Acta Oecologica **20** (5) (1999) 499–508 /

Post-fire regeneration patterns in the eastern Iberian Peninsula

Juli G. Pausas *, Ester Carbó, Rosa Neus Caturla, José M. Gil, Ramon Vallejo

Centro de Estudios Ambientales del Mediterráneo (CEAM), C. Darwin 14, Parc Tecnològic, 46980 Paterna, València, Spain.
* *Corresponding author (fax: +34 96 131 8190; e-mail: juli@ceam.es)*

Received April 28, 1999; revised August 19, 1999; accepted August 20, 1999

Abstract — Post-fire regeneration patterns (plant cover and richness) in the Valencia region (eastern Iberian Peninsula) are studied by analysing data from two different samplings after two periods of large fires (1991 and 1994). Emphasis is given to comparing different environmental conditions (thermo-Mediterranean vs. meso-Mediterranean; south facing vs. north facing slopes) and different bedrock types (limestone vs. marls). Results suggest that the highest post-fire cover and species richness is reached in thermo-Mediterranean conditions on limestone, and the main species are the resprouters *Quercus coccifera* and *Brachypodium retusum*. North-facing sites have higher plant cover than south-facing ones, and most life forms (trees, shrubs, grasses) have higher cover in these sites. Species richness is higher on north-facing sites than on the south-facing ones at the small scale (1 to 200 m^2), but differences were not significant at the highest scale studied (1 000 m^2). Plant species richness with increasing sampling area follows the classical log-log relationship; however, when species are segregated by life forms (woody species and herbs), different species-area relationships were found. © 1999 Éditions scientifiques et médicales Elsevier SAS

Fire / resprouting / recovery / large fires / life form / species richness / species-area / Spain

1. INTRODUCTION

Wildfires are an important feature of Mediterranean ecosystems and many species have evolved strategies that allow them to survive periodic fires [24, 45]. However, the statistics compiled for Spain [23, 32] show that during the last decades, a notable change in fire regime has taken place, whereby forest fires have changed from being few in number and affecting a small area, to becoming very numerous and affecting large extensions. This change has been attributed mainly to socio-economic and land use changes [23] together with climatic warming [35]. Mediterranean vegetation is probably not adapted to this new fire regime and negative consequences may occur.

Within Spain, the eastern area (e.g. the Valencia region) is strongly influenced by fire (*figure 1*). During the last decades, the mean annual burnt area in this region was about 23 kha·year^{-1}, that is, on average, ca. 2 % of the total forest area (woodlands and shrublands) were burnt every year. However, this varies largely with years, and in the worst year ever recorded, 1994, the burnt area reached 140 kha, i.e. ca. 12 % of the forest area. During the summer of that year, more than 400 kha were burnt in Spain [1, 23].

The aim of the present study was to describe vegetation recovery after large fires in eastern Spain. Emphasis is given to the different patterns in contrasted environmental conditions (e.g. north/south slopes) and at different spatial scales. Many studies have been carried out on post-fire recovery of vegetation in the Mediterranean basin [2, 8, 11, 15, 21, 22,

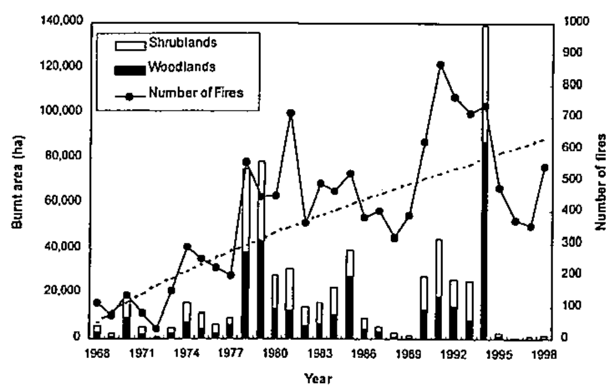

Figure 1. Yearly course of number of fires (dots and trend-line) and burnt areas (bars) in Eastern Spain (Valencia region) during the last decades (1968–1998).

25, 27, 28, 46, 47, 48, 49]; however, environmental factors have rarely been addressed [19, 49]. Furthermore, very few studies have considered the importance of scale in post-fire studies [18, 22, 41]. The specific questions addressed are: is the post-fire recovery of vegetation dependent on the climatic conditions? and on the bedrock types? Do different plant types behave differently in the recovery process? What is the species-area relationship after fire in two contrasted conditions (north/south slopes)? At which spatial scale does species richness differ between these conditions? These questions are addressed by analysing data from two different samplings elaborated by the CEAM team after two periods of large fires: the 1991 and the 1994 fires.

2. METHODS

2.1. Study area

The study area is the Valencia region, located in the eastern part of the Iberian Peninsula (Mediterranean coast). The climate is typically Mediterranean, with two main distinctive bioclimatic zones from the point of view of temperature [39]: a thermo-Mediterranean (TM) zone right next to the coast (mean annual temperature: 17–19 °C; vegetative period: 12 months) and a meso-Mediterranean (MM) zone a bit inland (mean annual temperature 13–17 °C; vegetative period: 9–11 months). Supra-Mediterranean areas (mean annual temperature: 8–13 °C) are less abundant further inland in the northern mountains. The precipitation regime is mainly dry (annual precipitation from 350 to 600 mm) and subhumid (from 600 to 1 000 mm) with some areas in the south with lower precipitation (semiarid area, with < 600 mm). The annual precipitation regime is strongly bimodal, with precipitation concentrated (> 60 %) in spring and autumn and with a dry summer (< 20 % of the annual precipitation).

