Post-fire succession in two Quercus pyrenaica communities with different disturbance histories

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Abstract – *Quercus pyrenaica* is a widely distributed oak species in the Iberian Peninsula which has been subjected to drastic disturbances, such as fire, leading to a significant decrease in its cover. The main objective of this study was to carry out a comparative analysis of the post-fire regeneration of two *Quercus pyrenaica* ecosystems. Prior to being burned by a wildfire at the end of the summer in 1985, the first ecosystem presented a developed tree layer, whereas the second one was in a shrub layer stage. In each ecosystem a permanent plot was established and sampled for a period of 6 years after the disturbance. Colonisation rates of different biological types were estimated, as well as the structural parameters defining the community: species diversity, richness and evenness. These results allowed us to determine a post-fire successional model for these ecosystems. Post-fire species composition of the two sites was similar, but abundance of particular species varied as a function of pre-fire abundance. (© Inra/Elsevier, Paris.)

fire / shrub / forest / regeneration / secondary succession

Résumé – Succession végétale après incendie dans deux peuplements de *Quercus pyrenaica.* *Quercus pyrenaica* est une espèce largement répandue dans la Péninsule Ibérique. Cette espèce a été soumise à des perturbations, notamment par le feu, qui a conduit à un fort recul de sa couverture. Le principal objet de cette étude est de réaliser une analyse comparative de la régénération après le feu dans deux écosystèmes de *Quercus pyrenaica.* Dans l'un des écosystèmes, cette espèce présentait, avant d'être brûlée par un incendie naturel (à la fin de l'été 1985), un bon développement de la strate arbustive, tandis que dans l'autre elle était au stade de maquis. On a alors établi une parcelle permanente dans chaque écosystème, d'où on a prélevé des échantillons pendant une période de six ans après l'incendie. On a ainsi estimé le taux de colonisation des différents types biologiques ainsi que les paramètres structurels qui définissent la communauté : diversité, richesse et uniformité. Les résultats obtenus ont servi à définir pour les deux écosystèmes un modèle de succession végétale après le feu. Après l'incendie, la composition spécifique était similaire dans les deux zones mais l'abondance de chaque espèce varie en fonction de la situation d'origine de chaque zone. (© Inra/Elsevier, Paris.)

feu / maquis / forêt / régénération / succession secondaire

1. Introduction

Quercus pyrenaica is one of the most abundant and characteristic oak species in the Iberian Peninsula. In Spain, the main areas covered by this species are found in León province, where they used to represent 20 % of the total surface area [14]. Today, this large surface has significantly decreased because of human action, mainly forest fires. Frequent fires result in previous tree-covered areas being replaced by shrub communities [2, 3, 5, 6, 13, 17, 26, 28], which represent seral stages of the forest climax.

The seral shrublands dominated by *Erica australis* resulting from frequent wildfire of *Quercus pyrenaica*

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forest occupy large areas in León Province [1]. These communities are also frequently subjected to human action: being burnt in order to obtain pasture for the domestic herbivores and croplands. Therefore, both tree and shrub communities are altered by fire, which implies that a secondary succession is initiated.

Studies on the structural changes of these tree and shrub communities after fire are needed to complete our knowledge of secondary succession patterns. The main aim of this study was to analyse comparatively the post-fire regeneration response of these two types of communities, one representing the stage of tree layer and the second one the shrub stage of the same climax series of *Quercus pyrenaica.*

2. Materials and methods

Two permanent plots were established at random in an area in which the climax is *Quercus pyrenaica*. They were burnt at the end of the summer of 1985. The first plot was covered in its initial pre-fire state with a small oakwood of 4 m tall trees on average ('forest community'). The second plot was in an area covered by an *Erica australis* subsp. *aragonensis* heathland ('shrub community'). Both plots were situated in the north of León province (NW Spain), in an area with almost no slope and at an altitude of 1 150 m (Universal Transverse Mercator, UTM coodinates: 30TUN243292). According to Rivas [20] these communities are included in the Mediterranean region. According to the Papadakis classification (cited in [15]), all the area is included in the moderate cold Mediterranean climate.

