

Wood pasture in an ancient submediterranean oak forest (Peloponnese, Greece)

Sylvopastoralisme dans une ancienne forêt méditerranéenne de chênes (Péloponnèse, Grèce)

P. D. Dimopoulos¹, E. Bergmeier²

1. Department of Environmental and Natural Resources Management, University of Ioannina, Seferi 2, GR-30100 Agrinio, Greece; Fax +30 641 39576; E-mail: pdimopul@cc.uoi.gr

2. Albrecht-von-Haller-Institut für Pflanzenwissenschaften, Georg-August-Universität Göttingen, Untere Karspüle 2, D-37073 Göttingen, Germany; Fax +49 551 39 2287; E-mail: erwin.bergmeier@bio.uni-goettingen.de *corresponding author

137

Abstract

In this study the effects of wood-pasturage on species composition and forest structure in the Quercus frainetto forest of Folói are described. This is the most extensive broadleaved forest of Peloponnese and southern Greece and unique in that there is evidence of several thousand years of existence. The variation in plant species composition among, and the differences between, grazed and ungrazed forest stands are analysed by means of ordination (correspondence analysis). Species indicative for grazing or its withdrawal are listed. Annuals and certain perennials with good regeneration capacity are indicative for grazed plots, while a dense shrub layer with Arbutus unedo and Erica arborea is related to ungrazed plots. Generally, in the absence of grazing the development of the herb and shrub layer is enhanced. Forest stands in exclosures tend to produce denser canopies, oak rejuvenation is more abundant, and the trees are higher and more vital than outside. In grazed woodland, litter and organic matter are less abundant and the degree of parasitism by Loranthus europaeus is higher. Our results suggest two possible conservation options for the study area, viz. (a) controlled grazing regime in the framework of a traditional but sustainable agro-silvopastoralistic system or (b) a concept towards a natural forest ecosystem.

Key-words

Grazing, Greece, Old forest, Quercus frainetto, Silvopastoralism

Résumé

Dans la présente étude sont décrits les effets du sylvopastoralisme sur la composition spécifique et la structure de peuplements dans la forêt à Quercus frainetto de Folói. Cette forêt, la plus étendue du Péloponnèse et du sud de la Grèce, est unique par le fait de son existence probablement plurimillénaire. La variation de la composition spécifique au sein de peuplements pâturés ou non, et les différences entre ces deux types de peuplements ont été analysées par ordination (analyse des correspondances). Des espèces indicatrices du pâturage et de son absence sont listées. Les espèces annuelles et certaines vivaces avec une bonne capacité de régénération sont liées aux placettes pâturées, tandis qu'une strate arbustive dense formée par Arbutus unedo et Erica arborea caractérise les placettes non pâturées. De façon générale, en l'absence de pâturage, les strates herbacées et arbustives sont mieux développées. Les forêts à l'intérieur des enclos ont tendance à produire des canopées plus denses, la régénération des chênes y est plus abondante, et les arbres sont plus hauts et plus vigoureux qu'à l'extérieur. Dans les peuplements pâturés, la litière et la matière organique sont moins abondantes, et le degré de parasitisme par Loranthus europaeus est plus élevé. Nos résultats suggèrent deux options possibles pour la conservation de la zone étudiée : a) un régime de pâturage contrôlé dans le cadre d'un système agropastoral traditionnel mais durable ou b) un régime visant un écosystème forestier à caractère naturel.

Mots-clés

Pâturage, Grèce, vieille forêt, Quercus frainetto, Sylvopastoralisme

INTRODUCTION

Interest in wood pasture has increased a great deal lately in many European countries (Papanastasis *et al.*, 1999; Redecker *et al.*, 2002). In western and central Europe re-introduction of wood pasture is currently under discussion, with the principal aims of enhancing forest dynamics and increasing biodiversity (Pott, 1999; Vera, 2000; Schmidt & Heile, 2001; Spencer, 2002). Modern forestry supports tall dense forest for economic reasons and, owing to the browsing of seedlings and juvenile trees, considers wood-pasture as detrimental to the forest and chiefly responsible for the decline of wooded areas and the structural senescence of the tree stands. Present silvopastoralism in Europe is largely restricted to countries of the wider Mediterranean and the Balkans. Grazing by domestic animals has widely been practiced in virtually all forests except for the most remote ones. In traditional silvopastoral farming systems, submediterranean deciduous and mediterranean sclerophyllous woodlands are chiefly involved. Deciduous oak forest is highly esteemed due to its mast production in autumn as food for pigs. But also other domestic animals such as sheep, goats and cattle benefit from the relatively light conditions in oak woodlands which support a fairly dense and plant-rich ground vegetation.

For the present study, the forest of Folói (Kápellis; Pholóë in antiquity; Ilía, Peloponnisos, Greece) was chosen. It has been used for charcoal burning and pasturage for centuries, as travellers' reports suggest (Philippson, 1892; Pritzel, 1908; Rothmaler, 1943). The major part has been used as wood pasture for sheep and pigs within the local rural economies but remote parts show little or no signs of grazing at present.

In Greece, as elsewhere in the Mediterranean, most oak woodlands have been, or still are, subject to coppicing at more or less regular intervals. Single-stemmed old-growth oak woodlands as in our study area, however, are exceedingly rare (Bergmeier *et al.*, 2004). The forest of Folói is the most extensive submediterranean non-coppiced oak forest in Peloponnisos, and certainly among the oldest existing. It was known already in Greek mythology, according to which it was frequented by centaurs, horses with human body, the personifications of mountain forest wilderness. Among the many myths around the Greek hero Herakles is one with the forest of Folói as the scenery of a guest meal provided for the hero that ended up in a massacre among the centaurs. Herakles also encouraged prehistoric people to clear part of the extensive forest. The myth can be interpreted figurati-

vely as an attempt to civilize wilderness and to establish cultivation in less favourable regions. Although close to Olympia the hinterland of Ilía remained a little attended region in antiquity. To our knowledge, the first mentioning of an historical event in the forest area of Folói dates back to the battle between Alarichos and Stilichon in AD 397 (Christopoulos, 1978).

