Effects of shrub encroachment on herbage production and nutritive value in semi-arid Mediterranean grasslands

M. P. Zarovali, M. D. Yiakoulaki and V. P. Papanastasis

Department of Range Science and Wildlife-Fresh Water Fisheries, School of Forestry and Natural Environment, Aristotle University of Thessaloniki, Thessaloniki, Greece

Abstract

There is limited information on the effects of the increase in the density of shrubs on herbage production and nutritive value of natural grasslands in the Mediterranean region, currently facing major land use changes. Herbage production of drymatter (herbaceous fractions, of plant functional groups and by species), crude protein (CP), neutral-detergent fibre (NDF), acid-detergent fibre (ADF), acid-detergent lignin (ADL) and hemicellulose concentrations and *in vitro* organic matter digestibility were determined at the time of peak of annual growth across four types of grassland vegetation each characterized by different shrub cover regimes. A sharp reduction in herbage production and a reduction in nutritive value were found as a result of the increase in shrub cover. These changes appeared to be closely related to the shift in plant functional groups detected as shrub density increased. Herbage production from grasses and legumes was found to be more sensitive to shrub cover changes than herbage production from forbs, whereas, as grassland types became denser, annual species were gradually replaced by perennials and C_4 grasses by C_3 ones. The impact of shrub encroachment on Mediterranean grasslands is discussed in relation to their use by livestock.

Keywords: herbage production, herbage quality, extensification, shrub cover, functional groups, Mediterranean grasslands

Correspondence to: Maria P. Zarovali, Department of Range Science and Wildlife-Fresh Water Fisheries, School of Forestry and Natural Environment, Aristotle University of Thessaloniki, 541 24 Thessaloniki, Greece.
E-mail: mzaroval@for.auth.gr

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Introduction

Grasslands contribute only a small proportion of forage resources in the Mediterranean region of Europe but are essential for supporting ruminant production, especially sheep and cattle (Papanastasis and Mansat, 1996). In these grasslands, although the dominant vegetation is herbaceous, consisting of both annual and perennial species, there is often a small proportion of shrubs (0·10–0·15) (Papanastasis, 1999), which are kept under control by a traditional, rather intensive, pastoral management. Such a management may include high stocking rates, mixed flocks of sheep and goats, periodic burning and fuelwood collection (Papanastasis and Chouvardas, 2005). If it is altered or becomes less intensive then natural succession leads to the invasion by woody plants. This is because the majority of grasslands in the Mediterranean, as elsewhere in Europe, are successional plant communities having derived from natural forests after the removal of trees; without management, most of them would revert to forests (Snaydon, 1987; Spatz and Papachristou, 1999).

Over the last few decades, traditional pastoral management of many Mediterranean grasslands has been largely extensified leading to shrub encroachment, particularly in dry and semi-dry areas. The main reasons behind these changes are the abandonment of hilly and mountainous areas by rural populations who have migrated to urban and coastal areas, leading to the gradual encroachment of shrubs and trees onto former grasslands in marginal areas (Naveh, 1991; Lepart and Debussche, 1992; Le Houerou, 1993). Correia (1993) suggests that socio-economic problems in marginal areas are closely connected with human depopulation and that land abandonment can in fact be considered both an effect and a cause.

Encroachment by woody plants is a physiognomically and functionally important stage of plant succession with effects both at a landscape level, especially with the reduction of 'open' habitats and at an ecosystem level, with the modification of their structure and function (Debussche and Lepart, 1992; Grove and

Rackham, 2001). Succession starts immediately after abandonment and proceeds to different stages depending on particular environmental conditions; hence, the type of vegetation indicates the time since abandonment started (Tasser and Tappeiner, 2002). The reasons that woody plants invade grasslands are associated with their specific characteristics, which give them a competitive advantage over herbaceous species, especially in semi-arid areas. They include increased seed production and effective seed dispersal, exponential growth rate, tolerance to nutrient and water stress, vegetation reproduction and extended longevity (Fuhlendorf, 1997).

There are several consequences of shrub encroachment in Mediterranean grasslands. Among the most important ones are the reduction of biodiversity and the increase in fire risk. When shrubs invade grasslands, the open habitats are decreased and the semi-natural grasslands develop progressively into phrygana, maquis and ultimately forests, which are very vulnerable to wildfires (Mitchley and Ispikoudis, 1999).

