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Role of Species Diversity and Secondary Compound Complementarity on Diet Selection of Mediterranean Shrubs by Goats

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Abstract Goats foraging on Mediterranean shrubs containing secondary compounds (toxins) may consume a variety of shrubs that contain different phytotoxins, thereby increasing shrub intake and avoiding toxicosis. We conducted eight experiments to examine whether goats offered different mixtures of shrubs containing different phytotoxins (tannins and saponins) would consume more shrub biomass than goats offered one shrub a single phytotoxin (tannin or saponin). In the first three experiments, goats fed a mixture of three tannin-rich shrubs (*Quercus ilex*, *Arbutus unedo*, and *Pistacia lentiscus*) ate more foliage than goats offered only one shrub (23.2 vs. 10.7 g/kg BW; 25.2 vs. 13.4 g/kg BW, and 27.9 vs. 7.9 g/kg BW), regardless of tannin concentration in individual shrub species. Goats also consumed more foliage when offered the same three tannin-rich shrubs than when offered the saponin-rich shrub *Hedera helix* (25.4 vs. 8.0 g/kg BW). However, goats offered a mixture of the same three tannin-rich shrubs consumed less foliage than goats offered a mixture of two shrubs containing tannins and saponins: *Quercus* and *Hedera* (21.6 vs. 27.1 g/kg BW), *Arbutus* and *Hedera* (21.8 vs. 27.1 g/kg BW), and *Pistacia* and *Hedera* (19.7 vs. 22.0 g/kg BW). Comparison of intake of shrubs containing only tannins or saponins to intake of shrubs containing both tannins and saponins indicated that goats consumed more total biomass when fed with shrubs with both classes of compounds than with either tannins or saponins alone. Our

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results suggest that goats can increase intake of Mediterranean shrubs high in secondary compounds by selecting those with different classes of phytotoxins. Simultaneous ingestion of shrubs containing tannins and saponins may promote chemical interactions that inhibit toxic effects of these phytotoxins in the intestinal tract. In addition to complementary interactions between tannins and saponins, biological diversity within Mediterranean maquis vegetation also plays a positive role in increasing shrub intake by goats.

Keywords Mediterranean shrubs · Maquis · Biodiversity · Secondary compounds · Tannins · Saponins · Goats

Introduction

Goats are primary consumers of the Mediterranean maquis vegetation and thereby shape the diversity, structure, and dynamics of these extensive ecosystems (Naveh, 1972; Hodgson and Illius, 1996; Kaiser, 2000). Vegetation of these plant communities usually consists of 20–25 shrubby species (Rogosic, 2000), and its diversity, function, and stability depend on biological/biochemical links between plant and animal components of these ecosystems (Dziba et al., 2005). Plants possess a variety of flavor intensities and nutritional qualities that influence diet selection by herbivores (Villalba and Provenza, 2000). Olfactory, gustatory, visual, and tactile stimuli are important sources of information that herbivores use to detect potentially nutritious or toxic plants (Augner and Bernays, 1998). Collectively, the phytochemicals in a plant give rise to the characteristic flavor of a shrub species. Traditionally, food selection has been attributed to the innate ability of animals to sense specific flavors, nutrients, and toxins in plants through taste and smell (Rhoades, 1979), but food preference is a learned process involving complex relationships between flavor and postingestive effects of the plant (Provenza et al., 1998).

Given the diversity of plant cues that herbivores typically encounter, their ability to learn to recognize food and to generalize over food cues are important traits (Augner et al., 1998). Herbivores learn to prefer food flavors associated with macronutrients (Ralphs et al., 1995; Villalba and Provenza, 1999) and to avoid flavors paired with toxins (Ralphs, 1992). Once flavor–postingestive feedback associations have been learned, herbivores use visual and olfactory cues to recognize specific plants (Launchbaugh and Provenza, 1993), and they generalize preference and aversion across familiar cues for nutrients and toxins (Launchbaugh et al., 1993).

