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Chapter 2

DIFFERENCES IN THE RESPONSE TO FIRE OF MEDITERRANEAN SHRUBLAND

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ABSTRACT

The response of shrubland species to burning was studied over fifteen years in a shrubland community dominated by Erica australis in NW Spain. Throughout history, fire has been the perturbation most frequently imposed by man on these shrub communities. Post-fire recovery in these areas occurs via an autosuccession process because the species appearing after the disturbance are the same as the one that occupied the area previously. The woody species that appear immediately after burning are sprouting species, namely Erica australis and Arctostaphylos uva-ursi. In general, the dominant species, Erica australis, influences the regeneration patterns of all other species which make up the community. There is a significant increase in the cover of woody species until the fourth year after burning. Highest values for annuals and perennials herbaceous were observed in the third and fourth years. Subsequently, Erica australis attains dominance, regaining its original spatial occupancy and cover values, reducing herbaceous species and negatively affecting the growth of woody taxa like Halimium umbellatum and Halimium alyssoides. The quantity of herbaceous species present is in inverse proportion to the quantity of woody taxa. Richness and diversity values attain a maximum between the fourth and fifth years post-fire, coinciding with the greater presence of herbaceous species. Subsequently, woody species are strongly dominant and this produces a reduction in both parameters. Erica australis, Chamaespartium tridentatum and Arctostaphylos uva-ursi regenerate by sprouting. Halimium alyssoides, Halimium umbellatum, Erica umbellata and Calluna vulgaris regenerate by germination. Differences in cover values during the first years of succession tend to be eliminated twelve-fifteen years after burning and most of the species tend to recover their initial cover values. These shrubland communities have a high degree of resilience due to the strong sprouting potential of the component species.

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INTRODUCTION

The present state of vegetation depends partly on human factors which have influenced the plant communities in the past, and which still continue to do so (Godron et al. 1981). The Mediterranean ecosystems of Europe have been subject to a long history of human use (Grove 1996, Margaris et al. 1996). For hundreds and even thousands of years they have been affected by intense anthropogenic perturbations. Among the most important forms of disturbance are forest fires (Trabaud 1980, 1991; Casal 1985, 1987; de Luis et al. 1989a,b; Clement and Touffet 1990; Calvo 1993; Le Houerou 1993; Calvo et al. 1998a,b; 2002 a,b; Naveh 1999). These long-term disturbances have led to the extensive destruction of tree-dominated vegetation formations in large areas of the Mediterranean basin (Naveh and Dann 1974; Barbero et al. 1990) and transformed it into shrubland, creating a mosaic of ecosystems indicative of degradation (Di Castri 1981). In the NW of the Iberian Peninsula (León province) these types of shrubland communities cover 33% of the total area, according to the Ministry of Agriculture (Ministerio de Agricultura 1984). *Erica australis* is the most characteristic shrub in these shrubland communities (de Luis et al. 1989a).

These shrubland communities have been considered marginal lands from the viewpoint of territorial development as they have low productivity. They have also been affected by human activity since ancient times. One of the most frequent forms of disturbance is the use of fire to create open areas for grazing. These shrublands are characterized by rapid post-fire recovery of vegetation (Keeley 1986; Westman and O'Leary 1986; Clemente et al. 1996). After burning, the community begins a secondary succession process, which has been identified as autosuccession in these formations (Calvo et al. 1998b; 2002b).

The study area has been affected by burning due to the fact that it was traditionally used as a grazing area for sheep. Shepherds frequently burnt the shrub during the spring in order to obtain pasture of a high nutritional quality, palatability and protein content. After burning, most of the woody species that make up this type of community are capable of regenerating either by vegetative resprouting from below ground vegetative buds (Keeley 1986,1992; Trabaud 1987; Ojeda et al. 1996; Lloret and Vilá 1997) or from seed (Keeley and Zedler 1978; Valbuena et al. 2000, 2001). However, germination from the seed bank is slower than vegetative resprouting (González- Rabanal 1992, Calvo el al. 1998 b). Life form and other life history features interact with regeneration strategies and with physical and chemical components of the environment, creating a complex framework within which regeneration takes place (Clemente et al. 1996).