There is limited information on the effects of the increase in shrub cover on herbage production and nutritive value of grasslands in the Mediterranean region. Most of this information comes from silvopastoral systems where trees rather than shrubs grow with herbaceous species. Several such studies have shown that both herbage production and nutritive value decrease as the tree canopy or density increases (e.g. Msika and Etienne, 1989; Armand and Etienne, 1995; Braziotis and Papanastasis, 1995; Papanastasis *et al.*, 1995; Garcia *et al.*, 1999). However, certain types of tree cover may increase pasture production while some species may have a beneficial role only on dry sites (Etienne, 1996). In shrublands, available herbage production was found to decrease with increased shrub cover (Platis and Papanastasis, 2003). However, no information was provided by such studies on the plant functional groups involved. The objective of this paper was to assess the impact of shrub encroachment on herbage production and nutritive value of semi-arid Mediterranean grasslands and discuss its implications to their management.

Materials and methods

Study area

The research was conducted in Lagadas county, central Macedonia, northern Greece (40°47′N, 23°12′E). The study area was nearly 575 ha and is located at an altitude of 450–550 m a.s.l. Mean annual precipitation is 586 mm and mean annual temperature is 12·1°C, indicating a semi-arid Mediterranean climate with cold winters (Le Houerou, 1981). The summers are hot and dry and have a duration of at least four months. Soils, which are mainly derived from metamorphic rocks, are shallow and acidic (pH 5·2–6·4), low in nitrogen, phosphorus and organic matter and have a sandy-loam texture (Zarovali, 2004). Grasslands are composed of both herbaceous and shrubby vegetation and are communally grazed by livestock (sheep, goats and cattle). During the study period, the grazing pressure was very light following a general trend of gradual abandonment of traditional activities in the whole Lagadas County over the previous 30-year period (Chouvardas *et al.*, 2006).

Experimental procedure

In early June 2003, four types of grasslands were identified in the study area based on their shrub cover. It was assumed that the higher the shrub cover the less space and light is available for herbaceous species growing between and under the shrubs. The mean values (and standard errors), determined by visual estimations by three independent observers, were: 0, 6·1 (2·1), 36·4 (2·6) and 60·5 (3·2)% respectively for the four shrub cover types, respectively. Hereafter, the four types are referred to as very open, open, dense and very dense shrub cover types respectively. The dominant shrub species was the evergreen species *Quercus coccifera*, while other deciduous shrubs, such as *Quercus pubescens*, *Pyrus amygdaliformis, Paliurus spina-cristii* and *Crataegus monogyna*, were also present. The mean of the shrubs height was 0·92, 1·56 and 2·27 m for the open, dense and very dense shrub cover types respectively. Each shrub cover type was replicated four times and in each replicate a plot of 0·09 ha (30 × 30 m) was randomly selected. In each of the sixteen plots, total above-ground herbage mass was harvested in mid-June. This period represents the peak of annual herbage growth in grasslands of the middle elevation zone in northern Greece (Papanastasis, 1982). Total above-ground herbage mass was obtained by cutting with hand-scissors at ground level from ten 0·50 m × 0·50 m quadrats placed randomly in each plot. Any woody vegetation falling within the quadrats was ignored.

The samples of the herbage mass were hand sorted into current year's production (refered to hereafter as herbage production) and previous year's production (refered to hereafter as old growth) while in half of them, i.e. from five quadrats for each plot randomly selected, herbage production was also sorted by species. The samples of each species were then grouped by plant functional groups, i.e. grasses, non-leguminous forbs and legumes. Plant functional groups were defined as non-phylogenetic groupings of species which perform similarly in an ecosystem, based on a set of common biological attributes (Woodward and Cramer, 1996;

Gitay and Noble, 1997). All samples were oven dried at 65°C for 48 h and weighed. Dry matter (DM) content was determined for herbage production and old growth separately and for each of the three plant functional groups. The latter were calculated as the mean of DM content of individual species belonging to each group. Grasses', non-leguminous forbs' and legumes' values were scaled up in order to correspond to herbage production values of each shrub cover type. Finally, the dominant species that contributed 0·80 of herbage production in each shrub cover type were identified. According to Cornelissen *et al.* (2003), the most abundant species are arbitrarily defined as those species that together make up about 0·70–0·80 of the standing biomass of the community and were used in order to obtain a good representation of the ecosystem or plant community under study. Except for the plant functional group that each of the dominant species belonged, additional data were collected for them including life cycle (i.e. annual or perennial species) and photosynthetic pathway (i.e. C_3 or C_4 species) based on Papadimitriou *et al.* (2004).

Chemical analyses

The chemical composition and *in vitro* organic matter digestibility (OMD) of herbage was determined on representative bulk samples for each plot in each shrub cover type. The bulk samples were composed of five samples for each plot that were not sorted by species. Each bulk sample was divided in two equal parts that were considered as replicates and were ground to pass a 1-mm screen of a Willey mill. Nitrogen concentration (N) was determined using the Kjeldahl method (AOAC, 1990). Crude protein (CP) was calculated as N × 6·25. Neutral-detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) concentrations were determined by the procedure described by Goering and Van Soest (1970). *In vitro* OMD was determined according to Moore's (1970) modification of Tilley and Terry's method (1963). Hemicellulose concentration was estimated from the difference between NDF and ADF concentrations (Harris, 1970).