Goats foraging on Mediterranean shrubs that contain secondary compounds may consume a variety of foods to avoid toxicosis (Freeland and Janzen, 1974). Different toxins have different physiological effects on herbivores (Cheeke, 1998), and herbivores are equipped with various physiological mechanisms to counter toxins (McArthur et al., 1991). A varied diet composed of plant species containing different kinds of nutrients and toxins may increase food intake and animal production by enabling individuals to select plants that are biochemically complementary (Freeland et al., 1985; Rogosic et al., 2003). The objective of this study was to examine the effect of feeding Mediterranean shrubs containing varying concentrations of tannins and/or saponins on intake by goats.

Methods and Materials

Study Shrubs and Animals

The four major shrub components of goat diets in the Mediterranean maquis plant community *Orno-Quercetum ilicis* (Horvatić, 1958) were examined in these experiments. These shrubs include *Quercus ilex* L. (Fagaceae), *Arbutus unedo* L. (Ericaceae), *Pistacia lentiscus* L. (Anacardiaceae), and *Hedera helix* L. (Araliaceae). *P. lentiscus* has the highest tannin index (1.50), followed by *A. unedo* (1.26) and *Q. ilex* (0.96). Other secondary compounds in these shrubs include a cyclic diterpene alcohol and quinic acid (*Q. ilex*), arbutoside and ethyl gallate (ethyl 3,4,5-trihydroxybenzoate; *A. unedo*), terpenes [including α-pinene, β-pinene, camphene, *trans*-caryophyllene, cubebene (or a similar sesquiterpene), and cadinene], and fatty acids (*P. lentiscus*; Rogosic and Clausen, unpublished data). *H. helix* is reported to contain a mixture of pentacylic 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.

We conducted eight trials at an experimental station 25 km from Split, Croatia, in the central area of the Adriatic seaside. Experimental animals were Alpine goats (mean body weight = 24.2 kg) with experience on grazing on Mediterranean shrublands near the Croatian coast. Animals were penned (1.5 × 2 m) individually. All shrubs offered were hand-harvested each week in the same location. Leaves and 1-yr old twigs, 10 cm long, were clipped and placed in bags. Within an hour, the plant material was ground to 1-cm length with a chipper, mixed for uniformity, placed in woven, polyethylene feed sacks, and refrigerated at 4°C. Every morning before the trial, bags of shrubs to be fed that day were removed from cold storage and offered immediately to animals.

Conditioning

Prior to the experiments, baseline intake of alfalfa pellets was determined for each animal on days 1–5. After baseline intake was established, all goats ($N = 12$) were offered all four shrubs simultaneously from 0900 to 1300 hr for 5 d. Shrub intake was monitored, and goats were stratified into two experimental groups ($N = 6$) based on total shrub intake. The same 12 goats were used in all experiments, and treatment groups were not changed between experiments. Between experiments, goats were fed with alfalfa pellets and barley at maintenance level for 3 d.

During experiments, goats received 100 g of barley from 0800 to 0830 hr and were offered 200 g of each shrub species simultaneously in separate feeders from 0900 to 1500 hr daily for 7 d. Feeders were monitored at 30-min intervals, and additional shrub biomass was placed in empty boxes. At 1500 hr, feed refusal was weighed and shrub consumption was calculated, and goats were fed with 550 g of alfalfa pellets. Throughout experiments, animals had free access to trace mineral blocks and freshwater.

Experiments 1–3

The objective of the first three experiments was to determine if goats consuming three high-tannin shrubs varying in nutrients and flavor would consume more biomass than goats offered only one shrub. Total intake when offered *Q. ilex*, *A.*

unedo, and *P. lentiscus* was compared to intake of only *Q. ilex*, *A. unedo*, or *P. lentiscus* in experiments 1–3, respectively.

Experiment 4

The objective of experiment 4 was to determine if goats offered the same three high-tannin shrubs would consume more biomass than goats offered one shrub (*H. helix*) containing saponins.

