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Consequences of plant–chemical diversity for domestic goat food preference in Mediterranean forests

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ABSTRACT

The domestic goat, a major herbivore in the Mediterranean basin, has demonstrated a strong ability to adapt its feeding behaviour to the chemical characteristics of food, selecting plants according to their nutritive quality. In this study, we determine some chemical characteristics related to plant nutritional quality and its variability among and within five tree species, these being the main components of the mountain forests of SE Spain, with the aim of determining their influence on food selection by this generalist herbivore. We analyse nitrogen, total phenols, condensed tannins and fibre concentration as an indicator of the nutritive value of the different trees. To determine the preference by the domestic goat, we performed two types of feeding-choice assays, where goats had to select between different species or between branches of the same species but from trees of different nutritional quality. The analysis of the plant nutritional quality showed significant differences in the chemical characteristics between species, and a high variability within species. However, when faced with different tree species, the domestic goat selected some of them but showed striking individual differences between goats. When selecting between trees of the same species, the goats showed no differential selection. This limited effect of chemical plant characteristics, together with the variability in foraging behaviour, resulted in a widespread consumption of diverse plant species, which can potentially modulate the effect of the goat on vegetation composition, and open the way for the conservation of traditional livestock grazing on natural protected areas.

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1. Introduction

For herbivores, plants may differ in their quality as food between different species, between individuals of the same species or between branches of the same plant (Orians and Jones, 2001). These variations can be measured as differences in nutritional value, concentration of chemical defences, as

well as morphological characteristics of twigs and tissues (Hartley and Jones, 1997). Genetic differences (Oiser and Lindroth, 2001), dissimilarities in environmental growing conditions (Coley et al., 1985; Larsson et al., 1985) or differing histories of relationships with herbivores (Provenza and Maléchek, 1984) provoke this high variability in plant characteristics, creating a nutritional mosaic for herbivores.

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Generalist herbivores prefer nutritious foods and avoid foods with low nutrient content or high toxin levels (Bryant et al., 1991; Provenza et al., 1992; Hódar and Palo, 1997). For example, nitrogen is a limiting element for herbivores, and therefore the N content in vegetation plays a key role in herbivore nutrition and diet selection (Mattson, 1980; Tipler et al., 2002). Moreover, almost all woody species contain potentially toxic or digestibility reducing secondary compounds (Bryant et al., 1991), such as phenols and tannins, which strongly sway food selection by herbivores (Provenza and Malechek, 1984; Bryant et al., 1991; Palo et al., 1997). Therefore, chemical characteristics and their variability influence the probability of a plant being eaten (Hartley et al., 1997), augmenting or diminishing herbivore consumption between different species (Pisani et al., 2001; Dziba et al., 2003; Alonso-Díaz et al., 2008), between plants of the same species (Riddle et al., 1996) or even between parts of the same plant (Hódar and Palo, 1997). However, most of these findings have been the results of totally controlled experiments, where animals are held under artificial conditions with only a few elements in its diet. Free-ranging animals foraging in diverse plant communities encounter a wide array of biochemicals that create a multidimensional feeding environment (Bryant et al., 1991). Interactions among these chemicals can lead to complementary relationships among foods when a combination of foods exceeds the benefit of consuming the foods in isolation (Lyman et al., 2008). Moreover, herbivores can learn to eat complementary mixtures of foods that contain nutrients and secondary compounds that enhance diet breadth and promote more uniform use of all plants in a landscape (Provenza et al., 2003).

The domestic goat (*Capra hircus* L.) has long been the most common livestock species in Mediterranean ecosystems, having an important economic value and strong impact on vegetation (e.g. El Aich, 1995; Papanastasis and Peter, 1998). Herbivory by livestock, including the domestic goat, has been described as a major historical biological factor determining the structure and composition of the Mediterranean forest (Carrión et al., 2003). Although the diet of the domestic goat depends heavily on plant availability, some plant species are actively selected, whereas others are totally or partially rejected (Barroso et al., 1995; Ngwa et al., 2000). The domestic goat has demonstrated a strong ability to adapt its feeding behaviour to food chemical characteristics (du Toit et al., 1991; Provenza et al., 1990, 1992; Villalba and Provenza, 2000). Moreover, several studies report selection by goats between diverse plant species (Dziba et al., 2003) or between individuals of the same plant species (Riddle et al., 1996) according to nutritional quality or the concentration of chemical defences. This potential food selection can, in turn, filter the composition and abundance of the Mediterranean forest. However, after hundreds of years of domestic herbivore pressure in the Mediterranean area, vegetation diversity is still high, without the extinction of the more palatable species. Only an unbiased use of all species in a community could maintain plant biodiversity under high herbivore pressure (Provenza et al., 2003; Dziba et al., 2007). In fact, there are other factors that can determine domestic herbivore diet selection (Papachristou et al., 2005) which can be equally or more important than plant chemical and morphological characteristics (Provenza et al., 2003; Duncan et al., 2007).