Grazing by domestic herbivores causes quantitative (number of plant individuals, species numbers) and qualitative (species composition, phenological traits) effects on Mediterranean open habitats (Noy-Meir *et al.*, 1989; Fernandez Alés *et al.*, 1993; Bergmeier & Matthäs, 1996; Bergmeier, 1998). However, not many studies have dealt with woodland grazing in the Mediterranean, or the effects of cessation of grazing to Mediterranean deciduous woodlands (Di Pasquale & Garfi, 1998; Debussche *et al.*, 2001). Few studies explicitly state which species in oak woodlands increase after silvopastoralism has been given up, and which decrease (Debussche *et al.*, 2001). Based on field studies in the Folói forest, our paper attempts to provide such information and addresses the following questions:

Is the species composition of oak forest a suitable indicator for wood pasture?

Which species of oak forest profit from grazing and which from its withdrawal?

To which extent differs the structure of ungrazed oak forest from that of grazed stands?

Is silvopastoralism an obstacle to the rejuvenation of oak?

Ancient Mediterranean forests are in urgent need of protection but conservation priorities have hardly been discussed, owing chiefly to the lack of ecological information. Our final point of discussion is therefore: Which conclusion can be drawn from our findings for the conservation and sustainable use of the specific study area?

STUDY AREA

The study area, the forest of Folói (Kápellis), comprises 3100 ha of broadleaved forest. It is situated in the eastern part of Ilía (Elis in antiquity) in western Peloponnisos (fig. 1). The Folói plateau constitutes the upper and most extensive in a series of conglomerate tables between Mt Erimanthos and the river Alpheios (Philippson, 1959). The plateau is very slightly inclined with less than 700 m of altitude in the north and almost 800 m in the south. It consists of Pleistocene continental

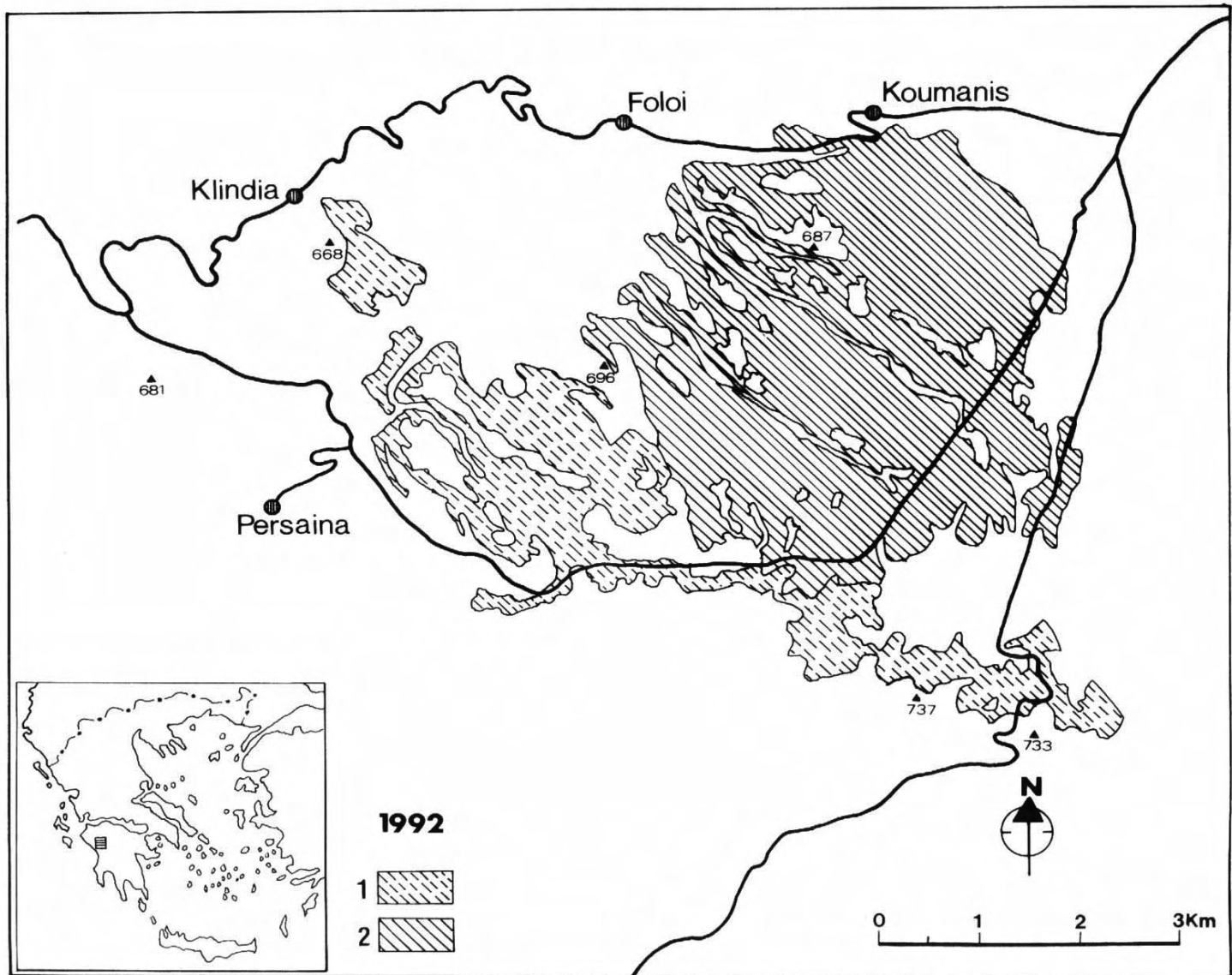


Figure 1. Position of the study area and distribution of *Quercus frainetto* forest drawn from an aerial photograph of 1992. Tree crowns in stands with open canopy (1) do not overlap and the cover is open or sparse (< 40 %); closed stands (2) with overlapping crowns represent dense canopy covers (> 60 %); intermediate stands (40-60 %) are infrequent and included into (2).