Both plots were annually sampled at the beginning of the summer. In the shrub plot, five sampling units of 1 m^2 each were studied for 6 years. The forest plot offered greater spatial heterogeneity. Therefore, in order to take into account the greatest possible variability, a larger number of samples were taken: twenty-five units of 1 m^2 were also analysed for 6 years. The sampling units were randomly selected in the 1st year and marked for subsequent monitoring. The cover percentages of all the species present (herbaceous and woody species) were visually estimated, as well as the percentage of bare soil in each sampling unit. One year after the fire, vegetation regrowth was very low in the shrub community, and therefore no inventories were carried out until the second growing season. Sampling was carried out from the 1st year in the forest community. Plant nomenclature followed that of Tutin et al. [29].

The diversity index [21] and the evenness index [18] were determined from the mean values of the cover data for each community. The similarity between the inventories of the two plots was calculated using the index attributed to Steinhaus by Motyka et al. [16]. The results were clustered by the UPGMA (Un-Weighted Peer Groups Method Using Arithmetic Averages) method [22].

Bare soil and woody, perennial herbs and annual herbs cover values were compared by two-factor repeated measures analysis of variance (ANOVA) as well as species diversity, richness and evenness values.

3. Results and discussion

Mean bare soil percentages were very high the 1st year after the fire in the forest community (*figure 1*), but they decreased in the following years owing to vegetation recovery. The increase in woody species was very

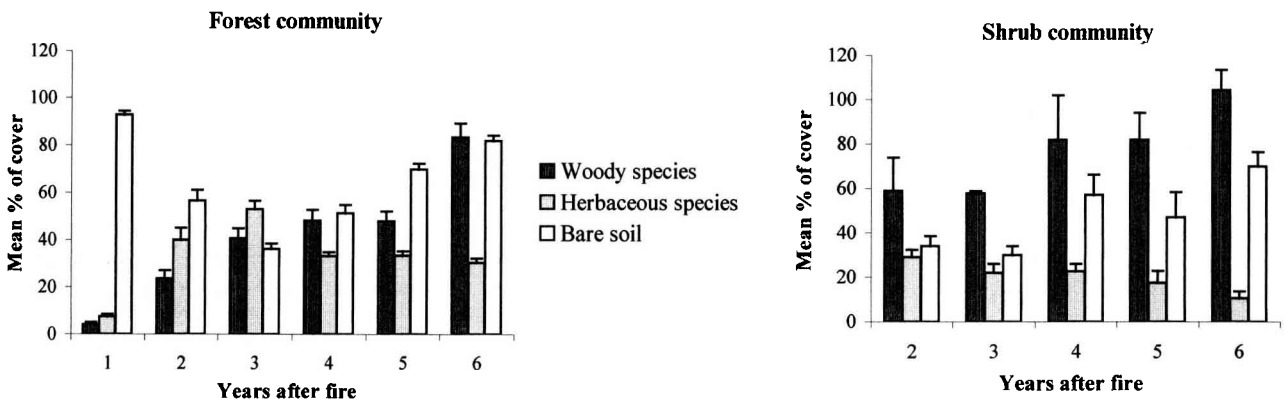

Figure 1. Mean cover percentages of woody species, herbaceous species and bare soil in the shrub and forest communities.

high in the shrub plot from the 2nd year onwards. Bare soil in the shrub plot was always lower than in the forest plot owing to the quick regeneration of woody species. Mean cover of herbaceous species was higher in the forest plot during the whole study period. The mean cover of herbaceous species was higher in both communities the 1st year after fire owing to the presence of gaps. Furthermore, since *Erica australis* showed allelopathic effects inhibiting the growth of herbaceous plants [4], when this species presented low cover values, this allelopathic effect could decrease. Both, pre-fire plant competition and allelopathy may have resulted in the reduction of the seed bank. The lowest bare soil values appeared, in both communities, in the 3rd year; afterwards, the cover of the herbaceous species decreased and the bare soil increased. The differences between both shrub and forest community, and among samplings were statistically significant (*table I*).

