

Goat preference for phylogenetical diverse compared to similar Mediterranean shrubs

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Abstract

Goat preference for phylogenetically diverse Mediterranean shrubs is key to understanding ecological relationships between plant and animal components of these shrubby ecosystems. In this study, we explore the preference of goats for phylogenetically diverse compared to similar Mediterranean shrubs. In four consecutive experiments, goats in group 1 were fed with one, two, three or four similar oak species (*Quercus pubescens*, *Q. ilex*, *Q. cerris* and *Q. petraea*), while goats in group 2 were fed with one, two, three and four phylogenetically diverse shrubs (*Fraxinus ornus*, *Arbutus unedo*, *Hedera helix* and *Juniperus oxycedrus*) that belong to different genera, family, order and subclasses. There was no difference in biomass intake between groups in Exp. 1 (17.76 ± 0.91 vs. 15.92 ± 0.79 g/kg BW; $P = 0.52$) and Exp. 2 (27.03 ± 0.86 vs. 30.79 ± 0.79 g/kg BW; $P = 0.12$). However goats in the phylogenetically diverse group 2 consumed more biomass in Exp. 3 (28.99 ± 0.91 vs. 39.57 ± 1.13 g/kg BW; $P < 0.001$) and Exp. 4 (31.67 ± 0.94 vs. 45.67 ± 1.01 g/kg BW; $P < 0.001$) in comparison to goats fed with phylogenetical similar oak (*Quercus*) species. Our results confirm the hypothesis that intake of plant biomass often increases when animals are offered different plant species which are phylogenetically more diverse.

Introduction

Mediterranean maquis type vegetation is generally composed of broadleaf evergreen small trees, with a mixture of several dominate oak species and diverse sclerophyllous shrubs. Plants as food for herbivores may differ in their quality between individuals of the same species and between different species of the same genus, but quality differences may be more pronounced between species which belong to different plant genera, families and orders because of greater phylogenetic distances (Crane et al., 2004; Rasmann and Agrawa, 2011). These variations include differ-

ences in nutritional value, concentration of plant secondary metabolites (PSM) as well as morphological and physiological characteristics of each plant species (Hartley and Jones, 1997). Genetic differences (Osier and Lindroth, 2001), dissimilarities in environmental growing conditions (Larsson et al., 1985) or differing histories of relationships with herbivores (Pfister, 2000; Provenza et al., 2003) instigate this high variability in plant characteristics, creating a nutritional disparity for herbivores.

Mediterranean shrubs with a diverse array of PSM may allow goats to harvest higher amounts of nutrients while maintaining PSM intake below toxic levels

(Pfister et al., 1997; Rogosic et al., 2007b). This is possible because PSM that affect different organs and detoxification pathways are likely to be less toxic when ingested as attenuate mixtures than when each PSM is ingested in a larger dose (Freeland and Janzen, 1974). Brushtail possums (*Trichosurus vulpecula*) have higher consumption of food when offered two diets containing phenolics and terpenes than when offered individually diets (Dearing and Cork, 1999). Mule deer (*Odocoileus hemionus*) also eat more sagebrush (*Artemisia tridentata*) and juniper (*Juniperus communis*), which contain different terpenes, when offered together than individual offerings (Smith, 1959). Sheep consume more when offered foods with different class of toxins that have different mechanisms of detoxification (Villalba et al., 2004; Lyman et al., 2008). A different class of PSM may also neutralize or inactivate toxins. Sheep eat more of a combination of Mediterranean shrubs containing tannins and saponins than shrubs containing only tannins, because tannins and saponins chelate in the intestinal tract, thus reducing the negative effects of both components (Rogosic et al., 2003; Rogosic et al., 2007b). Sheep and goat experiences with combinations of Mediterranean shrubs that contain complementary PSMs may elevate preference for these shrubs. Besides tannin and saponin complementary interactions, biological/biochemical diversity of a higher number of shrubs offered to goats is potentially important in increasing forage intake and animal performance on Mediterranean shrublands (Rogosic et al., 2006a, 2006b).

