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Space-time distribution patterns of *Erica australis* L. subsp. *aragonensis* (Willk) after experimental burning, cutting, and ploughing

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Abstract

The response of *Erica australis* to experimental burning, cutting and ploughing treatments was studied in two heathland communities where it was dominant. The treatments represent those most frequently originated by humans on these heathland communities throughout history. The response of this species in a community where it is dominant and there is no strong interspecific competition was also compared to that produced by it in a community where there is competition. It can be observed that the response to burning and cutting treatments is very similar with very fast spatial occupation in the first few years. From the point of view of time cover values increased in a pronounced manner during the first few years and this increase was stabilized from the fourth year. However, from this moment on a greater increase in this species' maximum height is evident. The response to ploughing is slower according to recovery mechanism (seedlings). Recovery is comparatively less in the area where there is no strong competition than in that where it exists between species.

Résumé

Dans deux communautés de bruyère dominées par *Erica australis* on a étudié la réponse de cette espèce aux traitements expérimentaux de brûlage, coupe et labour. Ces traitements représentent les actions les plus fréquentes que l'homme a exercé sur ces communautés de bruyère tout au long de l'histoire. De la même façon, on a fait la comparaison de la réponse de cette espèce quand elle se trouve dans une communauté dominée principalement par elle, où elle n'y a pas une forte compétition entre les espèces, avec la réponse quand elle se situe dans une communauté où plusieurs espèces coexistent. On observe que la réponse aux traitements de brûlage et coupe est très semblable, en présentant une occupation spatiale très rapide pendant les premières années. Du point de vue temporel, leurs valeurs de couverture augmentent de façon plus prononcée pendant les premières années, et c'est à partir de la quatrième année que ce développement se stabilise. Cependant, c'est à partir de ce moment là qu'on remarque une augmentation plus grande en ce qui concerne la hauteur maximale de cette espèce. La réponse au traitement de labour est plus lente en relation avec la régénération par semences. L'effet de la compétition se traduit par une récupération qui suit un mode d'augmentation opposé à la situation originaire. Dans la surface où il n'existe pas une forte compétition, la récupération est comparativement plus faible que dans la station où il y existait une compétition entre les espèces.

Mots clés: Maquis, Mécanismes reproductives, Perturbations expérimentales, Régénération, Rejets

Introduction

Shrub communities cover a wide surface area (33% of total area) in the province of León in the NW of the Iberian peninsula, according to the Spanish Ministery of Agriculture (1984). Heathland stands out as the dominant shrub formation (Luis et al. 1989). These communities reflect the way of life that has characterized our civilization throughout history. The first arboreal formations were subjected intensely to the actions of humans as time passed (Calvo 1993). Forest fires stand out amongst the most important ones (Le Houerou 1969; Naveh 1975; Trabaud 1980, 1991; Casal 1985, 1987; Luis et al. 1989; Clement & Touffet 1990; Calvo 1993) as well as cutting (Naveh 1982; Cody 1986). Both provoke the appearance of a mosaic of ecosystems which represents states of degradation (Di Castri 1981).

Amongst these states of degradation, shrub communities that have a long history of use and treatment by humans fundamentally based on the application of fire, cutting and ploughing are included. Fire has been the most frequently used of the three (Trabaud & Lepart 1980, 1981; Gimingham et al. 1981; Mallik & Gimingham 1983; Ariatnoutsou-Faraggitaki 1984; Casal 1987; Trabaud 1987, 1991; Calvo et al. 1990, 1992; Tárrega et al. 1995; Clemente et al. 1996). It has significant effects on the plant species composition of the community mainly due to the temporary destruction of dominant plants. This dominance is not generally reestablished until some years have passed and other woody and herbaceous species become established during this period, thus increasing their importance values (Mallik & Gimingham 1983).

The second type of action is cutting, the products of which have different purposes: fuel, fertilizers, etc. (Casal 1985; Calvo et al. 1992). However, this type of handling does not seem to have a very disturbing effect either at a biocoenosis or a soil level (Corns & La Roi 1976; Casal 1985).

The third type of action on shrubland is ploughing it up in order to turn it into agricultural lands, a common practice in León province during the 1960s. This mechanism produces a great change in the whole vegetation community and the soil (Calvo 1993).

This study simulates experimentally the three actions of humans (burning, cutting and ploughing) on two heathland communities dominated by *Erica australis* L. subsp. *aragonensis* (Willk.) P. Count, which have different species richness. One of them has only one dominant species (*Erica australis*) and the other the same species co-dominant with *Erica umbellata*, *Artostaphylos uva-ursi*, *Calluna vulgaris*, *Halimium alyssoides* and *Halimium umbellatum*. (Tutin et al. 1964–1980)

The basic aims of this paper is to define the different recovery patterns through time of *Erica australis*, dominant in both communities but with different shrub specific richness, after being experimentally disturbed.

Materials and methods

Two study areas in the north-east of León province were chosen. One of them, called Cota Isestil (C.I.) is at a elevation of approximately 1000 m, exposed to all winds and its UTM coordinates are 30TUN248336. The second one is called Palacios de Rueda (P.R.), located 5 km south of C.I. and its UTM coordinates are 30TUN243292. It is on a plain approximately 1150 m of altitude and exposed to all winds.

The communities in both areas are defined as a variant of the *Genistelo tridentatae-Ericetum aragonensis-Citisetosum laurifolii* community with *Erica australis* L. subsp. *aragonensis* (Willk) (Rivas et al. 1987) as the dominant species.

It is climatologicalli classified as Mediterranean Area, with a period of summer drought between July and August (Ministerio de Agricultura 1980).