The aim of this study is to analyze the development of the woody species and changes in vegetation over a period of 15 years after burning in shrubland communities dominated by *Erica australis*. Variations in plant community structure and composition were recorded throughout the regeneration process. We determine the type of regeneration mechanism in the different woody species. We also try to answer the following question: what length of time is needed by these species to attain a similar state to the original conditions as regards cover values?

MATERIALS AND METHODS

A study area was selected close to the highlands of the Province of Leon. This area is situated on level ground at UTM co-ordinates 30TUN2429, with an approximate altitude of 1050 m. The heathland community present in this area is classified as a variant of the *Genistelo tridentatae-Ericetum aragonensis-Cytisetosum laurifolii* community in which *Erica australis* L. subsp. *aragonensis* (Willk) P. Cout is the dominant species (Rívas Martínez et al. 1987). Apart from this species, other woody taxa were also well represented: *Arctostaphylos uva-ursi* (L.) Sprengel, *Erica umbellata* L., *Calluna vulgaris* (L.), Hull; *Chamaespartium tridentatum* (L.) P. Gibbs, *Halimium alyssoides* (Lam) C. Koch, *Halimium umbellatum* (L.) Spach and shrubby *Quercus pyrenaica* Willd. *Quercus pyrenaica* is the characteristic species of climax communities in these areas. Plant nomenclature follows Tutin et al. 1964-1980.

Mean annual precipitation for this area is 839.8 mm; mean annual temperature is 10.9 ºC; mean minimum in the coldest month is –1.1ºC and mean maximum in the warmest month is 26.9 ºC (Ministerio de Agricultura 1980). A period of summer drought occurs between July and August, and consequently the climate is classed as Mediterranean. The soil is classified as a humic cambisol (Junta de Castilla y León 1987). According to granulometric analysis, the soils of this area are very sandy and acidic (pH=5.5) (Calvo et al. 1998a).

In an area with homogeneous shrub cover, a plot of 10 m x 10 m was burned in July 1985. No aboveground biomass survived the burning. Before burning took place, a vegetation inventory was carried out in 100 units of $1m^2$, covering the whole plot surface. The percentage cover of each woody species was estimated visually in each sampling unit, whereas herbaceous species were considered as a whole because they represented a very low percentage of the total cover. After burning, in order to analyze the recuperation of woody species, 100 sampling units of 1 m^2 were studied at 1, 2, 3, 4, 5, 7, 9, 12, and 15 years. Percentage cover in vertical projection for each woody species was evaluated in each sampling unit. In order to analyze the dynamics of herbaceous species, 5 sampling units measuring $1m^2$ each were studied in the same dataset. These units were chosen at random for the first sampling and marked for later visits. Percentage cover in vertical projection for each herbaceous species was evaluated in each sampling unit. This sampling was carried out from the second year because, during the first year, herbaceous species represented < 1% of the total cover. Cover values were evaluated in the same way as before the treatment. The same people quantified percentage cover throughout the study period.

We compared the changes in the percentage cover of each species through time using a one-way (time, repeated measure) analysis of variance (ANOVA). To normalise errors percentage cover was arc sin transformed (Sokal and Rohlf 1979). The significance of the results was tested using the Scheffe test (Scheffe 1959).

Floristic diversity was calculated using species richness, evenness (J': Pielou 1969) and diversity (H': Shannon and Weaver 1949) from the second year after burning.

RESULTS

Changes in Woody Species Cover

The dominant species in the León Province heathlands, *Erica australis*, showed a very good regeneration response (Fig. 1), exceeding the original cover values from the seventh year after burning. Rapid regeneration by vegetative resprouting occurs during the first year after burning. The increase in cover values is pronounced until the fourth-fifth year. However, there are few subsequent changes, with no significant differences ($P<0.05$) in cover values. *Arctostaphylos uva-ursi* was another Ericaceae species of great importance in the original state (Fig. 1). The high water content of this species allows it to resist burning easily (Luis et al. 1989b). This (aspect), together with the ability to sprout from subterranean organs, allows very rapid recovery. Thus, one year after burning, it attains very significant cover values. By the 12th year, values are not significantly different ($P<0.05$) from the original state.