Many natural protected areas of the Mediterranean basin are traditional grazing areas for extensive herds of domestic goat and sheep (Zamora et al., 1996). These wooded rangeland areas are important for traditional livestock maintenance but are also important conservation areas for plant biodiversity (Blanca et al., 2002). Although herbivory by ungulates can represent harmful effects upon some species (Gómez-Aparicio et al., 2005), the traditional extensive grazing is considered a useful tool for plant biodiversity conservation (Bartolomé et al., 2000; Papachristou et al., 2005). However, good grazing management of wooded rangelands implies prior knowledge of the diet selection behaviour, since herbivores exert a major influence on vegetation composition through differential plant consumption (Papachristou et al., 2005, 2007).

In this work, we study the patterns of food selection of the free-ranging domestic goat on five important forest tree species in the western Mediterranean mountain areas. We examine the goat preferences at two levels: between species and between different individuals within species. Specifically, we seek to answer the following questions: (1) are there significant differences of nutritional quality in the tree species analysed, both between and within species? (2) Is there a differential selection by the domestic goat of the different tree species, both between and within species? and if so (3) is this selection explained by the nutritional characteristics of the trees? Our ultimate goal is to ascertain to what extent the nutritional variation between the main tree species in the Mediterranean mountains determines the food selection by the domestic goat.

2. Materials and methods

2.1. Study species

Five tree species were studied, all being major components of the Spanish Mediterranean mountain forests: two deciduous, Pyrenean oak (*Quercus pyrenaica* Willd.) and Spanish maple (*Acer opalus* subsp. *granatense* (Boiss.) Font Quer and Rothm.); one broadleaf evergreen, Holm oak (*Quercus ilex* L.); and two conifers, Scots pine (*Pinus sylvestris* L.) and Black pine (*Pinus nigra* Arnold). The trees were located in two mountain ranges, 45 km apart, the Parque Natural de la Sierra de Huétor (37° 17' N, 3° 27' W, 1350 m a.s.l.) and the Parque Natural de la Sierra de Baza (37° 23' N, 2° 50' W, 1800 m a.s.l.), both in south-eastern Spain. Scots pine, Black pine and Spanish maple were situated in the Sierra de Baza, in a mixed forest of Spanish maple together with reforested and natural Black and Scots pines, while Holm and Pyrenean oak were located in the Sierra de Huétor, in a sparse woodland surrounded by reforested Black, Scots, and Cluster (*Pinus pinaster* Aiton) pines. Both mountains are protected natural areas with conservation and recreational purposes as the main use. However, during summer, herds of domestic goat (*C. hircus*) and sheep (*Ovis aries*) are present in both mountains, traditional livestock being an important element for the local economy.

2.2. Plant sampling protocol

Thirty-two trees of Spanish maple, Holm oak, Scots and Black pine, and 19 of Pyrenean oak, were selected and individually

tagged. Adult trees were chosen primarily for the presence of canopy accessible to goats, with little attention paid to other tree characteristics. In August, when herbivory probability on woody vegetation by goats increased (Bartolomé et al., 1998; Baraza, 2004), four samples of current-year leaves or needles, coming from several branches situated in the part of canopy accessible to goats (between 0.5 and 1.5 m in height) were collected from each tree. Samples were dried to constant weight in an oven at 45 °C (Palmer et al., 2000) and milled to a particle size of 1 mm. Although goats preferentially eat leaves when foraging on shrubs and trees, they also ingest some woody materials; however, it is hard to quantify the exact proportion of wood ingested when the animal feeds on different plant species (see e.g. Mayes and Dove, 2000). In order to avoid uncontrolled sources of error and allow more direct comparisons between tree species, the samples collected belonged to a single tissue, the leaves, assuming that this sample is representative of the chemical characteristics of the tree.

2.3. Chemical analysis

Many chemical characteristics are related to plant nutritional value and herbivore intake (Tolera et al., 1997; Danell and Bergström, 2002). Thus, the following variables were chosen, not only because they showed an effect on ungulate diet selection, but also for their simplicity, repeatability, and widespread use.

2.3.1. Nitrogen content

N content was quantified by acid (sulphuric) digestion of 0.5 g dry leaves/needles powder, distillation in a semi-automatic Kjeldahl distiller (Büchi B-324, Switzerland) and subsequent manual titration. N concentration is expressed as percentage of dry weight.

2.3.2. Oxidative capacity of phenolic compounds

Phenolic compounds were extracted from 0.5 g dry powder with 10 ml of 50% (v/v) methanol in an ultrasonic bath for 15 min, and ultracentrifuged at 2500 rpm for 15 min. For the analysis of total phenols, an aliquot was diluted with water and assayed with the Folin–Ciocalteu phenol reagent and 20% sodium carbonate, and absorbance was then measured at 740 nm (Hódar and Palo, 1997). For the analysis of condensed tannins, the same extract was assayed with butanol–hydrochloric acid reagent (0.7 g of ferrous sulphate heptahydrate in 50 ml conc. HCl with n-butanol added up to 1 l of volume), and absorbance was measured at 550 nm (Waterman and Mole, 1994).