Our objective was to determine the preference of goats for different Mediterranean shrub species that belong to diverse plant genera, families, orders and subclasses that dominate the Mediterranean shrublands in parts of Croatia and Bosnia/Herzegovina. We hy-

pothesized that intake of shrub biomass would increase when goats were offered different shrub species which are phylogenetically more distant, and thus have higher biogenetical diversity than oak shrubs that belong to the same *Quercus* genus (*Quercus pubescens*, *Q. ilex*, *Q. cerris* and *Q. petraea*). Specifically, we seek to answer how more or less phylogenetic cognations between Mediterranean shrubs influences their preference by domestic goats.

Materials and Methods

Shrubs of the Same and Different Genera

Four trials were conducted at an experiment station in Zemunik Donji, 12 km from Zadar in the central part of the Croatian Adriatic coast (lat 44°06'N, long 15°23'E). Research protocols for the study were approved by the Ministry of Agriculture, Agency for Animal Care and Use Committee; No. UP/I-322-01/11-01/118, Republic of Croatia. In the four consecutive experiments the phylogenetical similar shrubs of the genus *Quercus* offered to the goats in the first experimental group, while the phylogenetical diverse Mediterranean shrubs offered to the goats in the second experimental group (table 1).

Shrubs were harvested each week from the vicinity of the feeding experiments. Shrub leaves and current season's growth (i.e., twigs) were clipped and ground to 1 cm length with a chipper, mixed for uniformity, placed in woven, polyethylene feed sacks, and stored at 4°C. Every day before the experiment, sufficient feed was removed from cold storage and offered to the animals.

Table 1. Experimental design: similar and diverse Mediterranean shrubs offered to the first and second experimental groups of goats during the 10 days.

Experiments	Phylogenetical similar shrubs in Group 1	Phylogenetical diverse shrubs in Group 2
Exp.1	<i>Quercus pubescens</i> L. (Fagaceae)	<i>Fraxinus ornus</i> L. (Oleaceae)
Exp.2	<i>Quercus pubescens</i> L. (Fagaceae)	<i>Fraxinus ornus</i> L. (Oleaceae)
	<i>Quercus ilex</i> L. (Fagaceae)	<i>Arbutus unedo</i> L. (Ericaceae)
Exp.3	<i>Quercus pubescens</i> L. (Fagaceae)	<i>Fraxinus ornus</i> L. (Oleaceae)
	<i>Quercus ilex</i> L. (Fagaceae)	<i>Arbutus unedo</i> L. (Ericaceae)
	<i>Quercus cerris</i> L. (Fagaceae)	<i>Hedera helix</i> L. (Araliaceae)
Exp.4	<i>Quercus pubescens</i> L. (Fagaceae)	<i>Fraxinus ornus</i> L. (Oleaceae)
	<i>Quercus ilex</i> L. (Fagaceae)	<i>Arbutus unedo</i> L. (Ericaceae)
	<i>Quercus cerris</i> L. (Fagaceae)	<i>Hedera helix</i> L. (Araliaceae)
	<i>Quercus petraea</i> (Matt.) Liebl. (Fagaceae)	<i>Juniperus oxycedrus</i> L. (Cupressaceae)

Animals and Diets

Twelve goats used in the experiments were 6-month-old crossbred Saanen and Croatian speckled goats. Each group was an equal mix of both sexes. Goats weighed 21.2 ± 1.07 kg at the beginning of the experiment and 21.54 ± 1.21 kg at the end. All animals were raised on the same farm on the island of Brač (Central Dalmatia) and were adapted to the shrubby vegetation of the Mediterranean maquis. To reduce neophobia, the experimental animals were offered each shrub singly for 120 minutes each day for five days before the trials commenced. Preference was then established for all eight shrubs simultaneously for five days. They were offered to each animal in individual feeding boxes, and continually replenished from 0830 to 1400 hours. Total individual shrub intake was also recorded for each animal. Goats were systematically divided into two treatment groups based on total shrub intake. Total shrub intake was ranked and all odd ranks were placed in one treatment and even ranks in the other. Animals remained in their respective treatment groups for all four experiments.

