

Vegetation Composition in a Post-Fire Successional Gradient of *Pinus halepensis* Forests in Attica, Greece*

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Abstract. The vegetation composition of a post-fire succession in Aleppo pine forests of Attica, Greece, was studied by a synchronic method. The sites form a post-fire chronosequence and have typical Mediterranean climate. Data on the flora of the burned sites, growth and life forms of the various plant taxa, as well as on vegetation structure are provided. The burned ecosystems recovered quite rapidly. During the first four years of the post-fire succession, herbaceous taxa dominate the flora of the forests, peaking at the second year. After 15 years little change in the vegetation was observed. The richest family in terms of the number of taxa was the Leguminosae, especially in the two first years of succession. Most of these taxa were herbaceous. The relative contribution of legumes to the flora after two years is gradually restricted.

Keywords: Life forms; Regeneration mode; *Pinus halepensis* forests; legumes; Greece

Introduction

Fire is known to be one of the primary factors affecting vegetation of Mediterranean - climate ecosystems (Naveh 1967, 1973). The flora of these ecosystems has evolved certain mechanisms in order to persist in a regime of stand - replacing fires (Naveh 1973, Rundel 1981, Arianoutsou-Faraggitaki and Margaris 1981a). Fire - resistant bark, enhanced seed germination and vegetative growth from root crowns are some of these mechanisms.

One of the main ecosystem types in Greece is that of the Mediterranean pine forests. In the mainland of Greece the dominant pine tree is *Pinus halepensis* Mill. (Aleppo pine), while on the islands of the East Aegean Sea and on Crete Aleppo pine is replaced by *Pinus brutia* Ter. (East Mediterranean pine). Together they cover 8.7% of the forested area of Greece (Ministry of Agriculture 1992).

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About 24.1% of the area burned each year during the dry summer in Greece is Aleppo and East Mediterranean pine forests (Kailidis 1992). Between 1965 and 1989, 122015 ha of *Pinus halepensis* forests burned, which is 33% of the total Aleppo pine forests in Greece (Kailidis 1992). The situation becomes more severe in the forests neighbouring urban areas and tourist resorts, as these forests are subjected to increasing pressure for land-use changes, especially when burned. In order to contribute towards accumulation of the knowledge needed to apply ecologically sound post-fire management plans, we undertook a study on post-fire succession of Mediterranean pine forests. This paper reports on the vegetation composition in a post-fire successional gradient of Aleppo pine forests in Attica, where these forests constitute approximately 40% of its forested cover and 18% of the overall *Pinus halepensis* cover in Greece (Ministry of Agriculture 1992).

Materials and Methods

Seven study sites were selected for sampling on hill-sides around Athens. Times since the last burn were 1, 2, 3, 4, 11, 15 and more than 30 years. We tried to select sites that were as similar as possible, but this was difficult because of high variability in bedrock types. As long as the dominant woody flora was identical and the degree of human interference with the ecosystem was similar the sites were considered for sampling. All sites have typical Mediterranean climate, that is mild, subhumid winters and long, dry hot summers. Sites descriptions are presented in Table 1.

The study was conducted from October 1992 to June 1993. Plant regeneration mode and life form were recorded at the one-year burned site, but information about these vital attributes is also provided for the later stages. A plant taxon can be a seeder, a resprouter or a facultative resprouter according to its regeneration mode, while it can be classified as a phanerophyte, a chamaephyte, an hemicyptophyte, a geophyte or a therophyte in the

Table 1. The characteristics of the study sites

Stand Age (yr)	Date of Fire	Locality	Bedrock Material	Altitude (m)
1	Sep 92	KAPANDRITI	Tertiary deposits	350
2	Sep 91	AVLONA	Limestone	400
3	Aug 90	STAMATA	Schists	350
4	Jul 89	FYLI	Limestone	400
11	Aug 82	DIONYSOS	Schists	450
15	Jul 78	PIKERMI	Tertiary deposits	200
>30	before 1960	PIKERMI	Tertiary deposits	200

Raunkiaer life form system. Raunkiaer (1934) defined the life form of a plant in terms of the position and degree of protection of its perennating bud relative to the ground surface (>25 cm for the woody phanerophytes; close to the ground but less than 25 cm from the surface for the chamaephytes - which are also woody perennials; renewal buds at the surface of the ground for the hemicryptophytes - many graminaceous and herbaceous plants; beneath the soil surface for the geophytes; and as an embryo in buried seeds for the therophytes). This system provides a means of classifying flora which focuses on the natural selection of vegetative organs in response to environmental pressures and the ultimate morphological adaptations that enable the plant to survive unfavourable conditions.