No single method will give satisfactory results for quantitative analysis of phenolic compounds in plant tissues (Yu and Dahlgren, 2000). Although there are problems with colorimetric analysis, caused by the variable structures of tannin polymers and the absence of satisfactory commercial standards (Appel et al., 2001), these procedures are considered adequate for relative comparisons (Yu and Dahlgren, 2000), or when the focus of the study is not the determination of the amount of phenols but its effects, as in our case (e.g. Alonso-Díaz et al., 2008). For better comparisons, phenolic compounds were quantified against commercial standards, tannic-acid

for total phenols (TAE), and quebracho-tannins (QTE) for condensed tannins (Waterman and Mole, 1994; Álvarez del Pino et al., 2005). However, the oxidative capacity of the particular phenols and tannins included in these standards is not directly equivalent to that of the plant material (Appel et al., 2001), so standard equivalents must be considered merely as an expression of the total oxidative capacity of phenolic compounds in comparable units (Álvarez del Pino et al., 2005) and not a measure of phenolic concentration.

2.3.3. Fibre content

The fibre content was analysed in 10 trees of each species used for the feeding assays (see Section 2.4). Leaves from the same tree were mixed, making two measurements per individual. Neutral-detergent fibre (NDF), acid-detergent fibre (ADF) and acid-detergent lignin (ADL) were analysed by the sequential procedure of Goering and Van Soest (1970) using the ANKOM200/220 fibre analyser (ANKOM Corporation® Technology, Fairport, NY). NDF, ADF and ADL were calculated based on dry matter as ash free. Ash was estimated by burning the residual ADL at 500 °C.

2.4. Feeding-choice assay

All feeding-choice assays were made with eight lactating domestic goats of the Murciano-Granadina breed, taken at random from a herd that usually pastures in the Sierra de Baza. Murciano-Granadina is a breed developed for milk production, traditionally managed in semi-extensive regimens in SW Spain (see Oklahoma State University Board of Regents, 1995–2008, for a diagnosis of the breed). Throughout the experimentation period, goats foraged with the rest of the herd in a typical Mediterranean mountain woodland comprised mainly of *Pinus*, *Quercus* and *Acer* species. At this time of the year (mid-summer), the herd forages at sunrise and sunset, and retreats to the pen during the hottest hours of the day. The use of previously free-ranging goats for the experiments limits the control of some important variables (e.g. previous experience of goats, feeding before the trials); however, it also provides a more realistic result about the preferences of goats that have these plant species available daily under field conditions.

The relationship between plant chemical characteristics and goat intake was explored through a series of cafeteria trials in which goats were allowed to browse experimental branches of tagged trees. Prior to the cafeteria trials, goats were fed with branches from all the experimental species for one week, combining several species each day and following the same protocol that was later used during feeding-choice assays, thereby ensuring the animal's familiarity with all the experimental tree species and the handling for trials. Trials were consistently made in the morning (7.00–10.00 solar local time), as soon as the herd returned to the pen. Goats were individually moved once a day into a test pen, where experimental branches were situated.

In the first experiment, goats were allowed to select between branches of similar size and number of twigs belonging to the five experimental species. Branches were collected daily, and two branches from one of the trees of each species were presented to each goat for 10 min or until all

leaves of the offered branches were finished. Branches were offered to goat tied to a vertical trunk so that they were kept in a position similar to the natural one. Trials were recorded on video to determine the order in which the goat browsed the different species (hereafter browsing rank), as well as the number of bites per branch. The position of each species with respect to the others was changed daily. The experiment was repeated with each goat on five consecutive days.

In the second experiment, goats were allowed to select between branches of the same species but different trees of contrasting chemical characteristics. Protein availability, calculated according to the equation proposed by Cooper et al. (1988): total protein minus half of the condensed tannin concentration (protein availability = [% N × 6.25] – [% QTE/2]), was chosen as the best chemical indicator of nutritional value because it links nitrogen with tannins and because previous studies found a good relationship between this variable and herbivore damage to plants under natural conditions (Cooper et al., 1988; Owen-Smith, 1994; Baraza, 2004; see also Danell and Bergström, 2002). From the results of the previous chemical analyses, two groups of five trees with the highest and the lowest protein availability were selected for maple, Pyrenean oak, and Holm oak. During the tests, two branches from a high-quality tree and two branches from a low-quality tree were offered to each goat for 10 min or until all leaves of the branches offered were finished. The branches offered were similar in size and number of buds, minimizing the possible effect of morphology on goat intake. Each day, two trees of the same species were offered to each goat, never repeating the same trees or trees combination with the same goat on consecutive days. The experiment was repeated on three consecutive days for each species with a day of rest between species.

Before the cafeteria trial, all the branches were weighed and the number of buds counted. Once the trial ended, branches were reweighed and the number of intact buds recorded. For the calculation of biomass intake, corrections for evaporative weight losses were made by weighing non-trial branches before and after each trial, and calculating the percentage of biomass decrease of branches due to dehydration. This percentage of biomass was subtracted from the biomass reduction of branches after each trial.

Goat intake was calculated using the proportion of dry biomass intake and proportion of eaten buds (Oosterheld and McNaughton, 2000). Furthermore, during the species selection trials, the number of bites per time unit was recorded, which together with the biomass intake data allowed the calculation of the average plant biomass removed per bite (hereafter bite biomass) for each tree species.

2.5. Statistical analysis

All the chemical variables were arcsine square root transformed prior to the analysis. The differences in the chemical characteristics, both between species and between trees of the same species, were analysed by ANOVAs, with species and tree nested into species, as fixed factors (Quinn and Keough, 2002). The tree was considered a fixed factor because we were interested in detecting significant differences between different trees of the same species, which allows the intra-species

selection of herbivores. The fibre content (of NDF, ADF and ADL) was analysed by a one-way ANOVA with species as a single factor since not enough replications within each tree were feasible.