Immediately following fire, herbaceous species may find favourable conditions to establish: there is no competition for light with the woody species, and they have superficial roots which allow them to take advantage quickly of the nutrients brought into the soil by the ashes. All these factors may facilitate the initial colonisation of the ecosystem. At the same time, the main woody species in both areas began to resprout, *Erica australis* in the shrubland and *Quercus pyrenacia* in the forest. The cover and size of these species increased after the 3rd year, which had a negative influence on the herbaceous species. This effect was more noticeable in the shrubland than in the forest.

The woody species mean cover increased in both areas during the study period (*figure 2* and *table II*). *Quercus pyrenaica* was the dominant species in the forest community, whereas *Erica australis* and *Arctostaphylos uva-ursi* were codominant in the shrub community. The most abundant annual herbaceous species in both communities was *Aira caryophyllea.* Annual herbaceous species reached the maximum cover in the 2nd and 3rd years after the fire, covering more surface in the forest than in the shrub community. The fact that the annual herbaceous species did not reach maximum cover values in the 1st year, as was reported by other studies [6, 26], could be because of the high frequency of the disturbances. Frequent burning reduces the seeds present in the soil [10, 12, 31]. Fire induces germination by scarification [8, 19], but it also increases mortality in a large number of seeds [7, 30]. Therefore, high frequency fires may decrease the germplasm bank in the soil [25]. Maximum herbaceous cover values may appear in the 2nd year because enough time has passed for the seeds to come from nearby areas [3].

Table I. ANOVA tables for two-factor repeated measure analysis of variance with bare soil, woody, total herbaceous species, perennial herbaceous and annual herbaceous species cover values.

Bare soil Source	df	Sum of squares	*F*-test	*P*-value
Plot (A)	1	2 757.13	6.274	0.0183
Subjects w. groups	28	12 304.45		
Repeated measure (B)	4	33 767.91	36.039	0.0001
AB	4	2 391.90	2.553	0.0429
B × subjects w. groups	112	26 235.39		
Woody species cover Source	df	Sum of squares	*F*-test	*P*-value
Plot (A)	1	16 511.15	9.290	0.0050
Subjects w. groups	28	49 762.59		
Repeated measure (B)	4	54 158.04	47.395	0.0001
AB	4	1 248.39	1.093	0.3638
B × subjects w. groups	112	31 995.17		
Herbaceous (annual + perennial) species cover Source	df	Sum of squares	*F*-test	*P*-value
Plot (A)	1	6 418.18	14.788	0.0006
Subjects w. groups	28	12 151.95		
Repeated measure (B)	4	7 974.67	11.864	0.0001
AB	4	1 150.41	1.712	0.1524
B × subjects w. groups	112	18 820.13		
Perennial herbaceous species cover Source	df	Sum of squares	*F*-test	*P*-value
Plot (A)	1	1 916.80	5.754	0.0234
Subjects w. groups	28	9 328.27		
Repeated measure (B)	4	751.31	5.363	0.0005
AB	4	297.05	2.120	0.0829
B × subjects w. groups	112	3 922.45		
Annual herbaceous species cover Source	df	Sum of squares:	*F*-test	*P*-value
Plot (A)	1	1 320.03	4.269	0.0482
Subjects w. groups	28	8 657.04		
Repeated measure (B)	4	7 609.37	14.748	0.0001
AB	4	718.31	1.392	0.2412
B × subjects w. groups	112	14 446.72		

Factor 1 sites (forest community and shrub community); factor 2 (repeated measure); year of sampling (2, 3, 4, 5 and 6 years after fire).

The cover percentages of perennial herbaceous species in the forest community were greatest in the 1st years because the bulbs and underground stems of these species were not affected by the fire and they were able to take advantage of the nutrients incorporated in the soil [9]. The most abundant perennial herbaceous species in the forest were *Luzula lactea, Festuca rubra* and