Quercus pyrenaica is considered to be the dominant species in the climax arboreal communities of this area. Recovery is relatively fast because *Q. pyrenaica*'s capacity to resprout increased its cover values from the fourth year. Significant increases in cover ($P<0.05$) occur in the 15th year after burning relative to the original situation. Another resprouting species in these communities is *Chamaespartium tridentatum* , which had very low cover (< 1%) values in the original state (Fig. 1). It recovers very slowly until the 9th year; from this period it exhibits a significant increase relative to original situation.

Two of the typical germinating species, *Calluna vulgaris* and *Erica umbellata*, (Fig. 1) are negatively affected by burning during the first years. These species begin to increase their cover values from the fourth year. However, original cover levels are only reached after fifteen years, without significant differences from the original situation.

Among the Cistaceae, *Halimium alyssoides* was the most important in the original state, and its recovery is favoured during the first few years of succession after burning (Fig. 1). This species uses germination as a regeneration mechanism and this starts during the first year. Cover values increase significantly during the first four years. Subsequently, coinciding with the quantitative increase and the wide spatial occupancy of *Erica australis*, growth is no longer significant. A comparison of the cover values attained by *H. alyssoides* after burning with those in the original state indicates that cover is significantly favoured by disturbance ($P<0.05$). The other Cistaceae species, *Halimium umbellatum*, had low abundance in the original state (0.2% cover) (Fig. 1). This species uses germination as a regeneration mechanism. Burning appears to have eliminated competition from species of greater size and this is reflected by higher cover values compared with the original state. This favourable effect can be seen until the seventh year, when species of greater size and cover begin to dominate, providing strong competition, and resulting in a decrease in *H. umbellatum*.