Experiments 5–7

The objective of experiments 5–7 was to determine if goats offered three shrubs containing tannins would consume more foliage than goats offered two shrubs containing two different classes of toxins (tannin and saponins). Intake of three shrubs (*Q. ilex*, *A. unedo*, and *P. lentiscus*) was compared to intake of two shrubs (*Q. ilex* + *H. helix*, *A. unedo* + *H. helix*, or *H. helix* + *P. lentiscus*) in experiments 5–7, respectively.

Experiment 8

The objective of experiment 8 was to determine the influence of saponins in *H. helix* on biomass intake of the three high-tannin shrubs. Intake of the three high-tannin shrubs was compared to intake of the same three shrubs + *H. helix*.

Statistical Analyses

The total daily shrub intake in each experiment was used as the dependent variable in the analysis. The experimental design for all eight experiments was a completely random design. Animals were a random factor in the mixed model analysis (SAS, 2000). The model included the two experimental groups (group 1 vs. group 2), shrub species (in different experimental groups), and the species × group interaction. The model also used days as a repeated measure with all other interactions included. All analyses on shrub intake were adjusted for body weight (g/kg BW). Data were analyzed by using analysis of variance (SAS, 2000), and means were separated using least significance differences ($P < 0.05$).

Results

In the first three experiments, goats fed with a mixture of three tannin-rich shrubs ate more foliage ($P < 0.01$) than goats offered only one shrub, regardless of concentration of tannins in the individual shrub (Fig. 1; experiments 1–3). In experiment 1, goats offered shrubs *Quercus*, *Arbutus*, and *Pistacia* ate more foliage ($P < 0.01$) than goats offered only *Q. ilex* (23.18 ± 2.62 vs. 10.66 ± 1.52 g/kg BW). Intake of *Q. ilex* did not differ between the two groups (9.49 ± 0.99 vs. 10.66 ± 1.52 g/kg BW). Goats offered the same three shrubs in experiment 2 also ate more foliage ($P < 0.01$) than goats offered only *A. unedo* (25.23 ± 2.53 vs. 13.36 ± 2.3 g/kg BW). Likewise, *Arbutus* biomass intake did not differ between groups (12.75 ± 2.7 vs. 13.36 ± 2.3 g/kg BW). In experiment 3, consumption was again greater ($P < 0.01$) for goats

