

Plant diversity in relation to overgrazing and burning in mountain mediterranean ecosystems

V.P. Papanastasis^{1*}, S. Kyriakakis² and G. Kazakis³

¹*Laboratory of Rangeland Ecology, Aristotle University, 541 24 Thessaloniki, Greece*

²*Direction of Forests, 731 00 Chania, Chrysopigi, Crete, Greece*

³*Mediterranean Agronomic Institute, 731 00 Chania, Crete, Greece*

* *Corresponding author*

Vasilios P. Papanastasis

Telephone +302310998933 - Fax +302310992721 - E-mail: vpapan@for.auth.gr

Keywords: Crete, endemic species, grasslands, life forms, phrygic ecosystems, Psilorites mountain

Abstract

There is a growing concern about the negative impact of livestock overgrazing on biodiversity of ecosystems in the Mediterranean region, particularly in the mountain areas where several rare or endemic species are usually found. This concern is aggravated by the fact that overgrazing is very often associated with wildfires set by the shepherds themselves to suppress undesirable to animals vegetation. In this paper, the relation between plant diversity and overgrazing with or without burning was investigated on Psilorites mountain of Crete at an average altitude of 1200 m. The study included grasslands and phrygic ecosystems that are communally grazed by sheep and goats for 6-7 months during the summer period at an average stocking rate of 4.6 sheep/ha/year which is at least four times higher than grazing capacity. In addition, they are frequently burned by the shepherds. In May 1996, 30 representative sites were selected, subjected to only overgrazing or to combined overgrazing and burning. In each site, 0.50 x 0.50 m each, were taken where the number of species and their abundance were measured. Subsequently, the species richness and equitability were calculated. In the phrygic ecosystems, it was found that the overgrazed sites produced slightly higher species richness compared with the protected sites (20 vs. 18 species per quadrat respectively) as well as equitability (0.46 vs. 0.45 respectively) but this increase was not statistically significant. On the contrary, overgrazed and burned sites had significantly lower values of species richness and evenness compared with the sites subjected to only overgrazing (17 vs. 20 species per quadrat and 0.43 vs. 0.46 index of equitability). An opposite effect of overgrazing was found in grasslands where overgrazed sites produced significantly lower species richness compared to the protected ones (13 vs. 15 species per quadrat) as well as equitability (0.39 vs. 0.42). These results suggest that overgrazing had a negative impact on plant diversity of grasslands but in phrygic ecosystems overgrazing was negative only when combined with burning.

Introduction

Grazing by domestic herbivores has a long history in the Mediterranean basin. It has acted as a major force in modifying and shaping Mediterranean ecosystems and very often resulted in the destruction of Mediterranean forests, especially when combined with wildfires (Papanastasis, 1998a). For this reason, livestock grazing is traditionally considered by conservationists incompatible with maintaining high biodiversity in the Mediterranean ecosystems (Thirgood, 1981; Tsoumis 1985).

This view however has been challenged in the last few decades. After reviewing the available literature,

Seligman & Perevolotsky (1994) have found that vegetation in the Mediterranean basin is well adapted to intensive herbivory by domestic ungulates and low grazing pressure can have undesirable ecological and management consequences. On the other hand, several experiments have shown that the impact of grazing on biodiversity mainly depends on its intensity. Naveh & Whittaker (1979), for example, have found higher diversity of herbaceous plants and particularly annuals and geophytes under moderate grazing than under complete protection and heavy grazing in Mediterranean grasslands and woodlands of Israel. Further studies in the same country which have been reviewed by Noy-Meir (1998) reveal that quite distinct

plant communities are developed under heavy, medium and no grazing and that ungrazed or undisturbed grasslands usually have low biodiversity. He concluded that total biodiversity tends to be higher in grazed than in protected plots and reduction may happen only at the extremely heavily grazed areas, such as near watering points or camping sites. Moreover, Stenberg *et al.* (2000) have found that species richness is affected not only by grazing intensity but also by the grazing regime, namely continuous vs seasonal grazing and early vs late in the season use of Mediterranean grassland by cattle.

Similar results have been also found in Spain, where it was observed that four years after protection from grazing species diversity was lower in the ungrazed than in the grazed sites (Montalvo *et al.* 1993). Also, Puerto *et al.* (1990) have found maximum biodiversity in moderately grazed communities on oligotrophic soils with intermediate levels of biomass. On the other hand, Peco *et al.* (1998) have found in dehesas a reduction in species richness in ungrazed as compared to grazed areas but this reduction was significant only when species richness was measured on small plots (10x10m). According to Noy-Meir (1998), all these results are consistent with the predictions of the dominance-disturbance hypothesis, the competition-defoliation trade-off hypothesis and the model of Milchunas *et al.* (1988) which postulate that species diversity increases with increasing intensity over a wide range from ungrazed grasslands up to a fairly heavy grazing rate.

Quite different are the results obtained in Greece. In grasslands dominated by annual species, heavy grazing resulted in a decrease of species composition compared with no grazing (Koukoura *et al.* 1998). In grasslands dominated by perennial warm-season grasses, however, even moderate grazing may reduce species composition, particularly of cool-season grasses which are more palatable to animals than the warm-season ones (Papanastasis, 1985). Several other studies have shown that overgrazing combined with wildfires both in grasslands and phrygic ecosystems may lead to severe degradation and desertification (Pantis & Mardiris, 1992; Arianoutsou-Faraggitaki, 1985; Vokou *et al.* 1986; Pantis & Margaritis, 1988; Koutsidou & Margaritis, 1998).