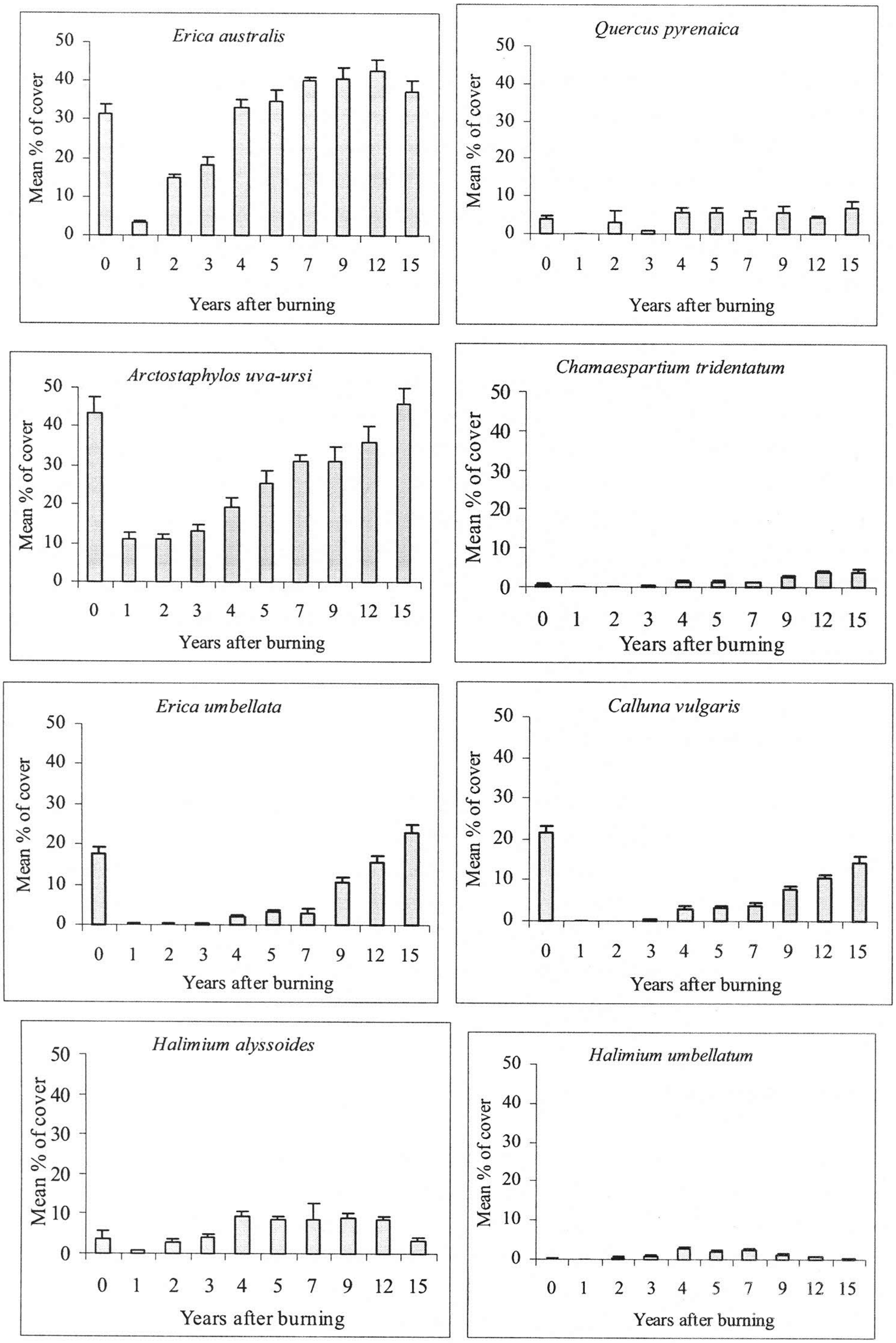

Figure 1.- Mean percentage cover and standard error for *Erica ustralis, Quercus pyrenaica, Arctostaphylos uva-ursi, Chamaespartium tridentatum, Erica umbellata, Calluna vulgaris, Halimium alyssoides* and Halimium umbellatum in original situation (0) and 1, 2, 3, 4, 5, 7, 9, 12, 15 (years after burning).

Behaviour of the Life Forms

The highest cover values for herbaceous annuals (or Therophytes according to the classical Raunkaier (1934) life forms classification) appear in the first five years after burning (Table I). The following are most important during throughout study period: *Aira caryophyllea*, *Crucianella angustifolia*, and *Arnoseris minima*. Several other herbaceous annuals (*Spergula morisonii*, *Sclerantus annus* and *Jasione montana*) only appear in the first years following burning. They are completely displaced from the zone from the fourth year, resulting in significant differences ($P<0.0005$) between the first 3-4 years of recovery and the remainder of the study period.

Perennial herbs behave differently, as their increase (Table I) shows no significant differences over time. Perennial species (or hemicryptophytes) exhibiting high cover values are: *Avenula marginata, Arenaria montana, Hypochoeris radicata, Lotus corniculatus* and *Tuberaria globularifolia*. It is important to emphasize that during the fifteen year period, cover of herbaceous taxa is very small. The space occupied by woody plants impedes the development and maintenance of herbaceous species for a long time period.

Cover of all the woody species increases significantly over time (Table I), although these increases are no longer significant from ninth year. The first woody species to appear are those with a vegetative sprouting capacity, like the chamaephytes: *Erica australis* and *Arctostaphylos uva-ursi*.

Seeders versus Resprouters

We considered as seeders the entire annual herbaceous and the seeders woody species. All perennial herbs were considered to be resprouters. Seeders comprise less than 35% in this shrubland community (Fig. 2). During the first year after the fire, resprouters represent more than 95% of the percentage cover. During the second year annual herbs comprise most of the seeders. From this year onwards, the rate of seeders does not show great changes until the 12th year, in which the proportions of woody seeders increase. Maximum values are attained during the 15th year and are similar to the original situation.

Structural Parameters

The richness values are higher during the first few years after burning and exhibit a significant decrease ($P<0.05$) over time (Table II). The maximum richness values appear during the fourth year. The evenness values show no significant differences ($P<0.05$) over time. H` diversity values were higher during the third and fourth year after burning due to the rise in the number of species and the relatively high evenness. During the 15th year diversity is significantly reduced due to the strong dominance of the woody species.