To describe the vegetation composition we used line-transects, which are especially advantageous and efficient for use in studies of succession in transition zones (Brower et al. 1990). In every stand we randomly located three 100-m line transects, keeping a minimum distance of 50 meters between them. On a monthly basis, we recorded occurrence of all plant species that were intercepted by a one-meter-long line (vertical plane) crossing the main transect at a right angle at one meter intervals.

The sites were grouped in clusters with the aid of an hierarchical agglomerative method provided by the **PRIMER** statistical program (version 3.1, Clarke and Warwick 1994). This method takes a Bray-Curtis similarity matrix as its starting point and successively fuses the samples into groups and the groups into larger clusters, starting with the highest mutual similarity then gradually lowering the similarity level at which groups are formed. The result of this hierarchical clustering is a dendrogram, where x axis is the full set of sites and the y axis is defining a similarity level at which two samples are considered to have fused. Note that the Bray-Curtis similarity matrix is formed by coefficients calculated on species presence/absence (1/0) data, which practically is identical to Sorensen similarity coefficient (Brower et al. 1989, Clarke and Warwick 1994).

$$\text{Sorensen Similarity Coefficient: } CC_i = \frac{2c}{S_1 + S_2}$$

where c = the number of species common to both sites, S_1 and S_2 are the numbers of species in sites 1 and 2 respectively.

Plant nomenclature follows Med - Checklist (Greuter et al 1984-1989) and Flora Europaea (Tutin et al 1968-1980) for the families not included in the published volumes of Med - Checklist.

Results

Plant taxa found along the line transects at each study site are given in Table 2. Regeneration mode and life forms of these taxa are also shown in Table 2. During the first three years after the fire the richest family, in terms of number of taxa, was the legume family (Leguminosae). In the more mature stands of the post-fire chronosequence other families, such as Compositae, Gramineae and Liliaceae, appeared to have rather more representatives than the rest of the families.

The richest flora was observed on the two-year-old site, while the smallest number was noted on the eleven-year-old site (Figure 1).

As far as it concerns the various life forms represented in the plants recorded, it is evident that therophytes were important in the early successional stages, while phanerophytes and chamaephytes were dominant in later stages (Figure 2).

The regeneration mode of each plant taxon is closely related to its life form. All therophytes are exclusively seeders and the geophytes are exclusively resprouters. Plants in the other life forms appear to be facultative resprouters (Table 3).

Cluster analysis on the data collected from all study sites indicated that sites were primarily grouped in regard to their successional stage, and that bedrock material had little but not overwhelming influence on this grouping (Figure 3). Two major groups were distinguished. The first was formed by the two sites of the very early post-fire successional stages on tertiary deposits and limestone respectively, while the second consisted of all the other sites. The second group was divided in two sub-groups: that of the third and fourth post fire year (schists and limestone respectively), and that of the 11-year, 15-year and mature sites (schists and tertiary deposits respectively).

Discussion

Since 1934, when Raunkiaer introduced his life form system, it has met with a great deal of application in all the fields of terrestrial ecology. The system can be successfully applied in the study of post-fire succession, as a

Table 2. List of plant taxa observed in all study sites. The classification of the life form (LF) follows the Raunkiaer system (Ph: Phanerophytes, Ch: Chamaephytes, G: Geophytes, H: Hemicryptophytes, Th: Therophytes). According to their regeneration mode (RM) plants are classified as obligate seeders(OS), obligate resprouters (OR) or facultative seeders (FS).