As far as the role of the fire is concerned, Noy-Meir (1995) has found that burning has more remarkable and long lasting effects on species composition in ungrazed than in grazed sites due to the greater fuel load in the former than in the latter. Individual species though respond differently; grazing always increases biodiversity but fire tends to do the same only in grasslands dominated by perennials while no such effects occur in grasslands dominated by annuals.

Most of the studies on the effects of grazing and fire in the Mediterranean region have been carried out in low altitude grasslands. On the contrary, few such studies have been conducted in mountain Mediterranean ecosystems. Such ecosystems have lower biodiversity and are predominated by perennial species (Montalvo *et al.* 1991; Papanastasis, 1981; Athanasiadis *et al.* 2001); also, they are more sensitive to disturbances due to the harsher climatic conditions as compared to the grasslands of lower altitudes.

Crete is predominantly a mountainous island with phrygic ecosystems growing from the sea level up to the sub-alpine region while grasslands are restricted to karstic depressions (dolines) in the mountains (Egli, 1991). More than 10% of the Cretan flora are endemic to this island and about 30% of them are found above timberline (Montmollin, 1991). Grazing and fire are long practiced in the island and have severely affected Mediterranean ecosystems (Papanastasis *et al.* 1990). However, apart from a few studies on phrygic vegetation in south White Mountains by Bergmeier (1996; 1997; 1998a; 1988b) and Bergmeier & Matthäs (1996) no detailed research has been carried out on the effects of grazing and fire on high altitude Mediterranean ecosystems. In this paper, the role of overgrazing and fire on mountain phrygic and grassland ecosystems is investigated and explored.

Materials and methods

The research was carried out on Psilorites mountain of Crete (35° 08' - 35° 18' N - 24° 54' - 25° 18' E), at a mean altitude of 1200 m (Fig. 1). Psilorites is the highest mountain of the island (2456 m) and is characterized by a long history of human activities including livestock husbandry which have caused land degradation and desertification (Lyrintzis & Papanastasis, 1995; Lyrintzis, 1996; Papanastasis,



Figure 1. General view of the study area

1998b). The dominant bedrock is undivided limestone of the “platy series” of the Jurassic – Eocene period. Soils are shallow, mostly red, derived from limestone (Papanastasis, 1998b). Climate is humid Mediterranean with a mean annual precipitation exceeding 800 mm mostly falling in the winter period in the form of snow often covering the mountain until the month of April. Bergmeier & Matthäs (1996) report that the mean air temperature does not exceed 21°C in the hottest month of July at an altitude of 1200 m of the White Mountains while the mean minimum temperature gets near or below zero indicating severe winters. Phrygantic ecosystems are the main vegetation type covering 63% of the mountain and dominated by chamaephytes. These are dwarf shrubs, spiny or aromatic, with seasonal dimorphism and very flammable. Grasslands are limited to dolines and cover no more than 0.49% of the mountain (Papanastasis, 1998b). They are dominated by annual and perennial herbaceous species (Egli, 1991) but quite often dwarf shrubs are also present.

In addition, phrygantic ecosystems are often burned by the shepherds themselves at 3-5 years intervals in order to suppress the unpalatable to animals dwarf shrubs and promote the growth of herbaceous plants. Burned areas are overgrazed by large numbers of animals right after the fire. This practice is more rare in grasslands.

The whole area is communally grazed by sheep and goats during the summer time, from May to

October, at an average stocking rate of 4.6 sheep equivalents/ha/year (Menjli, 1994). This rate is considered at least four times higher than the grazing capacity of rangelands in Crete (Papanastasis *et al.* 1990) thus suggesting overgrazing.

In 1996, 30 sites of 0.1 ha each were selected to represent overgrazed and protected as well as burned and unburned regimes. Of those, 20 were placed in phrygantic and 10 in grassland ecosystems (Fig. 2).

For the protected treatments, we used existing exclosures 0.5 ha large each and 5-6 years old, which were established by the Forest Service for conservation purposes. Our attempt to establish new exclosures failed because shepherds are very suspicious and hostile to fences. As a result, it was not possible to fully combine the treatments of over grazing with burning: we could find burned and overgrazed sites but not burned and protected from grazing except one in grasslands. Burned sites were 1-10 years old and were identified on the basis of information provided by the local shepherds as well as on expert opinion.

In May-June 1996, 6 quadrats 0.50x0.50 m each were randomly selected in each site and the total number of species as well as their individuals were counted. The species were sorted into botanical families (Tutin *et al.* 1993) and life forms (Raunkiaer, 1934). For data analysis, species richness expressed as number of species per quadrat and equitability were cal