deposits, represented chiefly by conglomerates (IGME, 1983). The soils are commonly fairly deep cambisols, acidic, base-poor and waterpermeable. The climate is Mediterranean-type, with mild humid winters and dry warm summers, but in the western Peloponnese modified towards sub-oceanic conditions, particularly so in the mountains. That is why, in spite of the southern position, the annual precipitation is above 1000 mm, and the arid period restricted to comprise about 90 days (meteorological station Andritsena, unpubl. data). Due to the infertility of the soils, the area was never densely populated. This is why a considerable extent of the forest was preserved

to our days. Philippon (1892: 36), however, mentioned forest degradation caused by extensive charcoal production. Beside of charcoal industry, grazing by domestic animals (sheep, pigs, more rarely goats) has widely been practiced in the forest (Rothmaler, 1943) and is still of considerable importance for the local rural economies. The deciduous *Quercus frainetto* is the predominant oak, as was already mentioned by Heldreich (1862), Pritzel (1908) and Rothmaler (1943). There are no traces of fire in the present oak forest, nor is fire mentioned as a means of forest or grazing management by the early geobotanical travellers cited above. Extensive nearby areas of pine

forest, on the other hand, burnt in the 1990s. The fire did not expand to the oak forest. In spite of the serious human impact, major areas remained spacious tall forest of single-stemmed, non-coppiced trees, today an exceptionally rare type of woodland in southern Greece and elsewhere in the Mediterranean.

METHODS

Silvopastoral activities (expansion or decrease of the grazed area; intensity; composition of livestock) have always been fluctuating in history, along with various socio-economic factors. Major parts of the forest are currently subject to grazing, but as for the rest, there is no way telling when exactly a given site was grazed last. Therefore, we distinguished between stands which are presently grazed, and others without present grazing impact. The absence of grazing was judged from the absence of browsed or grazed plants and from the lack of droppings. The species composition of grazed and non-grazed stands was studied in 30 and 12 quadrats, respectively, each of 400 m². Minimum distance between quadrats was c. 150 m, but usually more than 300 m. In order to restrict the selection to sites comparable in terms of abiotic parameters, only forests with more or less closed *Quercus frainetto* canopy, *i.e.*, with more than 60 % canopy cover were included. Most stands have 65-85 % canopy cover (figure 1). Stands on steep slopes and in ravines were excluded. Species abundance in tree (t), shrub (s) and herb (h) layers were distinguished (t > 4 m; 4 m > s > 100 cm; h < 100 cm).

Four of the ungrazed quadrats were in two grazing exclosures of about two hectares in total which had been established in April 1964. In one of the exclosures (N37°46'39", E21°44'46"), for silvicultural purposes a stand analysis had been performed in November 1964 (Panagiotidis, 1965). Among other parameters, stem diameter at breast height (BHD) and tree height (TH) had been assessed. We performed a similar analysis in 1999 using one plot of 8 × 50 m in the exclosure, the other of the same size in a grazed site further east 30 m outside the fence. Stand profiles and crown projection maps were drawn, and pH as well as visual properties of soil profiles were assessed. The following parameters were recorded per tree: BHD, TH, number of oak mistles (*Loranthus europaeus*) as an indicator for reduced vitality (only medium-sized to large *Loranthus* individuals were counted since smaller ones would easily have been

overlooked). The number of juvenile oaks in ungrazed forest was assessed in 8 plots of 1 m² each, laid out at regular intervals along a diagonal inside the exclosure, and for the grazed forest the same number of plots was arranged along an outside extension of the diagonal.

In order to explore the relevance of grazing for explaining the variation in the data set, the 42 relevés (30 in grazed sites, 12 in ungrazed sites) were subjected to indirect gradient analysis (Correspondence analysis, CA). The settings were biplot scaling with focus on inter-species distances, no downweighting of species, and no transformation. The ordinations were performed using CANOCO 4 (ter Braak & Šmilauer, 1998). For statistical calculations on species frequency, forest and tree parameters, seedling numbers, and the degree of mistle infection, Mann-Whitney U-Test was used, with the significance levels expressed by 2-tailed Monte Carlo significance.

Nomenclature of taxa follows *Flora Europaea* (Tutin *et al.*, 1968-1980, 1993).

RESULTS

The ordination of the 42 quadrats of *Quercus frainetto* forest by means of CA revealed an arched plot structure which is expected for data sets with one predominant gradient (figure 2). Along the horizontal axis (axis 1), grazed plots formed the left wing of the arch, while the right wing was composed of non-grazed plots. Hence grazing regime constitutes the most important gradient explaining a great deal of variation in species composition. Species such as *Cynosurus echinatus*, *Poa bulbosa* and *Trifolium campestre* scored in the far left of the diagram, indicating their preferential occurrence in grazed stands. In contrast, *Arbutus unedo* and *Erica arborea* shrubs turned out to be characteristic for non-grazed plots. In the central part of the diagram taxa without clear preference to any management regime were assembled.

Species preferences for grazed and non-grazed forests are displayed in more detail in table 1. Annual species were found to be restricted largely to the grazed plots. Among the perennials, certain species with the potential to resprout from basal buds or subterranean tubers (*Oenanthe pimpinelloides*, *Asphodelus ramosus*, *Poa trivialis* subsp. *ylvicola*, *Poa bulbosa*) occurred significantly more frequently in grazed plots. Shrub species, in particular *Arbutus unedo* and *Erica arborea*, to somewhat lesser degree also juvenile plants of these species in the herb layer, are a specific feature of non-grazed plots.

