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Chapter 2

History of landscape changes in northwest Spain according to land use and management

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Abstract

The historical background in the northwest Iberian Peninsula has resulted in many changes in the landscape which have accounted for a special situation with high risk of forest fires. Post-fire recovery in these areas is by an autosuccession process because the species appearing after the disturbance are the same as occupied the area previously. Resprouting species predominate but obligate seeders are also important in these ecosystems. The degree of community maturity before the fire determines both fire damage and regeneration speed. Post-disturbance recovery phases are described for different ecosystems dominated by tree and shrub species. Soil seed bank influence is also described.

1 Historical background and problems of forest fires

It can be deduced from the remotest references to landscapes in northwest Iberia that there were large areas of forested gradients at the point of contact between two biogeographical worlds. The predominance of the Mediterranean climate, although subject to Atlantic or Continental influences, together with the alternatives determined by its orography, which in some cases can create mesoclimates of great interest, multiplied their diversification.

Characteristics natural to a strictly Mediterranean climate with long, dry summers, high temperatures and low summer rainfall usually in the form of storms, can be found at one end of the gradient. Precipitations occur in winter with the annual total not being relatively very high.

The other end of the gradient clearly corresponds to the Eurosiberian domination area where Atlantic disturbances from the polar front reach the north and northwest coasts of the Iberian Peninsula determining wetter conditions and, at the same time, moderating the atmospheric fluctuations with their marine influence. Precipitations above those of the Mediterranean region are spread more equally throughout the year, although the constant of minimum in summer remains with a decrease in the length of the dry period and moderations in temperature oscillations.

Keeping to this and in relation to the gradient mentioned, the northern subplateau was covered in holm oak (*Quercus ilex*), juniper (*Juniperus comunis*), oak (*Quercus pyrenaica*) and beech (*Fagus sylvatica*) trees in perfect spatial dynamics and with all the possible sets of mesoclimatic, edaphic and orographic influences. This in turn translates into a gradient of species, ecotypes or hybridization elements which show their predominance as regards latitude, height and edaphic humidity, keeping to physiological relations which basically tend to overcome strong seasonal influences and great annual variations.

Vegetation distribution and evolution of the most representative climatological parameters reinforce the special location character of this region. The analysis of the ombrothermal diagrams of some meteorological stations located in the direction of this variation gradient may serve as a summary, basically as regards precipitation intensity and the significance of the dry period (Fig. 1).

Those macroclimatic characteristics, and with them the vegetation type and distribution, could have been valid for some 3000 years. Palaeontological studies prove that there have been very few variations in climate from a geological viewpoint. The same model has existed throughout human history except for the supposed global climate change of the last few years.

That state of extensive wooded cover, which can be accepted as correct, means that the landscape was very different to the present one. That period of time was long enough for several historical facts to have contributed to the northern subplateau of the Iberian Peninsula being an area extraordinarily bare of trees on the climatic limit of unstoppably becoming a desert nowadays.

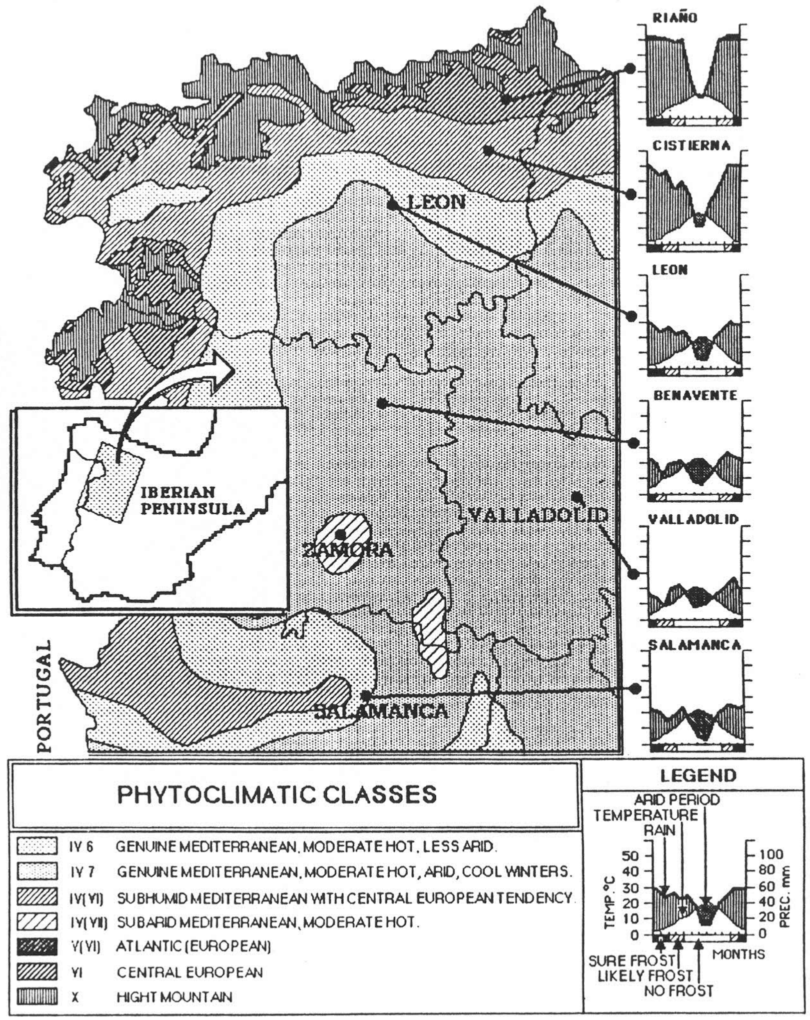

Figure 1: Phytoclimatic scheme from Allue Andrade[1].

Although there are few historical references, at least the behaviour and actions of the different populations of this territory can generally be traced.

Estrabon's (63 B.C. - A.D. 19) historical version is usually considered the first reliable one. In many narrations about the war campaigns of the Romans in Iberia it refers to the widespread, thick forests of oak, holm oak and juniper in Arevaco lands and only deforested close to populated Vacceo areas subjected to grazing. Those narrations made reference to places which can be identified now but have very different landscapes.

Estrabon also tells of campaigns against the peoples of the north (Cántabros and Astures). His comments coincide with those of other Roman historians in reference to these peoples' almost total dependence on forest resources. The mountains were practically covered in woods, except for some small cultivated plots in the forest valleys and clearings. Neither the Romans nor the subsequent civilizations that passed through the Iberian Peninsula managed to completely dominate these peoples and perhaps that is the reason for the present good state of conservation of the forest heritage in the Cantabrian Mountain range.

Population density in this region during the Roman period and until the 5th century was very low, not exceeding eight inhabitants per square kilometre. Thus deforestation was not very high except for the effects produced by communications and the impact on specific sites from mining.

It can be deduced from the Visigoths' code of laws (Lex Visigotorum) that they respected the forests, as was to be expected of a northern European people, with no timber farming or exploitation of the wood on a large scale.

Rapid domination by the Arabs, although with a completely different culture, did not modify tree distribution and density to any great extent. However, the slow process of the Christian reconquest which started in the north left significant traces of deforestation. War was continuous on the well-established frontiers and fire was often used for attack or defence. Where a fast reconquest took place areas of uninhabited no man's land remained with the forest communities doing rather better. These deserted lands were repopulated and colonized from the 12th century on.

The development of transhumant grazing with the foundation of the Mesta as a powerful livestock farming organization, formed in 1273 under the protection of the crown, was the origin of the first significant damage. This was caused by the change in use of the forests for grazing and the cutting down or burning by the shepherds to increase room for the Merino flocks, basically along and close to the cattle tracks, above all at the summer destination points. The Cantabrian mountain ranges were amongst the most important. That ancient treatment of shrub elimination by fire in order to create pastures is something that has continued down to our days, even when there are no sheep left to graze on those supposed pastures.

Huge areas were also cut down in that period to obtain wood to build prosperous cities, which, in turn, required more and more land for cultivation. Thus the wooded landscape changed into an agricultural one.

As no effective reforestation was carried out at the same time, deforestation was an extremely rapid process to the extent that it became alarming even on a social level and the first regulations for punishing intentional burning and cutting down were passed and reforestation with fast growing species was advised.

Even so, exploitation continued on a disproportionate scale: on the one hand as the raw material to build merchant and naval fleets to travel round and control all the empire colonies and, on the other, to increase the number of Merino sheep whose wool was one of the most important economic linchpins required to maintain that vast empire.

Maximum profitability from mountain pastures was attained with 800,000 head of livestock in the León province mountain passes, but it continued to increase up to 1,200,000 with the subsequent degeneration caused by overgrazing and trampling. This caused continual abandonment which produced plant communities dominated by shrubs of low economic efficiency which were then eliminated by fire at increasingly shorter intervals until edaphic erosion occurred.

The collapse of the Mesta meant the mountain pastures were abandoned and a very slow secondary succession started up which got bogged down in heathland or other shrub communities at high risk from fire.

After the Napoleonic and civil wars in the 19th century and, above all, after the civil war in the 1930's, large areas of forest were ploughed up for agriculture. In many cases they were residual woods on marginal lands with difficult orography so were of low profitability and abandoned a few years later, coinciding with a very marked migration from the country to the large population nuclei (Fig. 2). This desertion of the countryside coincided with a change in the traditional use to which wooded mountain areas were put, decreasing their use and exploitation as firewood or other biomass energy sources, which transform the landscape into masses at greater risk of fire.

Industrial development requires a greater production of raw materials for paper pulp, so an accelerated process of reforestation with rapid growth species was initiated in the 1940's which, due to their monotony and high combustibility, merely complicated the spectrum of fire as an impact.

In the last few years, and because of the demands of community policy, the abandonment of agriculture has been a common pattern within the CAP (Community Agricultural Policy) framework. Thus marginal lands, non-productive for man, continue to increase and slowly become serial heath communities and form part of the high risk areas.

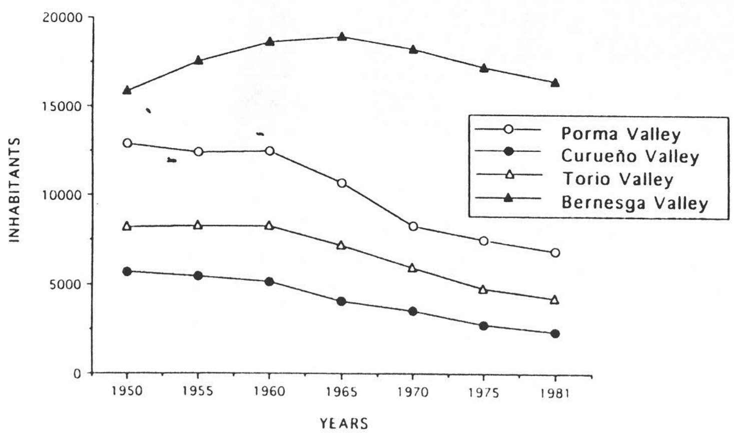

Figure 2: Population trends in four valleys of the León province between 1950 and 1981.