The relationship between different chemical characteristics was analysed using Pearson's correlations for the broad-leaf species. Browsing rank in the experiments of selection between different species was analysed using χ^2 tests comparing random probability to the frequency in which a species was selected the first. Due to non-normality of the data, the differences in bite biomass between species were analysed with the Kruskal–Wallis signed-rank test (Quinn and Keough, 2002).

A large proportion of branches were uneaten, giving rise to a non-exponential family distribution of the variables used as consumption estimators. Correlations of the two variables measured as intake indicators were therefore analysed by non-parametric Spearman's rank correlation. To evaluate the differences in goat intake between species, the semi-parametric multivariate analysis of variance approach of Anderson (2001) was used (hereafter PERMANOVA). This approach allows the testing of the responses of a non-normally distributed variable to one or more factors in an ANOVA experimental design based on any distance measure using permutation methods (see Anderson, 2001 for details). The goat intake estimators were separately analysed by PERMANOVA, including species as a fixed factor and goat as a random factor and the branches as experimental units ($n = 350$), in the case of the selection trials between different species. As a special case, one of the goats did not eat in any of the trials of the experiment of selection between different species, and therefore it was excluded for this analysis. Variation in goat intake during selection trials between different trees of the same species was evaluated by PERMANOVA with goat as a random factor, quality as a fixed factor, and each goat intake estimator for each branch ($n = 96$) as the response variable. Analyses were performed using PERMANOVA 1.6 software (Anderson, 2005; this can be freely downloaded from <http://www.stat.auckland.ac.nz/~mja/Programs.htm>). For these analyses we transformed the percentage of eaten branches to square root, and biomass intake to logarithms. We used the Bray–Curtis distance (appropriate for the datasets containing numerous zeros; Quinn and Keough, 2002) and 9999 permutations (permutation of raw data; Anderson and Ter Braak, 2003).

3. Results

3.1. Chemical differences

For all the chemical characteristics analysed, plant species was a significant factor, explaining a high proportion of the variability (Table 1). There were also significant differences between trees of the same species, but the explained variability was lower in all the cases except for % QTE (Table 1).

The highest percentage of N was found in the deciduous species, Spanish maple and Pyrenean oak. Within the evergreen species, the Holm oak had a higher percentage of N than did pines. Black pine was the species with the lowest percentage of N (Fig. 1). The tannin concentration (% QTE) was

Table 1 – Effect of the species and the tree nested in species on the chemical characteristics of the five tree species analysed

Variable	df Error	Species			Tree [species]		
		Explained variance	df	F	Explained variance	df	F
% N	426	0.59	4	458.03***	0.23	140	4.08***
% TAE	426	0.88	4	2090.91***	0.06	140	4.68***
% QTE	426	0.40	4	190.46***	0.39	140	5.21***
Protein availability	426	0.56	4	405.30***	0.29	140	5.92***

% N: percentage of nitrogen; % TAE: concentration of total phenols, expressed as the percentage of tannic-acid equivalents; and % QTE: condensed tannin concentration, expressed as the percentage of quebracho-tannin equivalents and percentage of protein availability. Values correspond to the proportion of the explained variance (SS_x/SS_{total}). Values remained significant after the Bonferroni correction ($P < 0.008$); the significance level is indicated as: *** $P < 0.0001$, ** $P \leq 0.001$, and * $P < 0.008$.

greater in the Holm oak than in the rest of species. Scots pine showed a higher % QTE than in maple and Pyrenean oak (Fig. 1). In the case of phenols, the three broadleaf species presented greater % TAE than the conifers, the interspecific differences within each group being non-significant (Fig. 1). Protein availability presented a similar behaviour as N except that Holm oak and Scot pines did not significantly differ (Fig. 1).

Fibre components were significantly different between species (% NDF, $F_{4,95} = 94.03$; ADF, $F_{4,95} = 158.74$; % ADL, $F_{4,95} = 179.54$; $P < 0.0001$ in all the cases; one-way ANOVA) this factor explaining a large proportion of the variability of all the variables analysed (% NDF, $r^2 = 0.80$; % ADF, $r^2 = 0.87$; % ADL, $r^2 = 0.88$; one-way ANOVA). The percentage of neutral-detergent

fibre (% NDF) in the broadleaf evergreen and coniferous species was greater than in deciduous ones, being higher in Pyrenean oak than in maple (Fig. 2). The percentage of acid-detergent fibre (% ADF) was higher in pines than in broadleaf species. There was no difference within deciduous, but Holm oak had a higher ADF% than in the two deciduous species but lower than in the two pines (Fig. 2). The ADL concentration was greater in pines than in the other species. Within broadleaf species, oaks showed greater ADL concentrations than did maple (Fig. 2).