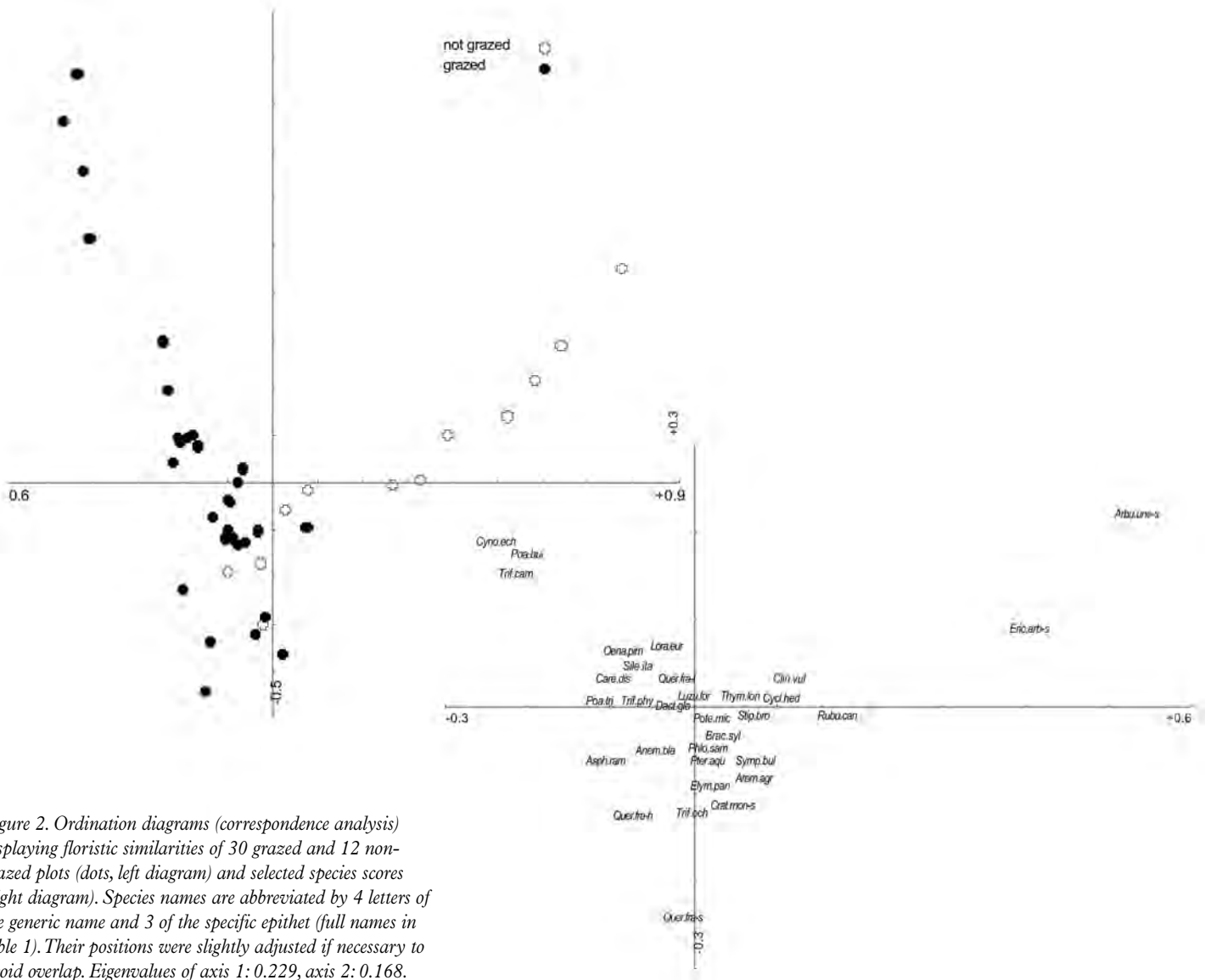


Figure 2. Ordination diagrams (correspondence analysis) displaying floristic similarities of 30 grazed and 12 non-grazed plots (dots, left diagram) and selected species scores (right diagram). Species names are abbreviated by 4 letters of the generic name and 3 of the specific epithet (full names in table 1). Their positions were slightly adjusted if necessary to avoid overlap. Eigenvalues of axis 1: 0.229, axis 2: 0.168.

The mean cover values of the *Quercus frainetto* canopy and the field layer tend to be higher in the non-grazed plots though not significantly (table 2). *Quercus frainetto* in the shrub layer occurred with high constancy in both regime types but was more abundant in the non-grazed plots. The cover of the shrub layer was very variable both in grazed and non-grazed stands, chiefly due to the variation in cover values of the *Q. frainetto* understorey, but significantly and altogether more than three times higher in non-grazed than in grazed stands (table 2).