Feeding

Throughout the experiments, animals had free access to trace mineral blocks and fresh water. Alfalfa pellets were used as the basal feed and were offered at 50% of basal *ad libitum* intake after the feeding trials each day. In all experiments both groups of animals were supplemented with barley (100g) at 0800 hours, then offered the ground shrubs from 0830 to 1400 hours. Shrubs were fed in individual boxes to each animal, and the amounts replenished as necessary during the day. Any uneaten amounts were weighed.

Trials were 10 days and ran consecutively. Goats in the *Quercus*-group were fed different species of oak (*Quercus*) genus. Goats in the diverse genera-group were fed species that belong to different genera, families, order and subclasses. From the phylogenetic point of view the shrubs species offered to goats in second group are very heterogeneous and much more phytochemical diverse.

Statistical Analysis

The total daily shrub intake of each goat was used as the dependent variable in the analysis. The experimental design for all four experiments was a completely random design. Animals were a random factor in the mixed model analysis (SAS 2000). The repeated measures model included the two experimental groups (group 1 vs. group 2) with individual animals nested within group, and day as a repeated measure with all

other interactions included. All analyses on shrub intake were adjusted for body weight (g/kg body weight). Data were analyzed by using Proc Mixed (SAS 2000).

Results

In Exp. 1 (Fig. 1; Exp.1), goats in group 1 were offered a high tannin shrub *Q. pubescens*, while *F. ornus* was offered to goats in group 2. Intake of *Q. pubescens* by goats in group 1 was 17.76 ± 0.91 g/kg BW and intake of *F. ornus* in group 2 was 15.92 ± 0.79 g/kg BW. There was neither treatment effect nor day x treatment interaction ($P > 0.5$), but there was a day effect ($P < 0.05$). Goats in both groups progressively increased intake of both shrubs from the first to the last day in experiment. In Exp. 1, shrub intake varied between 10 g/kg BW and 25 g/kg BW (Fig. 1; Exp. 1).

In Exp. 2 (Fig. 1; Exp. 2), goats in group 1 were offered two tannin-rich shrubs *Q. pubescens* and *Q. ilex*. Goats in the diverse group were given *F. ornus* and *A. unedo*. There was no treatment effect (27.03 ± 0.86 vs. 30.79 ± 0.79 g/kg BW, $P = 0.12$) nor day x treatment interaction ($P = 0.95$). Goats in group 1 (Fig. 2; Exp.2) ate significantly more *Q. pubescens* (19.77 ± 1.03 g/kg BW, $P = 0.017$) than *Q. ilex* (7.26 ± 0.77 g/kg BW). Likewise, goats in group 2 (Fig. 2; Exp.2) ate significant more ($P < 0.001$) *F. ornus* (22.59 ± 1.07 g/kg BW) than *A. unedo* (8.21 ± 0.48 g/kg BW). Here, it is important to emphasize that the experimental animals consumed considerable lower amounts of both new shrub species introduced in Exp. 2 than the original species. However, introducing new shrubs species into goats diet in Exp. 2 appeared to increase total shrub intake in both groups ($P < 0.001$). In Exp. 2, shrub biomass intake by goats varied between 25 g/kg BW and 35 g/kg BW.

In Exp. 3 goats in group 1 were provided a mixture of three high-tannin oak species (*Q. pubescens*, *Q. ilex* and *Q. cerris*). Total foliage intake did not increase in relation to Exp. 2 (from 27.03 ± 0.86 g/kg BW to 28.99 ± 0.91 g/kg BW, $P = 0.629$, Fig 4). In contrast, experimental goats in group 2 increased the amount of foliage consumed (from 30.79 ± 0.79 g/kg BW to 39.57 ± 1.13 g/kg BW, ($P < 0.001$)).