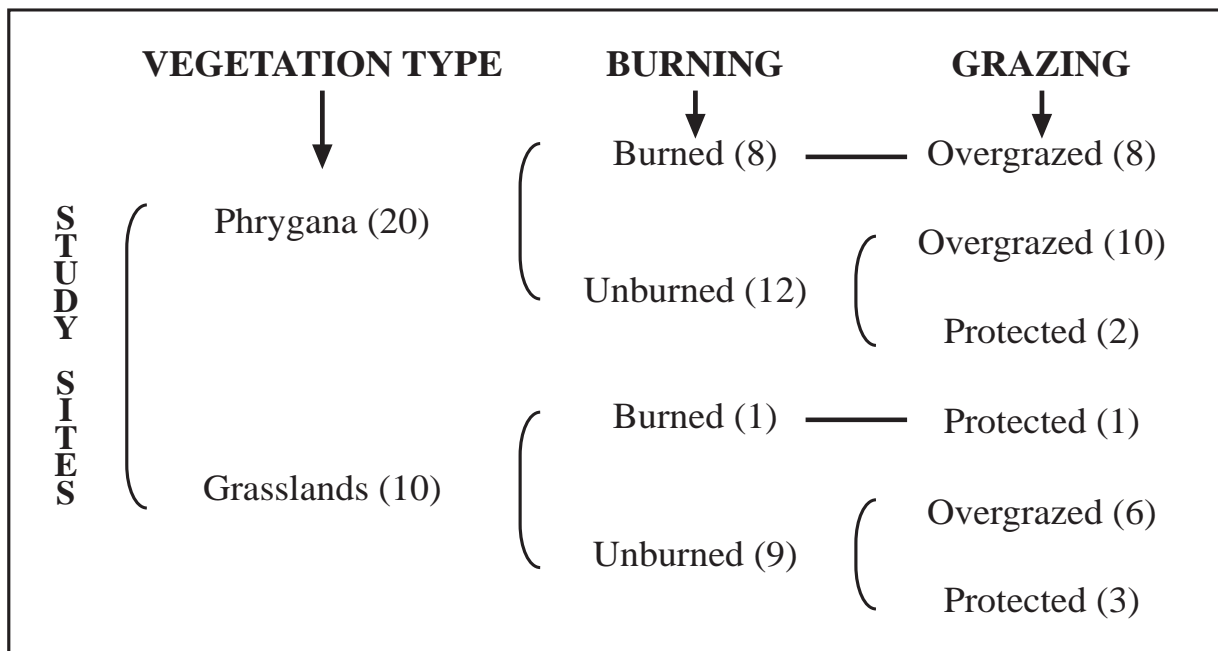


Figure 2. Breakdown of the 30 sites according to the vegetation type and the state of burning and grazing (numbers in parentheses refer to the sites allocated to each treatment).

culated for each site. For the latter, the formula $E = H'/H_{\max}$ (Magurran, 1988) was used. In addition, species richness was calculated separately for the various life forms, namely therophytes, hemicryptophytes, geophytes and chamaephytes. Subsequently, statistical comparisons were made between overgrazed and protected as well as between burned and unburned sites with a *t*-test (Magurran, 1988).

Results

Plant species profile and distribution

Altogether 310 plant species were recorded which belonged to 39 botanical families and 181 genera. The distribution of the various species to the families is shown on table 1. It is clear that the most populous family was Leguminosae with 51 species followed by Compositae and Gramineae with 45 species each. These three families contained 45% of the total number of species. All the other families had much fewer species while the majority of them had less than 5 species.

The frequency distribution of the families in the various study sites followed more or less their size; the most populous of them were the most widely distributed among the sites (Table 1). Nevertheless, there were some exceptions; the most notable example was the family Rubiaceae which was recorded in all the sites although it had only 16 species.

As far as the size of genera is concerned, the majority of them had only one species while only 6 genera had more than 5 species, namely *Trifolium* (13), *Medicago* (10), *Galium* (9), *Bromus* (8), *Crepis* (7) and *Veronica* (6) (Table 2).

Table 3 shows the number of species in the various life forms. It is clear that the majority (59%) of the species were therophytes. Of those, 13% were annual and biennial grasses with the most dominant being *Poa bulbosa* (L.), *Vulpia ciliata* (Dumort), and *Aira elegantissima* (L.); 21% were annual legumes with the most dominant being *Trifolium campestre* (L.), *T. subterraneum* (L.) and *Trigonella monspeliensis* (L.); and the remaining 66% were annual forbs belonging to all the other families except Gramineae and Leguminosae and with the most dominant being *Galium murale* (L.), *Crepis cretica* (L.) and *Lagoecia cuminoides* (L.). Hemicryptophytes were the second largest group (23%). Of these, 25% were perennial grasses with the most dominant being *Dactylis glomerata* (L.), *Lolium perenne* (L.) and *Catapodium rigidum* (L.); and the remaining 75% belonged to other than the Gramineae families with

the most dominant being *Centaurea idaea* (L.), *Eryngium campestre* (L.) and *Trifolium uniflorum* (L.). Chamaephytes were making 11% of the total number and dominated by *Onomis spinosa* (L.), *Sarcopoterium spinosum* (L.), *Euphorbia acanthothamnus* (L.) and *Corydanthus capitatus*. Geophytes were making 5% of the total number and dominated by

Table 1. Size and frequency distribution of botanical families in the study sites.

Family	No. of species	Frequency (%)
Acanthaceae	1	3
Berberidaceae	1	10
Boraginaceae	3	17
Campanulaceae	3	33
Caryophyllaceae	23	93
Cistaceae	2	37
Compositae	45	100
Convolvulaceae	2	17
Crassulaceae	3	27
Cruciferae	12	70
Cyperaceae	3	20
Dipsacaceae	3	17
Euphorbiaceae	2	43
Gentianaceae	2	13
Geraniaceae	4	30
Gramineae	45	100
Guttiferae	2	47
Iridaceae	2	7
Labiatae	13	77
Leguminosae	51	97
Liliaceae	11	50
Linaceae	2	23
Oleaceae	1	3
Orchidaceae	1	3
Orobanchaceae	1	3
Plantaginaceae	4	53
Plumbaginaceae	1	3
Polygalaceae	1	13
Polygonaceae	6	40
Primulaceae	2	37
Ranunculaceae	6	57
Rhamnaceae	1	7
Rosaceae	6	57
Rubiaceae	16	100
Santalaceae	2	13
Scrophulariaceae	9	50
Umbelliferae	13	73
Valerianaceae	4	20
Violaceae	1	3
Total	310	

Table 2. Distribution of species in the various genera.