Differences separated the trees into groups of significantly different chemical characteristics (Tukey's HSD *a posteriori* test); however, trees that significantly differed in one variable did not always differ in others. Different trees of the various

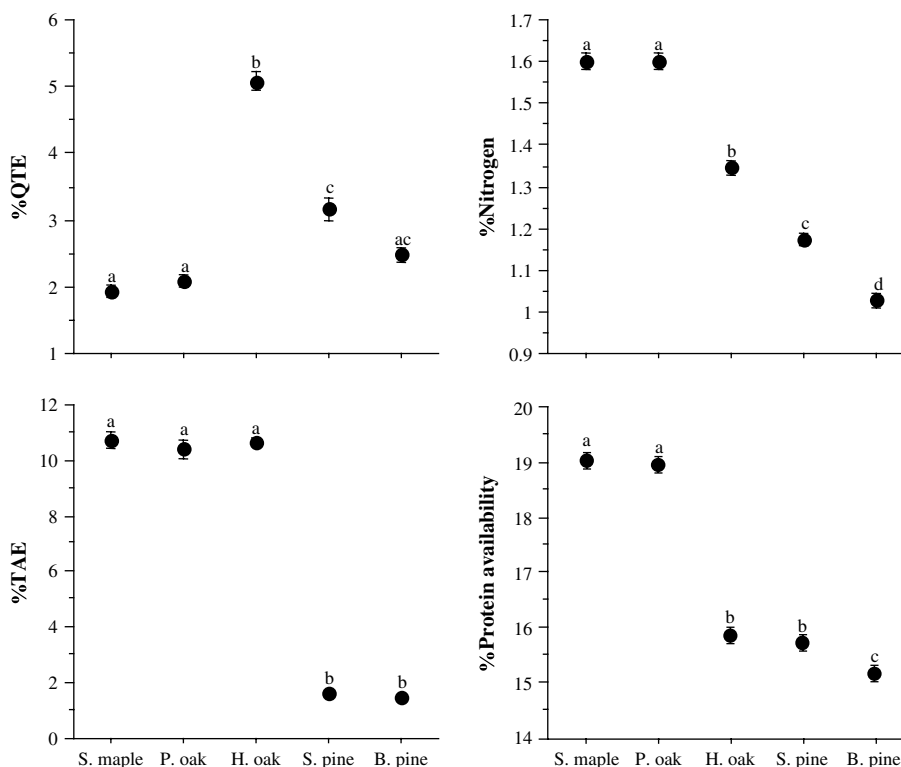


Fig. 1 – Mean chemical characteristics of the five tree species studied, % nitrogen, % QTE, concentration of condensed tannins, expressed as the percentage of quebracho-tannin equivalent; and % TAE, concentration of total phenols, expressed as the percentage of tannic-acid equivalent and percentage of protein availability [(% N × 6.25) – (% QTE/2)]. The lines on the bars correspond to the standard errors. Different letters indicate statistically significant differences by a Tukey HSD *a posteriori* test.

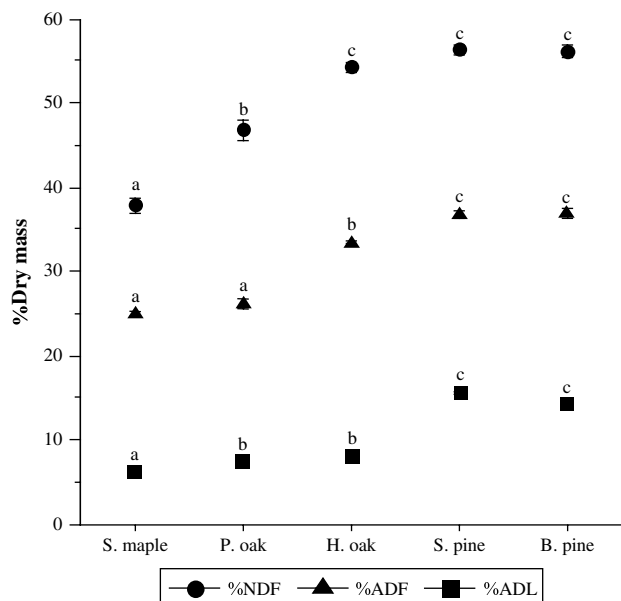


Fig. 2 – Mean of percentage of fibre content of the five tree species studied. % NDF, neutral-detergent fibre, % ADF, acid-detergent fibre, and % ADL, acid-detergent lignin. The lines on the bars correspond to the standard errors (some of them too small to see). Different letters between the same chemical variable indicate statistically significant differences by a Tukey HSD *a posteriori* test.

species significantly contrasted in percentage of protein availability (Table 1), which was negatively correlated with fibre components (Pearson's correlation: NDF vs. protein availability, $r = -0.436$, $n = 30$, $P = 0.0161$; ADF vs. protein availability, $r = -0.545$, $n = 30$, $P = 0.0019$) and total phenol oxidative capacity (Pearson's correlation: % TAE vs. protein availability, $r = -0.638$, $n = 30$, $P = 0.0001$).

3.2. Feeding-choice assay between species

There was no clear browsing rank since goats did not show a preferential order of consumption among experimental plant species ($\chi^2 = 5.74$, $df = 4$, $P = 0.219$).

There was a significant difference in bite biomass between species ($H = 37.71$, $df = 4$, $P < 0.001$; the Kruskal-Wallis). The greatest bite biomass was for Scots pine, while Holm oak and Black pine registered intermediate values, and deciduous species had the lowest average values (Fig. 3).