Two main bedrock types are found in the study area: limestone, that is, calcareous hard rocks producing very shallow and decarbonated brown-red soils with abundant outcrops and cracks, and marls which produce deeper and highly carbonated soils but without cracks [51].

Current vegetation cover [12] is the product of a long history of fire and land use [30]. Main vegetation types are evergreen shrublands (garrigues and heathlands with different abundance of *Quercus coccifera*, kermes oak) and pine woodlands (*Pinus halepensis*, Aleppo pine), often with abundant *Cistus* spp., *Ulex parviflorus* (gorse) and *Brachypodium retusum*; old fields are often dominated by these last two species. Through all the text, nomenclature for plant names follows the *Flora of Catalan Countries* [6].

2.2. Sampling after the 1991 fires

In 1991, 44 300 ha burnt in the Valencia region. A year later, two to three south-facing sites of 1 000 m^2 were selected for each combination of the four main environmental conditions (limestones/marls × TM/MM climate [50]). On each site, ten permanent parallel transects of 10 m were set up. At each transect, the floristic composition was recorded along the line every 10 cm (100 reading points), 10 and 34 months after the fire. Only south-facing (equatorwise) slopes were sampled because we were interested in studying the drier (harder) conditions for regeneration [50].

2.3. Sampling after the 1994 Requena fire

The Requena fire burnt 24 770 ha in the dry meso-Mediterranean bioclimatic zone in July 1994. Three localities were selected within the burnt area, and in each locality, a north-facing and a south-facing site was sampled (total of six sites). All sites are located on the same bedrock type (limestone) between 520 and 700 m a.s.l., and are part of a Spanish network for studying vegetation response to fire [24]. On each site a 50 × 20 plot (1 000 m^2) was installed. The cover of each species was sampled using three transects of 50 m with 500 points each (i.e. readings every 10 cm). The occurrence of plant species was recorded in nested plots of increasing size within the whole plot: sixteen plots of 1 m^2, eight of 10 m^2, six of 100 m^2, three of 200 m^2, and in the whole plot (1 000 m^2). Plots were visited at different times the second year (winter, spring and summer) after the fire in order to account for annuals and ephemeral species.

2.4. Data analysis

Vegetation cover is expressed as percentage points from the transect data, but subtracting outcrops (< 10 % in all plots). Vegetation information (number of species and plant cover) was compared for the different environmental conditions (climatic zones, aspect and lithology), and plant species richness was related to the sizes of the sampling areas. Means were compared by analysis of variance and multiple comparison. Percentage data (cover values) were arcsine square root-transformed and count data (number of species) were log-transformed, with data presented as untransformed means. Regression analysis was used to describe the species-area curves in both semi-log and log-log space.

Changes in plant cover were studied for total vegetation as well as by species (showing results for main species only) and by life forms. Life forms considered were (Raunkiaer names in brackets): trees (megaphanerophytes), shrubs (nanophanerophytes), scrubs (chamaephytes), perennial forbs (hemicrypto-

Table I. Plant cover (%) 10 and 34 months after fire in two climatic conditions (TM: thermo-Mediterranean and MM: meso-Mediterranean) and two lithologies (raw and column total means are also shown). After 34 months, all cover values were significantly ($P < 0.05$) higher than after 10 months, except for limestone in TM climate. Comparisons between climates are shown below the means compared. Comparisons between lithologies are shown at the right side of the mean values. ns, Not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

	10 months				34 months			
	Marls	Limestone		Mean	Marls	Limestone		Mean
TM	30.75	76.50	****	53.63	47.90	76.30	****	62.10
MM	50.15	66.25	****	58.20	58.30	69.40	***	62.74
	****	****		ns	**	*		ns
Mean	40.45	71.38	****	55.91	54.14	72.85	****	62.46

phytes), perennial grasses (idem), geophytes, and annuals (therophytes). The analysis was also carried out for total species, for the group of resprouters and for the legumes. Resprouters refer to the species with a capacity to resprout after fire (independently of the seed production; i.e. first and second type sensus Pausas [30]: *table III*), in opposition to non-resprouters (the remaining species, i.e. without this capacity; third and fourth type sensus Pausas [30]). Legume species were studied separately because it has been hypothesised that this group plays an important functional role after fire due to its capacity to fix nitrogen [3, 5].

3. RESULTS

3.1. Post-fire vegetation after the 1991 fires

Ten months after fire, vegetation covers about 56 % of the soil surface, and 24 months later (34 after fire), the cover reached 63 % (average figures). However, there were significantly different values depending on the bedrock type (limestone/marls, *table I*). When cover values were averaged by lithologies, significant differences were also observed under different climatic conditions (TM, MM, *table I*). Maximum cover values after 10 months were reached under TM conditions on limestone (76.5 %); however, in these conditions, there was no further increase in vegetation cover in the next 24 months. The minimum cover after 10 months was observed in TM conditions on marls (30.8 %), and there was a significant increase 24 months later (47.9 %). Intermediate values were observed in MM conditions (*table I*).

We found a mean of ten species per transect (10 m; 100 points) 10 and 34 months after fire, with some differences depending on the bedrock type and climatic conditions (*table II*). However, in no case in the climate × lithology matrix did the number of species change significantly by the second sampling (10 vs. 34 months after fire). The richest conditions were on limestone under TM climate, coinciding with the highest cover values (*tables I, II*).

