly. Typically, negative effects are attributed to effects on rumen microbial populations, digestion processes, intestinal damage, and/or metabolic toxicity post-absorption. In fact, some compounds may be beneficial at low concentrations (e.g., protein bypass with low tannin concentration). Animals have a number of behavioral and metabolic strategies to avoid, tolerate, and/or regulate intake of toxins. Herbivores cope with secondary compounds with pre-ingestive (taste, odor, etc.) cues (avoiding bitter and aversive compounds), detoxification (via intestinal microbes or tissue enzymes), learning (via social interactions and/or feedback), producing proline-rich salivary proteins, selecting plants/plant parts with lower concentrations, increasing diet breadth, cautious sampling, reducing absorption, altering frequency and length of feeding bouts (cyclic consumption), regulating intake below a threshold via conditioned aversions, ingesting soil, etc. (Freeland and Janzen, 1974; Robbins et al., 1987; Provenza et al., 1992; Pfister et al., 1997; Wink, 1998; Dearing et al., 2005; Wiggins et al., 2006).

2. Plant secondary metabolites as grazing deterrents in the mediterranean maquis

The Mediterranean maquis vegetation consists of numerous plant species differing in growth patterns and concentrations of nutrients and secondary compounds, and presumably possessing a variety of flavors and intensities that contribute to the differential palatabilities of these shrubs for browsing herbivores such as goats and sheep. Plant morphological characteristics and/or secondary compounds often limit utilization of shrubby species and adversely affect forage intake.

Understanding the role and significance of secondary metabolites in plant–animal interactions is crucial for managing plant and herbivore populations in Mediterranean grazing ecosystems. Small ruminants browsing on Mediterranean shrublands encounter a diverse range of dietary phytochemicals that affect animal performance and herbivory patterns in the maquis community (Silanikove et al., 1996a; Rogosic et al., 2006b,c, 2007b), and therefore likely have mechanisms to limit exposure to phytotoxins. By identifying these mechanisms, it should be possible to predict how the biochemical composition of plants influences their probability of being grazed.

2.1. Effect of plant flavors on preference

Olfactory, gustatory, visual, and tactile stimuli are all involved in the selection process (Goatcher and Church, 1970; Krueger et al., 1974). Sensory properties that contribute to a specific flavor can exert both pre-ingestive and post-ingestive effects on intake and/or dietary preference (Provenza et al., 1992; Pass and Foley, 2000; Burritt and Provenza, 2000). Flavor is a combination of taste, odor, and texture that provides sensory input about a particular food and can lead to positive or negative feedback associations and alter consumption of that food (Wang and Provenza, 1996; Burritt and Provenza, 2000). An animal can learn to associate high nutrient or toxin concentration of a diet with a specific flavor and alter preference (Burritt and Provenza, 1992; Launchbaugh et al., 1993; Villalba and Provenza, 1997). Flavor intensity is a function of olfaction and taste acting in concert (Corley et al., 1999). Herbivores may be able to develop preferences for varying flavor intensities if the flavor strength is associated with a desirable nutrient and/or toxin concentration (Launchbaugh et al., 1993; Villalba and Provenza, 2000).

The offensive flavors of some phytotoxins have long been considered to function as plant defense mechanisms against herbivores (Lindroth, 1989; Harborne, 1991). Bitterness is the primary aversive taste influencing consumption of diets in ruminants (Goatcher and Church, 1970; Krueger et al., 1974). Bitter secondary compounds include many sesquiterpenes, cyanogenic glycosides, alkaloids, flavonoids, and saponins (Gershenson and Croteau, 1991; Harborne, 1991; Molyneux and Ralphs, 1992), while tannins have an astringent taste that contributes to low palatability (Harborne, 1991). Herbivores may initially avoid foods with strong flavors (Launchbaugh and Provenza, 1994). Avoidance of bitter and other strong flavors may have important survival implications for herbivores in Mediterranean maquis ecosystems. However, the inherent avoidance of bitter

flavor is not universal (Nolte et al., 1994; Pfister et al., 2001). Because animals can identify toxins in a plant by associating flavor with post-ingestive effects (Garcia, 1989), the flavor of specific plant chemicals may contribute to a distinct flavor for a given plant. When plant flavor and toxicity are highly correlated, herbivores may learn to regulate food intake based on post-ingestive feedback and then adjust intake on the basis of flavor intensity (Launchbaugh et al., 1993; Villalba and Provenza, 2000).

2.2. *Transient food aversions*

Secondary compounds can alter plant palatability by causing negative gastrointestinal consequences in the herbivore to elicit a conditional food aversion. Herbivores generally sample small quantities when they encounter a new plant (Freeland and Janzen, 1974) and increase or decrease consumption over time depending on whether gastrointestinal malaise occurs (Provenza et al., 1992). Aversions or preferences formed as a result of the integration of sensory and post-ingestive consequences can alter intake (Provenza et al., 1992). Negative feedback can occur through activation of the emetic system resulting in malaise while positive effects arise from effects of digestion and fermentation end products and subsequent neural and hormonal responses (Provenza et al., 1992; Provenza, 1995a).

Herbivores typically select diets that maximize nutrient intake (Westoby, 1978) while minimizing consumption of harmful phytochemicals (Freeland and Janzen, 1974; Belovsky and Schmitz, 1994). However, herbivores generally consume a varied diet even when toxins are not a concern and nutritional needs are met (Provenza et al., 1996; Wang and Provenza, 1996; Early and Provenza, 1998; Ginane et al., 2000). This inconsistency may be due to the formation of aversions that decrease preference for a food just eaten due to the integration of sensory (flavor) input and post-ingestive effects (effects of nutrients and toxins on chemo-, osmo-, and mechano-receptors) of a food (Wang and Provenza, 1996; Provenza et al., 1996). Satiety and malaise are points on a continuum and preference can change even within a meal as satiety approaches (or is surpassed) and feedback changes from positive to negative, resulting in short term or long term aversions (Provenza, 1995b, 1996). Even preferred foods can be aversive if enough is eaten, but the effect is likely to be short-term when the nutritional properties are beneficial (Provenza, 1996; Early and Provenza, 1998). Thus, preference is the result of a complex learned process that is pliable (Provenza, 1995a, 1996).