Statistical analyses

Data on herbage DM production and CP, NDF, ADF, ADL and hemicellulose concentrations and IVOMD were averaged by plot and the latter six variables were also log-transformed before statistical analysis. All data sets were subjected to one-way analysis of variance (ANOVA) (Steel and Torrie, 1980) in order to test statistical significance across the four shrub cover types. Duncan's multiple-range test was applied in order to test statistical differences between means. The statistical analyses were carried out using SPSS 12·0 software for Windows (SPSS Inc., Chicago, IL, USA). All tests were performed at the level of significance of $P < 0·05$.

Results

Herbage production

The main part of the total above-ground herbage mass (~0·55 on average) was contributed by herbage production. It was gradually reduced as shrub cover increased. Compared with the very open type where shrub cover was absent, it decreased by 0·08, 0·49 and 0·62 in the open, dense and very dense types respectively. However, this reduction became statistically significant only when the shrub cover became dense (>0·36) (Table 1). There were no significant differences between the very open and open shrub cover types, or

Table 1 Dry matter (DM) production of herbage (g m^{-2}), and the s.e. of mean in parentheses, and proportion of herbaceous fractions in each of the four shrub cover types (very open, open, dense and very dense).

Herbaceous fraction	Very open: DM Production	Very open: Proportion	Open: DM Production	Open: Proportion	Dense: DM Production	Dense: Proportion	Very dense: DM Production	Very dense: Proportion
Herbage production	215·2 (11·8)^{a*}	0·56	198·8 (12·2)^{a}	0·55	110·3 (10·1)^{b}	0·63	82·2 (10·4)^{b}	0·48
Old growth	168·4 (11·8)^{a}	0·44	163·1 (11·7)^{a}	0·45	65·9 (5·3)^{b}	0·37	88·0 (7·9)^{ab}	0·52
Total herbaceous biomass	383·6 (16·6)^{a}	1·00	361·9 (16·5)^{a}	1·00	176·2 (10·9)^{b}	1·00	170·2 (11·7)^{b}	1·00

[1]Mean values within rows followed by different letters differ significantly ($P < 0·05$).

Table 2 Dry matter (DM) production (g m^{-2}), and the s.e. of mean in parentheses, and proportion of plant functional groups in each of the four shrub cover types (very open, open, dense and very dense).

Plant functional groups	Shrub cover type							
	Very open		Open		Dense		Very dense	
	DM Production	Proportion	DM Production	Proportion	DM Production	Proportion	DM Production	Proportion
Grasses	109·9 (18·4)^{ab*}	51	145·9 (11·1)^{a}	73	59·9 (12·5)^{bc}	54	29·0 (8·6)^{c}	35
Forbs	55·4 (14·4)^{a}	26	32·5 (10·9)^{a}	16	27·3 (9·8)^{a}	25	37·9 (11·0)^{a}	46
Legumes	49·9 (12·2)^{a}	23	20·4 (6·1)^{a}	11	23·1 (6·3)^{ab}	21	15·3 (5·5)^{b}	19
Herbage production	215·2 (11·8)^{a*}	100	198·8 (12·2)^{a}	100	110·3 (10·1)^{b}	100	82·2 (10·4)^{b}	100

[1]Mean values within rows followed by different letters differ significantly ($P < 0{\cdot}05$).

between the dense and very dense types. Old growth was also reduced as shrub cover increased, and was lowest in the dense type (Table 1). Total herbage mass followed the same pattern as herbage production.

Grasses were the main functional group, contributing more than 0·50 to herbage production, on average. Production of DM of grasses was greatest in the open and very open shrub cover types, with no significant differences between the two types. However, grasses were a greater proportion of herbage production in the open and dense than in the other two shrub cover types (Table 2).

The four shrub cover types differed in terms of the dominant grass species present (Table 3). In the very open shrub cover type, the dominant species were annual, with *Vulpia ciliata* being predominant and contributing 0·22 to herbage production. In the other three shrub cover types, the dominant species were perennials, with C_4 perennials making 0·59 of the herbage production in the open shrub cover type and 0·39 in the dense shrub cover type, while in the very dense shrub cover type they contributed only 0·05 as they were replaced by C_3 perennial grasses. In the very dense shrub cover type, *Stipa bromoides* was the dominant species, contributing 0·15 to herbage production (Table 3). No single species was common across the four types, only the C_4 grasses *Dichantium ischaemum* and *Chrysopogon gryllus* were common among the three latter shrub cover types.