In addition to this general outline the still important presence of well-conserved masses of forest dominated by beech groves, above all in the mountain areas of the northeast of León province close to the massif of the Picos de Europa mountain range, must not be forgotten. Relatively important tracts of *Quercus pyrenaica* oak woods also appear in lower lying areas but their structural characteristics have already been altered by human pressure.

Besides these forest masses huge areas of shrub communities, with different dominant species according to the location and soil alteration level, as well as arboreal plantations of species destined for wood production of widely differing extents, have a place in the landscape of current vegetation and of uses and exploitation in León province. The map is completed by formations of riverside corridors, also very altered in some valleys, and the grazing and crop lands.

Each of those environmental units possess a different potential fire risk due to its composition and structural characteristics. So the fire risk map for León province (Fig. 3) (Tárrega & Luis[2]), as in the most affected communities, is defined by a complex of spots with three different danger levels in the highest parts of the province. The low areas can be classified as without any risk of forest fire as a result of their basically agricultural character, although many agricultural activities in the last few decades have continued to use the bad practice of burning to eliminate fallow lands and can sometimes cause fires of great importance.

Fire statistics in the last few years show wide oscillations, in agreement with climatological characteristics, but a clear tendency towards a decrease in burnt surface area can be appreciated (Fig. 4). This is related to a significant increase in investment in prevention and basically to fire fighting.

The periods of greatest risk coincide with the end of the summer, although the presence of a by no means negligible risk in a dry spring must be mentioned (Fig. 5). The connection between the periods of maximum incidence and the huge percentage of intentional fires is simply proof of the socio-economic implications of those fires.

However, it cannot be deduced from the number of fires that the tendency is towards a decrease even though similar oscillations appear (Fig. 4). If the fact that there have been large fires, which have affected huge surface areas of importance to forestation, in the last few years is

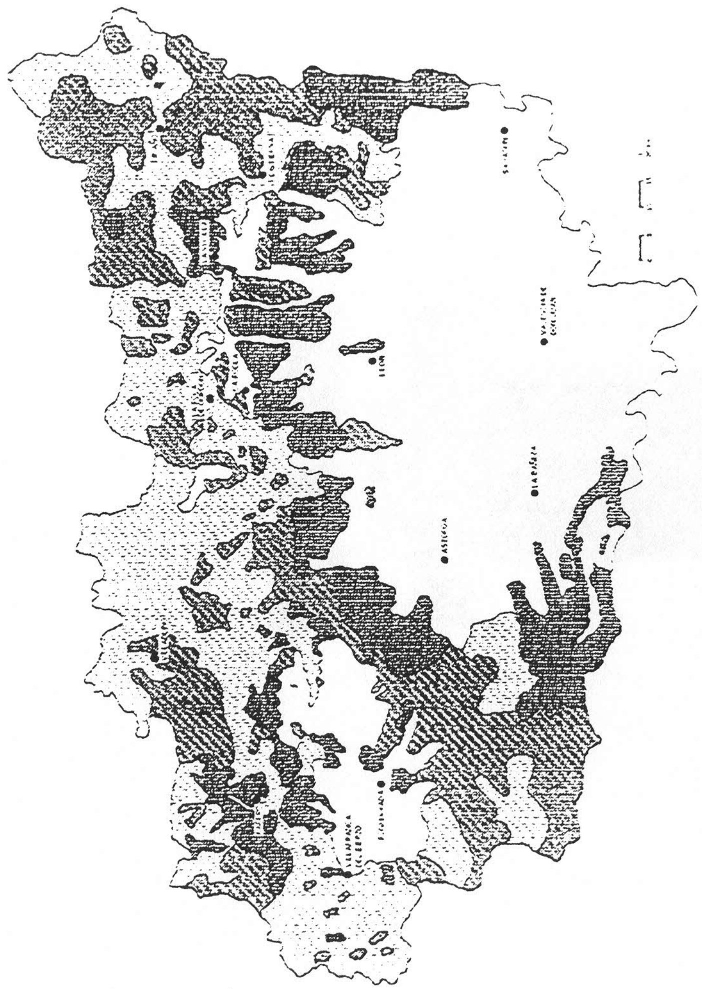

Figure 3: Fire danger map of the León province. (The darkest patches indicate the highest fire risk).

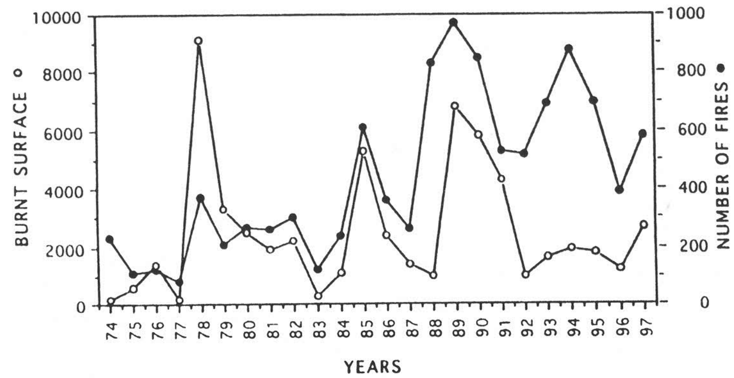

Figure 4: Surface burnt and number of fires in the province of León during a period of 24 years.

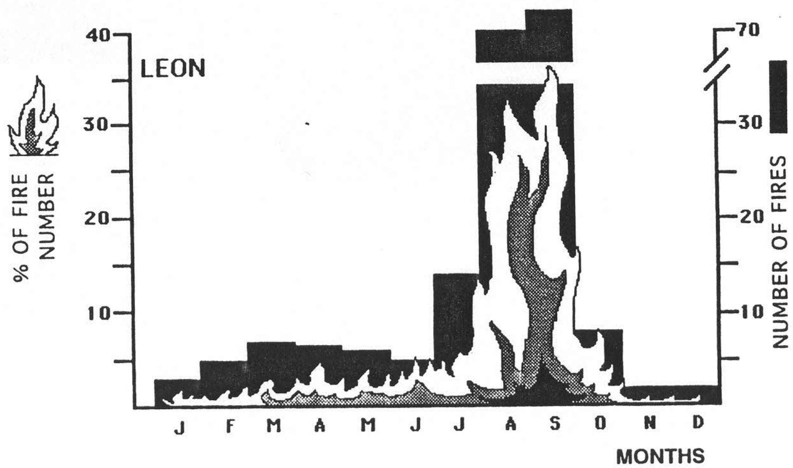

Figure 5: Monthly percentage distribution of fires in León province (Tárrega & Luis[2]).

added, then it is easy to understand why it is presented to society as a new social problem with enormous implications, which have forced new political and administrative reforms and which demand effective processes and procedures of awareness with greater frequency.

2 General tendencies in post-fire recovery

Forest fires are not a new phenomenon for most of our ecosystems, although the increase in frequency may be. Species adapted to rapid regeneration after disturbances caused by man and which have frequently occurred during thousands of years in the Mediterranean Basin predominate. Because of this, recovery is usually by autosuccession, that is, the species that appear after the disturbance are the same as those previously occupying the area (Hanes[3], Naveh[4], Keeley[5], Trabaud[6]). Vegetation recovery 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 at the same time. When germination is the main mechanism the process is often slower than when vegetative sprouting occurs.

2.1 Vegetative sprouting

The capacity to sprout vegetatively from subterranean organs which survive the fire is a characteristic common to many species of the Mediterranean Basin (Trabaud[6], Tárrega & Luis[2]). It appears in tree species, such as most *Quercus* spp. and is a highly developed mechanism in *Quercus pyrenaica*, as well as shrub species: many Ericaceae, like *Erica australis*, Leguminosae, such as *Genistella tridentata, Cytisus scoparius, Genista florida*, etc. It is also often found in herbaceous species with well-developed radicle systems which present subterranean shoots, rhizomes or bulbs capable of surviving due to bad heat diffusion in the soil, like many Graminae, Liliaceae, etc. Likewise the great abundance of *Pteridium aquilinum* after a fire is mostly due to regeneration from subterranean rhizomes.

These 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 on fire frequency to a great extent.

2.2 Germination

In addition to vegetative sprouting, a 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 amount and viability of the soil seed bank.

Studies of soil seed bank response after fire in different ecosystems, *Quercus pyrenaica* forests and shrubs dominated by *Erica australis,* was carried out (Valbuena[7], Valbuena & Trabaud[8]). Seeder species are always dominant in the soil seed bank (Table 1). In general, therophytes and hemicryptophytes are the dominant life forms in some areas and chamaephytes are dominant in others in relation to the pre-fire plant composition. Species with anemochory and autochory are dominant in these seed bank areas. The first ones may come from neighbouring areas and they do not appear in the field when the 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 way of regeneration resides in the maintenance of genetic diversity.

One way of checking the effect of fire on seed germination is to carry out laboratory tests subjecting the seeds to different temperatures for different lengths of time (similar to those the seeds in the soil would reach during a fire) and then incubating them in germination chambers. It has been proved, for example, that *Cytisus scoparius* and *Genista florida* germination are stimulated by heat (Tárrega *et al.*[9]). They are also capable of sprouting. This is also important when treating seeds used for revegetation as thermal treatment is cheaper and more effective than that with acid (for example, sulphuric). Heating to 100°C for 5 minutes determines about 80% germination in *Cytisus scoparius* and 50% in *Genista florida* (Fig. 6) compared with 20% germination in control seeds (untreated).

Table 1. Traits of species present in the soil seed bank in five plant communities after fire. Ar.uva-ursi= *Arctostaphylos uva-ursi*; Ca.vu = *Calluna vulgaris*; Cy.sc= *Cytisus scoparius*; Er.au = *Erica australis*; Hal.al= *Halimium alyssoides*; Qu.py= *Quercus pyrenaica*; Ag.ca= *Agrostis capillaris*; Av.su= *Avena sulcata*; Fe.ru= *Festuca rubra*; Lu.la= *Luzula lactea*.

T= Therophyte; He = Hemicryptophyte; C = Chamaephyte

	Shrub 1 (PARDAVE)	Shrub 2 (CORCOS)	Shrub 3 (CORCOS)	Oak forest 1 (PARDAVE)	Oak forest 2 (CORCOS)
Altitude over sea level	1000m	1063m	1063m	1000m	1063m
Vegetation dominant species	Er.au - Ca.vu Ha.al - Cy.sc Fe.ru	Er.au - Ca.vu Ar.uva-ursi Fe.ru - Ag.ca	Er.au - Ca.vu Ar.uva-ursi Fe.ru - Lu.la	Qu.py - Er.au Ca.vu - Cy.sc Av.su	Qu.py - Er.au Ca.vu - Lu.la Ar.uva-ursi
Soil	pH ≅ 5	pH ≅ 5	pH ≅ 5	pH ≅ 5	pH ≅ 5
Stations of fire	Spring	Summer	Spring	Spring	Spring
Biological traits	Herbaceous	Woody	Herbaceous	Herbaceous	Herbaceous/ Woody
Seed bank types of regeneration	Seed	Seed	Seed	Seed	Seed
Life forms	T/He	C	C	He	C
Seed dissemination types	Anemochory/ Autochory	Anemochory/ Autochory	Anemochory/ Autochory	Autochory	Autochory
Regeneration strategies in the field	Sprout	Sprout	Sprout	Sprout	Sprout

Cistus ladanifer seeds are also stimulated by heat with germination rates between 90% and 100% at 100ºC for 1 or 5 minutes and close to 80% at the same temperature for *Cistus laurifolius* (Fig. 7). The control seeds had germination rates of 60% and 20%, respectively (Valbuena *et al.* [10]). Besides, germination is much slower and more gradual without any heat. It seems that the strategy consists of rapid germination (in the first 10 days) to recolonize the burnt area fast. *Cistus ladanifer*, with its more Mediterranean character, is faster than *Cistus laurifolius* and thus probably better adapted to fire. When the temperature is kept at 150ºC for 1 minute, stimulation is maintained but if the heat is prolonged it becomes lethal. However, such high temperatures usually last for very short times in the soil even if reached in fires among shrubs of this type.