2.3. *Most common secondary metabolites in mediterranean shrubs*

Mediterranean shrubs produce a variety of secondary metabolites that are toxic and/or deterrent to herbivores (Silanikove et al., 1996a,b; Rogosic et al., 2006a,b,c, 2007a,b). These substances are usually assumed to serve as chemical defenses against herbivory in this ecosystem (Rogosic et al., 2006b). Tannins, terpenes, and saponins are three of the major classes of secondary compounds in Mediterranean shrubs.

2.3.1. *Tannins as defenses against herbivores*

Tannins are a group of phenolic compounds that are common in browse species. The two general categories of tannins are condensed tannins (proanthocyanidins; linear or branched polymers of flavonoid units) and hydrolyzable tannins (gallotannins and ellagitannins; parent polyol [e.g., glucose] esterified with gallic or hexahydroxydiphenic acid, respectively) (Hagerman and Butler, 1991; Murdiati et al., 1992; Reed, 1995). Tannins originate from the shikimate/chorismate pathway (De Bruyne et al., 1999). Proanthocyanidins are highly variable in structure because of variable hydroxylation patterns, the presence of three chiral centers, variable location and type of interflavan linkage, and variable structure of the terminal unit (De Bruyne et al., 1999). Hydrolyzable tannins range in size and molecular weight depending on the number of sugars in the parent group and the number of phenolic units esterified to them (Hagerman et al., 1992).

Tannins have traditionally been classified as hydrolyzable and condensed tannins based on their stability in the gut and potential for absorption. Hydrolyzable tannins are readily hydrolyzed in the intestinal tract (acid or microbial hydrolysis) to sugar moieties and simple phenolic compounds that may be absorbed and cause toxicity, while condensed tannins are large polymers with carbon–carbon bonds connecting flavan-3-ol units that are more difficult to degrade in the gut and are therefore not readily absorbed or as toxic (Jones and Mangan, 1977; Murdiati et al., 1992; Shimada, 2006). Toxic end products of hydrolyzable tannin degradation can result in hemorrhagic gastroenteritis, liver necrosis, and renal tubular necrosis (Murdiati et al., 1990; Reed, 1995), while condensed tannins typically exert their negative effects by binding and precipitating proteins and starch (Rhoades and Cates, 1976; Reed, 2001). Although these two classifications are entrenched in the literature, their distinctions are not clear cut and their significance in terms of nutritional effects may be overstated (Mueller-Harvey, 2006). Even though all

tannins by definition bind proteins, they are extremely diverse structurally, and these differences may affect binding strength and solubility of the complex (Mueller-Harvey, 2006).

Negative effects of tannins on intake and digestion are attributed to reduced protein availability, enzymatic inhibition, decreased palatability (astringency), reduced gut wall permeability, mineral chelation, and tissue effects of absorbed compounds (Bernays et al., 1989; Clausen et al., 1992; Reed, 1995). Decreased ruminal protein degradation can have negative effects on ruminal forage digestion and positive effects on amino acid availability in the lower tract (Waghorn and McNabb, 2003), depending on concentrations of dietary tannins and protein. While tannins typically reduce palatability/intake, digestibility, nutrient availability, and weight gain (Provenza and Malechek, 1984; Barry and Blaney, 1987; McArthur et al., 1993; Silanikove et al., 1996b), at low concentrations, condensed tannins may improve nutrition for ruminants by reducing protein degradation in the rumen and increasing protein bypass into the lower tract through reversible complexation with proteins (Barry and Blaney, 1987; Liu et al., 1998; Ben Salem et al., 2005; Min et al., 2006). Concentration of tannins in the diet along with structural properties that affect binding strength and solubility of the protein–tannin complex (e.g., molecular weight, type of binding [i.e., hydrophobic versus hydrogen bonding]) likely interact to dictate whether a particular dietary tannin exerts a positive or negative nutritional effect on an animal (Mueller-Harvey, 2006).

Nevertheless, tannins have been shown to exert negative effects on shrub intake, digestibility, and/or performance in a number of ecosystems. Provenza and Malechek (1984) reported that condensed tannins in blackbrush (*Coleogyne ramosissima*) reduced its palatability to goats. Goats learned to consume old-growth blackbrush and avoid tannin-rich current years growth quickly by associating flavor with internal malaise (Provenza et al., 1990). Condensed and/or hydrolyzable tannins have been negatively related to palatability and/or intake of browse by goats, sheep, and/or wildlife by several workers (Owen-Smith and Cooper, 1985; Degen et al., 1995; Woodward and Coppock, 1995; Alm et al., 2002). Furthermore, consumption of tannin-containing shrubs can negatively impact dry matter and/or protein digestibility, increase escaped protein, and shift excretion of nitrogen from urine to feces in browsing ruminants (Hagerman et al., 1992; McArthur et al., 1993; Woodward and Reed, 1997; Kaitho et al., 1998a,b).

Tannin/phenolic-containing Mediterranean shrubs have been associated with reduced intake by small ruminants (Silanikove et al., 1996b; Massei et al., 2000; Papachristou et al., 2003). High-tannin Mediterranean shrubs such as *Quercus ilex*, *Arbutus unedo*, and *Pistacia lentiscus* (Rogosic et al., 2006b, 2007b) cause a depression in animal production and in extreme cases can cause death. Tannin concentrations above 5% have been shown to reduce forage intake and digestibility of Mediterranean shrubs such as *Quercus calliprinos*, *Pistacia lentiscus* (Perevolotsky et al., 1993) and *Cerastium siliqua* (Silanikove et al., 1994).