There was a main treatment effect in Exp. 3 as goats in group 2 (Fig. 1; Exp. 3) ate significantly ($P < 0.001$) more foliage of the more diverse shrub species (*F. ornus*, *A. unedo* and *H. helix*) than goats in the *Quercus* group (39.57 ± 1.13 vs. 28.99 ± 0.91 g/kg BW). Further, there was a treatment x day effect ($P = 0.03$). In the first four days the difference in foliage intake between

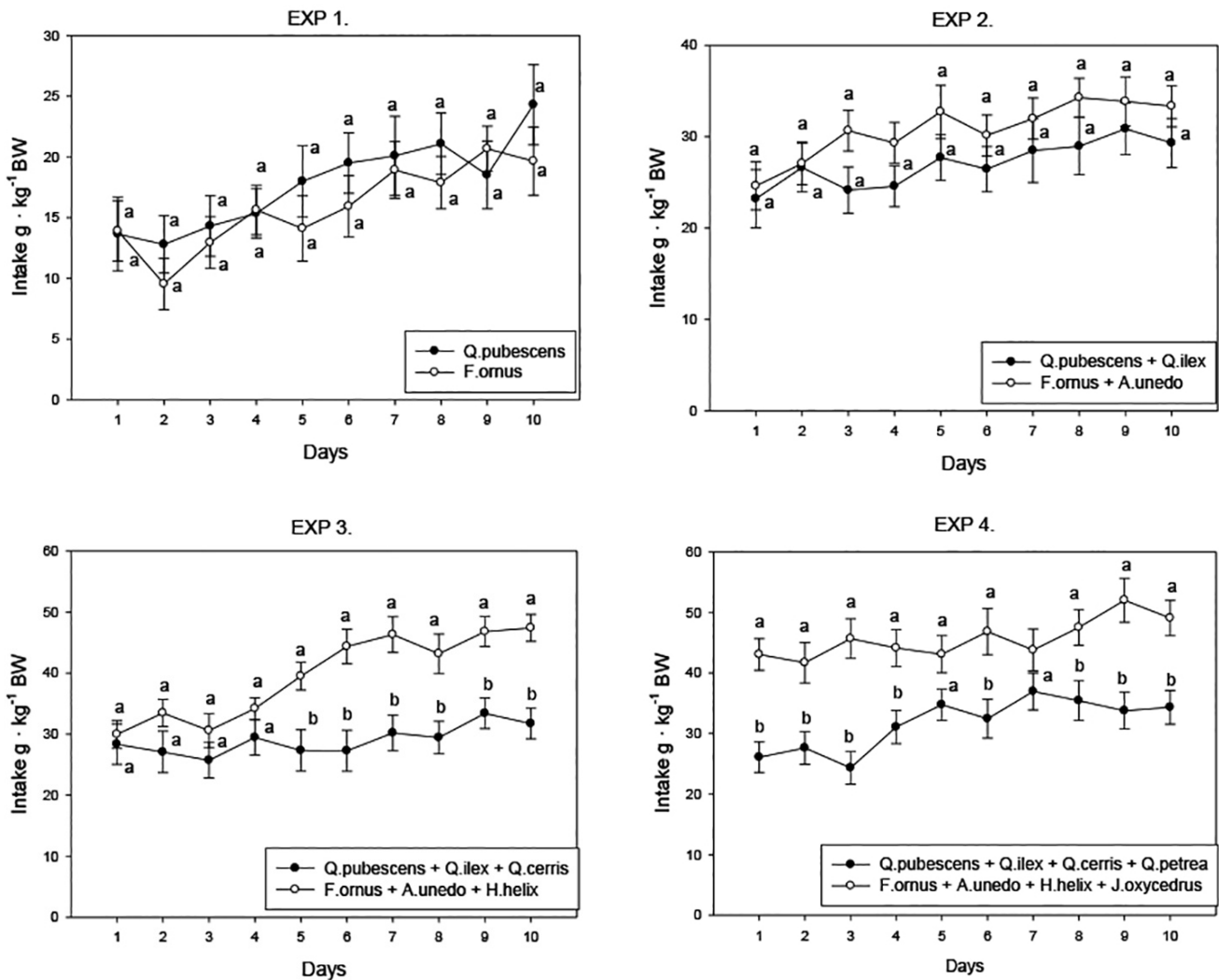


Figure 1. Daily shrub biomass intake ($\text{g/kg BW} \pm \text{SE}$) of the oak species (*Quercus pubescens*, *Quercus cerris*, *Quercus ilex* and *Quercus petraea*) offered to goats in group 1 and four phylogenetical diverse plant species (*Fraxinus ornus*, *Arbutus unedo*, *Hedera. helix* and *Juniperus oxycedrus*) offered to goats in group 2 during the four experiments. Different letters indicate the statistical significant differences ($P < 0.05$).

experimental groups was not significant, but there were treatment differences on days 5 to 10 (Fig. 1, Exp. 3). Shrub biomass intake in group 1 fluctuated around 30 g/kg BW , with a negligible increase from the first to the last day of the trial, while shrub biomass intake in group 2 was greatly increased, especially after the fourth day.