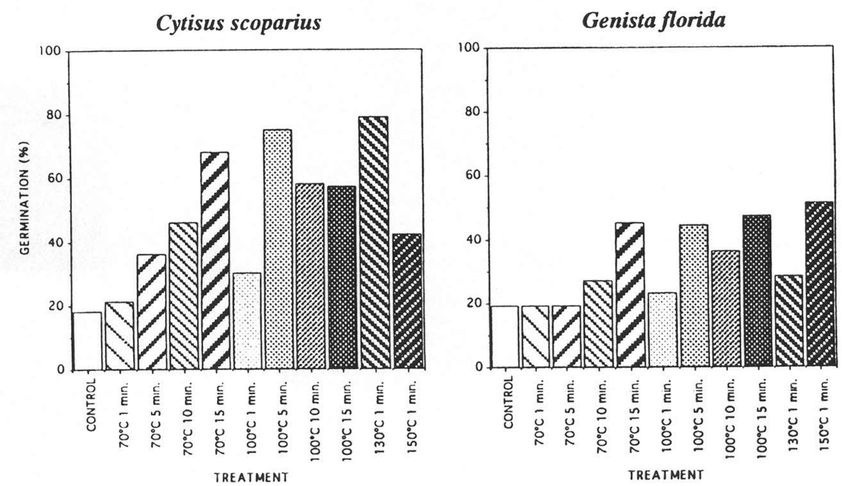

Figure 6: Percentage of germination of *Cytisus scoparius* and *Genista florida* subjected to different heat treatments.

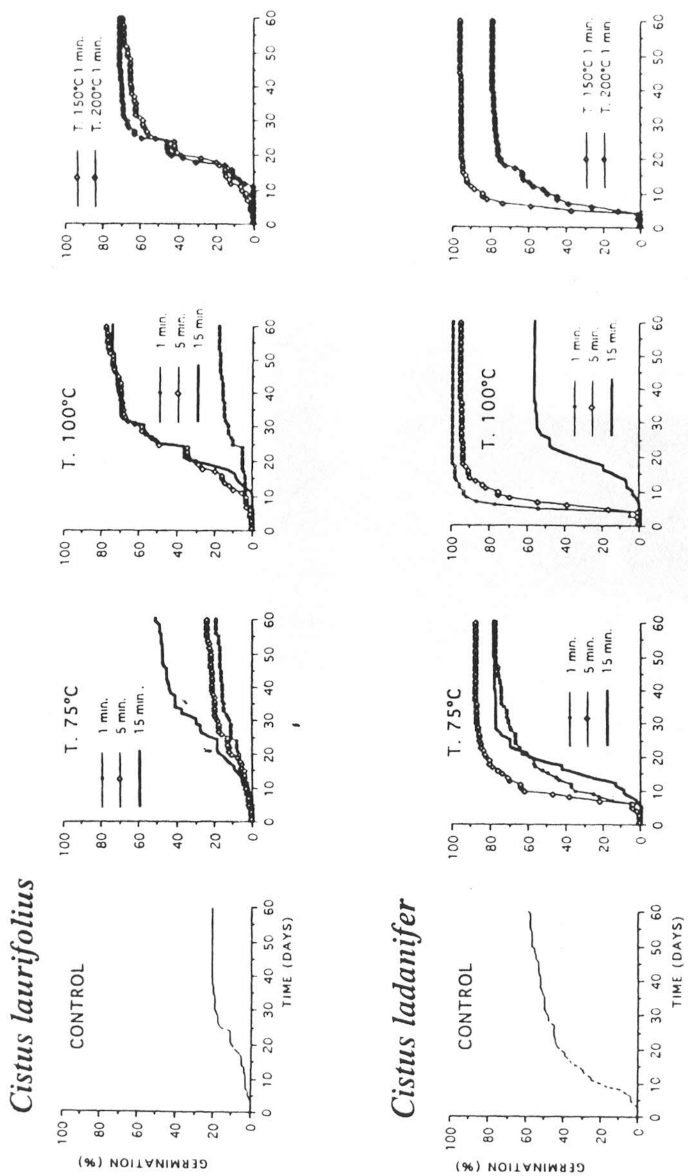

Figure 7: Cumulative germination percentage of *Cistus laurifolius* and *Cistus ladanifer* subjected to different heat treatments.

On the other hand, the seeds of species not adapted to fire are harmed by heat. Other seeds, such as *Quercus pyrenaica* acorns, germinate equally well with or without heat and no difference is detected between control seeds and those subjected to thermal treatment (Valbuena & Tárrega[11]). This allows them to regenerate after the fire as well as in its absence since this species is well-adapted to surviving disturbances, although it reaches greater maturity and forms true forests without them.

2.3 Effects of fire on soil properties

The effects of forest fires on the physical, chemical and biological properties of soils are directly related to the intensity and duration of soil heating (Wells *et al.*[12]). The fires occurring annually in León province are not too intense so they usually only affect the first few centimetres of soil (Fig. 8) and thus practically do not modify soil properties below this depth (Marcos[13], Marcos *et al.*[14]). The effect of fire on the soil is also related to the degree of degradation shown by the different communities before the fire and the season in which it occurs (Marcos *et al.*[15]).

3 Post-fire recovery in some plant communities

3.1 Recovery in *Quercus pyrenaica* oak groves

In spite of the good germination response by acorns in the laboratory, the main post-fire regeneration mechanism used by *Quercus pyrenaica* is vegetative. Oaks usually survive surface fires unless they are very small, when their trunks are very thin and the bark has not developed enough to protect the living tissues from heat. When the aboveground part of these smaller trees is destroyed by fire, active sprouting occurs with very rapid growth in the first few years because the radicle system has hardly been altered. They can reach heights of 2 m in two years and 3 m five years after the fire (Marcos *et al.*[16]). The trees with thicker trunks resist well and, although the lower branches dry out in some cases, the rest of the crown retains its vitality. Therefore this species' response to fire is quite good, which indicates that fires are not a new

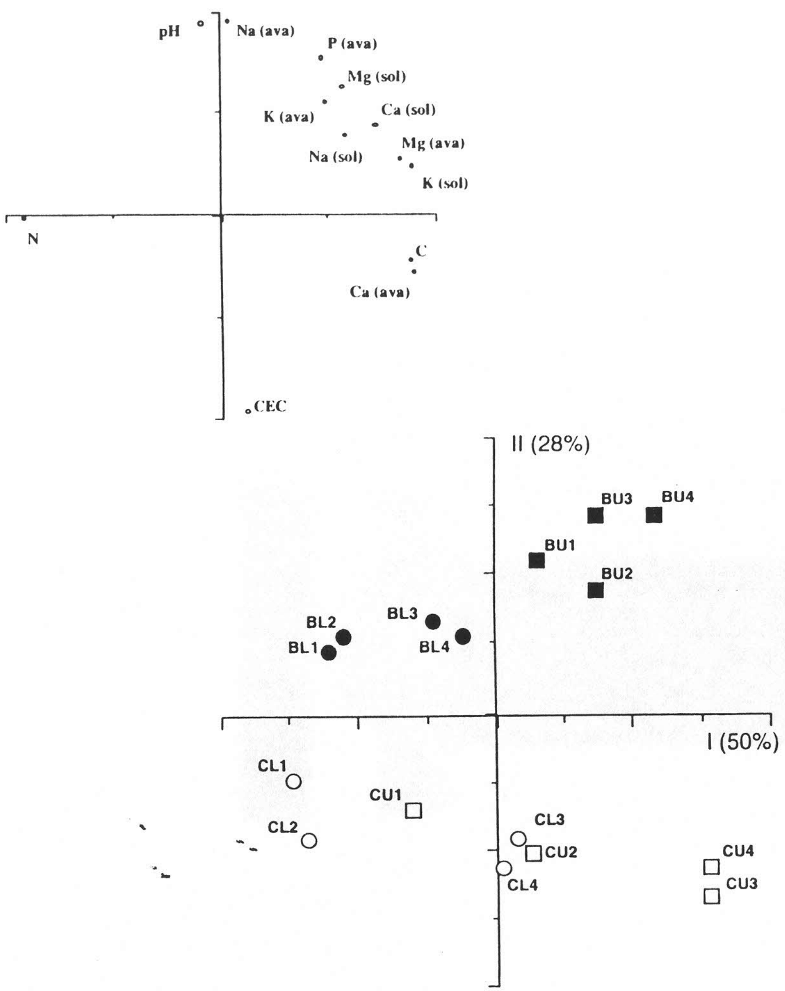

Figure 8: Location of the variables and samples in the plane defined by the first two axes of the principal components analysis. (ava = available, sol = soluble. B = Burnt, C = Control, U = Upper layer (0-2 cm), L = Lower layer (2-5 cm). 1, 2, 3, 4 = Four *Erica australis* heathland plots submitted to experimental fire).

phenomenon. Burning underbrush, which sporadically escaped man's control and which then spread to these formations, has probably been frequent since ancient times and thus they made these adaptations to survive. Nevertheless, the huge increase in fires in the last few decades may also negatively affect oak groves. If a second fire occurs shortly after the previous one, almost all the young oak trees that came up after the first fire are destroyed and will then sprout actively in even larger numbers than before. If this happens again, it will lead to formations of very thick oak shrubs which are much more susceptible to new fires and far removed from the optimum situation of a mature forest. In addition, the absence of vegetation immediately after a fire on sloping hillsides can lead to great soil loss, which could then not support the same plant mass as before the fire, but rather species with smaller demands on soil depth or even the same oaks with their growth restrained by the lack of soil.

A small scale experiment was carried out in order to determine the effect on the development of oaks from bushes to trees in thick, continuous shrub formations appearing as a result of repeated fires. An area burned three years previously with a mean density of 5.5 shoots per square metre and a mean height of about 2 m was chosen (Marcos *et al.*[16]). Three 25 m^2 plots were marked out: one was left as a control, all the woody species except the oak shoots were cut down in another and all the woody species except for 10 oak shoots were cut down in the third. Over a period of three years 10 trees were marked in each plot and their height and trunk circumference measured. It was observed that an increase in trunk circumference was favoured in comparison with height growth in the third plot (Fig. 9) because competition for light had decreased. This indicates that it would be possible to improve the structure of these ecosystems in the long run by using a forestry treatment.