2.3.2. Terpenes as defenses against herbivores

Terpenoids are the largest group of plant secondary chemicals, with over 30,000 terpenes identified structurally (Little and Croteau, 1999). Biosynthesis of this extremely diverse group of compounds originates from one of two pathways. In the mevalonate pathway, isopentyl phosphate isomerizes and condenses into an array of carbon skeletons that are modified to produce the wide array of specific terpenes in incremental five carbon units (McGarvey and Croteau, 1995). The mevalonate pathway operates in the cytosol, while a second recently discovered pathway (1-deoxy-D-xylulose-5-phosphate pathway) used to synthesize many of the terpenes operates in the plastids (Kreuzwieser et al., 1999; Dubey et al., 2003).

Terpenes have been found to decrease *in vitro* digestibility in ruminants, suggesting antimicrobial activity (Oh et al., 1967; Schwartz et al., 1980a), especially if the rumen microbial population is not adapted to the compounds (Oh et al., 1967). Nagy and Tengerdy (1968) reported sagebrush essential oil decreased bacterial numbers in deer rumen fluid, but observed no evidence of microbial adaptation. Actual effects of terpenes *in vivo* have been suggested to be less because of loss during mastication and rumination (Cluff et al., 1982), eructation of warm volatiles (Pederson and Welch, 1982), and/or absorption from the rumen (Freeland and Janzen, 1974). Newbold et al. (2004) reported that an essential oil mixture fed to sheep caused no major effects on fermentation, rumen ammonia, protozoa numbers, or digestion, although they did observe reduced *in sacco* protein degradation.

Terpenes that are not modified ruminally can be absorbed and exert toxic effects metabolically. Most small lipophilic compounds such as monoterpenes are readily absorbed (Sorensen et al., 2004; McLean and Duncan, 2006). Secondary metabolites that are absorbed by mammals are generally metabolized by a combination of Phase I (oxidation, reduction, and hydrolysis)

and/or Phase II (conjugation) processes (Smith, 1992; Dearing and Cork, 1999). Phase I enzymes change polarity by adding functional groups, primarily via mixed function oxidases of cytochrome P450s in the smooth endoplasmic reticulum, especially in the liver (Dearing et al., 2005). Conjugation involves reactions of metabolites with hydrophilic endogenous compounds such as glucuronic acid, sulfate, glycine, and glutathione, resulting in less toxic forms that are more readily excreted in urine or bile (Cheeke and Shull, 1985; Smith, 1992). These processes increase polarity and water solubility of lipophilic metabolites and facilitate their excretion (Smith, 1992; Dearing and Cork, 1999). Organic acids produced during detoxification can reduce urine pH upon excretion (Dearing and Cork, 1999; Dearing et al., 2000), and can perturb the acid/base balance if the system is overwhelmed (Illius and Jessop, 1996; Foley et al., 1999). The ability of animals to detoxify secondary compounds may depend on the combination of induction of enzymes due to toxin exposure and inhibition from competing metabolites (Pass and McLean, 2002).

The ability of animals to control absorption and elimination of phytochemicals has a major impact on their ability to consume shrubs. Although small lipophilic compounds are generally considered to be absorbed easily from the gastrointestinal tract (McLean and Duncan, 2006), recent evidence suggests efflux transporters in gut enterocytes (e.g., permeability glycoprotein) actively move some compounds back into the lumen to prevent absorption, which may be the reason specialists are more resistant to secondary compounds than generalists (Sorensen et al., 2006). Blood levels and clearance of these compounds also plays a major role in limiting intake (Foley et al., 1999; Dziba et al., 2006; McLean and Duncan, 2006). Dziba et al. (2006) reported reduced feeding with ruminal or intravenous infusion of 1,8-cineole in lambs, and suggested rate of absorption, distribution, and excretion interact to dictate cessation of feeding and length of time before animals return to feeding. Some herbivores may regulate intake (both amount and timing) to maintain phytotoxin levels below concentrations that cause acid/base imbalances and other negative feedbacks from secondary metabolites (Pfister et al., 1997; Foley et al., 1999; Stapley et al., 2000; Sorensen et al., 2005).

High-terpene shrubs and their extracts have been shown to negatively affect shrub intake, digestibility, and/or performance in various ecosystems. Terpene-containing shrubs and/or specific monoterpenes were related to intake of *Juniperus* spp. by goats (Riddle et al., 1996; Pritz et al., 1997), while total monoterpenes were negatively related to intake of big sagebrush

(*Artemisia tridentata* ssp. *tridentata*) by sheep (Yabann et al., 1985) and Sitka spruce (*Picea sitchensis*) by red deer (Duncan et al., 1994). Mule deer exhibited lower preference for diets containing extracts from *Juniperus* spp. (Schwartz et al., 1980b) and four *Artemisia* spp. (Bray et al., 1991). Ngugi et al. (1995) reported that feeding sheep mixtures with up to 30% mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) resulted in decreasing intake, dry matter digestibility, and nitrogen retention as dietary sagebrush increased. Goats and sheep also exhibit limited preference for terpene-laden shrubs (*Juniperus phoenicea*, *Helichrysum italicum*, and *Juniperus oxycedrus*) in the Mediterranean maquis (Rogosic et al., 2006b,c).

2.3.3. Saponins as defenses against herbivores

Saponins are glycosidic compounds composed of an aglycone and a sugar moiety varying in number and type of monosaccharides (Marston and Hostettmann, 1991; Majak, 2001). Although three major classes of saponins exist (glycosides of triterpenes, steroids, and steroidal alkaloids), triterpene glycosides are by far the most common (Marston and Hostettmann, 1991). Saponins can act as surfactants, cause red blood cell hemolysis, alter membrane permeability and cause cellular leakage, and can cause intestinal lesions and liver damage (Oleszek et al., 1999; Majak, 2001). Most saponins are poorly absorbed and are typically not toxic unless mucosal cell membranes are lysed and intestinal lesions are formed (Marston and Hostettmann, 1991; Majak, 2001).