The most abundant species was the perennial grass *Brachypodium retusum*, with mean cover ranging from ca. 24 to 46 % depending mainly on the bedrock type (with the highest cover on limestone, *table III*). Similar values were observed 34 months after fire (*table III*). Cover was not significantly different between climatic areas. A similar pattern was found for the second most important species, *Quercus coccifera* (kermes oak), with cover ranging from 7 (marls) to 29 % (limestone) 10 months after fire. *Stipa parviflora*, the second grass in importance, did not show any

Table II. Mean number of species per 10-m transect (100 points; considering all species) 10 and 34 months after fire in two climatic conditions and two lithologies (row and column total means are also shown). The mean number of species was not, in any case, significantly different between 10 and 34 months. ns, Not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

	10 months				34 months			
	Marls	Limestone		Mean	Marls	Limestone		Mean
TM	7.25	11.45	***	9.35	9.25	12.2	**	10.73
MM	10.67	10.35	ns	10.54	11.07	8.5	***	10.04
	**	ns		ns	*	****		ns
Mean	9.30	10.90	*	10.01	10.34	10.35	ns	10.34

Table III. Mean cover (%) of the main species 10 and 34 months after the fire in the two climatic conditions (TM: thermo-Mediterranean and MM: meso-Mediterranean) and in the two lithologies (marls and limestone). ns, Not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

	Brachypodium retusum			*Stipa parviflora*			*Quercus coccifera*			*Ulex parviflorus*		
Months after fire	10	34		10	34		10	34		10	34	
TM	38.26	36.00	ns	5.04	9.88	*	14.62	20.29	ns	2.56	5.50	***
MM	32.98	34.28	ns	2.44	4.09	ns	26.43	33.04	ns	2.27	5.95	ns
P	ns	ns		ns	**		ns	ns		ns	ns	
Marls	24.21	29.22	ns	4.69	9.79	*	7.00	8.85	ns	2.44	6.50	***
Limestone	46.23	41.83	ns	4.05	4.67	ns	29.17	37.72	*	2.55	3.88	ns
P	****	***		ns	**		****	****		ns	ns	

significant difference in cover after 10 months, but it did after 34 months. For this species, the cover was higher on marls and in thermo-Mediterranean localities. *Ulex parviflorus* (gorse), the second shrub in importance, did not show any significant difference in cover for the different climatic conditions or lithologies; however, it showed a clear increase over time in TM and on marls. Other species showed very low cover values and are not analysed in detail.

3.2. Post-fire vegetation after the Requena fire (1994)

A year after the fire, on average, the vegetation covered 42 % of the soil, and the cover was significantly greater on north slopes (52.4 %) than on south ones (32 %, *table IV*). The main life form covering the soil was shrubs (*table IV*) with 34.5 % on the N-slopes and 17.6 % on the S-slopes; the main species was *Q. coccifera* (*table V*) with a mean cover of 14.6 % (*Q. coccifera* did not show significant differences between facing slopes). The second life form in importance was perennial grasses (17.5 and 8.5 %) with its major representative being *B. retusum* (16.2 and 8.4 %, *table V*). The third species in order of abundance was the shrub *U. parviflorus* with a mean cover of 5.6 %. The remaining species showed a cover lower than 5 % (*table V*) and most of them had similar cover on both slopes or greater cover on the N-slope (e.g. *Cistus albidus*, *Rubia peregrina* and *Rhamnus alaternus*). There was a significant relationship between the seven life forms and species with resprouting capacity (*table VI*; $\chi^2 = 26.3$, $P < 0.001$) but not with legume species. Resprouting species cover about 31 % (39.7 in

Table IV. Mean and SD of cover data (%) for different species groups 1 year after the Requena fire. ns, Not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$).

Species groups	Total		North		South		*P*
	Mean	SD	Mean	SD	Mean	SD	
Total	42.17	13.25	52.40	7.80	31.94	8.74	****
Woody species	31.95	10.73	39.55	6.48	24.36	8.53	**
Shrubs	26.04	11.42	34.49	7.44	17.58	7.80	****
Trees	0.81	1.01	1.10	1.19	0.52	0.75	ns
Scrubs	6.66	4.73	6.05	5.53	7.27	4.01	ns
Herbs	14.76	8.08	19.51	8.89	10.02	3.00	**
Perennial grasses	12.98	8.24	17.46	9.54	8.51	2.90	*
Perennial forbs	1.80	1.10	2.08	1.01	1.52	1.16	ns
Geophytes	0.14	0.17	0.19	0.20	0.08	0.12	ns
Annuals	0.02	0.07	0.05	0.09	0.00	0.00	ns
Resprouters	31.16	12.65	39.73	9.75	22.58	8.90	**
Legumes	6.55	4.95	9.30	5.48	3.80	2.22	**

Table V. Mean and standard deviation (SD) of cover data (%) for the main species 1 year after the Requena fire and in their two aspects. ns, Not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