Non-leguminous forbs were the second most important functional group, contributing 0·28 to herbage production, on average (Table 2). Although the contribution of forbs to the total DM was greatest in the very open shrub cover type and least in the dense type there were no significant differences between the four types. Their contribution to herbage production was greatest in the very dense and least in the open types, while in the other two shrub cover types was intermediate (Table 2). As in the case of grasses, the dominant forb species differed between the four shrub cover types (Table 3). In the very open shrub cover type, a single annual species (*Crepis foetida*) was the dominant one, contributing 0·11 to herbage production, while in the other three types perennial forb species dominated. *Thymus sibthorpii* was the dominant species in the dense and very dense shrub cover types and the second dominant in the open shrub cover type (Table 3). No single forb species was common across the four types.

Legumes contributed the least to herbage production amounting to an average of 0·18 (Table 2). The contribution of legumes to the total DM was greatest in the very open type and least in the very dense type. In the dense and open shrub cover types it was intermediate without being significantly different from the other two types. As a proportion, legumes contributed almost equally to herbage production in the very open, dense and very dense shrub cover types, but least in the open one (Table 2). The dominant legume species were, as in forbs, annuals in the very open type and mainly perennials in the other three shrub cover types. In the very open type, seven species of legumes contributed to herbage production, the most important being the perennial *Vicia cracca*. In the other shrub cover types, the number of dominant legume species was lower and the perennial *Genista carinalis* became the dominant, except in the dense type where *Trifolium ochroleucon* was the dominant species. Only the annual legume *Trifolium hirtum* was common among the four shrub cover types. *Vicia cracca* was common among the first three and *G. carinalis* among the latter three shrub cover types.

Nutritive value

Crude protein, NDF, ADF, ADL and hemicellulose concentrations and IVOMD values of herbage for each

Table 3 Proportions of the dominant plant species in herbage production for the four shrub cover types (very open, open, dense and very dense).

Plant species	Shrub cover type: Very open	Open	Dense	Very dense
Grasses				
Aegilops neglecta[a][1]	0·048			
Anthoxanthum odoratum[p][2]		0·028		
Brachypodium sylvaticum[p]				0·012
Bromus sterilis[a]	0·020			
Bromus tectorum[a]	0·070			
C4 grasses[3] [p]		0·589	0·391	0·046
Dactylis glomerata[p]	0·047		0·100	0·077
Festuca ovina group[p]				0·018
Stipa bromoides[p]				0·153
Taeniatherum caput-medusae[a]	0·021	0·011		
Vulpia ciliata[a]	0·218			
Forbs				
Anthemis arvensis[a]		0·013		
Asparagus acutifolius[p]				0·028
Crepis foetida[a]	0·109			
Chondrilla juncea[p]	0·043			
Clinopodium vulgare[p]				0·011
Convolvulus cantabrica[p]			0·009	
Dianthus corymbosus[p]		0·032		0·017
Knautia ambigua[p]				0·013
Plantago lanceolata[p]	0·020	0·014		
Potentilla recta[p]	0·006			
Rumex acetosella[p]	0·036			
Sedum amplexicaule[p]		0·016		
Silene italica[p]				0·087
Tanacetum corymbosum[p]				0·028
Teucrium chamaedrys[p]				0·073
Teucrium polium[p]			0·041	
Thymus sibthorpii[p]		0·027	0·116	0·101
Legumes				
Genista carinalis[p]		0·057	0·035	0·115
Lotus angustissimus[a]	0·024			
Ornithopus compressus[a]	0·030			
Trifolium angustifolium[a]	0·025			0·013
Trifolium hirtum[a]	0·051	0·010	0·035	0·010
Trifolium ochroleucon[p]	0·010		0·058	0·018
Trifolium subterraneum[a]	0·015			
Vicia cracca[p]	0·065	0·015	0·047	
% of herbage production	0·858	0·812	0·832	0·820

[1][a]: annual species
[2][p]: perennial species
[3]*Dichantium ischaemum*and *Chrysopogon gryllus*

of the four shrub cover types are presented in Table 4. Crude protein concentrations were highest in the very open and dense shrub cover types and lowest in the very dense type and intermediate in the open shrub cover type without however being statistically different from the other types. Concentrations of ADF and ADL increased with increasing shrub cover and their highest values were obtained in the very dense shrub cover type. However, there were no significant differences between the four types for NDF and hemicellulose concentrations and IVOMD values.

Table 4 Crude Protein, NDF, ADF, hemicellulose and ADL concentrations (g kg^{-1} DM) and in vitro organic matter digestibility (IVOMD) of herbage for the four shrub cover types(very open, open, dense and very dense) (s.e. of mean in parentheses).