TAXA	Post-Fire Years						LF	RM	
	1	2	3	4	11	15			>30
1.PINACEAE									
<i>Pinus halepensis</i>			+	+	+	+	+	Ph	OS
2.FAGACEAE									
<i>Quercus pubescens</i>			-	-	+	-	-	Ph	OR
<i>Quercus coccifera</i>			+	+	+	+	+	Ph	OR
3.CARYOPHYLLACEAE									
<i>Stellaria media</i>	-	+	-	-	-	-	-	Th	OS
<i>Silene vulgaris</i>	-	+	-	-	-	-	-	H	FS?
<i>Silene colorata</i>	-	+	-	-	-	-	-	Th	OS
4.RANUNCULACEA									
<i>Anemone blanda</i>			+	-	-	-	-	H	OR
<i>Clematis vitalba</i>			-	-	-	-	-	Ph	OR
5.PAPAVERACEAE									
<i>Papaver rhoeas</i>	-	+	-	-	-	-	-	Th	OS
<i>Fumaria schleicheri</i>	+	+	+	-	-	+	-	Th	OS
6.CRUCIFERAE									
<i>Hirschfeldia incana</i>	-	-	-	+	-	-	-	Th	OS
<i>Capsella bursa-pastoris</i>	-	+	+	-	-	-	+	Th	OS
<i>Biscutella didyma</i>	-	+	+	-	-	-	-	Th	OS
7.ROSACEAE									
<i>Sarcopoterium spinosum</i>			-	+	+	+	-	Ch	FS
8.LEGUMINOSAE									
<i>Anagyris foetida</i>	-	-	-	-	+	-	-	Ph	FS
<i>Calicotome villosa</i>	-	-	+	+	-	+	-	Ph	FS
<i>Genista acanthoclada</i>	+	-	+	+	+	+	+	Ph	FS
<i>Anthyllis hermanniae</i>	-	+	+	+	+	+	+	Ph	FS
<i>Anthyllis vulneraria</i>	-	-	-	+	-	-	-	H	OS
<i>Bituminaria bituminosa</i>	-	+	-	-	-	-	-	Ch	OS
<i>Dorycnium hirsutum</i>	-	-	-	+	-	-	-	Ch	OS
<i>Onobrychis ebenoides</i>			-	+	-	-	-	H	OS
<i>Trifolium uniflorum</i>			+	-	-	-	-	H	OS
<i>Trifolium fragiferum</i>	-	+	-	-	-	-	-	H	OS
<i>Trifolium campestre</i>	+	+	+	+	-	+	+	Th	OS
<i>Trifolium arvense</i>	+	+	+	-	-	-	-	Th	OS
<i>Trifolium stellatum</i>	+	+	+	-	-	+	-	Th	OS
<i>Trifolium lappaceum</i>	+	-	-	-	-	-	-	Th	OS
<i>Vicia villosa</i>	-	+	-	-	-	-	-	Th	OS
<i>Vicia tetrasperma</i>	+	+	+	+	-	-	-	Th	OS
<i>Vicia sativa</i>	+	-	-	-	-	-	-	Th	OS
<i>Lathyrus setifolius</i>	-	+	-	-	-	-	-	Th	OS
<i>Lathyrus cicera</i>	+	-	-	-	-	-	-	Th	OS
<i>Lathyrus aphaca</i>	+	+	-	-	-	-	-	Th	OS
<i>Ononis variegata</i>	-	+	-	-	-	-	-	Th	OS
<i>Medicago arborea</i>	-	-	-	-	+	-	-	Th	OS
<i>Medicago lupulina</i>	-	+	-	-	-	-	-	Th	OS
<i>Medicago orbicularis</i>	+	+	-	-	-	-	-	Th	OS
<i>Medicago littoralis</i>	+	-	-	-	-	-	-	Th	OS
<i>Medicago polymorpha</i>	-	+	-	-	-	-	-	Th	OS
<i>Medicago minima</i>	+	-	-	-	-	-	-	Th	OS
<i>Lotus ornithopodioides</i>	+	+	-	-	-	-	-	Th	OS
<i>Securigera securidaca</i>	-	+	-	-	-	-	-	Th	OS
<i>Securigera cretica</i>	-	+	-	-	-	-	-	Th	OS
<i>Hippocrepis unisiliquosa</i>	+	+	-	-	-	-	-	Th	OS
<i>Scorpiurus muricatus</i>	+	+	-	-	-	-	-	Th	OS
9.GERANIACEAE									
<i>Geranium molle</i>	-	+	-	-	-	+	+	Th	OS
<i>Erodium malacoides</i>	+	-	-	-	-	-	-	Th	OS

continued on next page

Table 2. Continued.