In Exp. 4 (Fig. 1; Exp. 4) goats in group 2 fed with four very diverse shrubs (*F. ornus*, *A. unedo*, *H. helix* and *J. oxycedrus*) ate significantly more ($P < 0.001$) shrub biomass than goats in group 1 fed four species of oak (*Q. pubescens*, *Q. ilex*, *Q. cerris* and *Q. petraea*) (45.67 ± 1.01 vs. 31.67 ± 0.94 g/kg BW). Considering only *Quercus* intake by goats within group 1 (Fig. 2), goats consumed significantly ($P < 0.001$) more *Q. pubescens* biomass (22.42 ± 1.17 g/kg BW) compared to *Q. ilex* (4.34 ± 0.39 g/kg BW), *Q. cerris* (2.88 ± 0.33 g/kg BW) and *Q. petraea* (2.031 ± 0.22 g/kg BW). Likewise, goats in group 2 offered shrubs of diverse

geniuses (Fig. 3) ate a significantly ($P < 0.001$) higher amounts of *H. helix* (24.77 ± 1.09 g/kg BW) in relation to *A. unedo* (4.11 ± 0.28 g/kg BW), *J. oxycedrus* (3.89 ± 0.43 g/kg BW) and *F. ornus* (12.89 ± 0.65 g/kg BW). Also, goats in group 2 consumed more ($P < 0.001$) *F. ornus* biomass in relation to *A. unedo* and *J. oxycedrus*. It is important to note that intake of *F. ornus* decreased after the highly palatable shrub *H. helix* was included in the diet/experiment

In Exp. 3 and Exp. 4, goats in group 2 fed phylogenetically diverse shrubs ate significantly ($P < 0.001$) more foliage than goats in group 1 fed with combinations of high-tannin *Quercus* shrubs (Fig. 4). When we included *Q. ilex* in goat diets in group 1 in Exp. 2 total consumption of both oaks (*Q. pubescens* and *Q. ilex*) significantly increased ($P < 0.001$), but when the other two oaks (*Q. cerris* in Exp. 3 and *Q. petraea* in Exp. 4) were included there was not a significant increase ($P = 0.62$; $P = 0.37$) (17.76 ± 0.91 vs. 27.03 ± 0.86

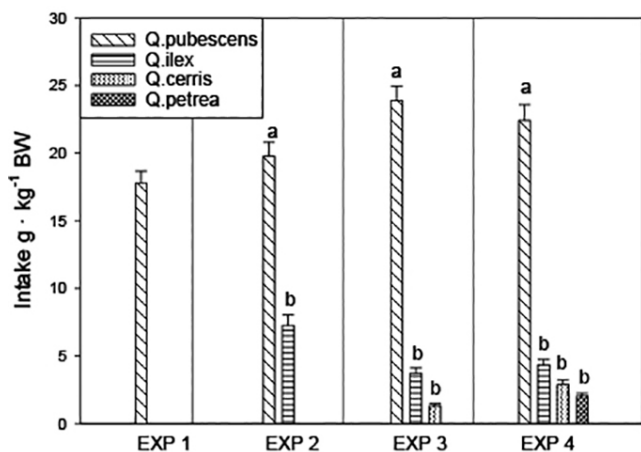


Figure 2. Average of oak shrubs (*Quercus pubescens*, *Quercus cerris*, *Quercus ilex* and *Quercus petraea*) biomass intake (g/kg BW \pm SE) by goats through the all experiments. Different letters indicate the statistical significant differences ($P < 0.05$) between species in each experiment.

vs. 28.99 ± 0.91 vs. 31.67 ± 0.94 g/kg BW). However, when goats in group 2 were provided a mixture of two, three and four phylogenetical diverse species (*F. ornus*, *A. unedo*, *H. helix* and *J. oxycedrus*) the total biomass intake significantly increased ($P < 0.001$; $P < 0.001$; $P = 0.005$) (15.92 ± 0.79 vs. 30.79 ± 0.79 vs. 39.57 ± 1.13 vs. 45.67 ± 1.01 g/kg BW).