Species	Total		North		South		P
	Mean	SD	Mean	SD	Mean	SD	
Resprouters:							
Quercus coccifera	14.64	7.35	17.60	6.50	11.69	7.28	ns
Brachypodium retusum	12.30	8.16	16.22	9.97	8.37	2.71	*
Rubia peregrina	2.54	3.06	4.44	3.28	0.63	0.98	**
Juniperus oxycedrus	0.82	0.94	0.90	0.85	0.74	1.07	ns
Brachypodium phoenicoides	0.59	1.37	1.18	1.79	0.00	0.00	*
Rhamnus alaternus	0.55	0.72	1.02	0.76	0.08	0.16	****
Daphne gnidium	0.48	0.80	0.75	1.05	0.22	0.33	ns
Erica multiflora	0.36	0.48	0.44	0.55	0.28	0.41	ns
Non-resprouters:							
Ulex parviflorus	5.63	4.83	7.54	6.04	3.72	2.20	ns
Helianthemum marifolium	3.99	3.91	3.77	5.16	4.20	2.40	ns
Cistus albidus	2.38	3.04	4.66	2.82	0.10	0.23	****
Ononis minutissima	0.70	1.00	1.40	1.01	0.00	0.00	****
Rosmarinus officinalis	0.68	1.02	0.22	0.29	1.15	1.27	*
Teucrium pseudochamaepitys	0.62	0.76	0.22	0.19	1.03	0.91	ns
Pinus halepensis	0.60	0.63	0.56	0.28	0.65	0.87	ns

the N and 24.4 % in the S) and legumes about 6.6 % (9.3 and 3.8 % respectively).

A total of 122 species were found in the Requena plots (*table VI*); 44 % of these were woody species. The number of species increased significantly when increasing the area sampled, from a mean of 6.7 species in 1-m^2 plots, to 48.8 species in 1 000-m^2 plot (*table VII*). There were more species on N-slopes than on S-slopes for all scales studied except for the total plot (1 000 m^2) where no difference was found between facing slopes. All species groups showed a significant increase in number of species with area (ANOVA, *table VIII*, *figure 2*), and most of them also showed a significant difference with aspect (ANOVA, *table VIII*). When area was taken into the analysis (as a covariant), aspect was significant for all groups. The better fit for the species-area curve is a log-log linear relationship (*figure 2*). However, when species are differentiated in woody species and herbs, the former showed a semi-log linear relationship while herbs follow a log-log linear relationship (*figure 3*, all with $R^2 > 0.97$).

Table VI. Total number of species, and number of resprouters and legumes for each life form on the Requena site 1 year after fire. Crosstab table results: Life form × Resprouters: $\chi^2 = 26.3$, $P < 0.001$; Life form × Legumes: $\chi^2 = 3.6$, $P < 0.5$.

Life forms	Total	Resprouters	Legumes
Woody species	54	25	5
Trees	2	1	0
Shrubs	18	14	2
Scrubs	34	10	3
Herbs	68	17	2
Perennial forbs	37	9	2
Perennial grasses	7	4	0
Geophyte	10	4	0
Annuals	14	0	0
Total	122	42	7

4. DISCUSSION

Comparison with long-term mean annual precipitation shows that in Requena during the year before the fire only 65 % of the mean precipitation fell, and during the post-fire year, 82 % of the mean precipitation fell (*table IX*). That is, the 1994 pre- and post-fire periods were dry. The number of days with mean temperatures greater than 30 °C was extremely high during the pre-fire period (30 % higher than the long-term mean), which may be the critical factor for the fire to spread, and consequently, for the extent of the fires of that year.

Table VII. Mean and standard deviation (SD) of the number of species at different scales and for the different facing slopes; n: number of samples; P: ANOVA P-values (ns, not significant; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$).

Scale (m^2)	Total			North		South		P
	Mean	SD	n	Mean	SD	Mean	SD	
1	6.72	2.62	96	7.81	2.55	5.63	2.23	****
10	17.63	5.41	48	20.96	4.99	14.29	3.43	****
100	26.39	5.56	36	29.89	4.80	22.89	3.82	****
200	32.50	6.57	18	37.11	5.62	27.89	3.52	***
1 000	48.83	11.20	6	56.00	11.36	41.67	5.51	ns
Overall	16.27	11.77	204	18.80	13.00	13.74	9.81	**

We have observed that the mean plant cover on south-facing slopes 10 months after the 1991 fire was around 56 %, and reached ca. 63 % 2 years later (*table I*). A large sampling on south-facing slopes of seven different 1994 fires showed cover values from ca. 17 up to ca. 40 % 10 months after the fire (unpublished). Results of the Requena fire (1994) showed a mean cover of ca. 32 (on south-facing slopes) and 52 % (north-facing slopes) a year after the fire. The maximum plant cover was observed under thermo-Mediterranean climate on limestone (ca. 76 %, *table I*), where the two main resprouting species were abundant (*Quercus coccifera* and *Brachypodium retusum, table III*). In general, these cover values are low compared with nearby garrigues which reached a mean value of 92 % 3 years after fire [13]. In this latter case, it was due to the high abundance of *Q. coccifera*, a strong resprouting species with rhizomes, and to the fact that during the sampling, outcrop patches were avoided. Ojeda et al. [27] also found higher cover values than ours: 36 and 85 % 5 months and 3 years after fire in a community dominated by *Q. lusitanica*, respectively. Lower values were found in Portuguese garrigues (30–35 and 45–50 % 1 and 2 years after fire [8]). Our results showed large spatial variation in plant recovery in different localities with the same aspect (*table I*) and in different aspects in the same locality (*table IV*). Different years, with different climatic conditions, also show different recovery rates. A year after fire, the average cover after the 1991 fire on

Table VIII. ANOVA and ANCOVA of the number of species in the different groups in relation to the plot, the aspect and the area. ns, Not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