Table I.- Mean cover values (X) and standard error (S.E.) for herbaceous species through the study period (2, 3, 4, 5, 7, 9, 12 and 15 years after burning). Total cover of annual herbs, perennial herbs and woody species.

	2		3		4		5		7		9		12		15	
	X	*S.E.*	X	*S.E.*	X	*S.E.*	X	*S.E.*	X	*S.E.*	X	*S.E.*	X	*S.E.*	X	*S.E.*
Aira caryophyllea	13.0	*2.0*	5.2	*1.3*	6.0	*2.3*	2.2	*0.8*	0.0	*0.0*	0.0	*0.0*	0.4	*0.2*	0.0	*0.0*
Airopsis tenella	0.4	*0.3*	0.6	*0.3*	0.2	*0.2*	0.4	*0.3*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Andryala integrifolia	0.0	*0.0*	0.2	*0.2*	0.0	*0.0*	1.0	*1.0*	0.6	*0.4*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Arnoseris minima	1.2	*0.4*	1.2	*0.5*	0.8	*0.2*	1.2	*0.2*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Crucianella angustifolia	0.4	*0.3*	0.4	*0.3*	0.2	*0.2*	1.2	*0.2*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Evax carpetana	0.2	*0.2*	0.2	*0.2*	0.2	*0.2*	0.2	*0.2*	0.2	*0.2*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Galium divaricatum	0.0	*0.0*	0.2	*0.2*	0.2	*0.2*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Jasione montana	0.0	*0.0*	0.0	*0.0*	0.4	*0.3*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Logfia minima	0.2	*0.2*	0.8	*0.2*	1.0	*0.0*	0.4	*0.3*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Scleranthus annus	0.0	*0.0*	0.0	*0.0*	0.2	*0.2*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Spergula morisonii	0.2	*0.2*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Tuberaria guttata	1.2	*0.7*	1.0	*0.3*	0.8	*0.2*	1.0	*0.3*	0.4	*0.3*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Annuals hebs total	16.8		9.8		10.0		8.0		1.2		0.0		0.4		0.0	
Agrostis capillaris	0.0	*0.0*	1.6	*0.7*	0.2	*0.2*	1.2	*1.0*	1.0	*0.6*	0.6	*0.4*	0.2	*0.2*	0.2	*0.2*
Arenaria montana	0.0	*0.0*	1.0	*1.0*	1.0	*0.5*	0.6	*0.6*	0.4	*0.4*	0.6	*0.6*	0.2	*0.2*	0.0	*0.0*
Avenula marginata	4.0	*4.0*	2.2	*2.0*	2.2	*0.8*	1.8	*1.6*	1.4	*1.0*	1.8	*1.6*	1.2	*1.0*	0.2	*0.2*
Hieracium castellanum	0.6	*0.4*	0.4	*0.4*	0.6	*0.4*	0.6	*0.4*	0.0	*0.0*	0.2	*0.2*	0.0	*0.0*	0.0	*0.0*
Hieracium pilosella	0.0	*0.0*	0.2	*0.2*	1.4	*0.3*	0.0	*0.0*	0.2	*0.2*	0.0	*0.0*	0.2	*0.2*	0.0	*0.0*
Hypochoeris radicata	2.8	*1.6*	2.8	*1.9*	1.8	*0.8*	2.0	*0.8*	1.6	*0.4*	0.6	*0.4*	0.6	*0.6*	0.0	*0.0*
Lotus corniculatus	1.8	*1.0*	1.6	*0.9*	1.0	*0.3*	0.2	*0.2*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Senecio vulgaris	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.2	*0.2*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Tuberaria globularifolia	2.4	*1.0*	2.4	*0.8*	4.4	*1.7*	2.8	*1.9*	1.8	*1.0*	1.4	*0.6*	0.8	*0.6*	0.0	*0.0*
Perennials herbs total	11.6		12.2		12.6		9.2		6.6		5.2		3.2		0.4	
Woody total	58.8		57.6		81.8		81.8		105.6		146.6		130.0		153.6	