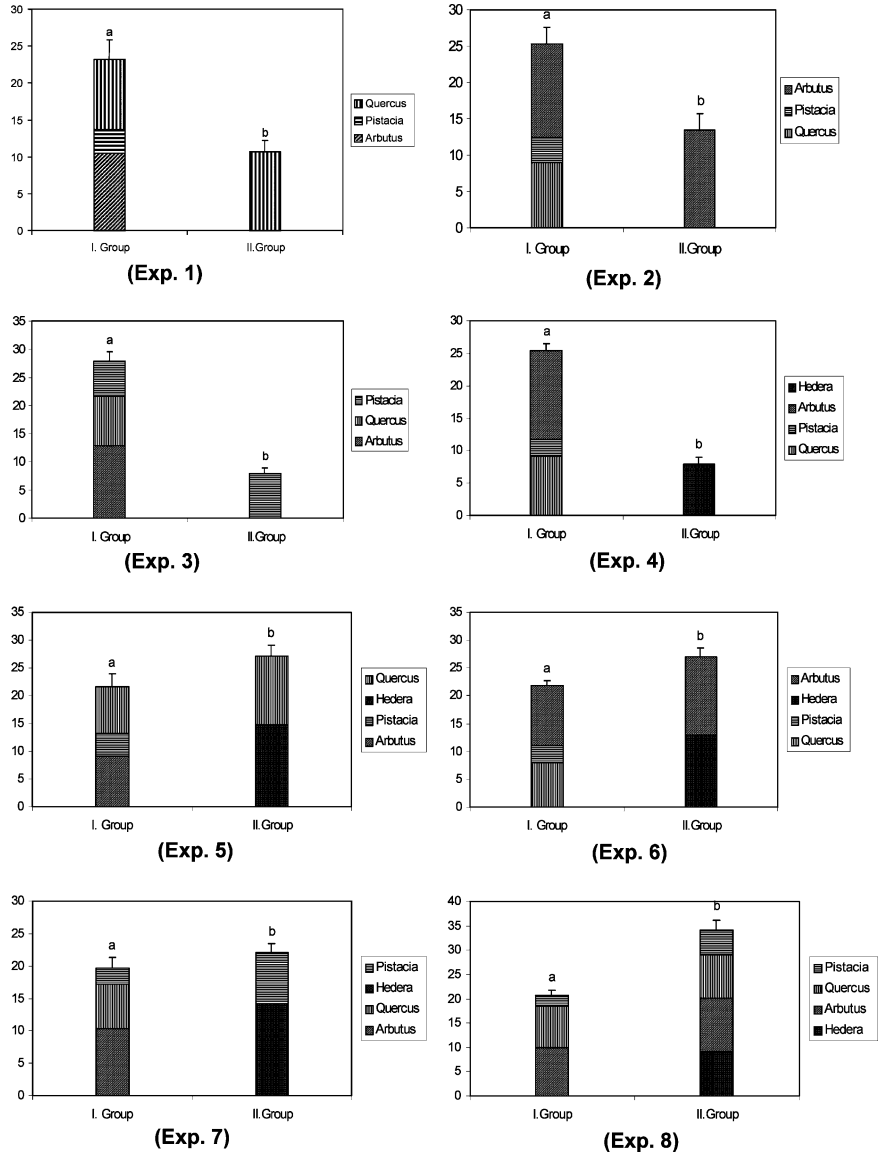

Fig. 1 Intake of goats (g/kg BW) fed with different combinations of high-tannin (*Quercus ilex*, *Arbutus unedo*, and *Pistacia lentiscus*) and/or high-saponin *Hedera helix* shrubs; $N = 6$ in each group. Standard error bars refer to total intake

fed the mixture of tannin-rich shrubs than for goats fed *P. lentiscus* (27.88 ± 1.72 vs. 7.85 ± 1.05 g/kg BW). In contrast to experiments 1 and 2, intake of *P. lentiscus* differed ($P < 0.01$, Fig. 1; experiment 3) between groups (6.22 ± 0.64 vs. 7.85 ± 1.05 g/kg BW). Goats with a choice of the same three tannin-rich shrubs also consumed more foliage ($P < 0.01$) than those receiving the saponin-rich shrub *H. helix* (Fig. 1; experiment 4; 25.37 ± 1.16 vs. 7.99 ± 0.93 g/kg BW).