Stand analyses of a non-grazed plot in an enclosure and a grazed one nearby outside the fence revealed significantly higher values for tree height (TH) in the non-grazed plot while mean stem diameter (BHD) was

lower than in the grazed plot (table 3). If compared with the mean values for all trees in 1964, the trees have become 5 m taller at an average within 35 years, and the BHD increment was 7 cm. The ratio TH/BHD remained almost constant in the enclosure while in the grazed stand a considerable decrease was noted (table 3). The age structure of the trees is uneven, and in 1964 11 % of the trees had BHD values > 40 cm (Panagiotidis, 1964). The crown projection revealed more than 80 % canopy cover in the fenced plot, as against about 70 % in the neighbouring grazed one (figures 3 and 4). The lower non-branched part of the stems is generally longer in the enclosure, and the branches in the lower two thirds of the trees are more scattered and with less foliage. Dead

Treatment	grazed	not grazed	<i>p</i>
Number of plots	30	12	
Woody species			
<i>Arbutus unedo s</i>	.	100	***
<i>Arbutus unedo h</i>	3	83	***
<i>Erica arborea s</i>	20	91	***
<i>Rubus canescens</i>	53	91	***
<i>Sorbus torminalis h</i>	3	33	ns
Annuals			
<i>Cynosurus echinatus</i>	63	.	***
<i>Trifolium campestre</i>	46	.	*
<i>Aira elegantissima</i>	30	.	ns
<i>Cerastium brachypetalum</i>	30	.	ns
Perennial herbs and subshrubs			
– more frequent in grazed plots			
<i>Oenanthe pimpinelloides</i>	96	58	***
<i>Poa trivialis ssp. sylvicola</i>	90	50	***
<i>Asphodelus ramosus</i>	67	25	**
<i>Trifolium physodes</i>	88	83	**
<i>Poa bulbosa</i>	50	16	ns
– more frequent in ungrazed plots			
<i>Stipa bromoides</i>	46	100	*
<i>Clinopodium vulgare</i>	36	75	*
<i>Potentilla micrantha</i>	76	100	*
<i>Brachypodium sylvaticum</i>	85	100	*
<i>Aremonia agrimonoides</i>	50	83	*
<i>Symphytum bulbosum</i>	43	75	*
<i>Brachypodium rupestre</i>	13	50	ns
<i>Teucrium chamaedrys</i>	3	41	ns
<i>Dorycnium hirsutum</i>	6	41	ns
<i>Cephalanthera longifolia</i>	6	41	ns
<i>Achillea ligustica</i>	6	33	ns
<i>Lathyrus laxiflorus</i>	76	100	ns
<i>Luzula forsteri</i>	82	100	ns

Table 1. Constancy values (given in %) and frequency differences of selected species in grazed and not grazed *Quercus frainetto* forest. *s* – shrub layer (1–4 m), *h* – herb layer (< 1 m). Frequency differences indicated by Mann-Whitney U-test significance levels: *P* < 0.05: *; *P* < 0.01: **; *P* < 0.005: ***; ns: not significant.

	Grazed	Not grazed	<i>p</i>
number of plots	30	12	
canopy cover	71.0 ± 11.8	75 ± 8.4	0.086 (ns)
cover shrub layer	11.1 ± 16.1	39.5 ± 22.2	0.000 (***)
cover herb layer	43.7 ± 20.7	50.5 ± 18.5	0.297 (ns)

Table 2. Oak forest parameters of the grazed and non-grazed plots. Mean cover values are in % with standard deviation. Significance levels are * (*p* < 0.05); ** (*p* < 0.01); *** (*p* < 0.001); ns, not significant.

branches are more numerous in the grazed plot. The oak mistle *Loranthus europaeus* occurred with a mean of 3.2 (± 2.6) individuals per tree while the ratio was 0.9 (± 1.2) *Loranthus* individuals per tree in the enclosure (*p* = 0.006). We have found 27 (± 19) juveniles of *Q. frainetto* per m² in the grazed and 60 (± 24) in the ungrazed plots (*p* = 0.012) (table 3).

The soil profiles were roughly 3-layered both inside and outside the enclosure, and the soil type was identified as cambisol (Braunerde). Base saturation is low, and the deep lime-free B horizon is markedly acidic (pH 4.6–5.5). Differences between the plots refer particularly to the humus layer. In the grazed plots, the latter is absent or, if present, thin (up to 2 cm) and largely without obvious mycelia. Litter is sparse and often absent. In the enclosures, there is high fungal activity in the humus layer, and litter in various stages of decomposition was 2–7 cm thick and covers most of the surface area.

DISCUSSION

The species composition of grazed *Q. frainetto* forests differs considerably from that of non-grazed stands. Annual species in particular qualify as grazing indicators, at least in dense stands with a more or less closed canopy. Among the perennial herbs and subshrubs, most species of deciduous oak forest seem to be not or negatively affected by grazing. Exceptions include *Oenanthe pimpinelloides* and *Poa trivialis* subsp. *sylvicola*, both supplied with subterranean tuberous or knotted swellings which enable regeneration; *Asphodelus ramosus*, largely avoided by herbivores and locally abundant in overgrazed pastures, and *Poa bulbosa*, a mat-forming pasture grass.

The forest structure in non-grazed stands, as exemplified by the enclosures, is denser, the trees are taller, and there is pronounced canopy competition. The trees in the

Year	1964	1999	1999	
Treatment	grazed	grazed	not grazed	
number of trees	524	10	9	
TH (m)	20.6 ± 1.6	23.9 ± 2.8	25.6 ± 1.8	p = 0.009 **
BHD (cm)	22.4 ± 3.1	34.5 ± 4.5	29.5 ± 4.5	p = 0.049 *
TH/BHD	92	69	87	
<i>Loranthus</i> individuals per tree		3.2 ± 2.6	0.9 ± 1.2	p = 0.006 **
number of juv. oaks		27 ± 19	60 ± 24	p = 0.012 *

Table 3. Tree and site parameters obtained from stand analyses in 1964 when the enclosure was installed, and in 1999 in the enclosure and outside next to it. Mean values with standard deviation are given. TH = mean tree height, BHD = mean breast height diameter. Significance levels refer to stand analyses in 1999; levels as in table 2.