The percentage of eaten branches depended on the goat (random effect, $F_{6,314} = 17.86$, $P < 0.0001$; PERMANOVA), and the interaction goat \times species ($F_{24,314} = 6.11$, $P < 0.0001$; PERMANOVA), with different proportions of eaten buds of different species, depending on the goat. By contrast, the tree species as a main factor did not significantly affect the percentage of buds consumed per branch ($F_{24,314} = 2.02$, $P = 0.1442$; PERMANOVA).

Biomass intake was affected by goat (random effect, $F_{6,314} = 22.59$, $P < 0.0001$; PERMANOVA), and the interaction goat \times species ($F_{24,314} = 14.81$, $P < 0.0001$; PERMANOVA), while the tree species as a main factor did not significantly affect the

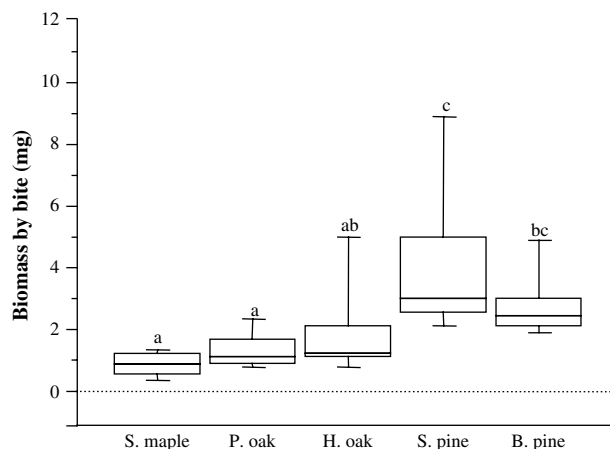


Fig. 3 – Box plot showing the distribution between species of average biomass (fresh weight) bite per goat. Different letters indicate statistically significant differences by *a posteriori* Dunn test.

biomass intake per branch ($F_{4,314} = 1.75$, $P = 0.0763$; PERMANOVA).

Spanish maple was the most selected species, since four of the seven goats significantly consumed higher proportions of buds of Spanish maple branches, while in some cases different goats significantly and positively selected Holm oak, Pyrenean oak or Scots pine. However, no goat significantly and positively selected Black pine (Table 2).

3.3. Feeding-choice assay between high- and low-quality branches

Goats did not select between branches of the same species since neither maple nor Pyrenean or Holm oak showed a significant effect, either of tree quality or goat \times tree quality interaction, regarding the proportions of buds eaten per branch (Table 3).

4. Discussion

4.1. Chemical variation within and between species

Our results showed significant variability in chemical traits between tree species, as well as significant differences between conspecific trees, for each of the five species analysed. Similarly, other authors have found major differences between chemical characteristics of conspecific trees, based not only on environmental conditions (Coley et al., 1985; Larsson et al., 1985), but also on genetic differences (Graglia et al., 2001; Oiser and Lindroth, 2001) or their interactions (Donaldson and Lindroth, 2007). This chemical variability has important consequences not only for herbivores fitness but also for plants (Donaldson and Lindroth, 2007), since plants have costs in maintaining genetic variation in chemical defences but increased fitness when the risk of herbivory is high (Donaldson and Lindroth, 2007).

Table 2 – Mean percentage of buds consumed and intake biomass as well as standard error for each species and each experimental goat

Goat	Species	% Buds, mean ± standard error		Biomass, mean ± standard error	
C1	Spanish maple	0.763 ± 0.062	a	8.594 ± 1.672	ab
	Pyrenean oak	0.125 ± 0.099	c	3.28 ± 1.55	c
	Holm oak	0.499 ± 0.111	b	7.72 ± 1.18	a
	Scots pine	0.706 ± 0.106	ab	20.21 ± 3.45	b
	Black pine	0.126 ± 0.049	c	7.69 ± 4.01	c
C2	Spanish maple	0.769 ± 0.066	a	10.26 ± 2.57	ab
	Pyrenean oak	0.035 ± 0.018	c	0.71 ± 0.26	c
	Holm oak	0.411 ± 0.103	b	4.44 ± 1.12	bc
	Scots pine	0.655 ± 0.098	ab	27.56 ± 4.36	e
	Black pine	0.063 ± 0.034	c	3.29 ± 1.83	d
C3	Spanish maple	0.008 ± 0.008	a	0.28 ± 0.28	a
	Pyrenean oak ^a	0.00	a	0.01 ± 0.1	a
	Holm oak	0.061 ± 0.050	a	0.77 ± 0.43	a
	Scots pine	0.00	a	0.00	a
	Black pine	0.020 ± 0.020	a	0.21 ± 0.21	a
C4	Spanish maple	0.005 ± 0.005	a	0.15 ± 0.15	a
	Pyrenean oak	0.539 ± 0.120	b	5.31 ± 1.03	b
	Holm oak	0.206 ± 0.120	a	2.88 ± 1.46	a
	Scots pine	0.018 ± 0.018	a	0.81 ± 0.81	a
	Black pine	0.020 ± 0.020	a	3.63 ± 2.62	a
C5	Spanish maple	0.032 ± 0.017	a	1.37 ± 0.78	a
	Pyrenean oak	0.005 ± 0.005	a	0.73 ± 0.64	a
	Holm oak	0.518 ± 0.111	b	7.40 ± 1.82	b
	Scots pine	0.686 ± 0.105	b	20.30 ± 2.29	c
	Black pine	0.079 ± 0.036	a	7.37 ± 3.54	b
C6	Spanish maple	0.109 ± 0.052	a	2.23 ± 0.85	a
	Pyrenean oak	0.014 ± 0.014	b	0.03 ± 0.03	b
	Holm oak	0.189 ± 0.099	ab	1.85 ± 0.89	a
	Scots pine	0.115 ± 0.067	ab	3.82 ± 2.08	a
	Black pine ^a	0.00	b	0.02 ± 0.02	b
C7	Spanish maple	0.412 ± 0.105	a	4.74 ± 1.59	a
	Pyrenean oak	0.589 ± 0.131	a	5.27 ± 1.01	a
	Holm oak	0.051 ± 0.026	b	1.80 ± 1.15	b
	Scots pine	0.054 ± 0.041	b	0.98 ± 0.77	b
	Black pine	0.00	b	0.00	b