Goats provided the mixture of three tannin-rich shrubs consumed significantly less foliage than those offered only two shrubs containing tannins or saponins (Fig. 1; experiments 5–7). In experiment 5, goats consumed more biomass ($P < 0.01$) when fed *Quercus* and *Hedera* than the group offered the three high-tannin shrubs (27.11 ± 2.03 vs. 21.64 ± 2.37 g/kg BW). Likewise, in experiment 6, goats receiving *Arbutus* and *Hedera* ate more ($P < 0.01$) than those offered *Arbutus*, *Quercus*, and *Pistacia* (27.05 ± 1.59 vs. 21.77 ± 0.89 g/kg BW). In experiment 7, goats fed the high-tannin mixture again consumed more foliage ($P < 0.05$) than those fed *Pistacia* and *Hedera* (22.03 ± 1.37 vs. 19.68 ± 1.6 g/kg BW). Cumulatively, the results of experiments 5–7 indicate that combinations of two shrubs containing both classes of phytotoxins resulted in a complementary interaction and greater intake than three shrubs containing only tannins. Goats ate more *Quercus* ($P < 0.01$) in experiment 5 when fed in combination with a saponin-containing shrub than in experiment 1 when fed either by itself or in combination with other high-tannin shrubs (12.29 ± 1.23 vs. 10.66 ± 1.52 or 8.49 ± 1.15 g/kg BW). Goats ate more *Arbutus* when fed in conjunction with *Hedera* (experiment 6) than when fed with two other high-tannin shrubs (experiment 2; $P < 0.01$; 14.01 ± 1.14 vs. 10.82 ± 0.76 g/kg BW), although intake of *Arbutus* in experiment 6 did not differ from experiment 2 when offered alone (14.01 ± 1.14 vs. 13.36 ± 2.3 g/kg BW; $P < 0.01$). Goats ate more *Pistacia* in experiment 7 in conjunction with *Hedera* than in experiment 3 when fed two other high-tannin shrubs (7.89 ± 0.64 vs. 6.22 ± 1.72 g/kg BW; $P < 0.01$), but intake of *Pistacia* in experiment 7 with *Hedera* did not differ ($P < 0.01$) from experiment 3 when *Pistacia* was fed alone (7.89 ± 1.05 vs. 7.85 ± 0.64 g/kg BW). Intake of *H. helix* was much lower ($P < 0.01$) in experiment 4 than in experiments 5–7 when fed in conjunction with a tannin-containing species (7.99 ± 0.93 vs. 14.82 ± 2.03; 13.04 ± 1.59; 14.14 ± 1.37 g/kg BW). In experiment 8, goats offered all three tannin-rich shrubs plus the saponin-rich *H. helix* ate more foliage ($P < 0.01$) than goats offered only the tannin-rich shrubs (34.06 ± 2.06 vs. 20.78 ± 0.99 g/kg BW). Tannin-rich shrubs increased the intake of *H. helix*, and conversely, *H. helix* positively influenced the consumption of tannin-rich shrubs.

Discussion

Plant phytochemicals play important ecological roles in plant defenses (Bryant et al., 1991), plant classifications (Levin, 1971), palatability (Provenza et al., 1992), phytotoxity (Pfister et al., 1994), and perhaps in fire ecology (Naveh, 1974). Tannins and saponins are two of the major groups of phytochemicals in Mediterranean shrubs. Tannins suppress shrub intake by reducing macronutrient digestibility and causing illness (Pritchard et al., 1992; Reed, 1995). Moreover, tannins bind to proteins, cell walls, and cell solubles (Kumar and Vaithiyanthan, 1990) and adversely affect rumen microbial and intestinal enzyme activity (Silanikove et al., 1996; Rogosic et al., 2005a), and consequently reduce ruminal volatile fatty acids (Makkar et al., 1995). Clinical signs of saponin toxicity include vomiting, excess salivation, and diarrhea, indicating both liver and digestive tract irritation (Harshberger, 1920). *H. helix* has also been reported to cause abortions in sheep and goats (Bondi et al., 1973). Specific roles of saponins involve modification of gut microbes, particularly in ruminants (Gee et al., 1993). Saponins suppress rumen protozoa by binding to cholesterol in the protozoa cell membrane, causing the

organisms to lyse and die (Makkar et al., 1998). Likewise, 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).

The first four experiments were designed to determine if goats offered a combination of three shrubs containing different concentration of tannins and presumably differing nutritional profile and flavor would consume more foliage than goats offered only one of those shrubs (experiments 1–3) or a shrub containing saponins (experiment 4). Goats offered a choice of three shrubs (experiments 1–3) containing different concentrations and types (molecular weights) of tannins consumed more foliage than goats offered each of these shrubs individually, regardless of tannin concentration in shrubs. Mule deer also consumed more sagebrush (*Artemisia tridentata*) and juniper (*Juniperus osterosperma*; plants high in different kinds of terpenes) than when consuming sagebrush or juniper alone (Smith, 1959). Phytochemicals such as tannins and terpenes apparently differ in their physiological effects and/or are detoxified by different means. The concentrations and specific molecular composition of toxins in Mediterranean shrubs fed to goats probably influences toxin satiation, which is not fixed but dynamically determined by the physiological state of an animal relative to the quality and quantity of nutrients and toxins available (Villalba et al., 2002). In essence, toxins cause herbivores to eat a variety of plants to meet their needs for nutrients because the pathways of detoxification are saturable (Freeland and Janzen, 1974; Foley et al., 1999). *H. helix* contains significant levels of saponins; these bitter, toxic compounds protect this shrub from browsing herbivores by affecting their feeding behavior (Rogosic et al., 2003). Goats offered three tannin-rich shrubs in experiment 4 ate more biomass than goats fed only *H. helix*. These results are consistent observations that a greater number of shrub species in the diet increase intake (Smith, 1959; Rogosic et al., 2005a,b).