The degree of maturity of the oak grove ecosystems before the fire also conditions recovery speed. The damage caused by fire is usually less in better preserved woods with survival of most of the trees and thus of the microclimatic conditions. The vegetation cover and diversity and species richness values are higher when dense formations of shrub oak are burnt and no aboveground biomass survives (Fig. 10) (Luis & Tárrega[17]). This is shown even on a very small scale, determining differences in the regeneration of stretches of a slope burnt in the same fire. The importance of the previous degradation level is also appreciable in the biotypes composition. One month after the fire perennial species specific to the community prevail in slightly altered oak groves in which quite a lot of trees survive. These are quicker to resettle as they can regenerate vegetatively. A slight increase in the number of therophytes takes place about one to two years after the fire and later the proportion of annual species goes down to the usual levels. There is also an invasion of therophytes with the highest percentages of annual species two years after the fire, in averagely disturbed areas with small oak trees that cannot outlive fire. In both cases oak shoots constitute the highest proportion of woody species (in the areas where there is survival, trees are not included) (Calvo *et al.*[18]) Finally, in communities dominated by *Quercus pyrenaica* forest but altered to the extent that only isolated oak trees or small woods appear, fire can cause major damage. Vegetative oak regeneration in these cases is scarce and nearly non-existent when starting from acorns. A high proportion of shrub species is observed shortly after the fire and after the therophyte stage, with an increase in woody species, among which the proportion of oak shoots is nearly non-existent (Luis & Tárrega[17]).

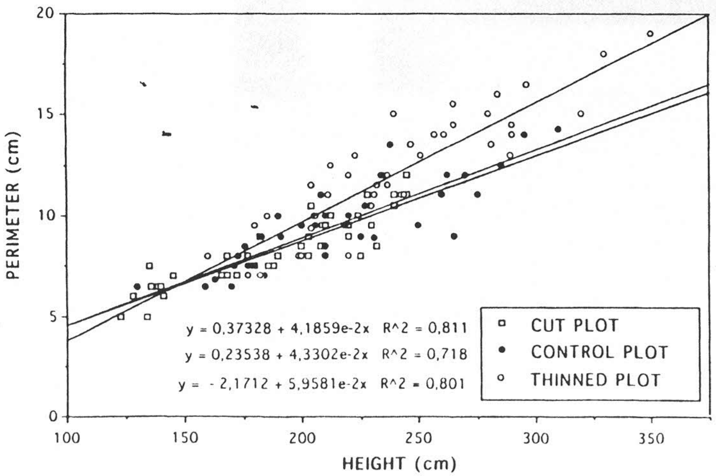

Figure 9: Regression analysis between height and trunk circumference of *Quercus pyrenaica* shoots in the experimental plots.

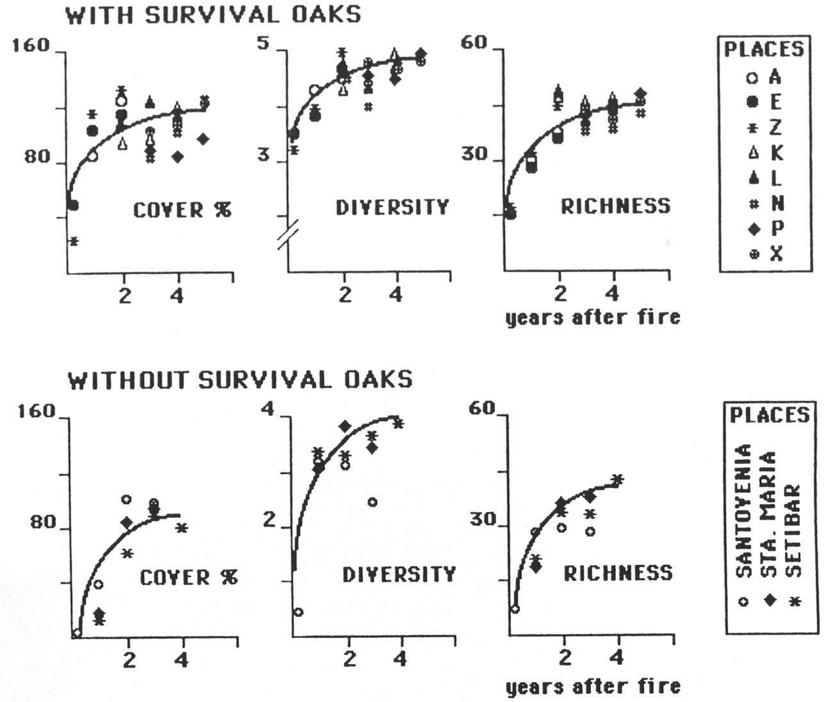

Figure 10: Changes in the first years of post-fire regeneration in the values of some parameters of the plant community, comparing areas with and without survival tress. (Modified from Luis and Tárrega[17]).

The predominance of sprouting species and those with short-distance seed dispersion (autochory and barochory) produces autosuccession after disturbances, so even comparing similar oak grove communities, with tree survival and fires on the same date, results in a greater similarity between successive samplings carried out on one community (with differing post-fire recovery ages) than between stages at the same recovery age (Fig. 11) (Tárrega & Luis[19]).

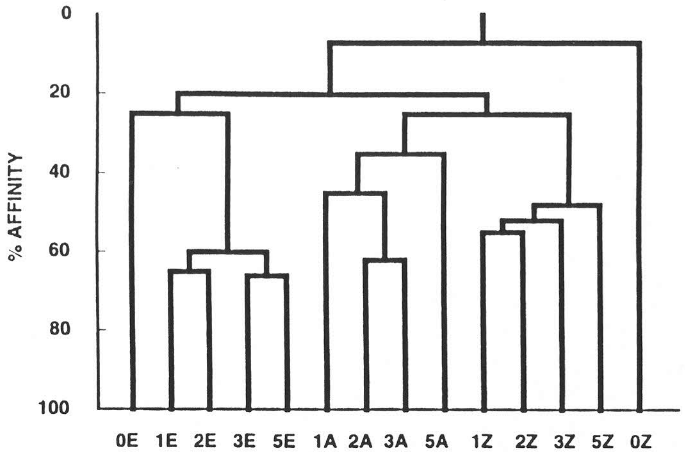

Figure 11: Affinity analysis (by Motika Index) between the samplings of three burnt *Quercus pyrenaica* ecosystems. (Zones A, E, and Z. Numbers indicate years after fire).

Although the degradation level before the fire is an important conditioning factor in the damage it causes and recovery of the ecosystem, the season in which the fire occurs also has an influence. Most of the fires in León province occur at the end of the summer, but a short drought sometimes also occurs in spring and this normally brings several fires, usually intentional ones. These fires are usually less intense and recovery is normally faster. Oak shoots more than 50 cm high were observed in an area burnt in spring one month post-fire, whilst they were no higher than 40 cm four months post-fire in a nearby area burnt in summer (Marcos *et al.*[16]). In addition, a higher percentage of bare soil can be seen in the areas burnt in summer in comparison with those burnt in spring. There plant recovery is faster as shown by Fig. 12, in which the first years of recovery of six oak groves, three burnt in spring and three in summer, were compared (Calvo *et al.*[20], Calvo *et al.*[18]). However, no differences are usually detected between the areas burnt in spring and in summer after three or four years. The ecosystem

characteristics have more influence than the disturbance on the recovery process, as is shown by the affinity analysis (Fig. 13). This is according to Egler's[21] theory of the importance of initial floristic composition.

There is great variability in the soil characteristics of these ecosystems so the effects of the fire will also vary from one area to another and the recovery capacity of the soil will, to a great extent, depend on the degree of degradation of the oak grove (Marcos *et al.*[15]). A big increase in phosphorus and assimilable cations is generally detected after a fire (Table 2). This increase is basically due to the ashes incorporated into the soil as they have a high mineral content and thus cause significant changes in the soil (Marcos *et al.*[22]). An increase of approximately one unit is also observed in pH. The changes in organic matter depend on the intensity of the fire with as many increases as decreases being found. However, no appreciable changes were detected in total nitrogen in any of the areas studied. The soil characteristics generally remain with higher values after one year, although a tendency for nutrients to decrease over time has been observed in some cases.

Table 2. Chemical properties of control (C) and burned soils (0 = immediately after fire, 1 = one year after fire) in two *Quercus pyrenaica* areas (0-5 cm).

	AREA 1			AREA 2		
	C	0	1	C	0	1
pH	5.63	5.90	5.91	4.86	5.61	5.56
N (%)	0.13	0.16	0.26	0.09	0.08	0.09
O.M. (%)	4.29	6.45	9.14	1.65	2.15	2.83
Available nutrients:						
Ca ($cmol_c\ kg^{-1}$)	54.45	82.54	136.16	62.31	48.40	41.73
K ($cmol_c\ kg^{-1}$)	10.66	13.28	9.59	4.45	4.19	5.07
Mg ($cmol_c\ kg^{-1}$)	4.94	8.71	10.66	7.09	5.04	6.03
P ($mg\ kg^{-1}$)	13.52	11.94	20.39	1.95	13.43	16.78

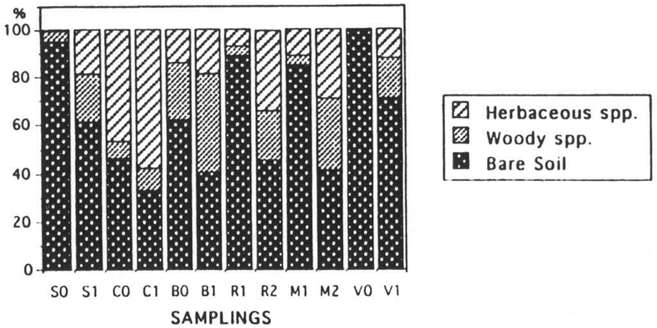

Figure 12: Cover percentage by woody species, herbaceous species and bare soil in the two first samplings of each *Quercus pyrenaica* ecosystem. (Zones **S**, **C** and **B** burnt in spring. Zones **R**, **M** and **V** burnt in summer. Numbers indicate years after fire: **0** = some weeks after fire, **1** = one year after fire, **2** = two years after fire).