No. of species per genus	No. of genera	% of the total
1	126	70
2	30	17
3	11	6
4	6	3
5	2	1
6	1	0.5
7	1	0.5
8	1	0.5
9	1	0.5
10	1	0.5
13	1	0.5
Total: 181		

Allium rubrovittatum (L.), *Asphodeline lutea* (L.) and *Urginea maritima* (L.). Finally, nanophanerophytes were making only 2% of the total number and dominated by *Calycotome villosa* (Poiret), *Rhamnus lysioidea* (L.) and *Prunus prostata* (L.).

Among the total species recorded, 15 are endemic to Crete (Table 5). All of them were present in phryganic communities, except *Polygonum idaeum*

Table 3. Distribution of plant species to various life forms

Life form	No. of species
Chamaephytes	33
Geophytes	15
Hemicryptophytes	72
Phanerophytes	7
Therophytes	183
Total	310

which was found only in grasslands. On the contrary, only a few of them were recorded in grasslands.

Between phryganic and grassland ecosystems, the therophytes, geophytes and chamaephytes were significantly more in the former than in the latter ecosystems, while the opposite was true for the hemicryptophytes (Table 5). As a result, species richness was much higher in the phryganic areas than in grasslands.

Effects of overgrazing and burning

In general, species richness was affected by both overgrazing and burning but this effect was different in the various life forms.

Irrespective of the vegetation type, total species richness was not affected either by overgrazing or bur

Table 4. Endemic species to Crete recorded in the various treatments

Species	Phrygana			Grasslands		
	Burned + Overgrazed	Unburned Overgrazed	Protected	Burned + Protected	Unburned Overgrazed	Protected
<u>Chamaephytes</u>						
<i>Asperula rigida</i> (Sibth. & Sm.)	+					
<i>Polygonum idaeum</i> (Hayek)					+	
<i>Phlomis lanata</i> (Willd.)		+				
<i>Tefcrium alpestre</i> (Sibth. & Sm.)	+	+				
<u>Hemicryptophytes</u>						
<i>Carlina curetum</i> (Heldr. ex Halacsy)	+					
<i>Centaurea idaea</i> (Boiss. & Heldr. in Boiss)	+	+	+	+	+	+
<i>Centaurea raphanica</i> (Sibth. & Sm.)	+	+			+	
<i>Hypericum trichocaulon</i> (Boiss. & Heldr. in Boiss)	+	+		+	+	+
<i>Petrorhagia candica</i> (P.W. Ball & Heywood)		+	+			
<i>Scariola alpestris</i> (Gand.)	+	+				
<i>Silene sieberii</i> (Fenzl)	+	+			+	
<u>Geophytes</u>						
<i>Allium rubrovittatum</i> (Boiss. & Heldr. in Boiss)	+	+				
<i>Muscari spreitzenhoferi</i> (Heldr.)		+				
<u>Therophytes</u>						
<i>Cerastium scaposum</i> (Boiss. & Heldr. in Boiss)	+	+				
<i>Crepis cretica</i> (Boiss.)	+	+	+	+	+	+

Table 5. Species richness (no/25m²) in phryganic and grassland ecosystems of Psilorites mountain (statistical comparisons are within the same life form).

Life form	Phrygana	Grasslands
Therophytes		
Grasses	2.21***	1.32
Legumes	2.41***	0.78
Forbs	8.56***	4.73
Total	13.18***	6.83
Hemicryptophytes		
Grasses	1.64	1.78
Total	4.04	5.72***
Geophytes	0.43**	0.17
Chamaephytes	1.93***	1.38
Total species	19.72***	14.13

** : P ≤ 0.01, ***: P ≤ 0.001

ning. However, the various life forms were affected more by the former than by the latter treatment (Table 6). More specifically, therophytes and especially forbs were found significantly more in the overgrazed than in the protected sites. The same was also found for geophytes and chamaephytes. On the contrary, hemicryptophytes were significantly more in the protected than in the overgrazed sites. On the other hand, burning did not significantly affect any life form category except annual legumes and total hemicryptophytes which were significantly reduced in the burned sites as compared to the unburned ones (Table 6).

In the phryganic sites, overgrazing did not affect

total species richness but significantly reduced annual legumes and increased annual forbs as well as geophytes. On the contrary, burning combined with overgrazing significantly reduced total species richness and specifically total therophytes and legumes as well as hemicryptophytes (Table 7).

More drastic were overgrazing and burning at the grassland sites, where total species richness was significantly reduced by the former but increased by the latter treatment (Table 8). More specifically, overgrazing significantly reduced annual grasses and total hemicryptophytes but increased geophytes and chamaephytes. Burning, on the contrary, significantly increased total therophytes including grasses but decreased perennial grasses (Table 8).

As far as equitability of the total number of species is concerned, overgrazing did not have any significant effects on phryganic ecosystems unless it was combined with burning, when it was significantly reduced (Table 9). On the contrary, overgrazing significantly reduced equitability in the grassland ecosystems but burning increased it.

Discussion

Species profile and distribution

An interesting finding of this study is the preponderance of therophytes (59%) among the total number of species recorded on the mountain. This is contrary to what was found in mountains of northern Greece (Papanastasis, 1981; Karagiannakidou

Table 6. Species richness (no/0.25m²) in overgrazed and burned sites of the mountain rangelands in Psilorites (statistical comparisons are within each life form and treatment).