The complementarity of tannin-rich shrubs and a saponin-rich shrub positively influenced biomass intake in experiments 5–7. Goats provided with a choice between shrubs containing tannins and saponins were able to consume combinations of the shrubs that may have reduced aversive feedbacks associated with consumption of either toxin alone. Our results are consistent with this hypothesis. Goats offered two shrubs containing different classes of secondary compounds (tannins and saponins) consumed more foliage than goats offered three shrubs that all contained only tannins. Complementary interactions between shrubs containing tannins and saponins (experiment 8) further support the idea that biochemical diversity (higher number of shrubs species in the diet) has a positive influence on shrub intake, enabling animals to better meet nutritional needs and avoid toxicity. Tannins, saponins, and other allelochemicals may form complexes within the intestinal tract, given that they form chelation complexes in *in vitro* systems (Freeland et al., 1985). Intestinal binding of tannins with saponins may minimize toxic effects by reducing absorption. Simultaneous consumption of plants containing chemical chelators (e.g., tannins) and those containing other toxins may provide a mechanism for reducing both pre- and postabsorption toxicity. If herbivores use phytochemical interactions as a means of neutralizing toxins, this mechanism could be important regarding management of ruminants on Mediterranean rangelands.

As each of these shrubs presumably exhibits different flavors, as well as different concentrations of nutrients and toxins, the flavor–nutrient–toxin interaction may also

explain why the efficacy of plant defenses varies with the mixture of plants, and why chemical attributes of a single shrub species must be considered within a larger context of the plant community. For a given plant compound, preference may range along a continuum from strongly aversive if nutrients and toxins are not complementary to strongly positive if nutrients and toxins (e.g., tannins and saponins) are complementary. Understanding the role of plant phytochemicals and their interactions will lead to a greater understanding of the influence of biochemical diversity on grazing herbivores and the effect of herbivores on plant diversity, both of which could have important implications for management of natural grazing ecosystems.

References

AUGNER, M. and BERNAYS, E. A. 1998. Plant defense signals and Batesian mimicry. *Evol. Ecol.* 12:667–679.

AUGNER, M., PROVENZA, F. D., and VILLALBA, J. J. 1998. A rule of thumb in mammalian herbivores? *Anim. Behav.* 56:337–345.

BONDI, A., BIRK, Y., and GESTETNER, B. 1973. Forage Saponins, Chemistry and Biochemistry of Herbage, p. 511, *in* G. W. Butler, and R. W. Bailey (eds.). Academic Press, New York.

BRYANT, J. P., PROVENZA, F. D., PASTOR, P. B., REICHARDT, B. P., CLAUSEN, T. P., and Du TOIT, J. T. 1991. Interaction between woody plants and browsing mammals mediated by secondary metabolites. *Ann. Rev. Ecolog. Syst.* 22:431–446.

BURROWS, G. E., and TYRL, R. J. 2001. Toxic Plants of North America. Iowa State University Press, Ames, IA, pp. 120–122.

CHEEKE, P. 1998. Natural Toxicants in Feeds, Forage and Poisonous Plants. Interstate Publ., Danville, IL.

DZIBA, L. E., PROVENZA, F. D., VILLALBA, J. J., and ATWOOD, S. B. 2005. Influence of terpenes and nutritional supplementation on intake of sagebrush by sheep. *Range Ecol. Manage.* (in press).