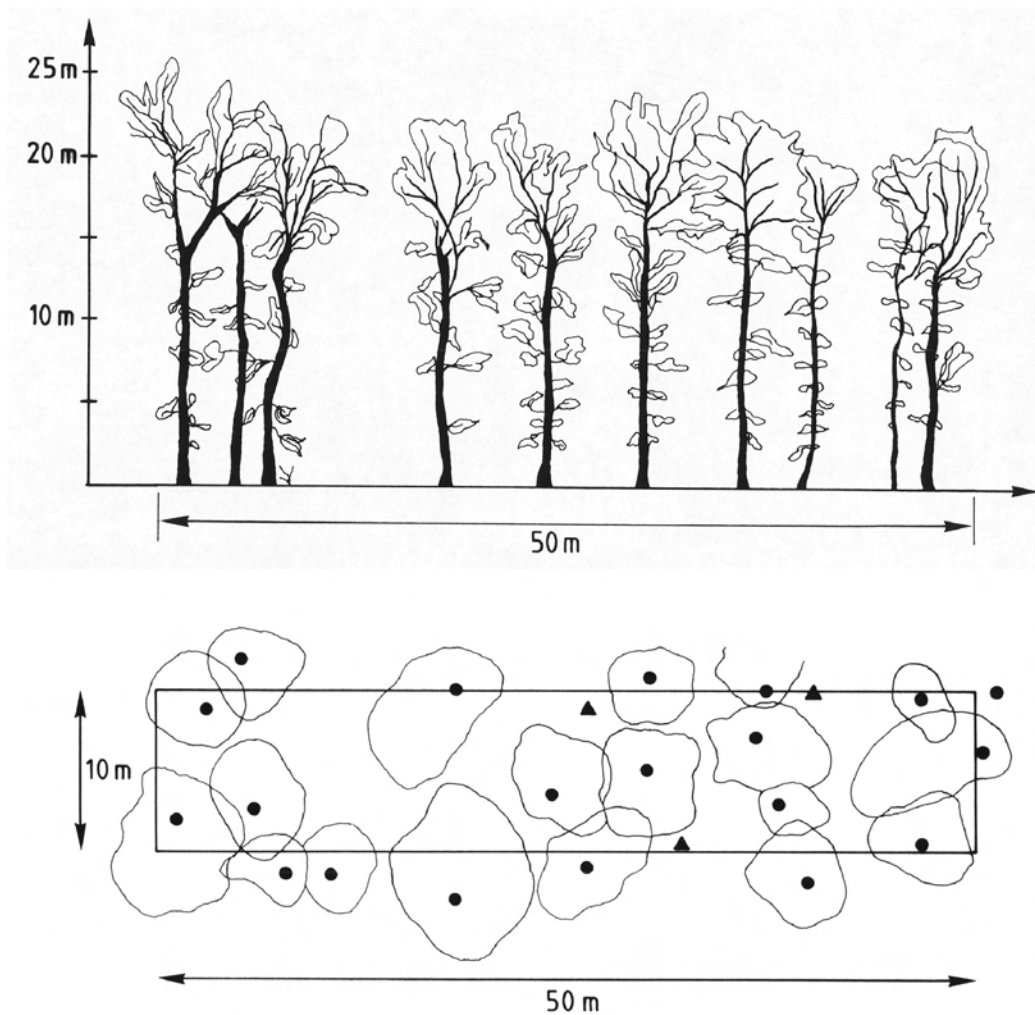
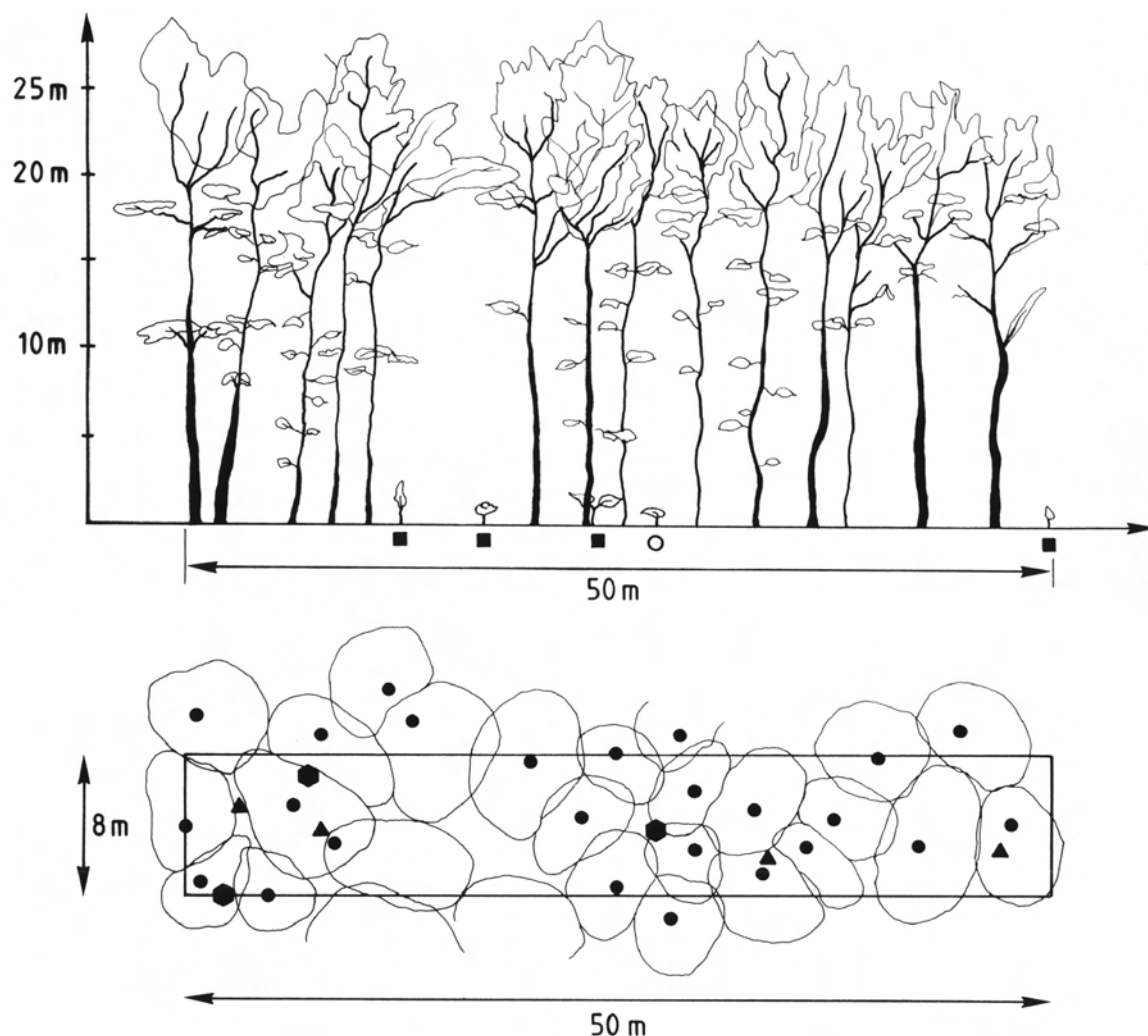