Life form	Grazing		Burning	
	Overgrazed	Protected	Burned	Unburned
Therophytes				
Grasses	1.88	1.86	2.30	1.78
Legumes	1.55	1.86	1.03	1.76*
Forbs	7.57**	5.69	7.47	7.06
Total	11.00*	9.42	10.80	10.60
Hemicryptophytes				
Grasses	1.58	1.83	1.33	1.71
Total	4.18	6.00***	4.00	4.75*
Geophytes	0.43***	0.00	0.37	0.29
Chamaephytes	1.78**	1.17	1.70	1.62
Total species	17.46	16.67	17.03	17.33

*: P ≤ 0.05, **: P ≤ 0.01, ***: P ≤ 0.001

Table 7. Species richness (no/0.25m²) in grazed and burned phryganic sites (statistical comparisons are within each life form and treatment).

Life form	Grazing		Burning ¹	
	Overgrazed	Protected	Burned	Unburned
Therophytes				
Grasses	2.28	2.00	2.21	2.28
Legumes	2.22	3.75**	1.17	2.22**
Forbs	9.28**	7.00	7.83	9.28
Total	13.78	12.75	11.21	13.78*
Hemicryptophytes				
Grasses	1.65	1.58	1.25	1.65
Total	4.22	3.92	3.13	4.22*
Geophytes	0.43*	0.00	0.46	0.43
Chamaephytes	1.90	1.33	1.75	1.90
Total species	20.40	18.08	16.88	20.40**

1: Burning and non-burning was also combined with overgrazing,

*: P ≤ 0.05, **: P ≤ 0.01

Table 8. Species richness (no/0.25m²) in grazed and burned grassland sites (statistical comparisons are within each life form and treatment).

Life form	Grazing		Burning	
	Overgrazed	Protected	Burned	Unburned
Therophytes				
Grasses	1.00	1.50**	2.67**	1.50
Legumes	0.69	1.06	0.50	1.06
Forbs	4.53	4.72	6.00	4.72
Total	6.22	7.28	9.17*	7.28
Hemicryptophytes				
Grasses	1.67	2.06	1.67	2.06*
Total	4.83	6.89***	7.50	6.89
Geophytes	0.28*	0.00	0.00	0.00
Chamaephytes	1.58*	0.94	1.50	0.94
Total species	12.92	15.28***	18.33***	15.28

*: P ≤ 0.05, **: P ≤ 0.01, ***: P ≤ 0.001

Table 9. Equitability of phryganic and grassland sites under overgrazing and burning (statistical comparisons are within the same vegetation type and treatment).

Life form	Grazing		Burning ¹	
	Overgrazed	Protected	Burned	Unburned
Phrygana	0.46	0.45	0.43	0.46*
Grasslands	0.39	0.42*	0.46***	0.42

1: In the case of phrygana burning was combined with overgrazing,

*: P ≤ 0.05, ***: P ≤ 0.001

& Kokkini, 1987) and in other parts of Mediterranean. Montalvo *et al.* (1991), for example, have found a decrease in “annuality” in favour of “perenniality” in grasslands of central Spain along an altitudinal gradient from 556 to 1718 m. a.s.l. They attributed this change to evolutionary strategies in the sense that the energy flow is faster in lower altitudes due to climatic reasons thus restricting the life expectancy of plant species and forcing them to follow the r strategy (primarily sexual reproduction); while in the higher altitudes energy is also stored in below-ground organs thus leading to a more persistent structure which means that plants follow the K strategy (primarily vegetative reproduction).

The high proportion of therophytes on Psilorites mountain suggests that the overriding factor in species distribution is not climate but land use. Annual or biennial plant species are more adapted to overgrazing because they can tolerate disturbance much more than perennials due to their shorter life cycle and their prolific seed production (Grime, 1979). Overgrazing is known to lead to rangeland retrogression characterized by the replacement of perennials with annuals in grasslands (Heady & Child, 1994; Papanastasis & Noitsakis, 1992). A high proportion of therophytes up to 1220 m altitude was also found in the rangelands of the White Mountains in Crete that are also subjected to long term overgrazing (Bergmeier & Matthäs, 1996).

Otherwise, the distribution of the various species to botanical families followed the general pattern of the Greek flora which is dominated by Compositae, Leguminosae and Graminae (Strid & Tan, 1997). On the contrary, apart of *Trifolium*, all the other dominant genera in Psilorites are not dominant of the Greek flora as well apparently reflecting the special environmental and land use conditions prevailing in the mountain.

The higher species richness found in phryganic ecosystems compared to grasslands should be attributed to the fact that the former are more heterogeneous plant communities than the latter. The increased presence of several species of chamaephytes, especially the dominant ones such as *S. spinosum*, *E. acanthothamnus* and *C. capitatus* which are largely unpalatable to animals create special habitats harboring a variety of therophytes, readily eaten by animals, especially sheep. This is the reason that the species richness of all groups of therophytes (grasses, legumes and forbs) were found significantly higher in phryganic communities than in grasslands. A positive role in preserving plant diversity by unpalatable weeds was also found in meadow plant communities of the Caucasus Mountains by Callaway *et al.* (2000).