	Shrub cover type			
	Very open	Open	Dense	Very dense
CP	62·2 (5·0)^{a*}	52·9 (1·0)^{ab}	56·0 (1·9)^{a}	46·4 (2·3)^{b}
NDF	687·3 (32·3)^{a}	742·1 (34·0)^{a}	732·4 (33·6)^{a}	707·8 (20·4)^{a}
ADF	420·9 (8·8)^{b}	424·4 (7·0)^{b}	432·7 (6·9)^{b}	466·0 (9·8)^{a}
Hemicellulose	266·4 (28·1)^{a}	317·8 (27·4)^{a}	299·7 (29·1)^{a}	241·9 (17·0)^{a}
ADL	69·1 (5·3)^{b}	68·3 (4·4)^{b}	80·3 (8·7)^{ab}	99·3 (8·7)^{a}
IVOMD	0·552 (0·021)^{a}	0·439 (0·070)^{a}	0·494 (0·040)^{a}	0·444 (0·014)^{a}

[1]Mean values within rows followed by different letters differ significantly ($P < 0·05$).

Discussion

Marriott *et al.* (2004) reviewed the results of a number of extensification experiments across Europe and concluded that the abandonment of traditional management practices results in both rapid changes in plant species composition and in decreases in species richness, biomass production and nutritive value of herbage. The four shrub cover types identified in this study represent successional stages of vegetation following extensification of human activities.

The findings are in agreement with other studies reporting that changes in tree cover and density significantly affect herbage production and nutritive value in grasslands (e.g. Msika and Etienne, 1989; Armand and Etienne, 1995). In silvopastoral systems, the effect of the tree layer on herbage production and its seasonal distribution was found to be either positive or negative, depending both on climatic conditions, such as drought, and on tree type, distribution, density and age (Frost and McDougald, 1989; Mosquera-Losada *et al.*, 2005). In plantations with pines (*Pinus* spp.), it is reported that the increase in tree-crown density results in a significant reduction in herbage production of the understorey (e.g. Pase, 1958; Braziotis and Papanastasis, 1995; Papanastasis *et al.*, 1995; Papanastasis, 1996; Garcia *et al.*, 1999). This reduction is attributed to reduced light reaching the herbaceous understorey. The same trend was identified in *Q. coccifera* shrublands of northern Greece where herbage production and forage availability (herbage and browse species) for small ruminants significantly decreased as shrub cover increased (Platis and Papanastasis, 2003). Conversely, Papachristou *et al.* (1997) reported that removal of woody vegetation in Mediterranean shrublands resulted in increased available herbage production and improved quality and availability for small ruminants. This means that, although not as tall as trees, shrubs do affect negatively herbage production and nutritive value as their shrub cover increases, apparently because of the reduction of available light to the herbaceous layer.

Herbage production by plant functional groups was found to significantly respond to increasing shrub cover. Grasses' and legumes' production was found to be more sensitive to shrub cover changes than forbs' production. The dominance, in terms of contribution to herbage production, of annual species in the very open cover type and of perennial species in the denser types agrees with the findings of other studies which report similar changes in the composition of plant communities, in the floristic and life form diversity and in the adaptive strategies during secondary succession in Mediterranean areas (Gondard *et al.*, 2001; Saïd, 2002). However, warm season (C_4) plants were gradually replaced by cool season (C_3) plants as shrub cover increased. Papanastasis (1981) found that, in open type grasslands of the same altitude in northern Greece, C_4 species contributed the most to herbage production (0·29 on average).

Results from the present study showed that different species were present depending on the amount of shrub cover with one single species being common among the four shrub cover types. In research conducted in the same locality as the present study, species richness was also found to be significantly different among the four shrub cover types; open type was the most diverse with thirteen species per 0·25 m^2, while in the very dense type the herbaceous species richness decreased to only six species per 0·25 m^2 (Papadimitriou *et al.*, 2004). Debussche *et al.* (1996) reported that floristic composition and species richness was altered in a study of succession in old-field plots in Mediterranean France. Other authors report that floristic composition and species richness are strongly dependent on management (Debussche *et al.*, 1996; Lavorel *et al.*, 1999; Kahmen *et al.*, 2002; Moog *et al.*, 2002).

The most important measures of the nutritive value of herbage are *in vitro* digestibility and the concentrations of CP and fibre (Wilkins and Humphreys, 2003). The higher CP concentration in the very open and dense shrub cover types might be attributable to the greater contribution of legume species (0·23 and 0·21 respectively) to herbage production of each shrub cover type. Plant species composition strongly determines the nutritional quality of vegetation since nutritive value varies greatly among species (Van Soest, 1982). In this study, CP concentration of herbage ranged from 46 to 62 g kg^{-1} DM. According to Vercoe *et al.* (1961), when CP concentration falls below 70 g kg^{-1} DM, the low intake of nitrogen might limit animal production. The results of this study are in agreement with Yiakoulaki and Nastis (1995) who reported that the nutritive value of herbage decreased as the proportion of shrub cover increased from 0·53 to 0·66 in *Q. coccifera* shrublands of northern Greece. This was evidenced by the greater concentrations of CP and values of IVOMD, and lower concentrations of NDF and ADL in goats' diets in the shrubland with the least shrub cover. The same authors reported that shrub cover also had a significant effect on goats' DM intake and that this intake was higher in the least dense type.