Different letters represent significant differences for a pair-wise *a posteriori* comparisons (PERMANOVA). In bold the significantly positively selected species.

a Branches with eaten leaves but not eaten branch.

Although there are many chemical characteristics that determine plant nutritional value (Tolera et al., 1997), in Mediterranean ecosystems, where tannins are a basic chemical defence of vegetation (Dafni, 1991), the percentage of

protein availability could be a good indicator of plant nutritive value (Cooper et al., 1988; Owen-Smith, 1994). This variable not only groups two very important nutritive characteristics of forage, nitrogen (Tipler et al., 2002) and tannins (Osuga

Table 3 – Result of the analysis of the effect of tree quality (fixed) and goat (random) on branch consumption, during selection trial between trees of the same species, by two-way, semi-parametric ANOVA (PERMANOVA)

	df	Spanish maple				Holm oak				Pyrenean oak			
		% Buds		Biomass		% Buds		Biomass		% Buds		Biomass	
		F	P	F	P	F	P	F	P	F	P	F	P
Goat random	7	6.27	0.0001	4.79	0.0002	2.05	0.0172	2.45	0.0033	13.50	0.0001	16.29	0.0001
Quality fixed	1	2.40	0.15	0.98	0.3635	2.80	0.0906	1.80	0.1819	1.06	0.3351	0.54	0.4874
Goat × quality	7	0.31	0.9721	0.77	0.6793	0.95	0.5192	0.97	0.4914	1.12	0.3456	1.14	0.3361

et al., 2007), but also is negatively correlated with the rest of variables analysed (see Section 3). As a consequence, the fibre and phenol oxidative capacity will decrease when this variable rises, increasing the plant's nutrient value. Using protein availability percentage as the principal nutritive indicator, but taking into account fibre and secondary compounds, we can predict a hierarchical order of the studied species, depending on their nutritional value. Deciduous species have greater nutritional value, because of the high protein availability and lower fibre proportion. Among the evergreen species, Holm oak and Scots pine showed similar values of protein availability; nevertheless, the Scots pine had a greater fibre proportion, and although Holm oak presented a greater proportion of phenols, the Scots pine had terpenoids as its main defence compound (Lewinsohn et al., 1991; see Baraza et al., 2003 for specific data of studied species). Consequently, Holm oak can be considered more nutritional than pine. Finally, Black pine appeared to be the least nutritious species, since it had the lowest protein availability and the highest fibre content; also, like Scots pine, it had terpenoids as an important component of its chemical defence.

4.2. Chemical variability and goat dietary selection

Although goats showed individual differences in the selection between the different species, all maintained a low consumption of Black pine. The low protein availability and high fibre proportion of Black pine are presumably the cause of this lower consumption. In the same way, Spanish maple was most frequently preferred by goats, presumably because of the high protein availability and low fibre content in this species. However, the mean consumption of Pyrenean oak, Holm oak, and Scots pine was similar, despite their chemical differences. These results agree with previous observational and experimental studies in the same area which have shown maple to be the species most consumed by livestock, whereas oaks and Scots pine are less consumed, and Black pine is the least preferred species (Baraza, 2004; Baraza et al., 2006). This suggests that, in addition to the chemical characteristics of the plants, other factors can influence the goat dietary selection, as for instance branch morphology (Villalba and Provenza, 1999). Herbivores demonstrate a preference for foods that allow them a greater consumption rate (Dziba et al., 2003). Thus, the branch morphology of pines, with needles more densely disposed on twigs than leaves of broadleaf trees, allows a greater consumption rate than do the other species, which could offset the negative effects of lower quality. In the case of Scots pine, the greater consumption rate presented in comparisons with the other species appeared to compensate for the poor nutritional value. As a result, Scots pine consumption was similar to that of other species with a high nutrient value but lower intake rate as Holm oak. On the contrary, Black pine, although its intake rate was higher than broadleaf species, presented lower consumption, probably because it presented lower intake rate differences and worse nutritional characteristics than Scots pine. Thus the goat, in its food selection, establishes a trade-off between faster and better quality consumption (Duncan and Gordon, 1999), this being solved based on the nutritional necessities of the moment (Villalba and Provenza, 1999).