Effects of overgrazing and burning

The results clearly suggest that overgrazing was effective in changing species richness. This is because sheep are selective grazers largely preferring legumes among therophytes as well as hemicryptophytes thus favoring less palatable groups of species such as annual forbs, geophytes and chamaephytes. The increase of the number of annual forbs as a result of grazing was also found by Bergmeier (1997) on phryganic communities of the White Mountains in Crete. Goats which are also part of the animal flocks on Psilorites mountain do not seem to profoundly modify this trend, although they are browsers, mainly feeding on chamaephytes. This may be attributed to the fact that their numbers were much less than those of sheep and also because they behave as grazers in seasons such as spring and autumn when herbaceous vegetation is of high nutritive value (Papachristou & Nastis, 1991).

The increase of therophytes and especially of forbs in the overgrazed sites at the expense of hemicryptophytes (Table 6) may be considered as a shift from “decreasers” to “invaders” (Dyskterhuis, 1949) in response to overgrazing. It can be explained by the hypothesis developed by Noy-Meir *et al.* (1989) and Noy-Meir (1998) that with increasing grazing intensity the main selection factor becomes the ability to colonize open space. It seems that annual forbs are effective colonizers of the open gaps created by the intensive selective grazing by sheep, because they are poor competitors for space and light. Similar explanation may be offered for the increase of geophytes, too. For the chamaephytes, however, their increase as a result of overgrazing (Table 6) may be attributed to the reduction of competition for soil water rather than for light. It seems that the reduction of hemicryptophytes by overgrazing releases soil moisture for the unpalatable chamaephytes which can survive more effectively over the dry summer period.

It can be postulated therefore that chamaephytes play a buffering role in phryganic communities towards increased grazing pressure. The fact that they are largely unpalatable to sheep which results in their increase in the overgrazed sites explains why there were found no significant differences in their total species richness between overgrazed and protected phryganic sites (Table 7). This outcome suggests that the response of diversity to grazing in phryganic communities does not follow the hump-shaped model proposed by Milchunas *et al.* (1988) for grasslands. These ecosystems are resilient to heavy and continuous grazing pressure thanks to their balanced structure with a large variety of plant forms

adapted to a long evolutionary history associated with grazing animals.

The buffering role of chamaephytes seems to be suspended in phryganic communities if overgrazing is combined with burning which destroys their aboveground biomass and consequently the protection that their crown offers to therophytes and hemicryptophytes thus making them more vulnerable to grazing animals. This is why the combination of overgrazing and burning resulted in significant reduction of species richness (Table 7). Another reason could be the rejuvenating effect that fire has in phryganic communities resulting in the production of very nutritious forage which attracts heavy grazing pressure (Papanastasis, 1977) that apparently eliminates several plant species, especially annual legumes and hemicryptophytes. Kazakis & Papanastasis (2000) have found that seed bank contained significantly more seeds in the overgrazed and unburned than in the overgrazed and burned sites of the same study area. The detrimental effects of the combined action of overgrazing and wildfires has been also documented in earlier studies in several parts of Greece (Papanastasis, 1977; Arianoutsou-Faraggitaki, 1985; Pantis & Margaritis 1988; Vokou *et al.* 1986; Koutsidou & Margaritis, 1998) including Crete (Tsiourlis *et al.* 1998). Similar results were found by Bergmeier (1998a) in phryganic ecosystems of the White Mountains of Crete, too.

In grasslands, on the contrary, chamaephytes are fewer and largely palatable to sheep (e.g. *O. spinosa*) (Kyriakakis *et al.* 1989). As a result, they do not seem to play any buffering role despite the fact that their species richness was increased with overgrazing. This may explain why the species richness of grasslands was significantly reduced in the overgrazed as compared to protected sites (Table 8). The same results were obtained in low elevation grasslands of Greece (Koukoura *et al.* 1998). Although no information is available on how the same grasslands would respond to light and moderate grazing, it seems that these ecosystems do not also follow the model proposed by Milchunas *et al.* (1988) postulating that sub-humid grasslands with a long evolutionary grazing history reach high diversity with high grazing pressure. Additional data are needed to develop a more general theory about the response to grazing of Mediterranean grasslands including the mountainous ones.

The information available in this study is not enough to fully evaluate the impact of burning alone on species diversity of Psilorites rangelands. Bergmeier (1997) reports that fire had only light effects on the overall diversity of phryganic communities in the White Mountains of Crete. This can not be confirmed for Psilorites where burning was only combined with overgrazing. The fact though that this combination produced significantly negative results on overall species richness while only grazing did not suggests that burning is causing rather significant effects. This however has to be confirmed with a specially designed study. On the other hand, the significant increase of species richness in the burned grasslands, although represented by only one site in the whole mountain, confirms the conclusions reached by Noy-Meir (1995) that fire causes increased biodiversity in grasslands dominated by perennials.

As far as the endemic species are concerned, the ones recorded in this study (Table 4) seem to be fairly well adapted to overgrazing based on their "browsing tolerance value" suggested by Bergmeier (1998a). On the contrary, none of the species he evaluates as intolerant to grazing was encountered in the study sites. On the other hand, Egli (1991) considers overgrazing an important agent for maintaining endemics such as *Polygonum idaeum* in grasslands grown on dolines, because it keeps off other plants with a higher competitive ability.

It may be concluded that despite their high altitude the rangelands of Psilorites mountain are dominated by therophytes due to their long history of overgrazing by domestic animals. This overgrazing does not seem to cause any problems in the plant diversity of phryganic areas unless it is combined with wildfires when detrimental effects may be produced. On the contrary, it does negatively affect plant diversity in grasslands without necessary eliminating creeping and prostrate endemic species.