Among the four shrub cover types studied, the first two (very open and open) did not differ significantly either in herbage production or nutritive value although their species composition was quite divergent (more annual species as well as legumes in the very open type). This means that having a shrub cover of less than 0·10 in semi-arid Mediterranean grasslands does not limit herbage production and nutritive value. On the contrary, it could be an advantage for grazing sheep flocks which usually (by tradition) have some goats as well. However, herbage production was significantly reduced when shrub cover exceeded 0·30. It should also be noted that the old growth was simultaneously reduced compared with the open types. This suggests that, as shrub cover increases, there is a decrease not only in herbage production but also in old growth, apparently because of the faster decomposition of organic matter as a result of the environmental amelioration caused by shrubs. This subject though needs further experimentation.

Management implications

Shrub encroachment in Mediterranean grasslands is a relatively recent phenomenon. In the study area, e.g. it started in 1970s when goat grazing was reduced due to rural depopulation and as the practice of using shrubs for fuelwood and charcoal was discontinued (Chouvardas *et al.*, 2006). Similar events elsewhere in Europe started earlier after World War II (Mitchley and Ispikoudis, 1999). This development creates significant problems for Mediterranean livestock production systems, which have to adapt if the traditional extensive use of grasslands is to be continued.

The sharp reduction in herbage production, together with the reduction in its nutritive value as a result of the increase of shrub cover, profoundly affects grassland management. Shrub-invaded grasslands can no longer support high numbers of sheep, which are the traditional grazers of Mediterranean grasslands, or cattle. Goats are the most suitable animals to utilize shrub-infested grasslands. Goats, however, are not capable of fully controlling shrubs particularly vigorous sprouting species such as *Q. coccifera*. In addition, they cannot reach shrubs if they are too dense to be penetrated or they exceed a certain height, typically 1·5 m. In such cases, additional measures such as shrub cutting by mechanical or chemical means or prescribed burning are also needed (Papanastasis and Liakos, 1991; Papanastasis *et al.*, 1991; Papachristou *et al.*, 1997). Shrubs need to be properly integrated in the grazing management of Mediterranean grasslands (Papanastasis and Mansat, 1996). In most cases, however, a balanced utilization of the shrub-invaded grasslands with mixed flocks of sheep and goats, assisted by additional measures such as shrub cutting for fuelwood or prescribed burning, could solve the problem provided that this utilization is well planned and operated.

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References

AOAC (1990) *Official methods of analysis, 15th edn*, 746 pp. Washington DC, USA: Association of Official Analytical Chemists.

Armand D. and Etienne M. (1995) Effet du couvert arboré sur la production du sursemis de trèfle souterrain dans le sud-est de la France. [Effects of tree cover on production of overseeded subterranean clover in the southeast of France]. *Cahiers Optons Méditerranéennes*, **12**, 184–187.

Braziotis D.C. and Papanastasis V.P. (1995) Seasonal changes of understorey herbage yield in relation to light intensity and soil moisture content in a *Pinus pinaster* plantation. *Agroforestry Systems*, **29**, 91–101.

Chouvardas D., Ispikoudis I. and Papanastasis V.P. (2006) Evaluation of temporal changes of the landscape of Kolchicos basin of lake Koronia with the use of Geographical Information Systems (GIS). In: Platis P., Sfougaris A., Papachristou T. and Tsiontsis A. (eds) *Rangeland of lowlands and semi-mountainous areas: means of rural development. Proceedings of the 4th Panhellenic*

Rangeland Congress, Volos, Greece, 2004, pp. 253–261. (In Greek with English summary)

Cornelissen J.H.C., Lavorel S., Garnier E., Díaz S., Buchmann N., Gurvich D.E., Reich P.B., ter Steege H., Morgan H.D., van der Heijden M.G.A, Pausas J.G. and Poorter H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.

Correia T. (1993) Land abandonment: changes in the land use patterns around the Mediterranean basin. *Cahiers Options Méditerranéennes*, **1**, 97–112.

Debussche M. and Lepart J. (1992) Establishment of woody plants in Mediterranean old fields: opportunity in space and time. *Landscape Ecology*, **6**, 133–145.

Debussche M., Escarré J., Lepart J., Houssard C. and Lavorel S. (1996) Changes in Mediterranean plant succession: old fields revisited. *Journal of Vegetation Science*, **7**, 517–526.

Etienne M. (1996) Research on temperate and tropical silvopastoral systems: a review. In: Etienne M. (ed.) *Western European silvopastoral systems*, pp. 5–19. Paris, France: Science update, INRA éditions.