Discussion

Based on the higher biological/biochemical diversity of shrubs, we predicted that goats would increase their intake of the phylogenetically more distant shrubs when compared to more related Mediterranean oak species regardless of their nutritional value. Overall, our results support these hypotheses, and show that goats ate more of the biochemically diverse shrubs than the biochemically similar oak species. Given a choice of two genetically more diverse and more similar shrubs categories offered to goats, we expected a higher preference for biochemically diverse shrubs and these differences increased from the second to the last experiment (Fig. 4).

The relationship between phylogenetic distances implies a greater diversity in plant secondary compounds, and is a key to understanding mechanisms of plant animal interactions in Mediterranean shrubby ecosystems. Secondary metabolites function as a defense against herbivores, so their class, concentrations and diversity determine herbivore preference (Hajer et al., 2005; Rogosic et al., 2007b), and therefore have an important role in the plant's survival in natural conditions. Likewise they represent adaptive characteristics

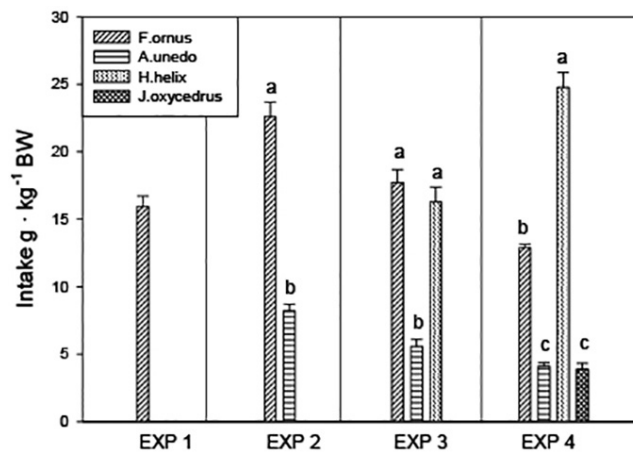


Figure 3. Average intake of four phylogenetical diverse species (*Fraxinus ornus*, *Arbutus unedo*, *Hedera helix* and *Juniperus oxycedrus*) (g/kg BW \pm SE) by goats through the all experiments. Different letters indicate the statistical significant differences ($P < 0.05$) between species in each experiment.

that have been subjected to natural selection during evolution (Rasmann and Agrawal, 2011).

Tannins in Oaks Determine Biomass Intake by Goats

The *Quercus* genus is one of the earliest angiosperms of the Miocene epoch (26-12 million years ago). Over time, oaks have divided into two main lineages (evergreen and deciduous species), with an intermediate subgenus for less genetically distinct species.. Because of their widespread distribution, oaks play a significant ecological role in many Mediterranean shrub communities. The *Quercus* genus, including the investigated oak species in this study (*Q. pubescens*, *Q. cerris*, *Q. ilex*