Acknowledgements

This paper is part of the European research project "Land use systems in the Mediterranean mountain and marginal lands" (contract AIR3 CT94 2426) carried out in Mediterranean Agronomic Institute of Chania, Crete (Dr M. Dubost, coordinator).

References

- Athanasiadis, N., Theodoropoulos, K. & Eleftheriadou, E. 2001. Flora and Vegetation of Greece. Teaching notes. Aristotle University Publications, Thessaloniki.
- Arianoutsou-Faraggitaki, M. 1985. Desertification by overgrazing in Greece: The case of Lesvos island. *Journal of Arid Environments* 9:237-242.
- Bergmeier, E. 1996. Zur bedeutung der beweidung für die griechische phrygana. *Ber. d. Reich. – Tüxen – Ges* 8:221-236.
- Bergmeier, E. 1997. Combined effects of fire and grazing on phryganic vegetation – a case study in SW Crete (Greece). *Ecologia Mediterranea* 23:1-10.
- Bergmeier, E. 1998a. Are Cretan endemics threatened by grazing? pp. 90-93. In: Papanastasis, V.P. & Peter, D. (eds), *Ecological Basis for Livestock Grazing in Mediterranean Ecosystems*. European Commission, EUR 18308 N, Luxembourg.
- Bergmeier, E. 1998b. Flowering intensity of phrygana plants after fencing. *Israel Journal of Plant Sciences* 46:41-46.
- Bergmeier, E. & Matthäs, U. 1996. Quantitative studies of phenology and early effects of non-grazing in Cretan phryganic vegetation. *Journal of Vegetation Science* 7:229-236.
- Callaway, R.M., Kikvidze, Z. & Kikodze, D. 2000. Facilitation by unpalatable weeds may conserve plant diversity in overgrazed meadows in the Caucasus Mountains. *Oikos* 89:275-282.
- Dyksterhuis, E.J. 1949. Condition and management of rangeland based on quantitative ecology. *Journal of Range Management* 2:104-115.
- Egli, B.R. 1991. The special flora, ecological and edaphic conditions of dolines in the mountains of Crete. *Botanica Chronika* 10:352-335.
- Grime, J.P. 1979. *Plant strategies and Vegetation Processes*. John Wiley, New York.
- Heady, H.G. & Dennis Child, R. 1994. *Rangeland Ecology and Management*. Westview Press. Oxford.
- Karagiannakidou, V. & Kokkini, S. 1987. The flora of mountain Menoikion in North East Greece. *Phyton* 27:267-283.
- Kazakis, G. & Papanastasis, V.P. 2001. Seed bank in rangeland ecosystems of the Psilorites mountain, pp. 139-144. In: Papachristou, T.G. & Dini-Papanastasi, O. (eds), *Range Management at the Threshold of the 21st Century*. Proc. Second Panhellenic Rangeland Congress, Thessaloniki (In Greek with English summary).
- Koukoura, Z., Tsiouvaras, C. & Papanastasis, V.P. 1998. Long term effects of grazing on biodiversity of a Mediterranean grassland in northern Greece. pp. 53-57. In: Papanastasis, V.P. & Peter, D. (eds), *Ecological Basis for Livestock Grazing in Mediterranean Ecosystems*. European Commission, EUR 18308 N, Luxembourg.
- Koutsidou, E. & Margaritis, N.S. 1998. The regeneration of Mediterranean vegetation in degraded ecosystems as a result of grazing pressure exclusion: the case of Lesvos island. pp. 76-79. In: Papanastasis, V.P. & Peter, D. (eds), *Ecological Basis for Livestock Grazing in Mediterranean Ecosystems*. European Commission, EUR 18308 N, Luxembourg.
- Kyriakakis, S., Kazakis, G., Abid, M., Doulis, A. & Papanastasis, V.P. 1999. Effects of grazing and burning on woody vegetation of Mediterranean rangelands of Crete, Greece. pp. 79-83. In: Papanastasis, V.P., Frame, J. & Nastis, A.S. (eds), *Grasslands and Woody Plants in Europe*, European Grassland Federation. *Grassland Science in Europe*, Volume 4, Thessaloniki, Greece.
- Lyrantzis, G. & Papanastasis, V.P. 1995. Human activities and their impact on land degradation – Psilorites mountain in Crete: A historical perspective. *Land Degradation & Rehabilitation* 6:79-93.
- Lyrantzis, G. 1996. Human impact trend in Crete: the case of Psilorites mountain. *Environmental Conservation* 23(2):140-148.
- Magurran, A. 1988. *Ecological Diversity and its Measurement*. Groom Helm Limited, London.
- Menjli, 1994. Effects of pastoral activities on desertification of mountain Psilorites. M.Sc. Thesis. Mediterranean Agronomic Institute of Chania, Crete.
- Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 130:168-198.
- Montalvo, J., Casado, M.A., Levassor, C. & Pinedo, F.D. 1991. Adaptation of ecological systems: compositional patterns of species and morphological and functional traits. *Journal of Vegetation Science* 2 :655-666.
- Montalvo, J., Casado, M.A., Levassor, C. & Pineda, F.D. 1993. Species diversity patterns in Mediterranean grasslands. *Journal of Vegetation Science* 4:213-222.
- Montmollin, B. de. 1991. Endemisme intra-cretois et trans-cretois-origine et differenciation. *Botanica Chronika* 10 :125-135.
- Naveh, Z. & Whittaker, R.H. 1979. Structural and floristic diversity of shrublands and woodlands in northern Israel and other Mediterranean regions. *Vegetatio* 41:171-190.
- Noy-Meir, I. 1995. Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. *Journal of Vegetation Science* 6 :701-710.
- Noy-Meir, I. 1998. Effects of grazing on Mediterranean grasslands: the community level, pp. 27-39. In: Papanastasis, V.P. & Peter, D. (eds), *Ecological Basis for Livestock Grazing in Mediterranean Ecosystems*. European Commission, EUR 1830 N, Luxembourg.
- Noy-Meir, I., Gutman, M. & Kaplan, Y. 1989. Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology* 77:290-310.
- Pantis, J. & Margaritis, N.S. 1998. Can systems dominated by asphodels be considered as semi-deserts? *International Journal of Biometeorology* 32:87-91.
- Pantis, J.P. & Mardiris, Th.A. 1992. The effects of grazing and fire on degradation processes of Mediterranean ecosystems. *Israel Journal of Botany* 41:233-242.
- Papachristou, T.G. & Nastis, A.S. 1993. Diets of goats grazing oak shrublands of varying cover in northern Greece. *Journal of Range Management* 46:220-266.
- Papanastasis, V.P. 1977. Fire ecology and management of phrygana communities in Greece, pp. 476-82. In: Mooney, H.A. & Conrad, C.E. (coors), *Proc. Symp. Environmental Consequences Fire and Fuel Manage in Mediterranean Ecosystems*. USDA Forest Service, Gen. Tech. Rep. WO-3, Washington D.C.
- Papanastasis, V.P. 1981. Species structure and productivity