Frost W.E. and McDougald N.K. (1989) Tree canopy effects on herbaceous production of annual rangeland during drought. *Journal of Range Management*, **42**, 281–283.

Fuhlendorf S.D. (1997) Why does brush dominate our grasslands? In: Rollins D. (ed.) *Brush sculptors: innovations for tailoring brushy rangelands to enhance wildlife habitat and recreational value*. San Angelo, Texas, USA: TAMV Agricultural Research and Extension Centre.

Garcia A., Rozados M.J., Silva-Panto F.J. and Lindner R. (1999) Evaluation of natural populations of *Dactylis glomerata* for grazing under pinewoods. *Grassland Science in Europe*, **4**, 167–169.

Gitay H. and Noble I.R. (1997) What are plant functional types and how should we seek them? In: Smith T.M., Shugart H.H. and Woodward F.I. (eds) *Plant functional types: their relevance to ecosystem properties and global change*, pp. 3–19. Cambridge, UK: Cambridge University Press.

Goering H.K. and Van Soest P.J. (1970) *Forage fibre analyses, Agricultural Handbook No. 379*. Washington DC, USA: USDA.

Gondard H., Romane F., Grandjanny M., Junqing L.I. and Aronson J. (2001) Plant species diversity changes in abandoned chestnut (*Castanea sativa*) groves in southern France. *Biodiversity and Conservation*, **10**, 189–207.

Grove A.T. and Rackham O. (2001) *The nature of Mediterranean Europe: an ecological history*. London, UK: Yale University Press.

Harris L.E. (1970) *Nutrition research techniques for domestic and wild animals, Volume 1*, Logan UT, USA: Utah State University.

Kahmen S., Poschlod P. and Schreiber K.-F. (2002) Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation*, **104**, 319–328.

Lavorel S., Rochette C. and Lebreton J.-D. (1999) Functional groups for response to disturbance in Mediterranean old fields. *Oikos*, **84**, 480–498.

Le Houerou H.N. (1981) Impact of man and his animals on Mediterranean vegetation. In: di Castri F. (ed.) *Ecosystems of the World 11, Mediterranean-type shrublands*, pp. 479–521. New York, USA: Elsevier Scientific Publishing.

Le Houerou H.N. (1993) Land degradation in Mediterranean Europe: can agroforestry be a part of the solution? A prospective review *Agroforestry Systems*, **21**, 43–61.

Lepart J. and Debussche M. (1992) Human impact on landscape patterning: Mediterranean examples. In: Hansen A.J. and di Castri F. (eds) *Landscape boundaries, consequences for biotic diversity and ecological flows*, pp. 76–106. New York, USA: Springer.

Marriott C.A., Fothergill M., Jeangros B., Scotton M. and Louault F. (2004) Long-terms impacts of extensification of grassland management on biodiversity and productivity in upland areas. A review. *Agronomie*, **24**, 447–462.

Mitchley J. and Ispikoudis I. (1999) Grassland and shrubland in Europe: biodiversity and conservation. *Grassland Science in Europe*, **4**, 239–251.

Moog D., Poschlod P., Kahmen S. and Schreiber K.-F. (2002) Comparison of species composition between different grassland management treatments after 25 years. *Applied Vegetation Science*, **5**, 99–106.

Moore J.E. (1970) Procedure for the two-stage in vitro digestion of forages. In: Harris L.E. (ed.) *Nutrition research techniques for domestic and wild animals, vol. I*. Logan UT: Utah State University.

Mosquera-Losada M.R., Pinto-Tobalina M. and Rigueiro-Rodriguez A. (2005) The herbaceous component in temperate silvopastoral systems. In: Mosquera-Losada M.R., McAdam J. and Rigueiro-Rodriguez A. (eds) *Silvopastoralism and sustainable land management*, pp. 93–100. Wallingford, UK: CABI Publishing.

Msika B. and Etienne M. (1989) Modification de facteurs biotiques par la présence d'arbres en région méditerranéenne francaise: effets sur la production herbagère. [Modification of abiotic factors by the presence of trees in the Mediterranean region of France: effects on herbage production]. In: *Proceedings of XVI Congrès International des Herbages, Montpellier, France*, pp. 1619–1620.

Naveh Z. (1991) Mediterranean uplands as anthropogenic perturbation-dependent systems and their dynamiconservation management. In: Ravera O. (ed.) *Terrestrial and aquatic ecosystems: perturbation and recovery*, pp. 545–556. New York, USA: Ellis Horwood.

Papachristou T.G., Platis P.D. and Papanastasis V.P. (1997) Forage production and small ruminant grazing responses in Mediterranean shrublands as influenced by the reduction of shrub cover. *Agroforestry Systems*, **35**, 225–238.