Species groups	Plot	ANOVA		ANCOVA
		Aspect	Area	Aspect (Area)
Total	ns	**	****	****
Woody species				
Shrubs	**	**	****	****
Trees	*	ns	****	****
Scrubs	ns	ns	****	****
Herbs				
Perennial grasses	ns	****	****	****
Perennial forbs	ns	****	****	****
Geophyte	**	**	****	****
Annuals	**	ns	****	****
Resprouters	ns	****	****	****
Legumes	ns	**	****	***

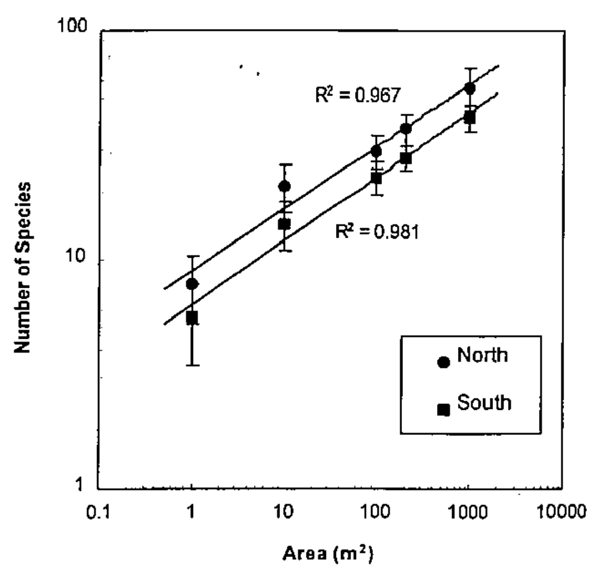

Figure 2. Species-area relationship for north and south slopes. Vertical lines are standard deviations.

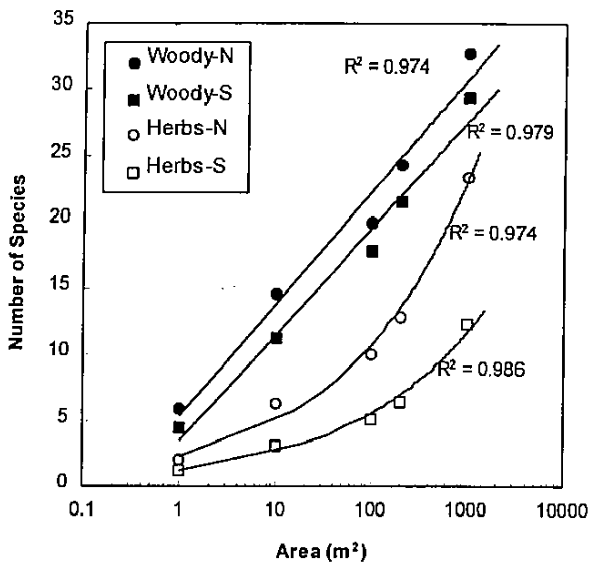

Figure 3. Species-area relationship for woody species and for herbs on north- and south-facing slopes. For making the different patterns clear, the graph is displayed in a semi-log space.

Table IX. Climatic data from the Requena Meteorological Station. Long-term mean values (1961–1990 [33]) and values for the year before and after the Requena fire (from meteorological records).

	Mean 1961–1990	Sept/93–Aug/94	Sept/94–Aug/95
Precipitation (mm)	452.1	297.6	370.2
Temperature (°C)	14.20	13.86	14.65
No. days with T > 30	55	71	51

south slopes was ca. 56 % (*table I*), and after the Requena fire in 1994, post-fire cover on south slopes was 32 % (*tables I, IV*). This could be related to the climatic conditions of the post-fire year (1994 was a dry year compared to the long-term mean, *table IX*). Unfortunately, climatic data for Requena during 1992 were incomplete and unreliable, but data from surrounding meteorological stations (in fact, most meteorological stations in the Valencia region) confirm that 1992 was a moister year than 1994/95, especially in spring. If we consider between 30–60 % of plant cover as a reference threshold for effective soil protection [43, 44], south slopes in the study area may have had some proneness to erosion during the first post-fire year in dry years.

In our monitoring of plant cover after the 1991 fires (*tables I, III*), we have observed that species with different strategies show different patterns: sprouting species reach relatively high cover values very soon after fire (< 10 months) and they do not increase significantly in the following months (*table III*). The percent cover of *B. retusum* was stabilised 1 year after fire in other localities of the same region (Caturla, Raventós and Guardia, unpubl. results and [50]). However, the increase in cover of *Ulex parviflorus* (an obligate seeder) is slower, and we observed a highly significant increase in the second sampling. *U. parviflorus* is the only species that registered a clearly significant increase in the second sampling; other species showed some slight increases but they had low abundance (e.g., *Stipa parviflora, Cistus clusii, Helianthemum marifolium*). *Q. coccifera* and *B. retusum* displayed a clear preference for limestone, while *S. parviflora* seems to prefer marls (*table III*). *S. parviflora* showed a preference towards the driest climate (TM). The preference for limestone shown by *Q. coccifera* may be explained by the fact that limestone has cracks that allow better foraging by the root system. Rambal observed water uptake by this species at 470 cm of soil depth in a limestone bedrock with a very shallow soil mantle [37]. However, the previous land use needs to be considered for interpreting these results [30]. Most areas with marls were cultivated long ago and later abandoned. Before cultivation, *Quercus* species were removed (including the roots), and the rate of colonisation of these species in dry areas is very low. So, the observed preference of *Q. coccifera* for limestone may be influenced not only by ecological preferences but also by historical land uses [30].