TAXA	Post-Fire Years							LF	RM	
	1	2	3	4	11	15	>30			
10.LINACEAE										
<i>Linum pubescens</i>			-	-			-	-	Th	OS
11.EUPHORBIACEAE										
<i>Euphorbia taurinensis</i>			-	+			-	-	Th	OS
12.ANACARDIACEAE										
<i>Pistacia lentiscus</i>	+	+	+	+			+	+	Ph	OR
<i>Pistacia terebinthus</i>	+	+	-	-	+		-	-	Ph	OR
13.MALVACEAE										
<i>Malva sylvestris</i>			+	-	+		+	+	H	OR
14.THYMELAEACEAE										
<i>Thymelaea tartonraira</i>			-	+	-		-	-	Ch	FS
15.HYPERICACEAE										
<i>Hypericum empetrifolium</i>			+	+	+		+	+	Ch	FS
16.CISTACEAE										
<i>Cistus creticus</i>	+	+	-	+	+		-	+	Ph	OS
<i>Cistus salvifolius</i>	-	-	+	+	+		+	-	Ph	OS
<i>Cistus monspeliensis</i>	-	-	+	-	+		-	-	Ph	OS
<i>Fumana thymifolia</i>	+	+	+	+	-		+	+	Ch	OS
17.UMBELLIFERAE										
<i>Tordylium apulum</i>	-	-	+	-	-		-	-	Th	OS
<i>Scandix pecten-jacobeus</i>	-	+	-	-	-		-	-	Th	OS
<i>Daucus carota</i>	-	+	-	-	-		-	-	Th	OS
18.ERICACEAE										
<i>Arbutus unedo</i>	+	-	-	-	+		-	-	Ph	OR?
<i>Arbutus andrachne</i>	-	-	-	-	+		-	-	Ph	OR?
<i>Erica arborea</i>	-	-	+	-	+		-	-	Ph	FS
<i>Erica manipuliflora</i>	-	-	-	-	+		-	-	Ph	FS
19.PRIMULACEAE										
<i>Cyclamen graecum</i>			+	+	+		+	+	G	OR
20.OLEACEAE										
<i>Olea europaea</i>	-	+	-	+	+		+	+	Ph	OR
<i>Phillyrea latifolia</i>	-	+	+	+	+		-	+	Ph	OR
21.RUBIACEAE										
<i>Gallium aparine</i>	-	+	-	-	-		-	-	Th	OS
<i>Rubia peregrina</i>	+	+	-	-	-		-	-	H	OR
22.CONVOLVULACEAE										
<i>Convolvulus elegantissimus</i>			+	+	-		+	+	H	OR
23.BORAGINACEAE										
<i>Alkanna tinctoria</i>			-	-	-		+	+	H	OR
24.LABIATAE										
<i>Ajuga chamaepitris</i>	+	-	-	-	-		-	-	H	OR?
<i>Teucrium sp.</i>	-	-	-	+	-		+	+	Ch	OR?
<i>Prasium majus</i>	-	+	-	-	-		-	+	Ch	OR?
<i>Ballota acetabulosa</i>	-	+	-	-	-		-	-	H	OR?
<i>Stachys sp.</i>	-	+	-	-	+		+	+	H	OR?
<i>Satureja thymbra</i>	-	-	+	+	+		+	-	Ch	FS?
<i>Coridothymus capitatus</i>	-	-	-	-	+		+	+	Ch	FS?
25.SCROPHULARIACEAE										
<i>Veronica cymbalaria</i>	+	+	-	-	-		-	-	H	FS?
26.GLOBULARIACEAE										
<i>Globularia alypum</i>			-	-	-		+	-	CH	OR
27.PLANTAGINACEAE										
<i>Plantago sp.</i>			+	-	-		-	-	H	OR
28.CAPRIFOLIACEAE										
<i>Lonicera etrusca</i>	+	-	-	-	-		-	-	Ph	OR
29.VALERIANELLACEAE										
<i>Valerianella sp.</i>	-	-	-	+	-		-	-	Th	OS
30.DIPSACACEAE										
<i>Lomelosia brachiata</i>	-	+	+	+	-		-	-	Th	OS
31.CAMPANULACEAE										
<i>Campanula drabiflora</i>	-	+	-	-	-		-	-	Th	OS

Table 2. Continued.