Figure 3. Stand profile (a depth of 8 m is recognized) and crown projection of a grazed *Quercus frainetto* forest stand. Dots on the projection indicate the position of stems, triangles that of weathered stumps.

grazed stands tend to be less high, with more branches in the trunk area and with more investment into radial stem growth. The higher degree of infection by parasitic *Loranthus* suggests that oak trees are less vital in heavily grazed forest. Since geological and topographic conditions are largely identical for all plots, differences in the

vitality of trees and in species composition are almost certainly related to the considerable differences observed in present litter and humus layers. The litter layer and the higher content of organic matter are important in maintaining rapid infiltration rates, absorbing many times its own weight of water (Pritchett & Fisher, 1987).

Figure 4. Stand profile (a depth of 5 m is recognized) and crown projection of an ungrazed *Quercus frainetto* forest enclosure plot. Dots on the projection indicate the position of stems; triangles that of weathered, sixangles that of resprouting stumps. Quadrats in the profile indicate *Arbutus* rejuvenation of >1 m, circle: resprouting *Q. frainetto* stump.



In the enclosure, litter covers the ground almost totally, and moisture is retained much more effectively. Annuals occur only on naked mineral soil, in conditions which are absent in the enclosure (or restricted to stem bases). This is the result of wind turbulence dislocating foliage and preventing accumulation of organic matter (Wilke *et al.*, 1993). The wind effect is reduced if a shrub or subshrub layer is developed. Such a layer is represented in the oak forest by the regrowth of *Q. frainetto*, the most frequent species in the herb layer, and, in non-grazed stands, also by *Arbutus unedo* and *Erica arborea*. In a study on post-grazing successional oak woodland in southern France Debussche *et al.* (2001) found shrub species among the increasing taxa but not among the decreasing. Grazing (by sheep and pigs as in the study area) does not prevent oak rejuvenation but young oaks are less abundant. In fact, since grazing is likely to prevent a dense *Arbutus* and *Erica* understorey, moderate silvopastoralism might even favour *Q. frainetto* rejuvenation. In enclosures, the

dense herb layer of oak seedlings and saplings supports litter and humus accumulation, thus improving soil water and nutrient conditions which, in turn, are favourable for rejuvenation. Browsing may be of little direct effect on the juveniles but trampling is destructive to the herb layer. Soil compaction and depletion are common features in grazed woodlands (Bezkorowajnyj *et al.*, 1993; Sibbald, 1999). Our findings suggest that they may be interpreted as an indirect effect of animals due to decreased litter accumulation rather than directly by trampling.

CONCLUSION AND FINAL REMARKS

The forest of Folói forms part of an area named 'Oropedio Folois' (9723 ha), chosen to become a Special Conservation Area, eligible to be included in the European 'Natura 2000' network of Sites of Community

Interest. Regulative arrangements and administrative measures for Special Conservation Areas are currently initiated, including the establishment of a management plan. Such a plan, however, cannot be worked out unless the conservation priorities are clearly defined. From our study two possible concepts may be suggested:

- (a) Folói represents an outstanding example of an agrosilvopastoral system. Such ecosystems are vanishing in Europe and almost lost in most countries. They are considered a traditional asset worthy of protection. The history of human interference in the Folói area is long but today's combined impacts on the forest (grazing, charcoal production, forestry, agriculture) are far from sustainable. Maintaining wood pasture in Folói requires a balanced grazing regime and a strict control of other kinds of impact.
- (b) On the other hand, Folói constitutes a unique example of submediterranean tall oak forest. As our study shows, it is severely suffering in places from grazing but the conditions of regeneration towards a natural forest are better than anywhere else.

Any management plan and conservation measures depend on which alternative is given priority. It is clear, from the results of our paper, that the two conservation visions can hardly be realized simultaneously in one and the same site. It is also evident that a Special Conservation Area cannot be established without the acceptance and co-operation of the resident farmers and villagers. The management plan will have to make an attempt to accommodate both options: *e.g.*, by installing a core zone where grazing is to be prohibited, and a buffer zone with controlled grazing regime. With the establishment of a European network of conservation sites the problem of harmonization of the options natural forest and traditional silvopastoralism will be of increasing relevance. Folói may well serve as a model on how to balance the respective management and conservation measures.

ACKNOWLEDGEMENTS

We thank L. Boskos, F. Galanos, G. Karetsos and K. Varelides, Research Forest Institute of Athens (NAGREF), for supplying us with stand analysis data from the late N. Panagiotidis; H. Dres, retired forester of the Folói forest, for discussions and informations on the study area; U. Bergmeier for support and assistance in the field; C. Adamidis, Ioannina, for statistical advice; P. Lampropoulos, Patras, and G. Amschliger, Freiburg,

for skilfully preparing the figures; M. Klescewski and H. Gondard, both Montpellier, for their linguistic help with the résumé; E. Vidal and an anonymous reviewer for suggestions to improve the manuscript.