Despite chemical differences found within species, the results of the feeding assays did not show differential consumption between branches from conspecific trees of different quality. There are at least different, non-exclusive explanations for this lack of selectivity. First, it is possible that the differences between trees detected in the chemical analyses were not sufficient to prompt goats to select, since both the toxins and the nutrients need to reach a certain concentration in order to exert a physiological effect, and consequently a result on diet selection (Villalba et al., 2002). Second, free-ranging goats have access to a mixed diet, which probably has the ability to attenuate the effect of potentially toxic plant constituents (for example, by modifying or buffering the effects on rumen microflora), and thus a larger amount of toxic plant could be consumed without a detrimental effect on the animals (Lyman et al., 2008). Free-ranging animals can learn to mix foods by eating more of a combination of plants containing different kinds of nutrients, and secondary plant compounds which are complementary promoting more uniform use of all plants with different chemical characteristics (Provenza et al., 2003; Papachristou et al., 2007). Finally, it is doubtful whether a free-ranging goat searching to find the most nutritive food gains a net benefit or avoids a net cost, since the search time needed could not compensate for the small increase in food quality (Bergman et al., 2001). Several authors have found an important effect of chemical characteristics of plants in goat foraging behaviour under experimental conditions (e.g. du Toit et al., 1991; Provenza et al., 1990, 1992; Riddle et al., 1996; Villalba and Provenza, 2000). However, when goats are offered more diversity of food at the same time or they are in natural conditions, the effect of the chemical compositions of plants in foraging behaviour decreases or disappears (Bartolomé et al., 1998; Duncan and Young, 2002). In this way, some recent studies suggests that the ability of ruminant herbivores to assess food quality primarily on the basis of post-ingestion consequences is limited at the scale of diet mixing typical of free-ranging animals (Yearsley et al., 2006; Duncan et al., 2007).

Ungulate herbivores such as the goat consume great quantities of food and are highly mobile, and thus their food selection is necessarily coarse-grained. Therefore, the food selection of the domestic goat would be more influenced by availability than by small differences in chemical characteristics (Barroso et al., 1995), and a strong contrast in nutritive quality is necessary to promote differential selection between species (Bartolomé et al., 1998).

4.3. Differences between goats

The feeding assays revealed a marked variability between animals in their feeding behaviour. Moreover, the significant goat × species interaction highlights the importance of the individual differences between goats in diet selection. Goats are able to select the food that satisfies their nutrient requirements, but the food selection varies between individuals, among other reasons because of prior experience, the food previously ingested, and the animal's physiological state (Parsons et al., 1994; Baraza et al., 2005), or the social influence of the herd and the mother (Biquand and Biquand-Guyot, 1992). For example, there are major individual differences in

detoxification capacity of secondary plant compounds, even within the same species (Foley et al., 1999). Moreover, under experimental conditions, when allowed to mix several different foods, each animal made a different mixture (Sahin et al., 2003), and animals with a mixed diet increased in productivity when compared to those fed with only a commune-suitable diet (Görgülü et al., 1996). Moreover, herbivores do not show a fixed behaviour, but rather may take different foraging decisions depending of circumstances; thus influencing plant communities in different ways (Papachristou et al., 2007).

4.4. Consequences of goat foraging behaviour on vegetation

The variability in foraging behaviour between animals has important consequences for plants, since it can promote the consumption of a higher number of plant species in the community (Provenza et al., 2002). Moreover, the utilization of a high number of plants minimizes the competitive advantages that occur when some plants are unbrowsed, and enhances the conservation of the vegetation biodiversity (Villalba et al., 2002).

Domestic herbivores have long exerted a decisive influence in vegetation at landscape level in the Mediterranean area (Le Houérou, 1981; Perevolotsky and Seligman, 1998). During the last two millennia, overbrowsing combined with fires, either natural or man-made, has driven the degradation of forests in favour of grass, thorny scrubs, and nitrophilous communities in the Mediterranean ecosystem of Iberian Peninsula (Carrión et al., 2003). This pattern is based mainly on the maintenance over time of a consistent herbivore pressure on palatable species, with a consequent benefit for the less palatable ones, promoting significant changes in forest composition (Le Houérou, 1981; Papanastasis and Peter, 1998, and references therein). However, the high variability in free-ranging goat foraging behaviour restricts generalizations about the effects of herbivory on plant communities, implying that herbivores are not invariant outputs of ecosystems, but rather show different foraging strategies when having even as few as five food choices (Papachristou et al., 2007). Thus, a coarse selection above the species level maintained over a long period of time, combined with a high variability foraging behaviour of goat, can promote the high vegetation biodiversity in Mediterranean forest (Bartolomé et al., 2000; Papachristou et al., 2005).

5. Conclusion

The results presented here confirm the high variability in nutritional quality of woody Mediterranean vegetation, not only between but also within species. However, although goats are able to select their food based on its nutritive value, the selection was made between contrasting species but not between species of similar characteristics or plants of the same species. This coarse level of selection, together with the variability in foraging behaviour shown by goats, permits the coexistence in the same habitat of diverse woody species with different nutritional value. The traditional extensive

grazing is considered a useful tool for the conservation of plant biodiversity (Bartolomé et al., 2000; Papachristou et al., 2005). Our results demonstrate that the foraging behaviour of free-ranging goats can explain the high plant biodiversity found in environments with heavy herbivore pressure, thus emphasizing the utility of maintaining traditional livestock grazing on natural protected areas.

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