Papadimitriou M., Tsougrakis Y., Ispikoudis I. and Papanastasis V.P. (2004) Plant functional types in relation to land use changes in a semi-arid

Mediterranean environment. In: Arianoutsou M. and Papanastasis V.P. (eds) *Proceedings of the 10th MEDECOS Conference, Rhodes Greece, 2004*, pp. 1–6. Rotterdam, the Netherlands: Millpress.

Papanastasis V.P. (1981) Species structure and productivity in grasslands of northern Greece. In: *Components of productivity of Mediterranean-climate regions*, pp. 205–217. The Hague, the Netherlands: Dr. W. Junk Pubs.

Papanastasis V.P. (1982) Production of natural grasslands in relation to air temperature and precipitation in northern Greece. *Dassiki Erevna III*, (in Greek with English summary).

Papanastasis V.P. (1996) Silvopastoral systems and range management in the Mediterranean region. In: Etienne M. (ed.) *Western European silvopastoral systems*, pp. 143–156. Rome, Italy: FAO.

Papanastasis V.P. (1999) Grasslands and woody plants in Europe with special reference to Greece. *Grassland Science in Europe*, **4**, 14–24.

Papanastasis V.P. and Chouvardas D. (2005) Application of the state-and-transition approach to conservation management of a grazed Mediterranean landscape in Greece. *Israel Journal of Plant Sciences*, **53**, 191–202.

Papanastasis V.P. and Liakos L. (1991) Effects of kermes oak brushland improvement on vegetation and livestock gains of goats in Greece. In: *Proceedings of IV International Rangeland Congress, vol. 2, Montpellier, France*, pp. 850–853.

Papanastasis V.P. and Mansat P. (1996) Grasslands and related forage resources in Mediterranean areas. *Grassland Science in Europe*, **1**, 47–57.

Papanastasis V.P., Papachristou T. and Platis P. (1991) Control of woody plants with mechanical means in a rangeland of Macedonia, Greece. In: *Grassland renovation and weed control in Europe. Proceedings of EGF Conference, Graz, Austria*, pp. 203–205.

Papanastasis V.P., Koukoura Z., Alifragis D. and Makedos J. (1995) Effects of thinning, fertilization and sheep grazing on the understorey vegetation of *Pinus pinaster* plantations. *Forest Ecology and Management*, **77**, 181–189.

Pase C.P. (1958) Herbage production and composition under immature ponderosa pine stands in the Black Hills. *Journal of Range Management*, **11**, 238–243.

Platis P.D. and Papanastasis V.P. (2003) Relationship between shrub cover and available forage in Mediterranean shrublands. *Agroforestry Systems*, **57**, 59–67.

Saïd S. (2002) Floristic and life form diversity in post-pasture successions on a Mediterranean island (Corsica). *Plant Ecology*, **162**, 67–76.

Snaydon R.W. (1987) Managed Grasslands. Analytical Studies. In: Goodall D.W. (ed.), *Ecosystems of the World*, 17B, p. 285. Amsterdam, the Netherlands: Elsevier.

Spatz G. and Papachristou T.G. (1999) Ecological strategies of shrubs invading extensified grasslands: their control and use. *Grassland Science in Europe*, **4**, 27–36.

Steel R.G.D. and Torrie J.H. (1980) *Principles and procedures of statistics*, 2nd edn. New York, USA: McGraw-Hill Book Corporation.

Tasser E. and Tappeiner U. (2002) Impacts of land use changes on mountain vegetation. *Applied Vegetation Science*, **5**, 173–184.

Tilley J.M.A. and Terry R.A. (1963) A two stage technique for the *in vitro* digestion of forage crops. *Journal of British Grassland Society*, **18**, 104–111.

Van Soest P.J. (1982) *Nutritional ecology of the ruminant*. Corvallis, OR, USA: O and B Books.

Vercoe J.E., Tribe D.E. and Pearce G.R. (1961) Herbage as a source of digestible OM and digestible N for the grazing sheep. *Australian Journal of Agricultural Research*, **12**, 689–695.

Wilkins P.W. and Humphreys M.O. (2003) Progress in breeding perennial forage grasses for temperate agriculture. *Journal of Agricultural Science, Cambridge*, **140**, 129–150.

Woodward F.I. and Cramer W. (1996) Plant functional types and climatic changes: introduction. *Journal of Vegetation Science*, **7**, 306–308.

Yiakoulaki M.D. and Nastis A.S. (1995) Intake by goats grazing kermes oak shrublands with varying cover in Northern Greece. *Small Ruminant Research*, **17**, 223–228.

Zarovali M.P. (2004) *Relationship between land use changes and above ground herbage production in rangelands of Lagadas County, Thessaloniki, Greece*. M.Sc. thesis, Aristotle University of Thessaloniki: Laboratory of Rangeland Ecology (in Greek with English summary).