Raunkiaer's life forms were defined mainly in terms of the position and degree of protection of their perennial buds [38]. This system provides a mean of classifying floras in response to morphological adaptations that enable the plant to survive unfavourable climatic conditions. It has been postulated that this system may also be used to provide a measure of predicting the survival of plants under fire [7]. Although our results support the hypothesis of some correlation between life form and capacity to resprout (*table VI*), more accurate fire-specific classifications need to be developed, perhaps as subcategories of life forms [20, 24] and based on regenerative strategies after fire [26, 30].

Plant species richness is higher in the area with thermo-Mediterranean climate and limestone bedrock (*table II*) and on north-facing sites (*table VII*). Our plots are richer in species (6.7 and 26.4 species·100 m^{-2}) than the nearby garrigues (18 species·100 m^{-2} 3 years after fire [11]) but poorer than the garrigues in the NE Iberian Peninsula (12–20 species·m^{-2} 3 years after fire [28]). Species richness in our results are also lower than in the fynbos communities at all scales [41]. Several works in different ecosystems have shown that species richness is related to aspect [19, 29, 31] or directly to available energy [9]. Our results corroborate this observation, but they also suggest that the difference in species richness is scale-dependent; at the large scale, no differences were found (*table VII*). Schwilk et al. [41] have also demonstrated that species richness response to fire frequency in fynbos vegetation is scale-dependent.

In our systems, few annual species and few legume species occur after fire, and none of the annuals were legumes (*table VI*), unlike in other Mediterranean ecosystems (such as Greece [3]). It has been postulated that post-fire vegetation may be rich in nitrogen fixing species (such as legumes) because of their high competitive ability in environments where part of the nutrients has been lost by fire. Our results do not seem to support this hypothesis and the proportion of legume species after fire (5.7 %) was lower than the proportion of legumes of the whole flora of the study area (8.4 %). However, there is a species of this family, the shrub *U. parviflorus*, which is abundant after fire, especially when resprouter species are absent (old fields). Germination of this species is strongly stimulated by fire [4] (for related species see also e.g. [3, 15]) and in a few years, it can dominate most of the plots (especially when resprouters are not abundant). However, no evidence of changes in soil nutrient availability has been shown under the dominance of this species in a nearby site [16].

We have found few annual species and those in very low abundance; the mean number of annual species after the Requena fire was 0.10 in 10 m^2 and 1.17 in 1 000 m^2. None of the annual species recorded at the study sites is apparently restricted to or strongly favoured by burnt areas and, thus, cannot be equated to the 'fire-annuals' group described in the Californian chaparral [17]; only opportunistic annuals were found. Studies in other Mediterranean systems found more annual species [13, 17, 18, 25, 27, 42]. In southern California, annuals may cover most of the soil surface, especially in hot well-drained inland sites [18]. In the eastern Mediterranean basin, it seems that after fire, annual species are more abundant in siliceous bedrock types [10, 13, 27, 34] than in calcareous types (this study among others [28, 47]). For example, our analysis of the data after two recurrent fires in Cap de Creus [13], a coastal siliceous area in the north-eastern

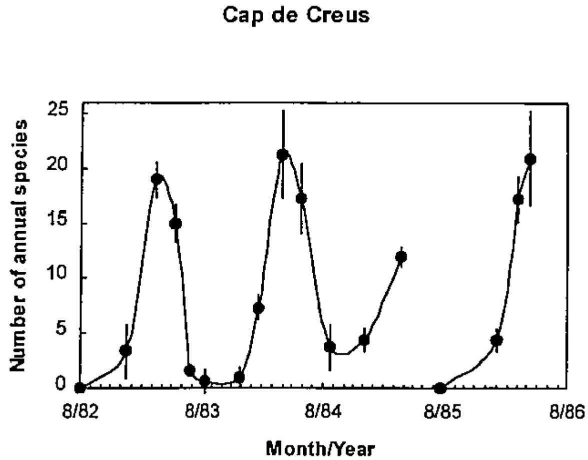

Figure 4. Mean (and SD) number of annual species in 25-m^2 plots in a siliceous area (Cap de Creus, Catalonia, north-eastern Iberian Peninsula) after two recurrent fires (8/1982 and 8/1985). Elaborated from data in Franquesa [13].

Iberian Peninsula, showed up to 25 annual species in 25 m^2, and the richness follows the typical annual cycle with summer depressions (*figure 4*). This annual species richness is much higher than the annual richness recorded in any calcareous area in the eastern Mediterranean basin. However, the reason for the differential annual species richness in different soil types is still poorly understood.

Species-area curves for total species in the Requena sites follow the classic power function (linear log-log relationship) for nested plots [36, 40], suggesting that local assemblages are proportional to large-scale richness. Keeley [18] indicated that while their data on California diversity also showed a log-log relationship, the data from other Mediterranean ecosystems (South Africa, SW Australia heath and Mediterranean basin [42]) tend to show a semi-log relationship. However, when different species types were considered in our study sites, different patterns were elucidated: woody species followed better a semi-log relationship, while herbaceous species fitted well a log-log relationship. That is, herbaceous species have a higher rate of species addition at the large scale than woody species. This different pattern may be due to the different spatial scales in which each life form operates. This result suggests that the pattern of diversity of different life forms is scale-dependent. Harte and Kinzig [14] have recently suggested that there might be different patterns in species-area curves for different types of species in the context of rare vs. abundant species. The study of the species-area relationship for total species may offer information on the average distribution of species, but different types of species may have different spatial distribution. Our results also emphasise that patterns of diversity in plant communities are clarified if total species are divided into growth-forms or functional types.