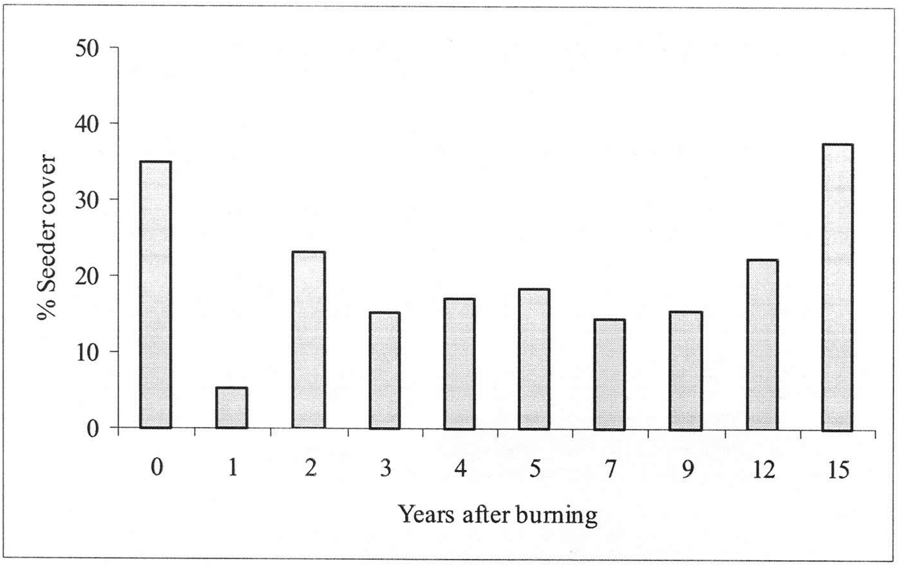

Figure 2.- Variations in percentage cover of seeders originally and 1, 2, 3, 4, 5, 7, 9, 12, 15 years after burning

Table II. Mean values and standard error of species richness (S), evenness (J') and diversity (H') during the study period.

Years	S		J'		H'	
	X	SE	X	SE	X	SE
2	9.8	*0.86*	0.67	*0.03*	2.43	*0.54*
3	12.2	*1.32*	0.64	*0.05*	2.83	*0.38*
4	15.0	*0.45*	0.67	*0.04*	2.7	*0.52*
5	14.6	*1.17*	0.62	*0.09*	2.37	*0.43*
7	8.6	*0.68*	0.56	*0.04*	2.21	*0.55*
9	7.2	*0.49*	0.57	*0.04*	2.37	*0.50*
12	7.8	*0.86*	0.61	*0.06*	2.34	*0.43*
15	6.2	*0.73*	0.69	*0.05*	1.45	*0.44*

DISCUSSION

Mediterranean shrubs are mainly associated with nutrient-poor, acidic soils and relatively mild climatic conditions (Ojeda 2001) which are widespread in the northwest of the Iberian Peninsula (Rívas-Martínez 1979; de Luis et al. 1989a). These communities occur in areas which are frequently subjected to perturbations, especially fires associated with human activity (Vázquez and Moreno 1998). Vegetation recovery after burning can start in various ways, either by germination of the seeds available in the soil seed bank, or vegetatively from the unaffected organs, or using both mechanisms simultanously. The use of one mechanism or another determines the speed at which species are capable of returning to the predisturbance state. When germination is the main mechanism, the process is often slower than when vegetative sprouting occurs (Forgeard 1990).

In these shrub communities resprouting and germinating species clearly coexist and it is common to find species which can use both mechanisms. It is also obvious that vegetation structure in autosuccession processes will be more similar to the original when the recovery mechanism is vegetative resprouting.

The capacity to sprout vegetatively from subterranean organs which survive the fire is a characteristic common to many species of the Mediterranean Basin (Trabaud 1987). It appears in tree species, such as *Quercus pyrenaica*, that resprouts from the shoots on the rhizome or the stem of the subterranean roots (Calvo et al. 1991, 1999, Luis-Calabuig et al. 2000). The resprouting capacity of this species is shared by others of the genus *Quercus*, distributed over the Mediterranean area, including *Quercus coccifera* (Trabaud 1980, Lloret and Vilá 1997) and *Quercus ilex* (Pausas and Vallejo 1999).