TAXA	Post-Fire Years							LF	RM
	1	2	3	4	11	15	>30		
32.COMPOSITAE									
<i>Helichrysum</i> sp.	-	-	-	+	-	-	-	Ch	OR?
<i>Phagnalon graecum</i>	-	-	-	-	+	+	+	Ch	OR
<i>Anthemis chia</i>	-	+	+	-	-	-	-	Th	OS
<i>Senecio vulgaris</i>	-	+	-	+	-	-	-	Th	OS
<i>Calendula arvensis</i>	-	+	-	+	-	-	-	Th	OS
<i>Carduus pycnocephalus</i>	-	+	-	+	-	-	-	Th	OS
<i>Hypochoeris achyrophorus</i>	-	+	+	+	-	+	+	Th	OS
<i>Atractylis cancellata</i>	-	+	-	+	-	-	-	Th	OS
<i>Centaurea raphanina</i>	+	+	+	+	-	-	+	H	OR
<i>Tragopogon</i> sp.	-	+	+	+	+	+	+	H	OR
<i>Scorzonera crocifolia</i>	+	-	+	+	+	-	+	H	OR
<i>Reichardia picroides</i>	+	+	-	+	+	+	+	H	OR
<i>Dittrichia viscosa</i>	-	-	-	+	-	-	-	Ch	OR
33.LILIACEAE									
<i>Asphodelus aestivus</i>	-	-	+	+	-	+	+	G	OR
<i>Asphodeline lutea</i>	-	-	-	+	-	-	-	G	OR
<i>Gagea graeca</i>	-	-	-	-	-	-	+	G	OR
<i>Scilla autumnalis</i>	-	-	-	-	-	-	+	G	OR
<i>Ornithogallum divergens</i>	-	+	-	-	-	-	-	G	OR
<i>Muscari comosum</i>	+	+	+	+	-	+	+	G	OR
<i>Asparagus acutifolius</i>	+	+	+	-	-	+	+	Ch	OR
<i>Ruscus aculeatus</i>	-	+	-	-	-	-	-	Ch	OR
<i>Smilax aspera</i>	+	+	+	+	-	-	-	Ph	OR
34.IRIDACEAE									
<i>Crocus cartwrightianus</i>	-	+	+	+	+	+	+	G	OR
<i>Romulea</i> sp.	-	-	-	-	-	+	-	G	OR
<i>Gladiolus</i> sp.	+	-	-	-	-	-	-	G	OR
35.GRAMINEAE									
<i>Cynosurus echinatus</i>	+	-	-	-	-	-	-	Th	OS
<i>Briza maxima</i>	-	+	-	-	-	-	-	Th	OS
<i>Aegilops geniculata</i>	-	-	-	+	+	-	-	Th	OS
<i>Lagurus ovatus</i>	-	+	-	+	+	+	-	Th	OS
<i>Bromus ramosus</i>	-	+	+	+	-	-	-	Th	OS
<i>Avena sterilis</i>	-	-	-	+	-	-	-	Th	OS
<i>Brachypodium sylvaticum</i>	+	+	+	+	+	+	+	H	OR
36.ARACEAE									
<i>Arisarum vulgare</i>								G	OR
37.ORCHIDACEAE									
<i>Ophrys lutea</i>								G	OR
<i>Serapias</i> sp.								G	OR

tool that allows us to predict the post-fire behaviour of a plant according to its life form (Chapman and Crow 1981). Of course in many cases things might not be so simple. For example, phanerophytes in general are regarded as resprouters but *Pinus halepensis* and *Cistus* spp. are obligate seeders. Chamaephytes and hemicryptophytes also seem to exhibit a diverse post-fire behaviour. For hemicryptophytes, in particular, it seems that post-fire behaviour is more or less a characteristic depending on the family in which the taxon belongs. For example all the hemicryptophytes of the Compositae recorded are resprouters (Table 2). On the other hand, it is known that the hemicryptophytes of the Leguminosae that colonise the burned pine forests are seeders (Papavassiliou and Arianoutsou 1993). Finally, therophytes are obligate seeders, and geophytes seem to be obligate resprouters.