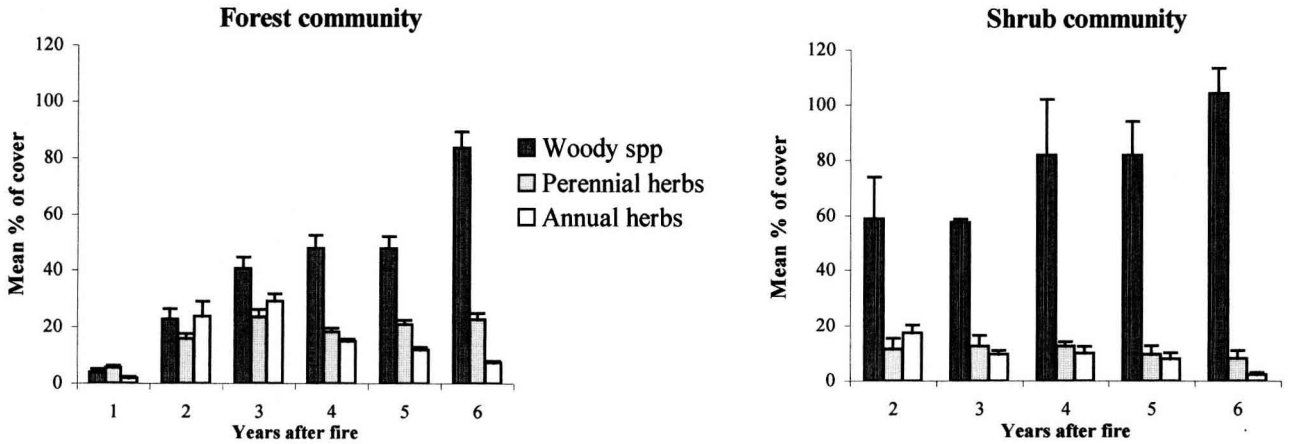

Figure 2. Mean cover percentages of woody species and annual and perennial herbaceous species in the shrub and forest communities.

Avenula marginata, whereas in the shrubland they were *Avenula marginata,* and *Tuberaria globularifolia.*

In general, the herbaceous species, which had a high cover during the first stages, were substituted after the 3rd year by the woody species owing to the competition for light and the allelopathic effects in the case of shrubland.

In the forest community, the cover percentages for the perennial herbaceous species were higher than in the shrub community; in the shurbland the cover values for the woody species were the highest.

Regarding structural parameters, the highest richness values (*table III*) appeared in both areas around the 4th year; at the same time there was a high number of herbaceous and woody species. From this moment on, the cover woody species began to dominate, which caused a decrease in the herbaceous species. This switch was reflected in a decrease in diversity values, mainly in the shrubland. The richness values were always higher in the forest than in the shrubland, where a very noticeable decrease in the herbaceous species was observed in the 6th year.

The highest values of evenness were recorded for both areas in the 1st year of the study, the species showing very similar abundance distribution. Diversity was maximum in the shrubland during the 2nd year owing to the fact that after the 3rd year *Erica australis* began to dominate. However, in the forest the maximum value of diversity was not reached until the 5th year, when the herbaceous species richness started to decrease.

The ANOVA detected statistically significant differences between the shrub and forest plots and for each plot in different samplings (*table IV*).

The similarity analysis (*figure 3*) showed two clusters, one for the samples from the shrubland and the other for the samples from the forest. This aspect indicates the importance of the initial floristic composition in the regeneration process [1–3, 23, 24, 27]. The cluster corresponding to the shrubland was characterised by high cover values of *Erica australis,* and the presence of *Erica umbellata,* which was not found in the forest. Among the species that were more abundant in the forest community, *Quercus pyrenaica* and some herbaceous species such as *Agrostis capillaris*, *Festuca rubra, Luzula lactea,* etc., stand out in the cover.

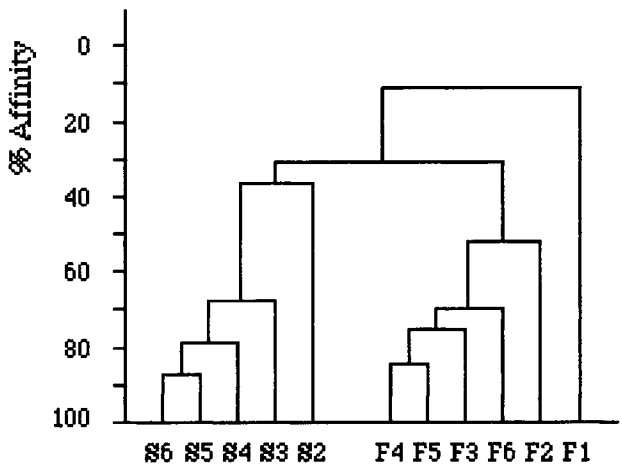

Figure 3. Similarity analysis. S: shrub community; F: forest community; 1, 2, 3, 4, 5, 6: years after fire.