A capacity for resprouting also occurs in the following shrub species: many Ericaceae, like *Erica australis*, *Arctostaphylos uva ursi*, Leguminosae, such as *Chamespartium tridentatum*. The buds of *Erica australis*, a resprouting species typical of these communities, are found in the lignotuber (Canadell and López –Soria 1998). The presence of a lignotuber gives these ecosystems a great advantage in their response to burning (Moreno et al. 1999). The presence of this type of storage mechanism is probably associated with recurring perturbations that eliminate all the aboveground biomass. The potential capacity for storing starch is much greater in species of *Erica* genus species than in other resprouters (Bell and Ojeda 1999). This starch is degraded and freed to supply the sprouts (Canadell and López-Soria 1998). However, in addition to resprouting vigorously, it is also capable of germinating from the seeds stored in the soil seed bank. Several authors have studied the germination capacity of various Ericaceae after perturbations such as fire (Calvo 1993; Ojeda et al. 1996; Obeso and Vera 1996; Calvo et al. 1998a, 1998b, Valbuena et al. 2000).

The resprouter *Arctostaphylos uva-ursi* has the greatest regeneration speed one year after burning, reaching 10% cover. Del Barrio et al. (1999) found an even more marked response in a monoespecific stand of *Artostaphylos uva-ursi*, which reached 30% cover from the fourth month after an experimental fire.

Herbaceous species with a well-developed radicle system often contain subterranean shoots, rhizomes or bulbs which are capable of surviving due to poor heat diffusion in the soil. This mechanism is used mainly by the perennial herbaceous or hemicryptophytes, many of which keep their buds protected at ground level. These include: *Tuberaria globularifolia, Hypochoeris radicata* and *Avenula marginata*. In these resprouting species the radicle system is always present and allows them to use water and nutrients quickly.

In addition to vegetative sprouting, the predominant mechanism in post-fire recovery, there are many species whose seeds are stimulated by heat, thus favouring their germination. This way of regeneration depends directly on the quantity and viability of the soil seed bank. Studies of soil seed bank responses after fire in shrub ecosystems dominated by *Erica australis* were carried out by Valbuena (1995), Valbuena and Trabaud (1994). Seeder species are always dominant in the soil seed bank. In general, therophytes and hemicryptophytes are the dominant life forms in some areas and chamaephytes are dominant in others, reflecting the pre-fire plant composition. Species with anemochory and autochory are dominant in these seed bank areas. The first species to appear may come from neighbouring areas and do not appear in the field when environmental conditions for germination and development are not favourable. Less than 25% of species present in the soil seed bank are found in the aboveground vegetation in the field. However, the importance of this method of regeneration resides in the maintenance of genetic diversity (Valbuena 1995).

Several authors (Naveh 1975; Berdowski 1993) consider two woody Ericaceous species (*Erica umbellata* and *Calluna vulgaris*) to be resprouters, but in this study they only reappear by germination. In the case of *Calluna vulgaris*, this has previously been described as the only recovery method after experimental fires in the north of Portugal (Rego et al. 1991), and in communities in SW Spain (García Novo 1977). One possible explanation for the exclusive use of germination is that given by Gimingham (1960) in studies of *Calluna* communities in Scotland: *Calluna vulgaris* only resprouts when in mature growth stages and not when it has reached a senescent phase. A similar process has been observed in *Calluna* communities in high areas of the Cantabrian mountain range, where populations of more than 30 years old do not resprout after cutting (personal observation). Resprouting capacity also declines with plant age in other species of Californian chaparral shrub (Hobbs and Mooney 1985). It therefore seems that the different mechanisms used by this species are not related to fire intensity, as questioned by Pausas (1999), since it uses germination in this area after any perturbation; it is possibly related to aspects of plant age. In general, the recovery of both species is slower than in resprouters during the first few years of succession, but after the 4th or 5th year post-perturbation both show very considerable increases in cover. This means that they are not pioneering species as far as colonisation is concerned, but they will not be replaced by competition with the dominant species, since *Erica australis* dominates the community from the moment its cover increases. These results concur with another experiment carried out in a similar shrubland dominated by *Erica australis* situated in a neighbouring area. Ten years after the fire, cover of *Erica australis* is higher than in pre-fire situation and *Calluna vulgaris* exhibits the opposite behaviour (Fernández Abascal et al., in press). However, in soil seed bank studies in the same area, Valbuena et al. (2000) find that the temperature reached during the fire improved the germinability of *Calluna vulgaris* seeds, the opposite occurring in the *Erica australis* seeds. The different response of *Erica australis* in the field and in the seed bank is easily explained by its resprouting capability, but the behaviour of *Calluna vulgaris* is not so clear.