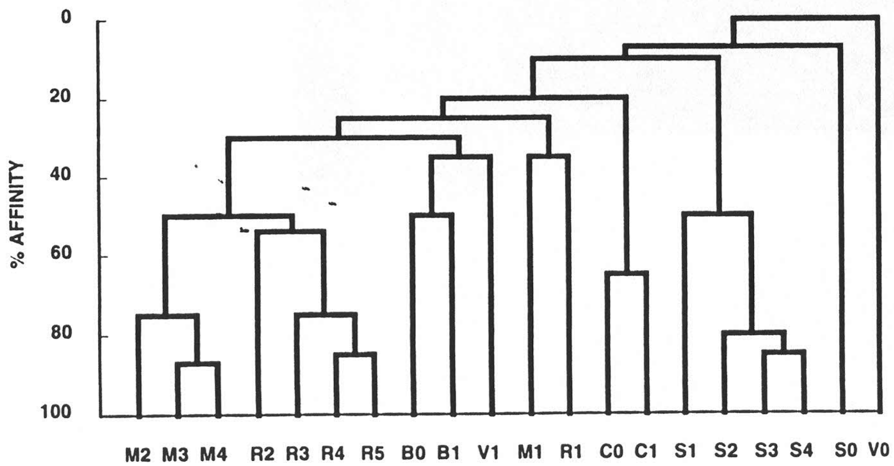

Figure 13: Affinity analysis (by Motika Index) between the samplings of each *Quercus pyrenaica* ecosystems. (Zones **S**, **C** and **B** burnt in spring. Zones **R**, **M** and **V** burnt in summer. Numbers indicate years after fire. The most degraded zone is S and the least degraded is C).

3.2 Response in shrub communities

3.2.1 Communities dominated by *Erica australis*

Shrub communities cover a large surface area in Spain (26%). The presence of this type of formations reflects the influence of man throughout history. According to data from the Ministerio de Agricultura[23] 32% of the surface area of León province is covered by woody shrub formations. If fires, as one of the main causes of the formation of these communities, are considered to have increased exponentially in the last few years, it is to be excepted that the surface area they now occupy has been greatly increased.

The main causes of shrub community origins are:

- Forest fires of tree masses directly or indirectly caused by man.
- Cutting down or felling of trees to satisfy the need for wood for different purposes throughout history.
- An indirect action through excessive grazing followed by abandonment.

Table 3. Mean cover (and standard deviation) in original state: previous treatments of a shrub community dominated by *Erica australis*.

	Plot 1		Plot 2		Plot 3	
	X	d	X	d	X	d
Erica australis	31.4	24.5	28.6	19.9	38.3	25.9
Erica umbellata	17.6	16.2	38.4	18.2	5.0	11.1
Arctostaphylos uva-ursi	43.6	39.4	14.6	24.2	43.1	34.9
Halimium alyssoides	3.9	7.2	6.7	6.6	5.8	6.7
Genistella tridentata	0.5	2.5	1.6	4.3	1.5	4.8
Calluna vulgaris	21.5	18.6	17.8	14.2	25.1	18.1
Quercus pyrenaica	3.9	7.2	1.0	5.0	0.9	4.6
Halimium umbellatum	0.2	0.8	0.4	1.8	0.3	1.7
Herbaceous spp	+		+		+	

X = Mean values of cover
d = Standard deviation
+ = Mean cover < 1%

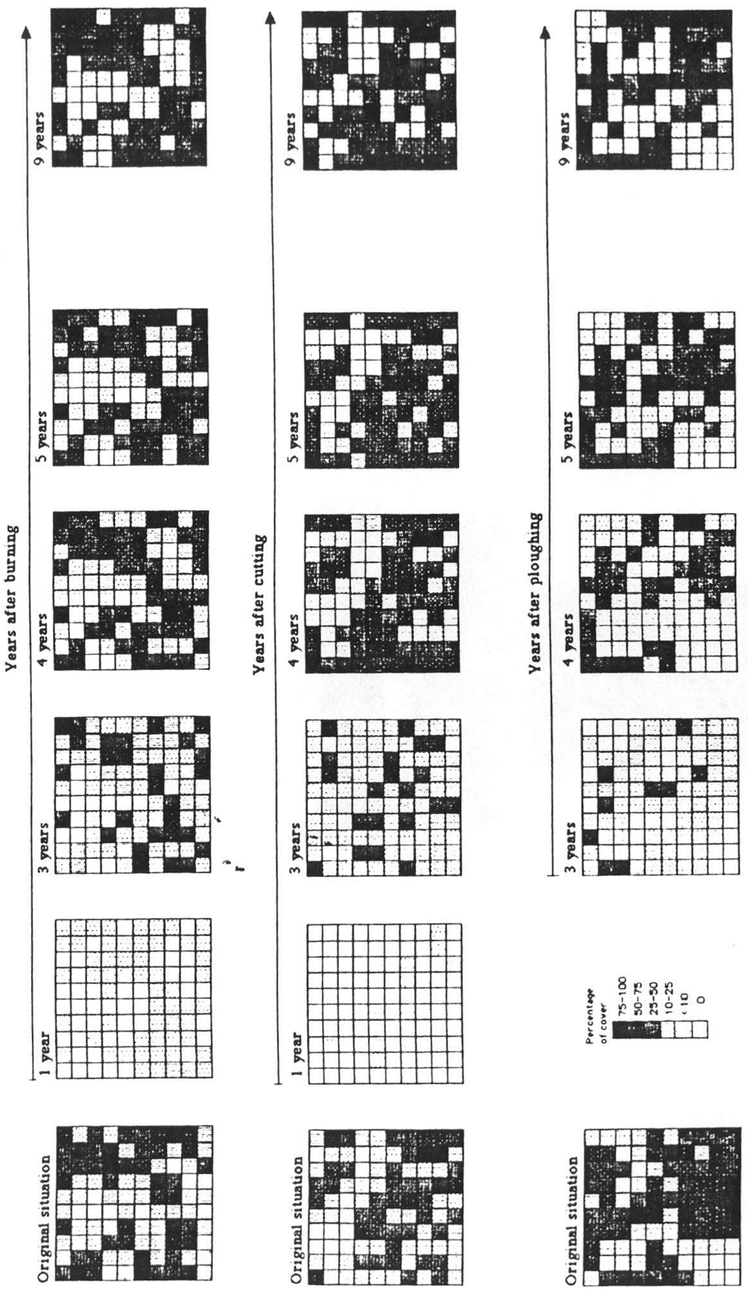

Figure 14: Spatio-temporal dynamics of cover of *Erica australis* after different treatments (burning, cutting and ploughing).

Among shrub communities those that appear most frequently are heathlands dominated by *Erica australis*. Other species also accompany the dominant species: *Erica umbellata, Calluna vulgaris, Halimium alyssoides, Halimium umbellatum, Genistella tridentata, Arctostaphylos uva-ursi* and *Quercus pyrenaica* in a shrub state (Table 3).

Vegetation begins to recover fast in the heathlands dominated by *Erica australis*. Dominance by the woody species, basically *Erica australis*, is clear from the first moments post-fire (Calvo *et al.*[24,25]). This species uses vegetative sprouting as its main mechanism, which allows very rapid spatial occupation and increases its cover values over time (Fig. 14). Cover values are high from about the fourth year and do not present any significant differences in comparison with the original values (Fig. 15). From this moment on the increase in height is much more marked than that in cover. The rest of the woody species typical to these heathlands show different response patterns. *Halimium alyssoides, Halimium umbellatum* and *Genistella tridentata* are species favoured by fire, since it allows an increase in their cover values, in comparison with

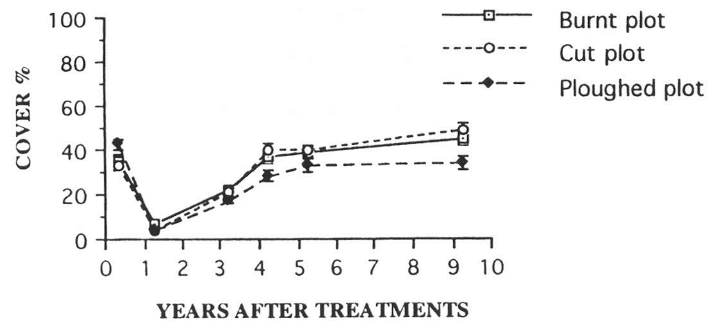

Figure 15: Cover percentage and standard error of *Erica australis* after experimental treatments.

the initial ones, and in spatial occupation. *Arctostaphylos uva-ursi* protects itself easily from fire because of its characteristics and fleshy leaves. Sprouting is the main recovery mechanism and so its distribution and cover increase in space and time after a fire. Practically all the recovery comes from seed in *Erica umbellata* and *Calluna vulgaris*, and so they are at a disadvantage when competing with sprouting species (Table 4). Both are capable of occupying their original space but do not attain original cover values at the same speed as the dominant species (Calvo[26], Calvo *et al.*[27]).

Germination tests have been carried out with seeds from the dominant species in these communities in order to study their response to high temperatures during a fire. It has been observed that species like *Erica australis*, whose recovery mechanism after a disturbance is sprouting Calvo *et al.*[27]), have very low germination under control conditions and the same occurs when their seeds are subjected to high temperatures. In contrast, species like *Halimium umbellatum, Halimium alyssoides* and *Genistella tridentata*, which use seeds as the main recovery mechanism, respond positively with high germination percentages when their seeds are subjected to high temperatures.

The highest values for herbaceous vegetation (Fig. 16) appear in the first two years post-fire, as this allows the creation of open spaces which these species can occupy as competition from woody ones has been eliminated. From the eighth year post-fire herbaceous species are very scarce. This is due to competition for light, nutrients and space between the woody and herbaceous species. The herbaceous annuals in these areas reach maximum cover values during the second to third year. However, they are not dominant due to these communities being subjected to this type of disturbance with great frequency over many years. This has therefore had an influence on the decrease in seeds present in the soil (Calvo *et al.*[27]).

The richness and diversity values are maximum between the fourth and fifth years post-fire (Fig. 17), coinciding with the greater presence of herbaceous species. From that moment on the woody species are strongly dominant and this produces a decrease in both parameters.

Table 4. Mean cover values of the most abundant species in the original situation (0) and in the subsequent years (2, 4...12) after burning in a shrub community dominated by *Erica australis*.

	years after fire																	
	0		2		4		5		7		8		9		11		12	
	X	*sd*	X	*sd*	X	*sd*	X	*sd*	X	*sd*	X	*sd*	X	*sd*	X	*sd*	X	*sd*
Woody spp																		
Arctostaphylos uva-ursi	43.6	*39.6*	27.0	*25.1*	25.0	*32.8*	23.2	*35.0*	38.0	*37.5*	55.0	*39.2*	50.0	*38.9*	27.0	*29.5*	41.0	*38.6*
Calluna vulgaris	21.5	*18.6*			2.0	*2.7*	1.4	*0.9*	3.8	*1.8*	7.6	*4.3*	7.2	*5.2*	8.4	*5.0*	10.2	*5.7*
Genistella tridentata	0.5	*2.5*			4.0	*6.5*	0.4	*0.6*	0.2	*0.5*	1.0	*2.2*	0.2	*0.5*	1.6	*2.0*	1.0	*1.2*
Erica australis	31.4	*24.6*	25.4	*19.4*	34.0	*8.9*	44.0	*32.1*	48.0	*16.8*	64.0	*26.6*	67.0	*14.4*	33.0	*34.8*	42.0	*19.2*
Erica umbellata	17.6	*16.3*			1.6	*3.6*	3.0	*4.5*	3.0	*4.5*	4.4	*6.3*	8.6	*12.6*	14.0	*16.4*	10.0	*9.4*
Halimium alyssoides	3.4	*5.0*	2.8	*4.2*	2.2	*2.6*	3.4	*3.1*	6.0	*5.5*	5.8	*8.6*	6.2	*6.3*	4.6	*4.6*	5.6	*5.2*
Halimium umbellatum	0.2	*0.7*	0.6	*0.9*	2.0	*4.5*	2.4	*2.4*	2.6	*3.7*	1.4	*2.2*	1.4	*2.2*	1.6	*2.3*	1.6	*2.1*
Quercus pyrenaica	4.0	*7.3*	3.0	*6.7*	11.0	*13.4*	4.0	*6.5*	4.0	*8.9*	6.0	*10.8*	6.0	*10.8*	8.0	*8.4*	3.6	*6.5*