Acknowledgments

The sampling design of post-fire vegetation after the 1994 fire was based on the REGINFO project co-ordinated by J.M. Moreno. We thank A. Ferran and W. Delitti for their comments on the manuscript. Contributors to the sampling were (in alphabetic order): N. Abad, F. Bellido, R. Guàrdia, F. Marin and L. Orts. This work has been financed by the regional government of Valencia ('Generalitat Valenciana') and the Spanish government ('Ministerio de Educación y Ciencia' special action REGINFO, num. AMB95-1236-E SGPN I+D and a post-doctorate contract to the first author).

REFERENCES

[1] Anonymous, Los incendios forestales en España durante 1994, ICONA, Madrid, 1995.

[2] Arianoutsou M., Post-fire successional recovery of a phyganic (East-Mediterranean) ecosystem, Acta Oecol. Oecol. Plant. 5 (1984) 387–394.

[3] Arianoutsou M., Thanos C.A., Legumes in the fire-prone Mediterranean regions: an example from Greece, Int. J. Wildland Fire 6 (1996) 77–82.

[4] Ballini C., Écophysiologie de la germination des graines d'*Ulex parviflorus* Pourr, Bull. Ecol. 23 (1992) 119–130.

[5] Ballini C., Bonin G., Nutrient cycling in some *Ulex parviflorus* Pourr scrubs in Provence (southeastern France). 2. Nutrient release from decomposing litter, Eur. J. Soil Biol. 31 (1995) 143–151.

[6] Bolòs O., Vigo J., Masalles R.M., Ninot J.M., Flora Manual dels Països Catalans, Pòrtic, Barcelona, 1990.

[7] Chapman R.R., Crow G.E., Application of Raunkiaer's life form system to plant species survival after fire, Bull. Torrey Bot. Club 108 (1981) 472–478.

[8] Clements A.S., Rego F.C., Correira O.A., Demographic patterns and productivity of post-fire regeneration in Portuguese Mediterranean maquis, Int. J. Wildland Fire 6 (1996) 5–12.

[9] Currie D.J., Energy and large-scale patterns of animal- and plant-species richness, Am. Nat. 137 (1991) 27–49.

[10] Faraco A.M., Fernández F., Moreno J.M., Post-fire vegetation dynamics of pine woodlands and shrublands in the Sierra de Gredos, Spain, in: Trabaud L., Prodon R. (Eds.), Fire in Mediterranean Ecosystems, Commission of the European Community, Brussels, 1993, pp. 101–112.

[11] Ferran A., Delitti W., Vallejo V.R., Effects of different recurrences in *Quercus coccifera* communities of the Valencia region, in: Viegas D.X. (Ed.), Forest Fire Research, Proceedings of the III International Conference on Forest Fire Research, and 14th Conference on Fire and Forest Meteorology, Luso, Coimbra, November 16-20 1998, ADAI, Coimbra, Portugal, 1998, pp. 1555–1569.

[12] Folch R., La vegetació dels Països Catalans, 2nd ed., Ketres, Barcelona, 1986, 541 p.

[13] Franquesa T., El paisatge vegetal de la península del Cap de Creus, Institut d'Estudis Catalans, Barcelona, 1995.

[14] Harte J., Kinzig A.P., On the implications of species-area relationships for endemism, spatial turnover, and food web patterns, Oikos 80 (1997) 417–427.

[15] Herranz J.M., Ferrandis P., Martínez-Sánchez J.J., Influence of heat on seed germination of seven Mediterranean Leguminosae species, Plant Ecol. 136 (1998) 95–103.

[16] Huesca M., Cortina J., Bellot J., Soil fertility as affected by gorse (*Ulex parviflorus*), in: Viegas D.X. (Ed.), Forest Fire Research. Proceedings of the III International Conference on Forest Fire Research, and 14th Conference on Fire and Forest Meteorology, Luso, Coimbra, November 16-20 1998, ADAI, Coimbra, Portugal, 1998, pp. 1643–1652.

[17] Keeley J.E., Resilience of Mediterranean shrub communities to fire, in: Dell B., Hopkins A.J.M., Lamont B.B. (Eds.), Resilience in Mediterranean-type ecosystems, Dr W. Junk Publishers, Dordrecht, 1986, pp. 95–112.

[18] Keeley J.E., Postfire ecosystem recovery and management: the October 1993 large fire episode in California, in: Moreno J.M. (Ed.), Large Fires, Backhuys Publishers, Leiden, 1998, pp. 69–90.

[19] Kutiel P., Spatial and temporal heterogeneity of species diversity in a Mediterranean ecosystem following fire, Int. J. Wildland Fire 7 (1997) 307–315.

[20] Lavorel S., McIntyre S., Landsberg J.J., Forbes T.D.A., Plant functional classifications: from general groups to specific groups based on response to disturbance, Trends Ecol. Evol. 12 (1997) 474–478.

[21] Malanson G.P., Trabaud L., Vigour of post-fire resprouting by *Quercus coccifera* L., J. Ecol. 76 (1988) 351–365.