Both *Halimium alyssoides* and *Halimium umbellatum* can be considered as colonisers. Changes in cover values over time show that both species take advantage of the empty spaces to germinate and increase cover as well as the space they occupy. However, when the dominant species (mainly *Erica australis*) reaches cover values similar to the original (4th year), that is, close to 60%, *H. alyssoides* stops spreading and *H. umbellatum* cover starts to decrease.

One herbaceous species that stands out after burning and which uses germination as a regeneration mechanism is the leguminous *Lotus corniculatus*. Other authors in Mediterranean areas (Arianoutsou-Faraggitaki and Margaris 1982) have already stated the role played by leguminous species in post-fire plant recolonization. This species probably came from a soil seed bank, as it is known that the seeds of leguminous species are very long-lived, allowing them to form large soil seed banks (Trabaud et al. 1997). The hardness and impermeability of the seeds of many woody genera are also well known. This makes their germination under normal conditions difficult (Casal 1987). High cover values for this species may therefore be produced by factors associated with the fire stimulating germination (temperatures, exposure to light, reduction of toxins) (Martinez-Sanchez and Herranz, 1999).

Species which respond to disturbances by vegetative sprouting, or by sprouting and seeding at the same time, have an advantage when recolonizing burnt areas as they can begin to occupy the space immediately after the fire has passed and, in addition, only have to regenerate their aboveground parts. In contrast, those that only reproduce by seed appear later, as the seeds remain in the ground and only germinate after the first rains. Success, and therefore the persistence of species with one or another type of strategy in an area, depends to a great extent on fire frequency.

In these types of communities which are subject to very frequent burning, the possibility of replacement by a different vegetation type is very low. The strong sprouting capacity of the component species confers a high degree of resilience in the spatial structure of shrub communities (dominated by Ericaceous) during recovery from perturbations in the short term (Clemente et al. 1996, Calvo et al. 1998a). This is also supported by the long term studies carried out by Kadmon and Harara-Kremer (1999) in maquis communities. This high resilience, in the sense of recovery capacity, is not only attributed to the strong resprouting potential of these species, but also to their germination capacity. In other types of Mediterranean communities, such as those dominated by *Cistus ladanifer* and *Cistus laurifolius*, which are obligate seeders, germination also confers high resilience, as shown in the studies of Tarrega et al. (1995, 1997).

At the entire plant community level, changes were most marked until the fourth-fifth year after the fire. This is due to the fact that it is a period when many herbaceous species, mainly annuals (Therophytes), enter to take advantage of the lack of competition from woody taxa. Once the woody species reach high cover values, this competition displaces the annuals, with only some herbaceous perennials remaining for 15 years. The abundance of herbaceous perennials is inversely related to the amount of woody cover, i.e. where woody plants have less total cover, herbaceous species are of greater importance. This is due to competition for space and light. Competition for light is very important in multilayer communities similar to these (Vilá 1997).

These marked changes in the cover values of the different life forms during the first few successional stages are reflected in the changes observed in the floristic diversity parameters, especially richness and diversity. The highest values for the two parameters coincide with the maximum explosion of herbaceous species during the first 4-5 years and then both decrease. This increase in the richness values in the first few stages has been described by other authors analysing post-fire vegetation recovery (Naveh and Dann 1974, Trabaud and Lepart 1980, 1981; Casal et al. 1990, Bond and Van Wilgen 1996, Cavero and Ederra 1999, Naveh 1999). The decrease in diversity values is produced by the community starting to stabilise or the changes being brought to a standstill and this results in a marked dominance of woody species and, in theses zones, of *Erica australis*.

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