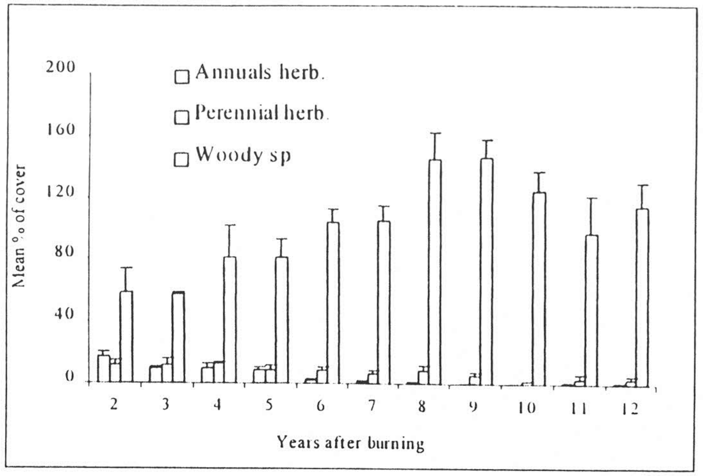

Figure 16: Mean percentage cover of biotypes (annual herbaceous species, perennial herbaceous species and woody species) and standard error in a heathland dominated by *Erica australis*.

The following stages in post-fire succession can be established in this type of community (Calvo[26]):

1st. 3-6 months. There is vegetative sprouting of woody species like *Erica australis* from the stocks present in the soil. Bare soil is present with a high percentage.

2nd. 1 year. Herbaceous annuals and perennials begin to germinate. The woody species continue to increase and sprout.

3rd. 2-3 years. Maximum herbaceous annuals and perennials are recorded. Cover increase by the woody species is considerable since seed germination appears as well as vegetative sprouting. Bare soil percentages are low.

4th. 4-5 years. The shrubland evolves towards a state similar to the original one and the herbaceous species begin to decrease.

5th. More than 5 years. The shrubland acquires a composition and structure similar to the original ones. The maximum increase is in height. The herbaceous species decrease significantly on being eliminated by competition from the woody ones. Bare soil values are as high as in the original state (Calvo[26]).

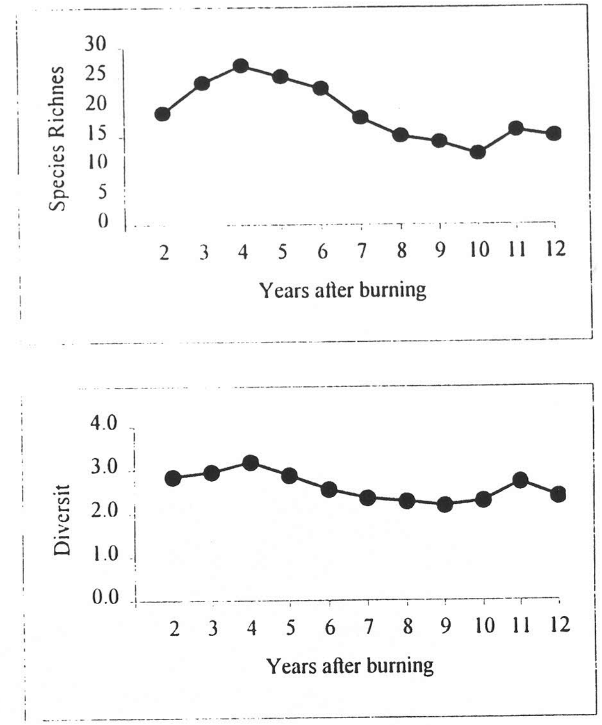

Figure 17: Values over time of species richness and diversity after burning in a community of *Erica australis*.

These communities usually develop on basically very acid sandy or sandy loam soils with a high organic material content and deficient in nutrients.

An increase in pH from 4.5 to 5.5 in the first cm of soil (Table 5) was found after the experimental burning of a shrubland dominated by *Erica australis*, although this pH increase is smaller at depth (Marcos[13]). The increase in pH is due to the incorporation of ashes into the soil as they have a pH of about 10. The effects of fire on organic material vary according to fire intensity. A slight increase in the organic matter content occurs post-fire in most cases but sometimes a significant reduction in content can be observed (Table 5). This is due to the high heterogeneity of these areas as regards soil and vegetation characteristics which determine fire behaviour to such an extent that high temperatures are reached at some points and remain high in the soil for some time (Marcos *et al.*[14]). The recovery of organic matter in these areas is slow with its two years, post-fire content remaining lower than that in the unburnt areas. The changes in total nitrogen content are related to the changes in organic matter, although not in the same proportion (Christensen[28]). The variations in nitrogen content are generally minimal after a fire as the temperatures reached on the surface do not usually exceed 200°C and so no significant transformations occur. The nitrogen content tends to increase slightly as time passes (Table 5) but does not show any important changes in general (Marcos[13]).

The phosphorus and assimilable cations increase after the fire to a smaller or greater degree depending on the initial soil content and the addition of these elements from the ashes left in the soil. It remains two years post-fire except for calcium and potassium, whose contents diminish (Table 5).

Table 5. Changes in soil properties before (C) and after experimental fire (0 = immediately after fire, 2 = two years after fire) in *Erica australis* heathland (mean values from four plots, in the first 2 cm).

	C	0	2
pH	4.55	5.34	5.77
C (%)	10.34	8.31	6.69
N (%)	0.57	0.57	0.62
Available P (ppm)	0.17	0.33	0.46
Available K (meq/100g)	0.49	0.69	0.32
Available Na (meq/100g)	0.02	0.04	0.02
Available Mg (meq/100g)	0.41	0.44	0.62
Available Ca (meq/100g)	1.03	0.87	0.62
Texture (%)			
Sandy	84.50	90.00	84.50
Silt	10.00	5.50	10.00
Loam	5.50	4.50	5.50

Texture and structure remain practically unchanged since fires are not usually so intense as to modify these properties. The small changes detected during community recovery are due to seasonal variations and the establishment of vegetation.

Two years after the fire some of the changes produced by it can still be observed, such as a higher phosphorus and assimilable cation content and a higher pH value. The rest of the properties will already have returned to their initial values. The difference as time passes between 0-2 cm depth and the rest is patent, the former showing the first clear seasonal change patterns whilst no tendency was observed in the rest (Marcos[13]).

In comparison with burning, the behaviour of these plant species after cutting is very similar, since the main recovery mechanism is vegetative sprouting. In contrast, after uprooting, considered the most drastic disturbance, the only reproductive strategy that can be used is germination, as the possibility of sprouting has been eliminated by pulling out the roots. This means that the time needed to start regeneration is longer (two years), although the situation is similar to that of the other two treatments and the original one after four-five years (Calvo *et al.*[25]).

3.2.2 Communities dominated by *Calluna vulgaris*

Another of the shrub communities widely extended throughout the Cantabrian mountain range is that of damp heathlands dominated by *Calluna vulgaris*, which represent birch (*Betula*) grove substitution stages when degradation is marked. Besides the dominant woody species the others, which have high cover values, are *Erica tetralix* and *Vaccinium myrtillus* (Table 6). None of these species has a height over 50 cm. The origin and maintenance of these formations is related to disturbances caused by humans, such as burning, cutting vegetation followed by pasture abandonment, and ploughing. Burning occurs most frequently (Calvo[26], Calvo *et al.*[29]).

The herbaceous species are generally clearly dominant in the first few years after the three disturbances. Perennials are the most dominant herbaceous species in the first five years after burning. This can be explained by their using underground organs as survival mechanisms. In addition the elimination of competition with ericaceae and the appearance of favourable environmental conditions, such as an increase

Table 6. Mean cover and standard deviation of the most abundant woody species in the original situation (0) and in subsequent years (1, 2, 3...10) after experimental treatments (Burning = B; Cutting = C; Ploughing = P) in a heathland dominated by *Calluna vulgaris*.

	Calluna vulgaris	*Erica australis*	*Erica tetralix*	*Vaccinium myrtillus*
B0	**86.7 (10.5)**	**2.0 (9.6)**	**0.8 (3.0)**	**2.4 (1.5)**
B1		0.4(0.5)		2.0 (1.2)
B2	13.3 (12.3)	0.4 (0.9)		8.6 (3.5)
B3	15.0 (5.0)	0.6 (0.9)		16.0 (6.5)
B4	0.2 (0.4)			16.0 (2.2)
B5	0.8 (1.3)			14.2 (10.6)
B9	15.0 (10.6)	1.6 (3.6)	3.6 (6.5)	16.0 (8.9)
B10	22.0	1.2 (1.6)		19.6 (14.9)
C0	**75.2 (12.6)**		**18.5 (11.0)**	**0.5 (1.0)**
C2	0.4 (0.5)		9.2 (10.5)	7.6 (4.7)
C3	1.4 (0.9)		17.2 (14.5)	4.4 (2.5)
C4	7.2 (4.1)		32.0 (18.2)	6.6 (2.3)
C5	2.8 (4.2)		25.0 (22.4)	18.0 (15.6)
C9	7 (10.9)		68.0 (30.5)	9.0 (4.2)
C10	10.0 (5.0)		44.2 (35.3)	5.8 (2.2)
P0	**86.5 (14.4)**	**1.3 (7.2)**	**1.2 (4.5)**	**2.6 (1.7)**
P1				
P2	1.2 (2,2)			0.8 ((0.5)
P3	2.4 (4.3)	0.2 (0.4)		1.4 (2.1)
P4		0.2 (0.4)		4.8 (3.4)
P5	1.6 (1.9)	0.2 (0.4)		3.8 (2.8)
P9	16.6 (10.1)	3.6 (6.5)		4.4 (2.6)
P10	36.0 (9.6)		0.6 (1.3)	9.2 (3.7)

in light and soil nutrient availability, have to be taken into account. The woody species increase their cover values slightly in the first three years, due to the recovery of the dominant species, *Calluna vulgaris*. However, many days being covered by snow and the secondary effects this can produce, like decomposition processes caused by fungi, occasion a high death rate among this species. Recovery of this species is high from the sixth year with no significant differences in comparison with the initial situation. Elimination of aboveground biomass after cutting does not

affect the regenerative organs but competition with woody species disappears and so the herbaceous species gain in importance. This treatment favours massive sprouting by *Erica tetralix* and its spatial occupation is considerable after 10 years. Ploughing is more drastic and influences by delaying recovery (Calvo[26]).