Saponins from some plant species modify gut microbes, particularly in ruminants (Gee et al., 1993). Saponins can reduce rumen protozoa populations by binding to cholesterol in the protozoal cell membrane, causing lysis and cell death (Makkar et al., 1998). However, Abreu et al. (2004) observed increased protozoal numbers in sheep receiving the high-saponin fruits of *Sapindus saponaria*. No effect of saponins was detected on organic matter digestibility (Abreu et al., 2004). Because few shrub species have been reported in the literature to be high in saponins and because saponin toxicity is less common than for many other classes of secondary compounds, little information is available regarding the feeding deterrent properties of high-saponin shrubs. Although saponins may be aversive to mammalian feeding behavior in some cases (Gershenson and Croteau, 1991), effects of saponin-containing shrubs on intake, digestibility, and productivity are not well understood. *Hedera helix* is one Mediterranean shrub that contains significant saponin levels; these bitter, toxic compounds apparently protect this shrub from browsing herbivores

by affecting their feeding behavior (Rogosic et al., 2003, 2006a, 2007a).

3. Influence of nutrients and feed additives on utilization of mediterranean shrubs

Sheep and goats browsing on Mediterranean shrublands cannot avoid ingesting secondary compounds such as tannins, saponins, and terpenes that commonly occur in shrubs in that area (Silanikove et al., 1994; Rogosic et al., 2003, 2006c, 2007a,b). Although secondary compounds can limit intake, animals have a variety of behavioral and metabolic strategies to deal with them. For example, animals can modify feeding behavior in time or space to maintain blood metabolite concentrations below a certain level or use cautious sampling and diet mixing to maintain inducible enzymes for potential encounters with plant toxins (McLean and Duncan, 2006).

While herbivores have evolved mechanisms to deal with phytochemicals to a certain extent, practical management methods to safely increase shrub intake by livestock are needed. A variety of management practices and diet additives have been examined to increase intake of secondary metabolite-laden but otherwise highly nutritious shrub species. One approach involves supplementation of various nutrients that would be expected to counteract negative effects on nutrient absorption in the intestinal tract and/or enhance clearance of secondary compounds post-absorption. Depletion of body protein and glucose may occur during detoxification to counteract losses from conjugation, enzyme synthesis, maintenance of acid/base balance, etc.; consequently, supplementation and improved nutrient status should permit animals to consume more phytotoxins (Illius and Jessop, 1995, 1996; Foley et al., 1999). Burritt et al. (2000) reported no improvement in sagebrush intake with either protein or energy supplementation, while Banner et al. (2000) reported improved sagebrush intake with supplemental energy. However, Villalba et al. (2002a) reported increased intake of sagebrush by sheep and goats when fed a protein supplement, but generally found energy to have no effect or a negative effect on sagebrush intake. Villalba et al. (2002a) suggested the discrepancy with the two previous studies was probably due to the high protein basal diet used in those studies. Villalba et al. (2002b) also reported protein supplementation increased intake of a diet containing condensed tannin compared to a high-energy supplement. Sheep consumed more total toxins when fed three diets containing terpenes, tannins, or oxalates in association with a high quality diet (both in terms of protein and energy)

than with a low quality diet, presumably because the high quality diet supplied the necessary nutrients for ruminal and hepatic detoxification (Shaw et al., 2006).

In addition to nutritional manipulation, a variety of treatments and dietary additives that enhance detoxification, reduce absorption, or otherwise counteract limitations of secondary compounds on intake have been examined. Increased dietary diversity (greater number of shrub species consumed) and complementarity of shrubs containing different classes of secondary compounds have also been examined as methods to increase the ability of ruminants to consume shrubs. The potential for three such additives (activated charcoal, polyethylene glycol, and calcium hydroxide) as well as dietary mixing and shrub complementarity to increase intake of Mediterranean shrubs by sheep and goats are discussed below.

3.1. Effect of activated charcoal on intake of terpene-rich mediterranean shrubs

Activated charcoal can adsorb and decrease bioavailability of phytochemicals in the gastrointestinal tract through the interaction of its positively charged surface with negatively charged toxins, allowing them to be excreted in the feces of browsing herbivores (Buck and Bratich, 1986; Poage et al., 2000). Sheep and goats receiving 20 g of activated charcoal consumed more total biomass of high-terpene Mediterranean shrubs (Fig. 1) when offered either three (*Juniperus phoenicea*, *Helichrysum italicum*, and *Juniperus oxycedrus*), two (*Juniperus phoenicea*, and *Helichrysum italicum*) or one shrub (*Juniperus phoenicea*) species (Rogosic et al., 2006c). Charcoal presumably reduced the impact of terpenes on intake of the shrubs. Only in the second study (three shrub species) was this shown conclusively. In that study, the controls received the barley carrier and the treated group received barley plus charcoal, while the controls received no grain in the third (two shrub species) and fourth (one shrub species) studies; thus, an effect of energy cannot be ruled out in the latter studies. However, as mentioned earlier, energy supplementation has generally not been successful for increasing intake of sagebrush (Villalba et al., 2002a). Also, Banner et al. (2000) reported a positive effect of charcoal on sagebrush intake by lambs. In contrast, Villalba et al. (2002a) observed no effect of charcoal on sagebrush intake by sheep and goats. Bisson et al. (2001) reported that charcoal increased intake of redberry juniper (*Juniperus pinchotii*) initially (first 5 days of study), but had no effect on intake of ashe juniper (*Juniperus ashei*) by goats.