FOLEY, W. J., IASON, G. R., and MCARTHUR, C. 1999. Role of plant secondary metabolites in the nutritional ecology of mammalian herbivores: How far have we come in 25 years? pp. 130–209 *in* H. G. Fahey (ed.). Nutritional Ecology of Herbivores. Proceedings of 5th International Symposium on Nutrition of Herbivores. American Society of Animal Science, Savoy, IL.

FREELAND, W. J. and JANZEN, D. H. 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. *Am. Nat.* 108:269–288.

FREELAND, W. J., CALCOTT, P. H., and ANDERSEN, L. R. 1985. Tannins and saponins: interaction in herbivore diets. *Biochem. Syst. Ecol.* 13:189–193.

GEE, J. M., PRICE, K. R., RIDOUT, C. L., JOHNSON, I. T., and FENWICK, G. R. 1989. Effect of some purified saponins on transmural potential difference in mammalian small intestine. *Toxicol. in vitro* 3:85–90.

GEE, J. M., PRICE, K. R., RIDOUT, C. L., WORTLEY, G. M., and HURRELL, R. F. 1993. Saponins of Quinoa (*Chenopodium quinoa*): Effect of processing on their abundance in Quinoa product and their biological effects on intestinal mucosal tissue. *J. Sci. Food Agric.* 63:201–209.

HARSHBERGER, J. W. 1920. Pastoral and Agricultural Botany. Blakiston's Son & Co., Philadelphia, PA, p. 87.

HODGSON, J. and ILLIUS, A. W. (ed.) 1996. The Ecology and Management of Grazing Systems. CAB International, Wallingford, UK.

HORVATIĆ, S. 1958. Typological division of the Adriatic littoral vegetation of the garrigues and pine forest. *Acta Bot. Croat.* 17:7–78 (In Croatian).

JOHNSON, I. T., GEE, J. M., PRICE, K. R., CURL, C. L., and FENWICK, G. R. 1986. Influence of saponins on gut permeability and active nutrient permeability "*in vitro*." *J. Nutr.* 116:2270–2277.

KAISER, J. 2000. Rift over biodiversity divides ecologists. *Science* 289:1282–1283.

KUMAR, R. and VAITHIYANTHAN, S. 1990. Occurrence, nutritional significance and effect on animal productivity of tannins in tree leaves. *Anim. Feed Sci. Technol.* 30:21–38.

LAUNCHBAUGH, K. L. and PROVENZA, F. D. 1993. Can plant practice mimicry to avoid grazing by mammalian herbivores? *Oikos* 66:501–504.

LAUNCHBAUGH, K. L., PROVENZA, F. D., and BURRITT, E. A. 1993. How herbivores track variable environments: Response to variability of phytotoxins. *J. Chem. Ecol.* 19:1047–1056.