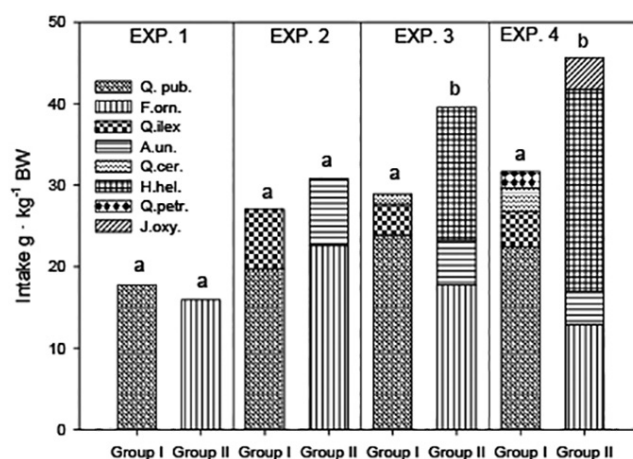


Figure 4. Total shrub intake (g/kg BW \pm SE) of goats fed with different combinations of high-tannin oaks in group 1 (*Quercus pubescens*, *Quercus ilex*, *Quercus cerris* and *Quercus petraea*), and shrubs in group 2 that belong to different species, genus, family, order and subclasses (*Fraxinus ornus*, *Arbutus unedo*, *Hedera helix* and *Juniperus oxycedrus*), $n = 6$ per treatment group; different letters indicate the statistical significant differences ($P < 0.05$) between treatment groups of each experiment.

and *Q. petraea*) contain both condensed and hydrolyzable tannins in highly variable amounts (5-15%) (Vovk et al., 2003; Okuda, 2005; Niemetz and Gross, 2005; Rogosic et al., 2006b). Tannins are a group of complex phenolic polymers that are distributed widely in a variety of plants (Silanikove et al., 1997). Based on the structural characteristics of the compounds and their reactions with hydrolytic agents, tannins are classified into condensed (MW 1000-20000) and hydrolyzable molecules (MW 500-3000; Mueller-Harvey, 1999). Hydrolyzable tannins have a central carbohydrate core to which a number of phenolic carboxylic acids are esterified, while condensed tannins are derived from the condensation of flavanol or flavan-diol. Hydrolyzable tannins are readily hydrolyzed in the stomach to sugar moieties and small phenolic compounds that may be absorbed and cause toxicity.

In contrast, condensed tannins are polymerized into larger molecules that are not absorbed readily and are unlikely to cause toxicity (Jones and Mangan, 1977). Condensed tannins bind and precipitate proteins and starch (Rhoades and Cates, 1976; Reed, 2001). Negative effects of condensed 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). However, 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 complexes with proteins (Ben Salem et al., 2005; Min et al., 2006). Other potential benefits of tannins include reduced flystrike and intestinal nematodes and nematode larvae (Waghorn and McNabb, 2003; Athanasiadou and Kyriazakis, 2004).

As the number of the oak species offered to the goats in group 1 increased, intake increased only in Exp. 2, when *Q. ilex* was added to *Q. pubescens*) (17.76 ± 0.91 vs. 27.03 ± 0.86 g/kg BW; $P < 0.001$). The oak intake did not increase ($P > 0.05$) when three oak shrubs in Exp. 3 (28.99 ± 0.91 g/kg BW) and four oak shrubs in Exp. 4 (31.67 ± 0.94 g/kg BW) were offered. Goats in group 1 received more closely related oak that are biochemically similar, which apparently resulted in an increase in the concentration of tannins in the goat diets. Thus, higher concentrations of tannins in their diet from similar oak species (similar chemical composition) appeared to adversely affect goats' oak intake.

High-tannin Mediterranean shrubs such as *Quercus ilex*, *Arbutus unedo*, and *Pistacia lentiscus* (Rogosic

et al., 2006b; 2007a) can depress 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 *Ceratonia siliqua* (Silanikove et al., 1994).

Phylogenetical/biological and Biochemical Diversity of Mediterranean Shrubs Increase Biomass Intake by Goats

In our study, as the number of the more phylogenetically distant Mediterranean shrubs offered to goats in group 2 increased from Exp.1 to Exp.4, shrub intake increased ($P < 0.001$; 15.92 ± 0.79 vs. 30.79 ± 0.79 vs. 39.57 ± 1.13 vs. 45.67 ± 1.01 g/kg BW). These results support the claim that phylogenetical/biological and biochemical diversity increase food intake (Provenza et al., 2003; Villalba et al., 2004; Rogosic et al., 2006a). Shrub species offered to goats in group 2 (*Fraxinus ornus*; *Arbutus unedo*; *Hedera helix* and *Juniperus oxycedrus*) belong to different genera, families, orders and subclasses, and thus represent biochemically more diverse shrub species. The introduction of new shrub species in every succeeding experiment, essentially offering a more biochemically diverse diet, may have resulted in a reduction in concentration of specific PSM in their diet, thus enabling the increased consumption of shrubs. To obtain needed nutrients on Mediterranean shrublands, goats must eat a variety of plant species that contain different kinds of PSMs. In principle, goats should be able to eat more plant biomass with different kinds of PSMs because they produce different effects in the body and they are detoxified by different mechanisms (Freeland and Janzen, 1974).