Table II. Mean cover values (and standard deviation) of the most important annual, perennial and woody plant species present in the shrub and in the forest communities.

	Years after fire					
	1	2	3	4	5	6
Annual herbaceous						
Shrub community						
Aira caryophyllea		13.0 (4.47)	5.2 (2.9)	6.0 (5.2)	2.2 (1.8)	1.0 (0.7)
Airopsis tenella		0.4 (0.5)	0.6 (0.5)	0.2 (0.4)	0.4 (0.5)	0.2 (0.4)
Logfia minima		0.2 (0.4)	0.8 (0.4)	1.0 (0.0)	0.4 (0.5)	
Tuberaria guttata		1.2 (1.7)	1.0 (0.7)	0.8 (0.4)	1.0 (0.7)	0.2 (0.4)
Forest community						
Aira caryophyllea	1.1 (1.6)	17.0 (23.7)	16.6 (11.3)	6.7 (4.2)	4.1 (2.7)	1.6 (1.2)
Andriala integrifolia			1.1 (0.8)	1.2 (0.7)	2.1 (1.3)	1.8 (1.6)
Arnoseris minima	0.4 (0.5)	1.6 (2.2)	2.0 (1.5)	0.8 (0.5)	1.0 (0.6)	0.6 (0.5)
Logfia minima	0.1 (0.3)	0.4 (0.5)	2.1 (2.1)	0.7 (0.5)	1.3 (0.8)	0.9 (0.4)
Perennial herbaceous						
Shrub community						
Avenula marginata		4.0 (8.9)	2.2 (4.4)	2.2 (1.8)	1.8 (3.5)	2.0 (4.5)
Hipochoeris radicata		2.8 (3.6)	2.8 (4.2)	1.8 (1.9)	2.0 (1.7)	0.8 (0.4)
Lolium perenne		1.8 (2.1)	1.6 (1.9)	1.0 (0.7)	0.2 (0.4)	0.2 (0.4)
Tuberaria globularifolia		2.4 (2.3)	2.4 (1.8)	4.4 (3.4)	2.8 (4.2)	2.2 (3.3)
Forest community						
Agrostis capillaris		0.3 (0.9)	4.3 (5.2)	3 (3.2)	3.9 (4.1)	3.6 (5.6)
Avenula marginata	0.3 (1)	0.7 (1.6)	2.4 (5.1)	3.4 (4.0)	2.3 (4.3)	3.2 (4.6)
Festuca rubra	1.6 (3.4)		3.4 (7.1)	3.8 (4.7)	3.2 (7.2)	4.1 (7.0)
Luzula lactea	1.3 (2.2)	4.3 (7.4)	4.9 (9.6)	0.1 (0.2)	3.6 (6.6)	2.8 (4.8)
Woody species						
Shrub community						
Arctostaphylos uva-ursi		27 (25.1)	21.0 (21.9)	25 (32.8)	23.2 (34.9)	43 (41.8)
Erica australis		25.4 (19.3)	30.0 (18.7)	34.0 (8.9)	44 (32.1)	43.0 (23.3)
Halimium alyssoides		2.8 (4.2)	2 (2.1)	2.2 (2.6)	3.4 (3.1)	3.6 (4.2)
Halimium umbellatum		0.6 (0.9)	0.4 (0.9)	2.0 (4.5)	2.4 (2.4)	0.6 (1.3)
Quercus pyrenaica		3.0 (6.7)	4.0 (6.2)	11.0 (13.4)	4 (6.2)	6.0 (10.8)
Forest community						
Erica australis	0.2 (0.5)	2.8 (4.6)	5.8 (7.8)	9.5 (8.8)	10.0 (11.7)	19.8 (21.7)
Genistella tridentata	0.1 (0.4)	0.6 (1.1)	1.2 (3.1)	2.5 (5.4)	3.2 (4.4)	6.1 (10.9)
Halimium alyssoides	0.1 (0.3)	1.0 (1.6)	4.0 (6.8)	5.2 (6.8)	7.2 (9.9)	10.2 (14.2)
Quercus pyrenaica	3.6 (5.6)	19.0 (17.1)	29.2 (21.6)	27.4 (22.7)	25.0 (21.6)	42.6 (30.8)