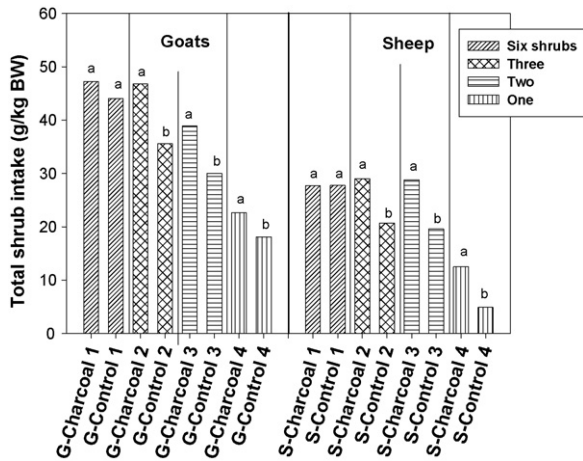


Fig. 1. Total shrub intake by sheep ($n=12$; 6 males and 6 females; mean weight = 23.1 ± 1.6 kg; cross between Pramenka and Wunterberg breeds) and goats ($n=12$; 6 males and 6 females; mean weight = 19.8 ± 1.9 kg; cross between Saanen and Alpine breeds) offered six (*Quercus ilex*, *Erica multiflora*, *Arbutus unedo*, *Juniperus phoenicea*, *Viburnum tinus*, and *Pistacia lentiscus*), three (*Juniperus phoenicea*, *Helichrysum italicum*, and *Juniperus oxycedrus*), two (*Juniperus phoenicea* and *Helichrysum italicum*), or one (*Juniperus phoenicea*) shrub species. Supplemented animals received 20 g of activated charcoal plus ground barley (100–200 g). Controls received the barley carrier in Exp. 1 and 2 and no grain in Exp. 3 and 4. Different letters indicate that charcoal-treated animals and controls differed ($P < 0.05$) within an experiment. From Rogosic et al. (2006c).

When six Mediterranean shrub species (three high-terpene and three high-tannin species) differing in amounts and classes of secondary compounds were fed together, activated charcoal had no effect on total intake by sheep and goats (Fig. 1). Complementary interactions of shrubs varying in nutrients and classes of secondary compounds (discussed below) may have negated the benefit of charcoal (Rogosic et al., 2006a, 2007a). However, because animals received a different basal diet than in the other studies, it is also possible that the higher plane of nutrition diminished the effects of charcoal.

3.2. Effect of polyethylene glycol on intake of high-tannin mediterranean shrubs

Polyethylene glycol is a polymer that binds irreversibly to tannins over a wide range of pH and decreases their ability to interact with dietary and ruminal proteins, and consequently affects ruminal degradation and fermentation (Jones and Mangan, 1977; Barahona et al., 1997; Ben Salem et al., 2005; Gasmi-Boubaker et al., 2006). Supplemental PEG has been found to increase intake of high-tannin diets and shrubs by sheep and/or goats (Barahona et al., 1997; Decandia et al., 2000; Provenza et al., 2000; Titus et al., 2000, 2001;

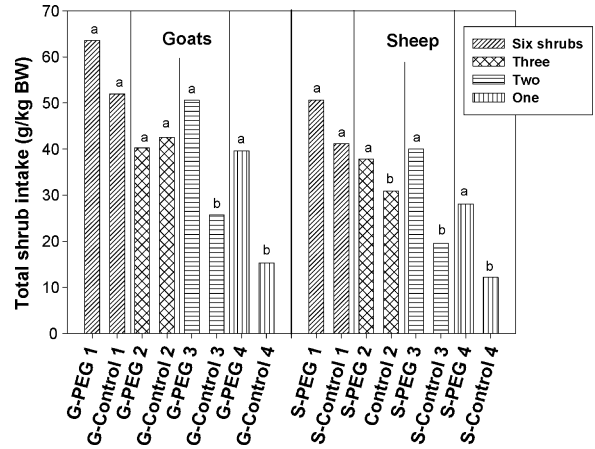


Fig. 2. Total shrub intake by sheep ($n=12$; 6 males and 6 females; 8 months of age; crossbred hair breed; mean weight = 23.0 kg) and goats ($n=12$; 6 males and 6 females; 6 months of age; purebred Alpine; mean weight = 21.2 kg) offered six (*Quercus ilex*, *Erica multiflora*, *Arbutus unedo*, *Juniperus phoenicea*, *Viburnum tinus*, and *Pistacia lentiscus*), three (*Quercus ilex*, *Arbutus unedo* and *Pistacia lentiscus*), two (*Arbutus unedo* and *Pistacia lentiscus*), or one (*Pistacia lentiscus*) shrub species. Supplemented animals received 25–50 g of polyethylene glycol (PEG) plus ground barley (100–175 g). Controls received the barley carrier in Exp. 1 and 2 and no grain in Exp. 3 and 4. Different letters indicate that PEG-treated animals and controls differed ($P < 0.05$) within an experiment. From Rogosic et al. (2007b).

Villalba et al., 2002b) and cattle (Landau et al., 2000b). When three high-tannin Mediterranean shrubs (*Arbutus unedo*, *Pistacia lentiscus*, and *Quercus ilex*) were offered (Rogosic et al., 2007b), PEG increased total shrub intake in sheep but not goats (Fig. 2). Also, increased intake was observed when two (*Arbutus unedo* and *Pistacia lentiscus*) or one (*Pistacia lentiscus*) shrub was offered to both sheep and goats receiving PEG; however, the PEG treatment was confounded with the barley carrier in the latter two studies. The relatively unpalatable shrub *Pistacia lentiscus* was consumed to some extent even when offered with another more palatable shrub (*Arbutus unedo*). Further, goats and sheep offered two shrubs with PEG (in a barley carrier) ate much more of both shrubs than controls (Fig. 2), suggesting the PEG effectively reduced the impact of tannins from *Pistacia lentiscus* and *Arbutus unedo* (again the effect of energy cannot be completely discounted). However, Decandia et al. (2000) reported that goats browsing Mediterranean scrubland increased percentage of *Pistacia lentiscus* in the diet (over two-fold) and total intake of condensed tannins when fed a concentrate carrier with PEG versus the carrier alone.