In the early post-fire years, herbaceous flora dominated Aleppo pine forests, as is true for other Mediterranean climate ecosystems (Hanes 1971, Naveh 1973, Trabaud 1980, Arianoutsou-Faraggitaki and Margaris 1981a, Arianoutsou-Faraggitaki 1984, De Lillis and Testi 1992, Keeley 1992, Faraco et al 1993). The majority of those taxa were restricted only to the first few years after fire and they were obligate seeders. Their seeds, which remain viable for many years and form soil seed bank, germinate primarily after fire (Keeley and Zedler 1978, Arianoutsou and Margaris 1981b, Papavassiliou et al 1994). An exception to this general trend seem to be South African fynbos, where the post-fire flora is dominated by geophytes (Kruger 1983). Part of the explanation is that bulbs and corms are an efficient nutrient pool (Le Maitre and Migley 1992), which is so crucial for the nutrient pool

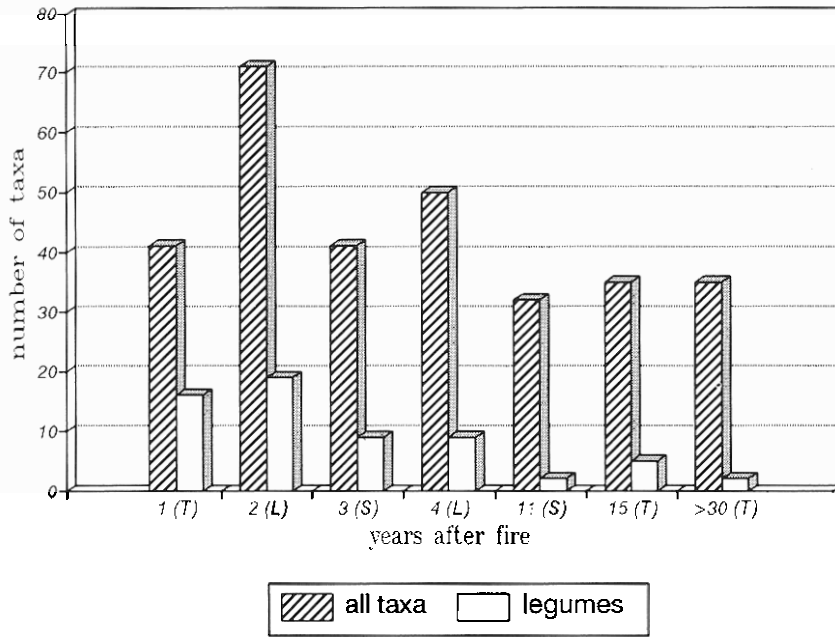


Figure 1. Total species richness and richness of leguminous taxa at each study site (T: tertiary deposits, L: limestones, S: schists).

fynbos soils. Another reason could be fire intervals. In the Mediterranean Basin and in California there are longer fire intervals as compared to those in South Africa (cited by Keeley 1992). These relatively long fire intervals (>40 years) may favour the formation of seed banks as a rather efficient mode of survival. In other words, the annual habit may be more compatible with longer, unpredictable fire-free periods (Keeley 1992). In fynbos, geophytes can persist for many more years after fire due to the more open

nature of the vegetation (Kruger 1983). Finally, the greater summer water stress faced by the Mediterranean and Californian systems (cited by Keeley 1992) may make survival of perennials less favourable in post-fire environments. This evidence is supported by the fact that in arid fynbos annuals become more important (Kruger 1979).