- in grasslands of Northern Greece. pp. 205-217. In: Margaris, N.S. & Mooney, H.A. (eds), Components of Productivity of Mediterranean – Climate Regions. T:V 54, Dr W. Junk Publ. The Hague.
- Papanastasis, V.P. 1985. Impact of grazing on a grassland of the Lahanas region of Thessaloniki. *Dassiki Erevna* VI(2): 155-168 (In Greek with English summary).
- Papanastasis, V.P. 1998a. Livestock grazing in Mediterranean ecosystems: an historical and policy perspective. pp. 5-9. In: Papanastasis, V.P. & Peter, D. (eds), *Ecological Basis for Livestock Grazing in Mediterranean Ecosystems*. European Commission, EUR 1830 N, Luxembourg.
- Papanastasis, V.P. 1998b. Grazing intensity as an index of degradation in semi-natural ecosystems: the case of Psilorites mountain in Crete. pp. 146-158. In: Enne, G., D'Angelo, M. & Zanollo, C. (eds), *Indicators for Assessing Desertification in the Mediterranean*. Nucleo Ricerca Desertificazione, Universita di Sassari, Italy.
- Papanastasis, V., Kyriakakis, S. & Ispikoudis J. 1990. Forestry and grazing practice in Crete. pp. 42-46. In: Grove, A.T., Rackham, O. & Moody, J. (eds), *Stability and Change in the Cretan Landscape*. Petromaroula 1, Corpus Christi College, England.
- Papanastasis, V.P. & Noitsakis, B.I. 1992. *Rangelands Ecology*. Giahoudis-Giapoulis Press. Thessaloniki (In Greek).
- Peco, B., Espigares, T. & Levassor, C. 1998. Trends and fluctuations in species abundance and richness in Mediterranean pastures. *Applied Vegetation Science* 1:21-28.
- Puerto, A., Rico, M., Matias, M.D. & Garcia, J.A. 1990. Variation in structure and diversity in Mediterranean grasslands related to trophic status and grazing intensity. *Journal of Vegetation Science* 1:445-452.
- Raunkiaer, C. 1934. *The Life Forms of Plants and Statistical Plant Geography*, translated by Carter et al. Oxford Univ. Press.
- Seligman, N.G. & Perevolotsky A. 1994. Has intensive grazing by domestic ungulates degraded Mediterranean basin rangelands? pp. 93-103. In: Arianoutsou, M. & Groves, R.H. (eds), *Plant-Animal Interactions in Mediterranean – Type Ecosystems*. Kluwer Academic Publ. The Hague.
- Sternberg, M., Gutman, M., Perevolotsky, A., Ungar, E.D. & Kigel, J. 2000. Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. *Journal of Applied Ecology* 37:224-237.
- Strid, A. & Tan, K. (eds). 1997. *Flora Hellenica*, Vol. 1. Koenigstein.
- Thirgood, J.V. 1981. *Man and the Mediterranean Forest*. Academic Press, New York.
- Tsiourlis, G.M., Kasapidis, P., Parnakelis, A. & Dretakis, M. 1998. Effects of grazing on the structure of phryganic ecosystems in the Asterousia mountain of Crete, Greece, pp. 94-97. In: Papanastasis, V.P. & Peter, D. (eds), *Ecological Basis for Livestock Grazing in Mediterranean Ecosystems*. European Commission, EUR 1830 N, Luxembourg.
- Tsoumis, G. 1985. The depletion of forests in the Mediterranean region- An historical review from the ancient times to present. *Scientific Annals of the Department of Forestry and Natural Environment* Vol. KH (11):281-300.
- Tutin, T.G., Burges, N.A., Chater, A.O., Edmondson, J.R., Heywood, V.H., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. 1993. *Flora Europea*. Second edition. Cambridge University Press.
- Vokou, D., Diamantopoulos, J., Mardiris Th.A., & Margaris, N.S. 1986. Desertification in northern Greece: the case of Kella. pp. 155-160. In: Fantechi, R. & Margaris, N.S. (eds), *Desertification in Europe*. D. Reidel Publishing Co. Dordrecht.