When sheep and goats were offered six dominant Mediterranean maquis shrubs (including three high-tannin shrub species) and when goats were offered three

high-tannin shrubs, PEG supplementation had no effect on intake (Fig. 2). In general, as number of shrubs on offer decreased, the effect of PEG on shrub intake increased, although not statistically comparable because of confounding in time and methodological inconsistencies among studies. Because tannins interact with overall animal nutrition in such a variable manner and because PEG is relatively expensive, its benefits should be examined for each specific situation (Mueller-Harvey, 2006).

3.3. Effect of calcium hydroxide on intake of tannin-rich mediterranean shrubs

The ability of hydrolyzable tannins to bind with proteins and other reactive substances could affect browsing animals positively if formation of complexes between these tannins and other agents prevents absorption from the alimentary tract. Calcium hydroxide supplementation has been used as an antidote for hydrolyzable tannin poisoning in rabbits (Dollahite and Camp, 1962), calves (Dollahite et al., 1966), and goats (Murdiati et al., 1990), while other calcium salts (acetate, carbonate, chloride, and lactate) were all ineffective in preventing tannic acid poisoning in rabbits (Dollahite and Camp, 1962). Formation of insoluble complexes between hydrolyzable tannins and calcium hydroxide that deter absorption is the likely mechanism of detoxification (Murdiati et al., 1990).

Intake of a mixture of three tannin-rich shrubs of the Mediterranean maquis (*Quercus ilex*, *Arbutus unedo*, and *Pistacia lentiscus*) by sheep and goats was increased with calcium hydroxide (Rogosic et al., unpublished data; Fig. 3). However, no beneficial effect on intake was detected for calcium hydroxide with the most diverse diets (six shrubs, three of which were high-tannin shrubs) in either sheep or goats (Fig. 3), possibly because the greater variety of shrubs in attenuated effects of the additive. However, there was also no difference for the single component diet (*Pistacia lentiscus*), in contrast to expectations.

3.4. Importance of biological and biochemical diversity on intake of mediterranean shrubs

Dietary combinations containing a greater number of Mediterranean shrub species generally resulted in greater total intake of both goats and sheep (Rogosic et al., 2006a,c, 2007a,b; Rogosic et al., unpublished data). This effect of increased species in the diet on intake was observed regardless of whether the shrubs represented a single class or two classes of compounds (Rogosic et al., 2006a, 2007a). Total intake decreased

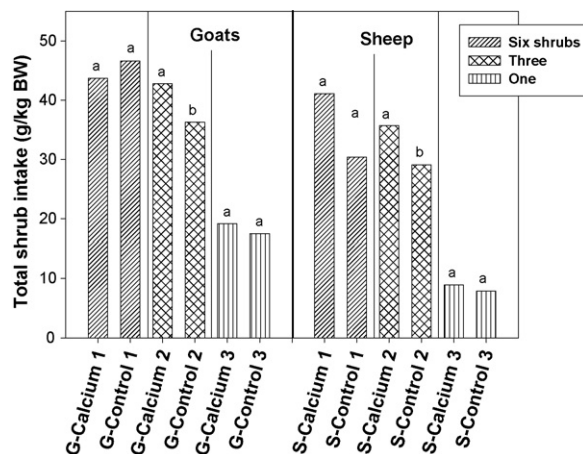


Fig. 3. Total shrub intake by sheep ($n = 12$; 7 males and 5 females; 4 months of age; crossbred Pramenka; mean weight = 17.7 ± 1.5 kg) and goats ($n = 12$; 6 males and 6 females; 5 months of age; Saanen and Alpine crossbreeds; mean weight = 16.8 ± 2.1 kg) offered six (*Quercus ilex*, *Erica multiflora*, *Arbutus unedo*, *Juniperus phoenicea*, *Viburnum tinus*, and *Pistacia lentiscus*), three (*Quercus ilex*, *Arbutus unedo* and *Pistacia lentiscus*), or one (*Pistacia lentiscus*) shrub species. Supplemented animals received 20 g of calcium hydroxide plus ground barley (180 g). Controls received the barley carrier in Exp. 1 and 2 and no grain in Exp. 3. Different letters indicate that calcium hydroxide-treated animals and controls differed ($P < 0.05$) within an experiment. Rogosic et al., unpublished data.

as number of high-tannin or high-terpene shrub species offered decreased numerically from six to three and from three to two or one species (Figs. 1–3). As noted earlier, statistical comparisons are not possible because of methodological differences and confounding in time among experiments. The likelihood of consuming more of a particular toxin and fewer classes of secondary compounds increases as biodiversity and number of dietary choices decreases, while the potential for positive toxin/nutrient interactions is diminished. Greater plant/biochemical diversity may allow animals to learn to mix diets and minimize the negative consequences of toxins and improve nutrient status, and to learn to consume different classes of toxins and minimize negative effects on metabolism (Provenza et al., 2003). Thus, the availability of a variety of shrub species varying widely in forage quality and secondary chemical concentrations in the maquis plant community (Rogosic et al., 2006a,b, 2007a) may influence intake as well as nutrient-toxin and complementary toxin–toxin interactions as well as the upper limit of intake of Mediterranean shrubs. If herbivores learn associations between flavor and different post-ingestive consequences, they should increase their preferences for different flavor intensities depending on the extent of the nutritional reward.