The difference between the response to these treatments may be found in the initial situation and is maintained and accentuated after them, as in the case of *Erica tetralix*, much more abundant in the cut plot both before and after cutting. The plots were more similar in their original state throughout the area due to the dominance of *Calluna vulgaris* (Calvo[26]). However, the fact that the dominant species takes a long time to recover accentuates the differences between the three disturbances. Nevertheless, no significant differences appear in the total cover vegetation percentages between the three disturbances in this type of community after 10 years. The temporal heterogeneity values (Fig. 18) do not decrease in time, which indicates that the community has not reached complete structural stabilization. Thus, regeneration in this type of community is much slower than that of *Erica australis* heathlands due to their short vegetative period and the prolonged period of time they are covered by snow.

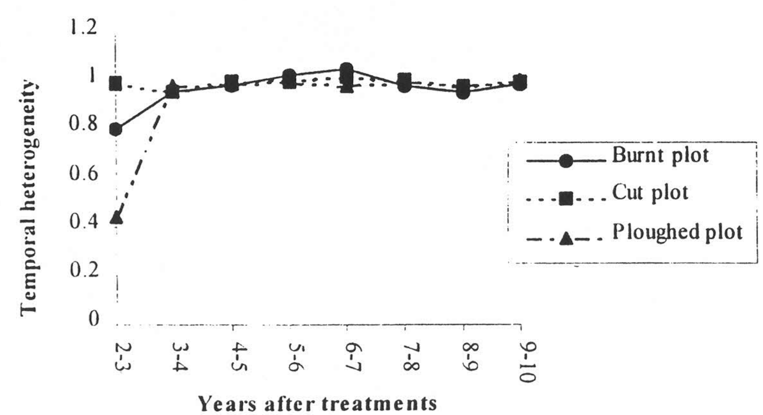

Figure 18: Values over time of temporal heterogeneity after burning in a community of *Calluna vulgaris*.

Germination tests were carried out in order to study the germination response of the dominant species, *Calluna vulgaris*, at high temperatures during the fire. Given that this species recovers from a disturbance by seed germination, the germination response to high temperatures was examined to see if it was really positive. High germination percentages are recorded when the seeds are subjected to more than 75°C.

3.2.3 Communities dominated by *Cistus*

Cistus species, which proliferate appreciably in some burnt areas, are among those considered as typical pyrophytes which reproduce actively after a fire but only via seeds. However, Trabaud[6], when discussing the term 'pyrophytes', considers these species rather as heliophilous which colonize the altered areas, free of aggressive competitors.

In a study carried out on two almost monospecific communities dominated by *Cistus ladanifer* and *Cistus laurifolius*, respectively, heat was seen to stimulate germination but also the regeneration capacity of both species after other types of disturbance (Tárrega *et al.*[30,31], Luis *et al.*[32]). The two communities were very close, less than 1 km apart. Experimental plots were established in each area: three in the case of the *Cistus ladanifer* community, which were subjected to burning, cutting and ploughing, and two in the *Cistus laurifolius* dominated one, which were subjected to burning and cutting. Differences were maintained eight years after the disturbances (Fig. 19). Cover was also greater in the burnt plots in the first few years but was then similar in all of them. However, the height reached by the *Cistus ladanifer* seedlings was significantly greater in the ploughed plot which had the lowest density. No seedling height differences were appreciable between the burnt and cut plots. Although recovery of both species was very good, and slightly faster in *Cistus ladanifer*, the characteristics existing before the disturbances had not yet been attained after eight years with lower density and greater height, although the cover values were fairly similar.

As regards community recovery a proliferation of herbaceous species was observed with a maximum in the first year and more marked in the cut plots than the burnt ones, due to the faster recovery by the dominant woody species after burning (Luis *et al.*[32]; Tárrega *et al.*[33]), which checks herbaceous expansion (Fig. 20), contrary to which happened in *Erica australis* heathlands. *Cistus ladanifer* recovery in the ploughed plot was initially slower but herbaceous cover was not so

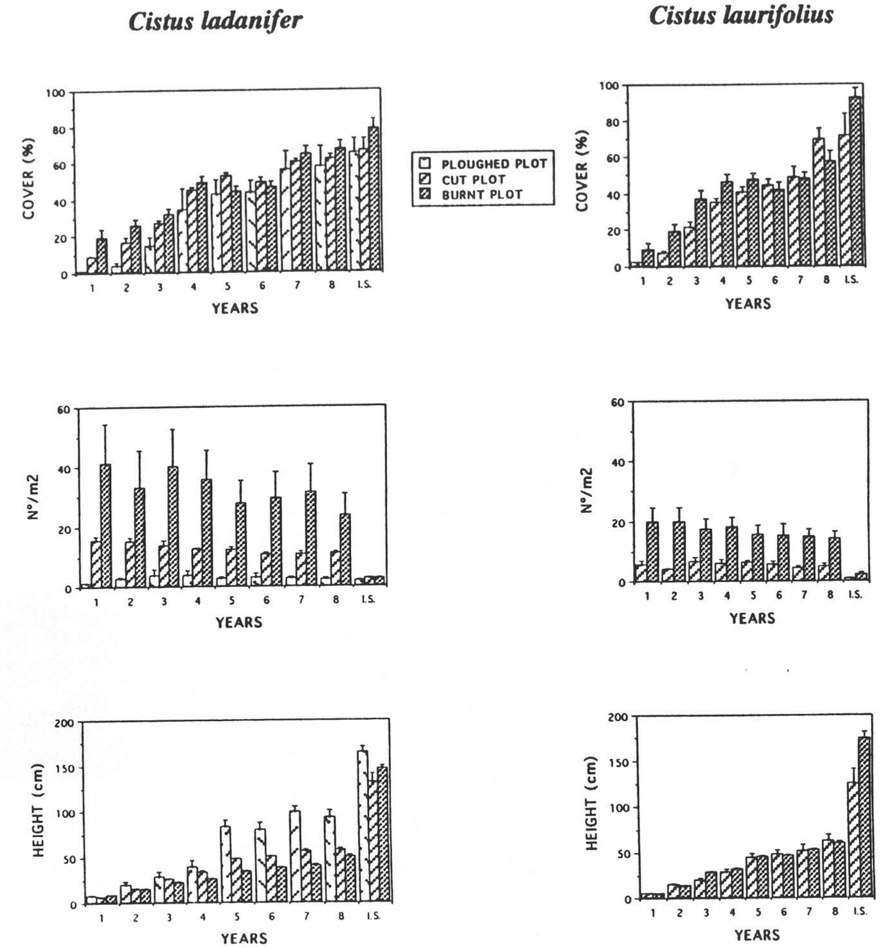

Figure 19: Cover, density and height values of both *Cistus* spp. seedlings in the experimental plots during the first eight years after disturbances, comparing with the initial situation (I.S.).

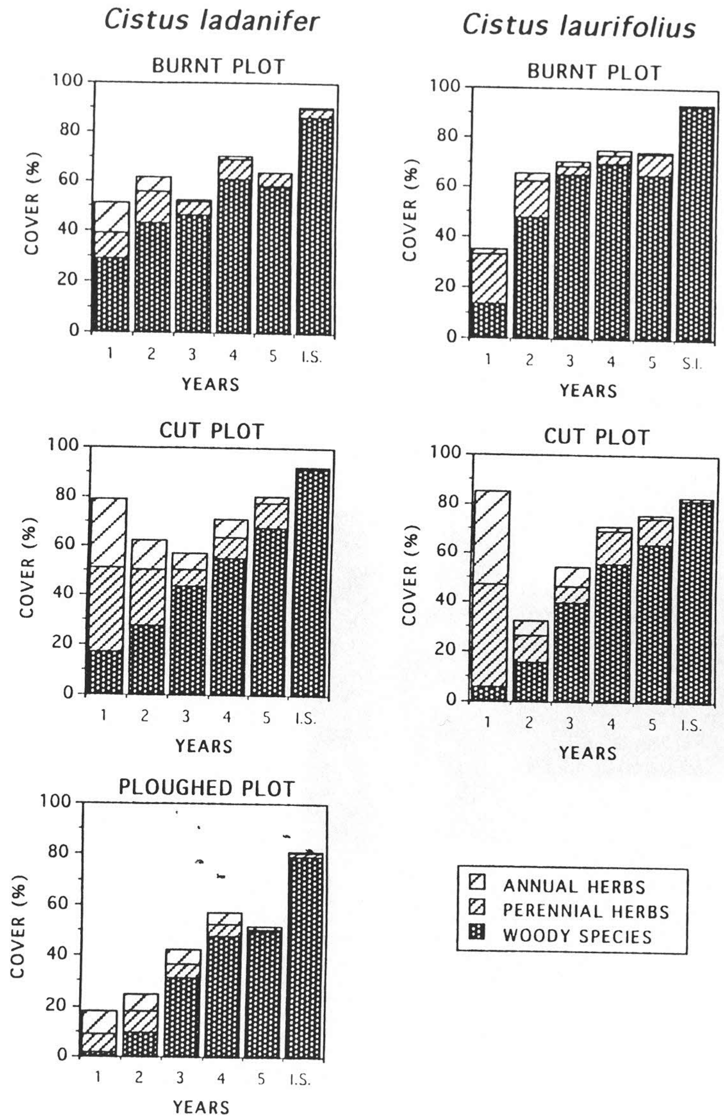

Figure 20: Cover percentage by annual herbaceous spp., perennial herbaceous spp. and woody spp. in the experimental plots during the first five years after disturbances, comparing with the initial situation (I.S.).

marked as in the cut plot (Tárrega *et al.*[30]); this was probably due to the alteration in soil structure caused by ploughing with the subsequent effects on the seed bank. Coinciding with this, the greatest species diversity and richness occurred in the first two years after the disturbances and then tended to diminish (Tárrega *et al.*[31]), (Table 7). On comparing the samplings carried out on the burnt and cut plots in both areas in the first five years after the disturbances using multifactorial analysis, a clear separation between the plots of both areas (one dominated by *Cistus ladanifer* and the other by *Cistus laurifolius*) can be appreciated, whilst none is detected as regards the type of disturbance. The tendency towards autosuccession is also clear if the analysis is repeated without the two dominant species. Separation between areas is still seen, above all in the initial samplings because of the presence of species like *Agrostis capillaris, Avenula marginata, Hypericum perforatum, Hieracium pilosella*, etc., which only appear in the area dominated by *Cistus ladanifer*, or like *Arenaria montana, Genistella tridentata, Adenocarpus complicatus, Centranthus calcitrapa* or *Trifolium arvense*, associated with the area dominated by *Cistus laurifolius* (Fig. 21). The differential presence of species is probably due to the fact that they were already in the area before the disturbances. The temporal tendency is also clear with an association among the samplings carried out in the first few years on herbaceous species, like *Senecio gallicus, Lactuca virosa* and *Holcus mollis* in the *Cistus ladanifer* dominated area, and *Tuberaria guttata, Rumex acetosella* and *Cerastium glomeratum* in the *Cistus laurifolius* dominated one, or those common to both, like *Hypochoeris radicata, Sonchus asper, Jasione montana, Trifolium campestre*, etc.