The highest increase in species richness occurs in the second post-fire year. This increase cannot be attributed to the enrichment of the flora of the burned forest by dor-

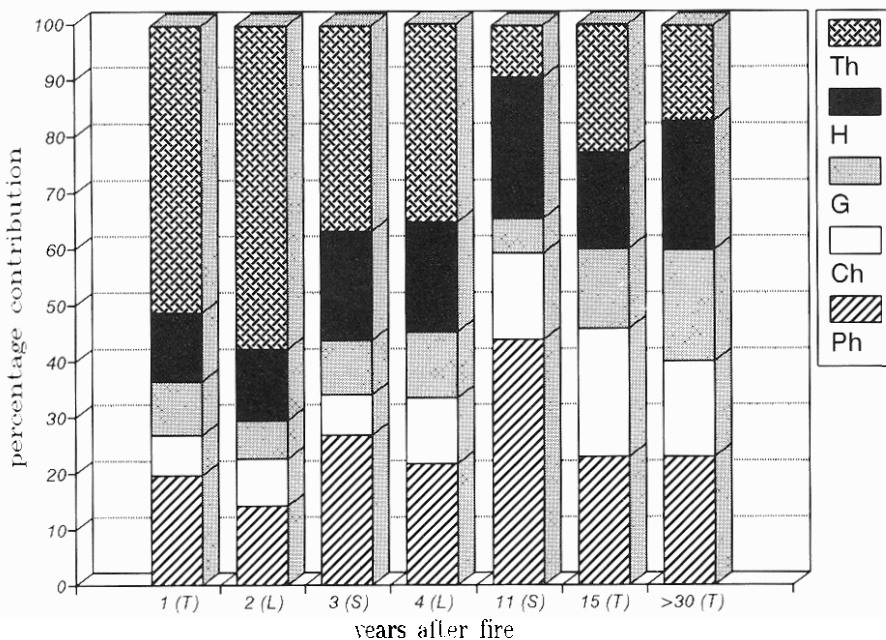


Figure 2. Percentage contribution of each life form to the flora of the study sites (T: tertiary deposits, L: limestones, S: schists).

Table 3. Regeneration mode (RM) and life forms in the recorded plant taxa.

REGENERATION MODE	PLANT LIFE FORMS				
	Ph	Ch	G	H	Th
obligate seeders	50.0	56.0	0.0	68.0	100.0
obligate resprouters	23.0	19.0	100.0	21.0	0.0
facultative seeders	27.0	25.0	0.0	11.0	0.0

mant seeds, since it is expected that all of the hard-coated seeds have already germinated in the first year. Data from other Mediterranean countries support our results on the increase of floristic richness early after fire. Trabaud and Lepart (1980) mention that floristic richness of *Pinus halepensis* woodlands, *Rosmarinus officinalis* garrigues, *Quercus ilex* coppices and *Quercus coccifera* garrigues grows gradually to reach a maximum between the 10th and the 40th month. Then the floristic richness diminishes. Finally, a relative stabilisation occurs from the 60th month onwards. Similarly, after the second post-fire year they noted a decrease in the number of taxa of the Aleppo pine forests, which was mainly due to the loss of the therophytes.

The presence of the therophytes in the early post-fire stages and their subsequent relative absence from the later stages may be related to their germination mechanisms. Most of the species which appear immediately after fire have seeds whose germination is directly or indirectly induced by fire. The direct induction is mediated through the mechanical eruption of the hard seed coat caused by soil heating. This mechanism has been proved for many woody and herbaceous plants with hard seed coats (Arianoutsou and Margaris 1981b, Keeley 1991, Roy and Sonie 1992, Thanos et al 1992, Keeley 1992). Indirect induction of seed germination can be related to the re-

moval of the canopy (Roy and Arianoutsou-Faraggitaki 1985). Once a fire consumes the vegetation, the incident light coming to the soil surface has a different spectrum, since there is no leafy filter to intercept it. This leads to a change in the Red:Far Red ratio which reaches the light sensitive seeds, which therefore germinate. It is possible that some of the soft-coated seeds are induced to germinate this way. We assume that further decrease in the herbaceous taxa which is observed in the more mature stands (3 yr old burn and onwards) is due to the restriction imposed by the competition for light and nutrients with the woody species which constantly occupy more space.

Although we expected that the species richness would decrease with increasing stand age, we found that in Fyli (4 yr-old burn site) the flora was richer than that of Stamata (3 yr-old burn site). This difference may have resulted from a thick layer of bryophytes at Stamata that may have negatively affected the plant community. In the 11-year stand woody species dominated the ecosystem. The vegetation was quite dense and the herbaceous cover was limited. Finally, in the 15-year stand the vegetation appeared less dense; the canopy opened slightly again and some herbaceous species reappeared.