[22] Moreno J.M., Fernández F., Vallejo V.R., Carbó E., Bocio I., Valle F., Retama X., Busquets I., Regeneración de la vegetación en zonas quemadas por los grandes incendios de 1994, in: Moreno J.M. (Ed.), Estado de la investigación y el desarrollo en protección contra incendios forestales en España. I Seminario Nacional, 20–21 de Marzo de 1997, Ponencias, 1997, pp. 177–190.

[23] Moreno J.M., Vázquez A., Vélez R., Recent history of forest fires in Spain, in: Moreno J.M. (Ed.), Large Fires, Backhuys Publishers, Leiden, 1998, pp. 159–185.

[24] Naveh Z., The evolutionary significance of fire in the Mediterranean region, Vegetatio 29 (1975) 199–208.

[25] Ne'eman G., Lahav H., Izhaki I., Spatial pattern of seedlings 1 year after fire in a Mediterranean pine forest, Oecologia 91 (1992) 365–370.

[26] Noble I.R., Slatyer R.O., The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbance, Vegetatio 43 (1980) 5–21.

[27] Ojeda F., Marañon T., Arroyo J., Postfire regeneration of a Mediterranean heathland in southern Spain, Int. J. Wildland Fire 6 (1997) 191–198.

[28] Papió C., Respuesta al fuego de las principales especies de la vegetación de Garraf (Barcelona), Orsis 3 (1988) 87–103.

[29] Pausas J.G., Species richness patterns in the understorey of Pyrenean *Pinus sylvestris* forest, J. Veg. Sci. 5 (1994) 517–524.

[30] Pausas J.G., Mediterranean vegetation dynamics: modelling problems and functional types, Plant Ecol. 140 (1999) 27–39.

[31] Pausas J.G., Carreras J., The effect of bedrock type, temperature and moisture on species richness of Pyrenean Scots pine (*Pinus sylvestris* L.) forests, Vegetatio 116 (1995) 85–92.

[32] Pausas J.G., Vallejo V.R., The role of fire in European Mediterranean ecosystems, in: Chuvieco E. (Ed.), Remote Sensing of Large Wildfires in the European Mediterranean Basin, Springer-Verlag, 1999, pp. 3–16.

[33] Pérez-Cueva A.J., Atlas climàtic de la Comunidad Valenciana, 1961-1990, Generalitat Valenciana, Valencia, 1994.

[34] Peter A.M., Étude de l'impact du feu sur la végétation de l'étage méditerranéen des Albères (Pyrénées Orientales), Mém. Étud. École Natl. Ing. Travaux Agr., 1981, 65 p.

[35] Piñol J., Terradas J., Lloret F., Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain, Clim. Change 38 (1998) 345–357.

[36] Preston F.W., The canonical distribution of commonness and rarity: part I, Ecology 43 (1962) 185–215.

[37] Rambal S., Water balance and pattern of root water uptake by a *Quercus coccifera* L. evergreen scrub, Oecologia 62 (1984) 18–25.

[38] Raunkiaer C., The Life Forms of Plants, Clarendon Press, Oxford, 1934.

[39] Rivas-Martínez S., Mapas de series de vegetación de España, ICONA, Madrid, 1987.

[40] Rosenzweig M.L., Species Diversity in Space and Time, Cambridge University Press, 1995, 436 p.

[41] Schwilk D.W., Keeley J.E., Bond W.J., The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos, Plant Ecol. 132 (1997) 77–84.

[42] Specht R.L. (Ed.), Mediterranean-Type Ecosystems. A Data Source Book, Kluwer Academic Publishers, Dordrecht, 1988.

[43] Stocking M.A., Assessing vegetative cover and management effects, in: Lal R. (Ed.), Soil Erosion and Research Methods, Soil and Water Conservation Society, Ankeny, Iowa, 1988.

[44] Thornes J.B., The interaction of erosion and vegetation dynamics in land degradation: spatial outcomes, in: Thornes J.B. (Ed.), Vegetation and Erosion, Wiley, New York, 1990, pp. 41–54.

[45] Trabaud L., Fire and survival traits of plants, in: Trabaud L. (Ed.), The Role of Fire in Ecological Systems, SPB Academic Publishing, The Hague, 1987, pp. 65–89.

[46] Trabaud L., Fire regimes and phytomass growth dynamics in a *Quercus coccifera* garrigue, J. Veg. Sci. 2 (1991) 307–314.

[47] Trabaud L., Lepart J., Changes in the floristic composition of a *Quercus coccifera* L. garrigue in relation to different fire regimes, Vegetatio 46 (1981) 105–116.

[48] Trabaud L., Grossman J., Walters T., Recovery of burnt *Pinus halepensis* Mill. forests. I. Understorey and litter phytomass development after wildfire, For. Ecol. Manag. 12 (1985) 269–277.

[49] Tsitsoni T., Conditions determining natural regeneration after wildfires in the *Pinus halepensis* (Miller, 1768) forests of Kassandra Peninsula (North Greece), For. Ecol. Manag. 92 (1997) 199–208.

[50] Vallejo V.R. (Ed.), La restauración de la cubierta vegetal en la Comunidad Valenciana, Fundación CEAM, València, 1997.

[51] Vallejo V.R., Alloza J.A., The restoration of burned lands: the case of Eastern Spain, in: Moreno J.M. (Ed.), Large Forest Fires, Backhuys Publishers, Leiden, 1998, pp. 91–108.