In spite of the dominant woody species being obligate seeders, recovery by autosuccession is very fast, germinating from the soil seed bank as soon as the first rains fall.

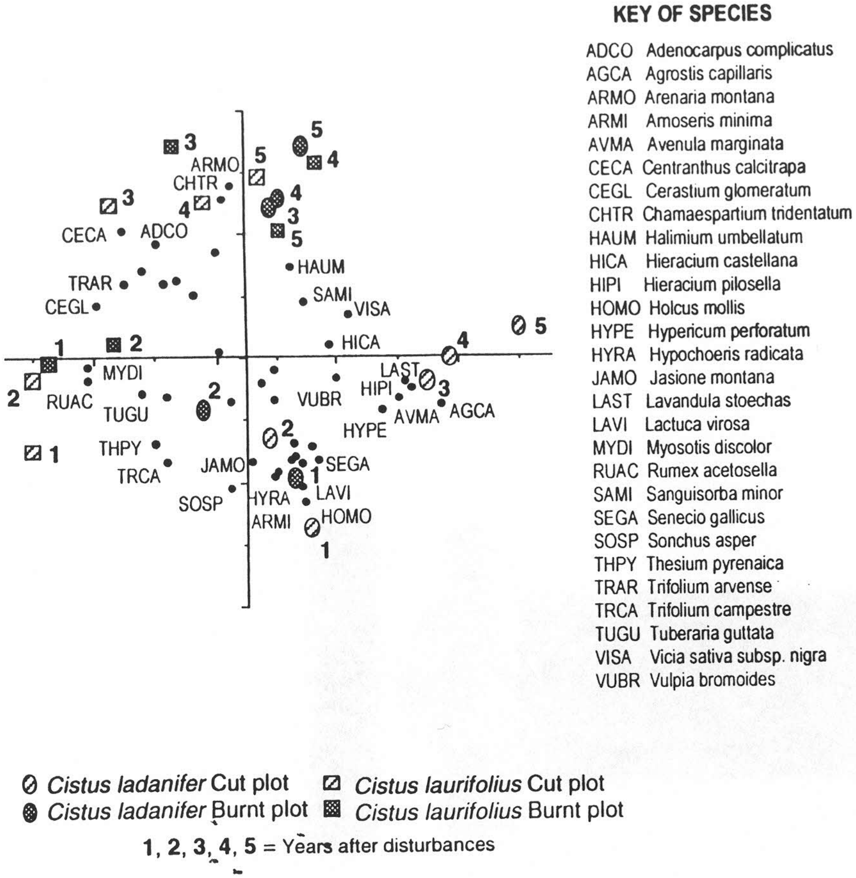

Figure 21: Location of samples and species from the cut and burnt plots of both *Cistus* shrubland in the plane defined by the first two axes of the Correspondence Analysis. Both *Cistus ladanifer* and *Cistus laurifolius* have been removed in this analysis.

Table 7. Species richness and diversity (Shannon Index, H′) in the *Cistus* experimental plots in the first five years after disturbances.

		Years after disturbances 1	2	3	4	5
Species Richness (no. of spp.):						
C. laurifolius	Cut plot	20	25	24	18	17
	Burnt plot	18	22	17	13	13
C. ladanifer	Cut plot	34	30	20	21	16
	Burnt plot	23	22	7	10	4
	Ploughed plot	18	22	16	18	18
Species Diversity (H′):						
C. laurifolius	Cut plot	2.7	3.1	2.4	1.9	1.7
	Burnt plot	2.8	1.9	1.6	1.7	1.7
C. ladanifer	Cut plot	4.1	3.0	2.2	2.3	1.8
	Burnt plot	2.9	1.9	1.1	1.3	1.0
	Ploughed plot	3.3	3.4	2.2	1.7	0.7

4 Final remarks

Four phases can usually be distinguished in post-fire recovery in these communities, differing in length according to fire intensity and the type of vegetation involved (degree of maturity before the fire):

1. Bare soil.

2. Sprouting of natural species to the ecosystem: generally woody ones but also herbaceous perennials whose underground organs survive the fire. They usually begin to appear a few weeks after the fire.

3. Proliferation of herbaceous species, usually annuals, whose seeds were already in the area before the fire but had to wait for the first rains and favourable temperatures for germination, or invading species which arrive by anemochory (wind) or zoochory (animal) dispersion. They are usually abundant one to three years after the fire and then displaced as the woody species regain their dominance.

4. Recovery of the structure similar to that existing before the fire, although always with some loss in maturity to a greater or lesser extent.

The decrease in diversity over time in shrub communities, to a situation similar to the one existing prior to the disturbances, is gradually regained according to most of the authors studying post-fire recovery (Hanes[3], Trabaud & Lepart[34], Casal[35], Bond & Van Wilgen[36]) and confirms the risk of using only this parameter to estimate ecosystem maturity. The greater diversity, associated with the first phases of herbaceous proliferation, is transitory in these secondary communities prone to frequent disturbances.

An awareness of the occupation of the tridimensional space in the development of the plant community to the climax is necessary. In this way, the evaluation of sectorial diversity in terms of biotypes is essential. A dynamic interaction is established between these elements in relation to theirs evolutive traits. Some mathematical expressions demonstrating these sectorial interactions among consecutive processes of disturbance in the ecological succession, could be the most correct mechanism for explaining numerical relationships between species and their significance in the maturity of the community.

Recovery by autosuccession is partly responsible for spatial microheterogeneity. The mechanisms of recovery by vegetative sprouting guarantee individual continuity in the same microspace previously occupied. In addition the soil seed bank is also characterized by high spatial variability because of the dominance of species with dispersion mechanisms like barochory or autochory, with a short spatial projection but with banks which persist through time (Trabaud[37]). This allows them to survive and germinate as soon as a disturbance leaves an empty space. Fire is also an additional heterogeneity factor on a small scale (Bond & Van Wilgen[36]) as it burns at different intensities, thus conditioning differences in the survival of the species and the effects on their seeds. Moreover, the unequal spread of ashes during the post-fire months also contributes to that heterogeneity by distributing the nutrients irregularly. This microheterogeneity has important implications when planning the experimental design for fieldwork (plot size or using the synchronic or diachronic method in succession studies).

On the other hand, the recovery response observed in these ecosystems confirms the importance of disturbances in the conservation of species and landscape diversity (Naveh & Liberman[38]). However, every concrete situation has to be studied. Bond & Van Wilgen[36] state that support for intermediate disturbance hypotheses from fire studies is less than unanimous and point out the problems of the extreme scale

dependence of measures of diversity and disturbance effects on community heterogeneity.

The present ecosystem pattern is the result of balanced exploitation-conservation, each situation corresponding with a different level of disturbance by human action (González-Bernáldez[39]). The search for the optimal situation in each area is of the utmost importance for correct management.

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Chapter 3

Functioning and dynamics of plant communities in central and southern Spain

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Abstract

The Iberian Peninsula presents a high number of plant species. However, the most important characteristic of the Spanish flora is its richness in endemic and subendemic taxa (27.63% of the flora), the highest among all the European countries. At least two-thirds of Iberian endemisms are found in the southern half of the Peninsula as a consequence of the paleoclimatic and greater environmental heterogeneity.

The central and southern parts of the Iberian Peninsula have suffered the same alterations as a result of human intervention as the rest of the Mediterranean region. The climax vegetation of extensive areas has completely disappeared, but in central and southern Spain well-preserved natural vegetation remains. In this chapter, the principal floristic, ecological and dynamic characteristics of the extensive plant formations existing in the southern half of the Iberian Peninsula are described. Responses of these formations after fire and the role that seed bank plays in the plant regeneration after this perturbance are noted. Furthermore, the very important ecological role of the bryophyte communities in the recolonization of burnt soils in this ecosystem is discussed.

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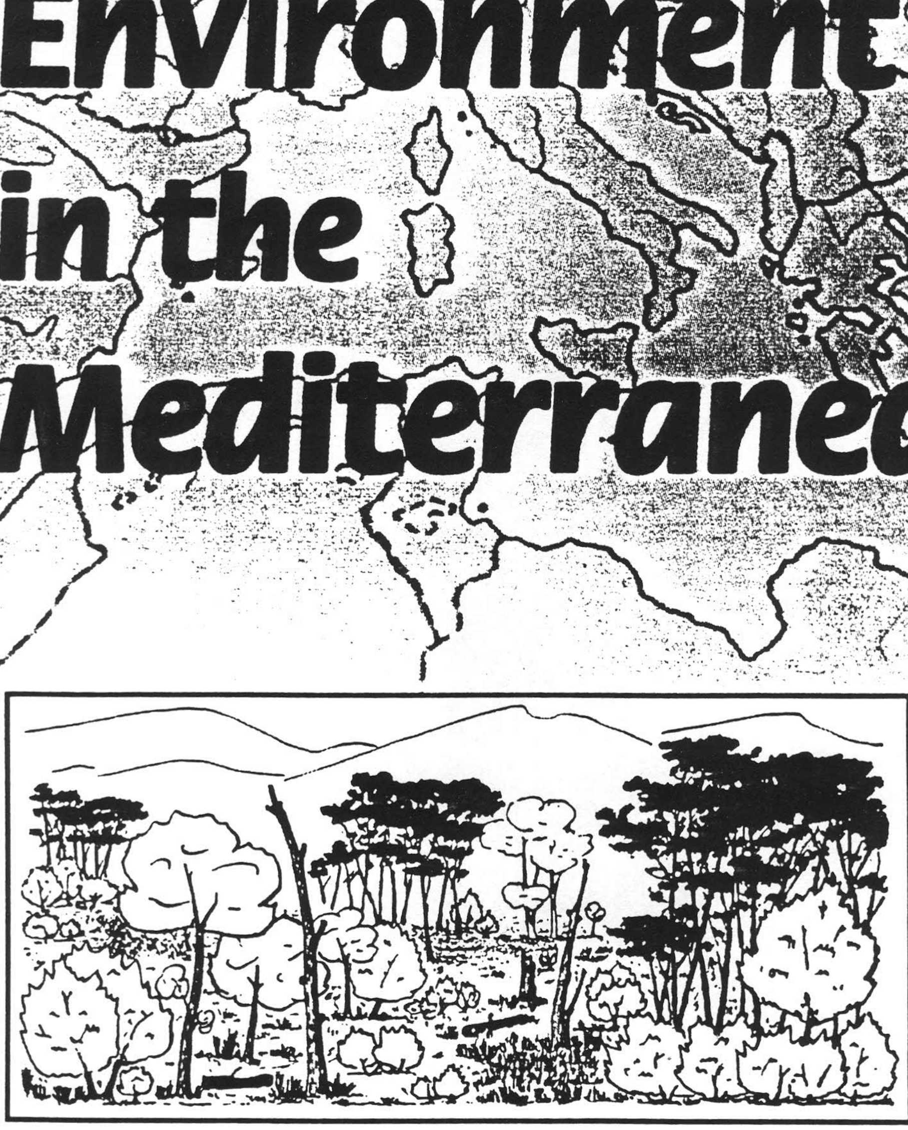

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