References

- BERGMEIER E., 1998. Flowering intensity of phrygana plants after fencing. *Israel. J. Plant Sci.* 46: 41-46.
- BERGMEIER E., DIMOPOULOS P., THEODOROPOULOS K. & ELEFTHERIADOU E., 2004. Zonale sommergrüne Laubwälder der südlichen Balkanhalbinsel. *Tuexenia* (in press).
- BERGMEIER E. & MATTHÄS U., 1996. Quantitative studies of phenology and early effects of non-grazing in Cretan phrygana vegetation. *J. Veg. Sci.* 7: 229-236.
- BEZKOROVAJNYJ P.J., GORDON A.M. & MCBRIDE A.A., 1993. The effect of cattle foot traffic on soil compaction in a silvopastoral system. *Agroforestry Systems* 21: 1-10.
- CHRISTOPOULOS G. (ED.), 1978. *Istoria tou Ellinikou Ethnous. [The history of the Greek Nation.]* Vol. 7 (Vizantinos Ellinismos-Protovizantini chroni). Ekdoti Athinon, Athina.
- DEBUSSCHE M., DEBUSCHEE G. & LEPART J., 2001. Changes in the vegetation of *Quercus pubescens* woodland after cessation of coppicing and grazing. *J. Veg. Sci.* 12: 81-92.
- DI PASQUALE G. & GARFI G., 1998. Analyse comparée de l'évolution de la régénération de *Quercus suber* et *Quercus pubescens* après élimination du pâturage en forêt de Pisano (Sicile sud-orientale). *Ecol. Medit.* 24: 15-25.
- FERNANDEZ ALÉS R., LAFFARGA J.M. & ORTEGA F., 1993. Strategies in Mediterranean grassland annuals in relation to stress and disturbance. *J. Veg. Sci.* 4: 313-322.
- HELDREICH TH. VON, 1862. *Die Nutzpflanzen Griechenlands.* Athens.
- IGME (ED.), 1983. Geological Map of Greece 1/500 000 (red. J. Bornovas & T. Rondogianni-Tsiambaou). 2nd ed. Athina.
- NOY-MEIR I., GUTMAN M. & KAPLAN Y., 1989. Responses of Mediterranean grassland plants to grazing and protection. *J. Ecol.* 77: 290-310.
- PANAGIOTIDIS N.TH., 1965. *Makrochronii dhasike piramatike epithanie. [Langfristige forstliche Versuchsflächen.]* Athine. 51 pp.
- PAPANASTASIS V.P., FRAME J. & NASTIS A.S. (EDS.), 1999. *Grasslands and woody plants in Europe.* Proceedings Internat. Occ. Symp. European Grassland Federation, Thessaloniki, Greece, May 27-29, 1999. Thessaloniki.
- PHILIPPSON A., 1892. *Der Peloponnes.* Versuch einer Landeskunde auf geologischer Grundlage. Berlin.
- PHILIPPSON A., 1959. *Die griechischen Landschaften 3 (2). Der Peloponnes, Teil 2: Der Westen und Süden der Halbinsel.* Klostermann, Frankfurt am Main.

- POTT R., 1999. *Diversity of pasture-woodlands of north-western Germany*. In: Kratochwil A. (ed.), Biodiversity in ecosystems. Kluwer Acad. Publ., Dordrecht: 107-132.
- PRITCHETT W. & FISHER R., 1987. *Properties and management of forest soils*. Wiley, New York.
- PRITZEL E., 1908. Vegetationsbilder aus dem mittleren und südlichen Griechenland. *Bot. Jahrb. Syst. Pflanzengesch. Pflanzengeogr* 41: 180-214.
- REDECKER B., FINCK P., HÄRDTLE W., RIECKEN U. & SCHRÖDER E. (EDS.), 2002. *Pasture landscapes and nature conservation*. Springer, Berlin, Heidelberg.
- ROTHMALER W., 1943. Die Waldverhältnisse im Peloponnes. *Intersylva* 3, 329-342.
- SCHMIDT M. & HEILE H., 2001. Beweidung von Hutewäldern im Reinhardswald – Pro und Kontra. *Jahrb. Naturschutz Hessen* 6: 184-190.
- SIBBALD A.R., 1999. *Silvopastoral agroforestry: soil-plant-animal interactions in the establishment phase*. In: Papanastasis V.P., Frame J. & Nastis A.S. (eds.), Grasslands and woody plants in Europe, Proceedings Internat. Occ. Symp. European Grassland Federation, Thessaloniki, Greece, 27-29 May 1999: 133-144.
- SPENCER J., 2002. *Managing wood pasture landscapes in England: the New Forest and other more recent examples*. In: Redecker B., Finck P., Härdtle W., Riecken U. & Schröder E. (eds.), Pasture landscapes and nature conservation. Springer, Berlin, Heidelberg: 123-136.
- TER BRAAK C.J.F. & ŠMILAUER P., 1998. *Canoco Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4)*. Microcomputer Power, Ithaca, NY, USA.
- TUTIN T.G. ET AL. (EDS.), 1968-1993. *Flora Europaea*, Vols. 2-5 and Vol. 1, 2nd ed. Cambridge University Press, Cambridge.
- VERA F.W.M., 2000. *Grazing ecology and forest history*. Oxon Cabi Publ.
- WILKE B., BOGENRIEDER A., WILMANN O., 1993. Differenzierte Streuverteilung im Walde, ihre Ursachen und Folgen. *Phytocoenologia* 23: 129-155.