Sheep and goats are primary consumers of Mediterranean shrublands, and therefore shape the diversity, structure, and dynamics of these extensive ecosystems. In many traditional systems in the Mediterranean Basin, people have mixed flocks of sheep and goats as a strategy to maximize utilization of natural resources (Bourbouze and Rubino, 1992). Although both are mixed feeders, goats typically consume more browse and use shrubs more efficiently than sheep (Landau et al., 2000a; Rogosic et al., 2006b). When a high biodiversity diet (six shrub species) was offered to sheep and goats (Figs. 1–3), goats consistently consumed more total shrubs than sheep (Rogosic et al., 2006b,c, 2007b; Rogosic et al., unpublished data). Both sheep and goats generally preferred *Erica multiflora*, *Viburnum tinus*, *Quercus ilex*, and *Arbutus unedo* over *Pistacia lentiscus* and *Juniperus phoenicea* (Rogosic et al., 2006b). Presumably the reason for low intake of the latter two shrubs was not poor nutritional quality (Rogosic et al., 2006b), but rather because they contained high concentrations of secondary compounds. High concentrations of tannins in *Pistacia lentiscus* (Perevolotsky et al., 1993) and high essential oil and terpene content of *Juniperus* spp. (Pritz et al., 1997; Sorensen et al., 2004) likely reduce preference by sheep and goats. Sheep and goats responded similarly to shrub diets in the sense that both species increased intake over time regardless of number offered or number of classes of secondary compounds present (Fig. 4), suggesting ongoing adaptation. Also, as number of shrub species offered decreased, total shrub intake decreased

for both goats and sheep. Even though goats generally ingested higher levels of shrubs than did sheep in all experiments, goats and sheep both responded similarly to supplemental charcoal, PEG, and calcium hydroxide. One exception was that when three high-tannin shrubs (*Arbutus unedo*, *Pistacia lentiscus*, and *Quercus ilex*) were offered, PEG increased total shrub intake in sheep but not goats (Rogosic et al., 2007b; Fig. 2).

Goats appear to be more tolerant of secondary compounds than sheep. Intake and dry matter digestibility of tannin-containing forages are often higher for goats than sheep (Salem et al., 2006). Browsing species (e.g., mule deer) have been shown to secrete more proline-rich tannin-binding salivary proteins than grazing animals such as cattle and sheep (Robbins et al., 1987; Makkar and Becker, 1998; Müller-Schwarze, 1991). These proteins form stable complexes that are excreted primarily via feces (Shimada, 2006). Although it has been hypothesized that mixed-feeders such as goats produce proline-rich salivary proteins as a means of coping with consumption of tannins, Distel and Provenza (1991) did not detect their presence in goat saliva, regardless of whether they had been adapted to a high-tannin diet. Possibly, differences in ruminal fermentation and adaptation of rumen microbes to tannins also may enable goats to more efficiently use tannin-rich foods than sheep (Landau et al., 2000a). Another possibility is that goats and sheep differ in their ability to absorb and/or detoxify tannins. Boyle et al. (2000) reported that specialist marsupials produce more extensively oxidized compounds than generalists and require less conjugation to make secondary compounds water soluble for excretion and therefore waste fewer nutrients during detoxification. Perhaps goats also utilize Phase I enzymes more effectively than sheep. Also, efflux transporters such as permeability glycoprotein that actively move lipophilic compounds back into the lumen to prevent absorption may afford specialist woodrats more resistance to secondary compounds than generalists (Sorensen et al., 2006). Possibly, goats utilize this mechanism more efficiently than sheep, although these metabolic processes have not been explored in small ruminants.

Irrespective of differences in shrub consumption between goats and sheep in previous studies (Rogosic et al., 2006b,c, 2007b; Rogosic et al., unpublished data), biological diversity plays an important role in foraging of herbivores on Mediterranean rangelands (Rogosic et al., 2007a). Increasing number of shrubs fed increased total intake in small ruminants, regardless of whether shrubs represented a single class of compounds or more than one (Rogosic et al., 2006a,c, 2007a). Croatian rangelands have a high diversity of plants that provide nutritional

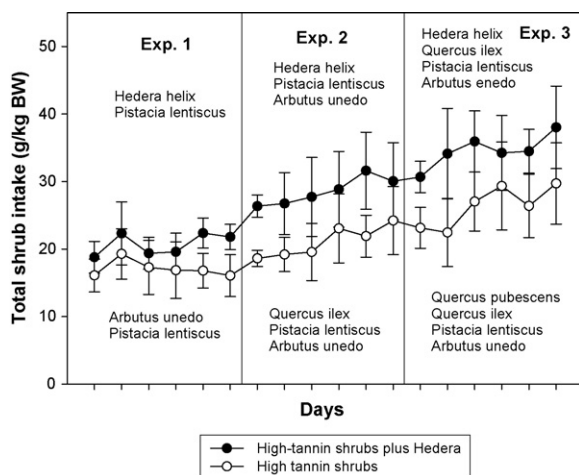


Fig. 4. Total daily shrub intake (\pm S.E.) by sheep ($n = 12$; 6 months of age, cross between Pramenka and Wunterberg breeds; mean weight = 27.2 kg) offered different combinations of high-tannin shrubs (*Quercus ilex*, *Quercus pubescens*, *Arbutus unedo*, and *Pistacia lentiscus*) with or without the high-saponin shrub *Hedera helix*. From Rogosic et al. (2007a).

forage and habitat for a variety of wildlife and livestock species (Rogosic et al., 2006b). If biodiversity is reduced and a few shrub species become dominant in the Mediterranean maquis, it will be more difficult for herbivores to select a variety of plants that maximize nutritional status while minimizing toxin consumption and enhancing secondary compound complementarity (Provenza et al., 2003). A note of caution is warranted when extrapolating results from pen studies to rangeland conditions, given the restrictions on an animal to browse plants and plant parts selectively, limitations on movement and associated energetic costs, etc., that may affect strategies for coping with secondary compounds.