Of all the samples, the one that differed the most was the first sample from the forest community, which was taken 1 year after the fire. It differs from the rest, not because of the presence of different species but rather for its lower vegetation cover. In each cluster, the greatest similarity among the samples can be seen after the 3rd year, with affinity values over 65 %, which shows that after that stage there were increasingly fewer changes in the plant community.

From these results it is possible to describe a post-fire recovery model that could explain the changes produced in both communities. The general succession model in these ecosystems is described as autosuccession [1, 11].

Each community has a particular species composition, which allows some distinctions between the two of them. It is important to stress that it is the abundance values for the species which vary, rather than the species themselves, as they are seral communities of the same climax. Both communities showed a similar post-fire variation pattern, in relation to biological types and bare soil percentages. This pattern results in certain structural parameters evolving in a similar way. Diversity has its maxi-

Table III. Species richness, evenness and diversity values in the shrub and forest communities.

	Years after the fire					
	1	2	3	4	5	6
Richness						
Shrub community						
Annual spp.		9	8	11	9	7
Perennial spp.		5	10	8	8	8
Woody spp.		5	6	8	8	8
Total spp.		22	24	27	25	23
Forest community						
Annual spp.	8	13	12	18	18	15
Perennial spp.	11	16	16	17	18	16
Woody spp.	4	5	5	7	6	7
Total spp.	23	34	33	42	42	38
Evenness						
Shrub community		0.71	0.68	0.61	0.62	0.57
Forest community	0.74	0.64	0.73	0.70	0.72	0.64
Diversity						
Shrub community		3.18	2.84	2.77	2.46	2.25
Forest community	3.36	3.25	2.68	3.78	3.86	3.40

Table IV. ANOVA tables for two-factor repeated measures analysis of variance with species diversity, richness and evenness values.

Species diversity (H') Source	df	Sum of squares	*F*-test	*P*-value
Plot (A)	1	4.39	6.912	0.0137
Subjects w. groups	28	17.77		
Repeated measure (B)	4	11.61	21.572	0.0001
AB	4	1.67	3.112	0.0181
B × subjects w. groups	112	15.07		
Species richness Source	df	Sum of squares	*F*-test	*P*-value
Plot (A)	1	208.03	9.036	0.0055
Subjects w. groups	28	644.64		
Repeated measure (B)	4	984.64	40.246	0.0001
AB	4	67.52	2.760	0.0312
B × subjects w. groups	112	685.04		
Evenness Source	df	Sum of squares	*F*-test	*P*-value
Plot (A)	1	0.11	4.861	0.0359
Subjects w. groups	28	0.62		
Repeated measure (B)	4	0.20	6.543	0.0001
AB	4	0.06	1.833	0.1274
B × subjects w. groups	112	0.84		

Factor 1 sites (forest community and shrub community); Factor 2 (repeated measure); year of sampling (2, 3, 4, 5 and 6 years after fire).

mum values in a different period in both communities, because of the effect of dominance of woody species, which is much more noticeable earlier on in the shrubland than in the forest.

The following phases may be described.

1. The 1st year after the fire was characterised by a high percentage of bare soil which is greater in the shrubland than in the forest, with the appearance of some herbaceous species and the vegetative resprout of two woody species, *Erica australis* and *Quercus pyrenaica,* respectively.

2. In the 2nd year, annual herbaceous species showed the highest cover. Woody species had a very low regeneration. The bare soil percentages decreased.

3. In the 3rd year, high cover values for the annual and perennial herbaceous species appeared, being greater in the forest community than in the shrub community. The woody species showed a higher increase in their cover values. The bare soil values were the lowest.

4. After the 4th year, the woody species began to dominate in both areas, replacing the herbaceous species. The bare soil values began to increase.

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