LEVIN, D. A. 1971. Plant phenolics: An ecological perspective. *Am. Nat.* 105:157–181.
MAKKAR, H. P., BLUMMEL, S., and BECKER, K. 1995. Formation of complexes between polyvinyl pyrrolidones or polyethylene glycols and tannins, and their implications in gas production and true digestibility in "*in vitro*" techniques. *Br. J. Nutr.* 73:897–913.
MAKKAR, H. P., SEN, S., BLUMMEL, S., and BECKER, K. 1998. Effect of fractions containing saponins from *Yucca schidigera*, *Quillaja saponaria* and *Accacia auriculoformis* on rumen fermentation. *J. Agric. Food Chem.* 46:4324–4328.
MCARTHUR, C., HAGERMAN, A. E., and ROBBINS, C. T. 1991. Physiological strategies of mammalian herbivores against plant defenses. pp. 103–114, *in* R. T. Palo and C. T. Robbins (eds.). Plant Defenses against Mammalian Herbivory. CRC Press, Boca Raton, FL.
NAVEH, Z. 1972. The role of shrubs ecosystem in present and future Mediterranean land use, pp. 414–427, *in* Wildland Shrubs, their Biology and Utilization. Academic Press, London, UK.
NAVEH, Z. 1974. Effect of fire in the Mediterranean region, pp. 401–434, *in* T. Kozlowski and T. Ahlgren (eds.). Fire and Ecosystems. Academic Press, Inc., New York.
PFISTER, J. A., PROVENZA, F. D., and MANNERS, G. D. 1994. Why do most cattle survive tall larkspur ingestion?, pp. 484–489, *in* S. M. Colegate and P. R. Dorling (eds.). Plant Associated Toxins. CAB International, Wallingford, UK.
PRITCHARD, D. A., MARTIN, P. R., and O'ROURKE, P. K. 1992. The role of condensed tannins in the nutritional value of mulga (*Acacia aneura*) for sheep. *Aust. J. Agric. Resour.* 42:1739–1746.
PROVENZA, F. D., PFISTER, J. A., and CHENEY, C. D. 1992. Mechanism of learning in diet selection with reference to phytotoxicosis in herbivores. *J. Range Manag.* 43:36–45.
PROVENZA, F. D., VILLALBA, J. J., CHENEY, C. D., and WERNER, S. J. 1998. Self-organization of foraging behavior: From simplicity to complexity without goals. *Nutr. Res. Rev.* 1:199–222.
RALPHS, M. H. 1992. Conditioned food aversion: Training livestock to avoid poisonous plants. *J. Range Manag.* 45:46–51.
RALPHS, M. H., PROVENZA, F. D., WIEDEMEIER, W. D., and BUNDERSON, F. B. 1995. Effect of energy source and food flavor on condition preference in sheep. *J. Anim. Sci.* 73:1651–1657.
REED, J. D. 1995. Nutritional toxicology of tannins and related polyphenols in forage legumes. *J. Anim. Sci.* 73:1516–1528.
RHOADES, D. F. 1979. Evolution of plants chemical defense against herbivores, pp. 3–53, *in* G. A. Rosenthal and D. H. Janezen (eds.). Herbivores: Their Interaction with Secondary Plant Metabolites. Academic Press, New York.
ROGOSIC, J. 2000. Management of the Mediterranean Natural Resources. Skolska naklada Mostar. ISBN 9958-774-00-, COBISS/BiH-ID 8755974. pp. 1–352 (in Croatian).
ROGOSIC, J., PFISTER, J. A., and PROVENZA, F. D. 2003. Interaction of tannins and saponin in herbivore diets. Proc. VII Internat. Rangel. Cong., Rangelands in the New Millennium, pp. 103–105.
ROGOSIC, J., PFISTER, J. A., and PROVENZA, F. D. 2005a. The effect of polyethylene glycol on intake of Mediterranean shrubs by sheep and goats. *Rangeland Ecol. Manag.* (in press).
ROGOSIC, J., PFISTER, J. A., PROVENZA, F. D., and GRBESA, D. 2005b. The effect of activated charcoal and number of species offered on intake of Mediterranean shrubs by sheep and goats. *Appl. Anim. Behav.* (in press).
SAS 2000. Statistical Analysis System. SAS/STAT User's Guide. Version 8, volume 2. Cary, NC.
SILANIKOVE, N., GILBOA, A., NITSAN, Z., and PEREVOLOTSKY, A. 1996. Goats fed tannin-containing leaves do not exhibit toxic syndrome. *Small Rumin. Res.* 25:195–201.
SMITH, A. D. 1959. Adequacy of some important browse species in overwintering mule deer. *J. Range Manag.* 12:9–13.
VILLALBA, J. J., and PROVENZA, F. D. 1999. Nutrient-specific preference by lambs conditioned with intraruminal infusions of starch, casein and water. *J. Anim. Sci.* 77:378–387.
VILLALBA, J. J., and PROVENZA, F. D. 2000. Roles of flavor and rewards intensities in acquisition and generalization of food preference: Do strong plant signals always deter herbivory. *J. Chem. Ecol.* 26:1911–1921.
VILLALBA, J. J., PROVENZA, F. D., and BRYANT, J. P. 2002. Consequences of the interaction between nutrients and plant secondary metabolites on herbivores selectivity: benefits or detriments for plants? *Oikos* 97:282–292.