3.5. Importance of secondary compound complementarity on intake of mediterranean shrubs

It has long been assumed that animals select diets that optimize nutrient intake and minimize intake of toxins or classes of toxins (Freeland and Janzen, 1974; Westoby, 1978). These hypotheses (based on nutritional constraints versus limitations of detoxification) are alternative (but not mutually exclusive) hypotheses for explaining food complementarity. The detoxification limitation theory suggests herbivores maximize intake by selecting a variety of plants to meet nutritional requirements while spreading detoxification over a greater number of pathways to minimize competition for and saturation (via enzyme and co-substrate depletion) of detoxification pathways (Marsh et al., 2006a). Although little actual metabolic evidence exists to support this hypothesis, feeding behavior and intake responses generally suggest that animals can detect that a detoxification pathway is becoming saturated and adjust feeding accordingly by modifying behavior (reducing intake, changing length or number of feeding bouts, etc.) or switching to another forage containing compounds that rely on a different metabolic pathway, presumably to allow time for clearance of saturated toxins (Wiggins et al., 2003; Marsh et al., 2006a; Wiggins et al., 2006). Marsh et al. (2006b) tested this hypothesis by feeding compounds that rely on similar or divergent detoxification pathways to brushtail possums in various combinations. In general, they found that intake did not differ when one versus two compounds were fed that used competing pathways, while intake differed when one versus two compounds with dissimilar pathways were fed. Because detoxification is very complex due to the number of factors involved (toxin detection by the animal, enzymes and co-substrates, end product removal, ATP supply, acid/base balance regulation,

etc.), there are probably no truly independent pathways, but rather, degrees of separation (Marsh et al., 2006b).

Tannins and saponins are two classes of secondary compounds prevalent in Mediterranean shrubs. Goats that were allowed to choose among shrub species containing tannins or saponins consumed combinations that increased total intake, apparently by reducing adverse effects associated with consumption of either toxin alone (Rogosic et al., 2006a). Sheep also consumed more total shrubs when fed a mixture containing both high-tannin and high-saponin shrubs than when fed an equal number of only tannin-containing shrubs (Rogosic et al., 2007a; Fig. 4). A complementary interaction may have occurred for shrubs containing both classes of compounds, especially considering intake of the shrub with the highest tannin content (*Pistacia lentiscus*) was increased in all experiments when fed with the saponin-containing *Hedera helix* (Rogosic et al., 2007a). Phytochemical complementarity is based on the premise that different plant species containing different types and concentrations of secondary metabolites enable herbivores to select different combinations of secondary compounds in order to minimize toxic effects. In addition, certain compounds (e.g., tannins and saponins) may form complexes in the gastrointestinal tract, thereby reducing negative effects of these compounds in the intestine and/or partially reducing absorption and the reliance on a particular detoxification pathway (Freeland et al., 1985). Complementary interactions may occur if detoxification is spread over more pathways in the case of readily absorbable compounds or through dilution of the impact on a specific pathway when plants with highly absorbable compounds are consumed in conjunction with poorly absorbed phytotoxins that cause other physiological problems (e.g., gut necrosis, decreased nutrient availability, etc.). Complementary interactions between high-tannin and high-saponin shrubs (Fig. 4) could decrease the impacts of toxin consumption if herbivores select diets that capitalize on these beneficial interactions. Complementary interactions between plant secondary metabolites and/or toxins have been reported to increase intake and/or modify feeding behavior in other systems (Freeland et al., 1985; Burritt and Provenza, 2000; Wiggins et al., 2003, 2006). The interactions of flavor, nutrients, and phytochemicals within a plant community may also partly explain why effectiveness of plant defenses varies with the mixture of plant species.

In general, our studies with Mediterranean shrubs indicate diet biodiversity (consumption of a greater number of shrub species) typically leads to increased total

shrub intake, regardless of number of classes of compounds contained (Rogosic et al., 2006a,c, 2007a,b; Rogosic et al., unpublished data). This may be partially attributed to the fact that classes of compounds in shrubs are not mutually exclusive (i.e., even though a particular shrub species is classified as high in a particular class of compounds, it may contain some level of another compound or class of compounds) and the fact that within a class of compounds, a great deal of variation exists in the chemical attributes and absorbability of specific compounds.

Furthermore, other factors (nutrients, associative effects among secondary compounds, animal experience, transient aversions from satiety, etc.) affect foraging activities, and detoxification pathways overlap and degrees of separation exist among them (Marsh et al., 2006b). Because each shrub species likely has a unique combination of primary and secondary compounds that creates a unique flavor and nutrient profile, it might be expected that intake would increase as diet diversity increases. However, the positive effect of the saponin-containing *Hedera helix* on intake was observed even as number of shrubs offered and biological diversity of the diet increased (Rogosic et al., 2006a, 2007a).

4. Conclusions

Garrigues and maquis plant communities are extensive vegetation types in the Mediterranean region and an important habitat for wild and domestic herbivores. Although most of these shrubs are nutritious, secondary compounds (tannins, terpenes, saponins, etc.) decrease their forage value. Nutrients and “medicinal” additives (e.g., activated charcoal, polyethylene glycol, and calcium hydroxide) may have potential for enhancing shrub intake through decreased absorption and/or increased elimination of secondary compounds. The biological diversity of Mediterranean maquis vegetation also positively influences shrub consumption by small ruminants. Consumption of shrubs containing complementary chemical classes (e.g., tannins and saponins) together may lead to chemical interactions within the intestinal tract that reduce their toxic effects and/or increase their efficiency of detoxification. In general, sheep and goats responded similarly. Both sheep and goats typically increased shrub intake from the beginning to the end of each experiment, indicating ongoing adaptation to shrubs. Although goats consumed more total shrubs than sheep across experiments, both species responded similarly to supplemental charcoal, PEG, and calcium hydroxide.

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