The richest plant family in terms of taxa during the first years of the post-fire chronosequence was Leguminosae. This has also been reported by other researchers (Martin 1966, Hanes 1971, Naveh 1973, Chen et al 1975, Arianoutsou 1979, Rundel 1981, Westman 1981, Van Wilgen 1981, Thanos et al 1989, Papavassiliou and Arianoutsou 1993, Cocks 1994) for Mediterranean climate ecosystems. For example, Martin (1966) reported a 245% increase in the density of Leguminosae genera *Amphithalea*, *Indigofera*, *Bituminaria* (ex *Psoralea*) and *Tephrosia* in a one-year old burned area of fynbos. Van Wilgen and Kruger (1981) observed a mean cover of 4.5 and 3.3% of *Rafnia capensis* for two four-year old sites; this species was absent from the nearby mature (21 and 35 years) stands. Westman (1981) working in California coastal sage scrubs reported a drop in cover of five legume species (three species of *Lupinus* and two species of *Lotus*) from 11.5% to 1.5% between the first and the seventh year after fire. After 21 years, legume cover had decreased to almost zero. Arianoutsou (1995) reported that taxa of Leguminosae consisted up to 77% of the above ground plant biomass in a 3-year burned pine forest in Attica, Greece. Plants of this family are particularly important because they are able to form symbiotic relations

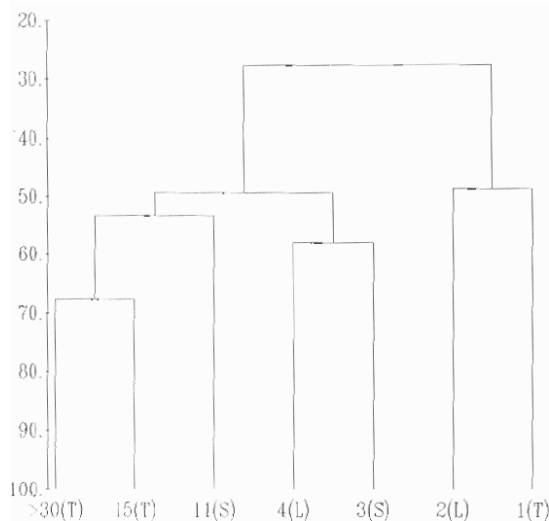


Figure 3. Patterns of Bray-Curtis similarity between clusters of plant taxa (T: tertiary deposits, L: limestones, S: schists).

with nitrogen-fixing soil bacteria, thus contributing to nitrogen enrichment of the soil (Rundel 1981, Arianoutsou-Faraggitaki and Margaris 1981a, c, Papavassiliou and Arianoutsou 1993; Arianoutsou and Thanos 1994, Cocks 1994).

The vast majority of the species in the first years after fire were herbaceous and their presence was restricted to the first post-fire stages. Only three woody species were recorded: *Calicotome villosa*, *Genista acanthoclada* and *Anthyllis hermanniae*.

It is known that Leguminosae can grow over a wide range of geological substrates (Antonovics et al 1971, Proctor and Woodell 1975). It is this wide preference that may explain the way the studied sites are grouped in the cluster analysis performed. The sites are clustered according to their post-fire stage and not according to the bedrock formation underlying them, as long as legumes are the main component dominating in the flora of the sites. On the three older sites data suggest a tendency for sites to be grouped according to substrate. However, more research is needed for the strong justification of this aspect.

Other families with a high number of taxa were those of Compositae and Gramineae. They were most important on the 4-yr-old site.

Our results show that post-fire succession at the Aleppo pine forests of Attica is similar to the succession of other Mediterranean ecosystems (Arianoutsou-Faraggitaki 1984, Espirito-Santo et al 1993, Lucchesi and Giovannini 1993, Ne'eman et al 1993 among others). Still, there are not enough data in the Mediterranean region, to develop a strong theory of species replacement during post-fire succession, primarily because it has been difficult to obtain long-term diachronic data on the same permanent plots in these human-disturbed areas. Many researchers use the synchronic method, which has the shortcoming arising from the difficulty in identifying sites which are different only in their post-fire age. It is our aim to contribute towards the filling of this gap by a combination of both methods under the framework of an ongoing project.

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