The chemical studies on *Fraxinus ornus* show the presence of many compounds belonging mainly to the groups of hydroxycoumarins, secoiridoid glucosides (hydroxyframoside A and hydroxyframoside B), phenylethanoids, flavonoids and the lignan 1-hydroxy-pinoresinol glucoside (Kostova and Iossifova, 2002). *Arbutus unedo* has a tannin index of 1.26 (Rogosic et al., 2006b). Other PSM in *Arbutus unedo* include an arbutoside and ethyl gallate (i.e., ethyl-3, 4, 5-trihydroxy benzoate) (Kouki and Manetas, 2002). *Hedera helix* contains a mixture of pentacyclic terpenoids (Burrows and Tyrl, 2001) classified as genins, monodesmosides (α -hederin and β -hederin), or bidesmosides (hederacosides C and B). This complex mixture is often referred to as saponins. Specific roles of saponins involve modification of gut microbes, particularly in ruminants (Gee et al., 1993). Saponins can damage intestinal mucosal

cells by altering cell membrane permeability and interfering with active transport (Gee et al., 1989), an effect that is dependent on the structure of the individual saponin molecule (Johnson et al., 1986). Generally, *J. oxycedrus* contains terpenes (Rogosic et al., 2011), but according to detailed chemical analyses the main constituents are α -pinene, α -phellandrene, γ -terpinyl acetate, *D*-3-carene, myrcene (Milos and Radonic, 2000). Intake of shrubs with high levels of PSMs such as terpenes is regulated by both serum and tissue concentrations and excretion rates (Dziba et al., 2006). If the excretion rate of toxins is slow the potential toxicity and metabolic cost of the detoxification are increased (Foley et al., 1987), and acid base balance may be disrupted (Illius and Jessop, 1997). This increase in organic acid load may initiate negative feedback and deter shrub intake by goats (Foley et al., 1995), though there is evidence that feedback from the toxin *per se* may be more important (Dziba et al., 2006).

Importance of Biodiversity in Mediterranean Shrubby Ecosystems

Our study provides evidence that goats prefer to eat biochemically diverse than biochemically similar Mediterranean shrubs, and indicates how ruminants cope with, and likely benefit from, secondary compounds in their diets. A stand of Mediterranean maquis contains a diverse array of PSMs which may allow goats to harvest higher amounts of nutrients while maintaining PSMs intake below toxic levels. Sheep eat more when offered choices of foods with various toxins that affect different detoxification mechanisms (Burritt and Provenza, 2000; Villalba et al., 2004). A diverse intake

of PSM from Mediterranean shrubs may also lead to toxin neutralization or inactivation, which in turn could reduce susceptibility to PSMs. Sheep and goats eat more of a combination of Mediterranean shrubs rich in tannins and saponins because tannins and saponins chelate in the intestinal tract, reducing the negative effects of both components (Rogosic et al., 2006a; Rogosic et al., 2007b). Thus, eating a combination of Mediterranean shrubs may lead to complementary interactions among PSM that may exceed the benefit of simply adding diversity to the diet s (Rogosic et al., 2006a, 2008).

Implications

Mediterranean shrublands are composed of a great variety of evergreen and deciduous shrub species widespread in Croatia and Bosnia/Herzegovina. Both evergreen and deciduous oak species are important components of these plant stands, as these species play a significant ecological role. Goats fed with phylogenetically distant and biochemically diverse shrubs that belong to different taxa increased intake in comparison to goats fed with the same number of oak species (genus *Quercus*) that are phylogenetically closely related and biochemically similar, regardless of their nutritional values. The feature of shrub communities in the Mediterranean region is the huge variation in plant species, biomass production and chemical composition. The resulting diversity of plant communities in nutrient levels and phylogenetical/biochemical similar and disparate PSMs are strong determinants of diet selection when animals forage on Mediterranean rangelands.

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