From the edaphic point of view the soil is classified as cambisol húmico (Junta de Castilla y León, 1987). Physico-chemical parameters of the soil of each communities were studied (Table 1) to determine whether structure values for both indicate reasonable stability, that is to say, they are not easily erodible (Cecconi & Polesello 1956). According to the granulometric analysis both areas are classified as very sandy. Organic material content as well as total nitrogen, Ca^{2+}, K^{+}, Mg^{+} is higher in P. R. than in C.I., whilst total phosphorus and assimilable phosphorus are higher in C.I. Both areas have acid soils (pH=5.5).

In each zone, a system of four plots, each measuring 100 m^2, with 3 m wide corridor in-betwing, was established in those areas with the most homogeneous characteristics possible in cover of species and in height. One of the four plots was kept with its original structure. The other three were subjected to experimental treatments of controlled burning of aerial biomass, cutting or felling at ground level of woody biomass and ploughing or uprooting of shrubs with the stump or roots.

The three treatments were carried out in the P.R. area in July 1985, and the burning and cutting in July 1985, and ploughing in July 1986, in the C.I. area.

In each plot, 100 sampling units measuring 1 m^2 were analyzed before and after carrying out the treatments at yearly intervals for the first five years of secondary succession and in the eighth and ninth years (uprooted C.I. plot and the rest of the plots, respectively). The percent cover in vertical projection of each woody species and the herbaceous ones considered as a whole, as well as the percentage of bare soil,

Table 1. Results of physico-chemical analysis of soil

Physical parameters	Humidity %	Structure	Sand	Lime %	Clay
C. I.	1.70	43.50	79.05	14.30	4.95
P. R.	4.10	46.45	74.50	18.50	2.90

Chemical parameters	O.M. %	C.E.C. meq/100gr	Nt %	Ca^{2+}	K^{+}	Mg^{2+} ppm	Na^{+}	P ppm	P_2O_5 ppm	pH
C. I.	4.50	65.00	0.16	1.0	2.0	0.4	0.5	16	36.64	5.5
P. R.	7.36	68.75	0.29	1.7	2.5	0.9	0.5	8	18.36	5.5

C.I.= Cota Isestil Area.
P.R. = Palacios de Rueda Area.
0.M. = Organic Matter.
C.E.C. = Catyon Exchange Capacity.

were evaluated for each sampling unit. From the fourth year, when the communities begin to show visible differences in maximun heights of the woody species, these values were noted for the higher plant for each sampling unit. This paper is only concerned with the results for *Erica australis*.

In order to compare the regeneration of this species an analysis of variance of repeated measurements in the comparisons of successive samplings of the same experimental treatment was used. In order to compare treatments with each other a two way analysis of variance followed by Scheffe's test (Scheffe 1959) was performed.

Results

The mean cover and standard deviation of shrub species in original state were represented in Table 2. Average cover values of *Erica australis* are higher in area C.I. (62–79%) than in P.R. (29–38%). However, from the spatial point of view the distribution of this species is similar in both areas. Average maximun heights were 80 cm in P.R. and 120 cm in C.I. (Calvo 1993).

Recovery after burning

It can be observed that *Erica australis* began to recover one year after burning in both areas (Figures 1 and 2) and occupied practically the whole plot spatially. Vegetative resprouting caused the spatial reoccupy from the same places in the original situation, with a similar pattern of cover in the sampling units. In successive years there is an increase in cover in each sampling unit. Considering the entire plots, temporally (Figure 3) the cover increased considerably until the fourth year with significant differences in this increase (Table 3). From the fifth year onwards the increase slowes.

Original cover values were surpassed and the increase stabilized in the P.R area from the fourth year. From this moment on, no significant differences were recorded (Table 3). However, the increase in cover in the C.I. area was pronounced throughout the study period, although it did not surpass the original values. It showed significant differences throughout the study period.

Recovery after cutting

Recovery began in the year after cutting (Figures 1 and 2) in both areas. From this moment on, there was an increase in spatial occupation with the whole plot covered in the end of the period of time observed. A quantitative increase in this species cover was also observed.

Cover increase in the C.I. area is lower than the increase shown after burning, whilst it is similar after both treatments in P.R.

Table 4 shows that significant differences exist in both areas during the study period.

Table 2. Mean cover (and standard deviation) of shrub species in original state

	Burnt plot		Cut plot		Ploughed plot	
	X	d	X	d	X	d
Cota Isestiil						
Erica australis	78.7	25.3	62.2	26.9	73.8	23.2
Halimium alyssoides	0.1	1.0	0.1	1.0		
Calluna vulgaris	0.2	1.4			0.1	0.5
Thymus zygis			1.2	2.6	0.6	1.9
Crataegus monogyna			0.5	3.6		
Lavandula stoechas			0.2	1.6		
Erica umbellata					2.3	8.3
Herbaceous spp	+		+		+	
Palacios de Rueda						
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
Chamaespartium tridentatum	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%.

Table 3. Results of comparison using the Scheffe test based on Repeated Measures Analysis of Variance of mean cover of *Erica australis* after burning treatment in both areas

	1st year	3rd year	4th year	5th year	9th year
Cota Isestil					
Original	211.578*	97.098*	50.771*	32.387*	12.562*
1st year		22.014*	55.062*	78.407*	121.03*
3rd year			7.445*	17.33*	39.809*
4th year				2.058	12.823*
5th year					4.608*
Palacios de Rueda					
Original	43.115*	6.783*	2.983*	2.857*	15.047*
1st year		15.695*	68.78*	68.17*	109.103*
3rd year			18.762*	18.445*	42,036*
4th year				0.00135	4.631 *
5th year					4.791*

* = Significant differences.

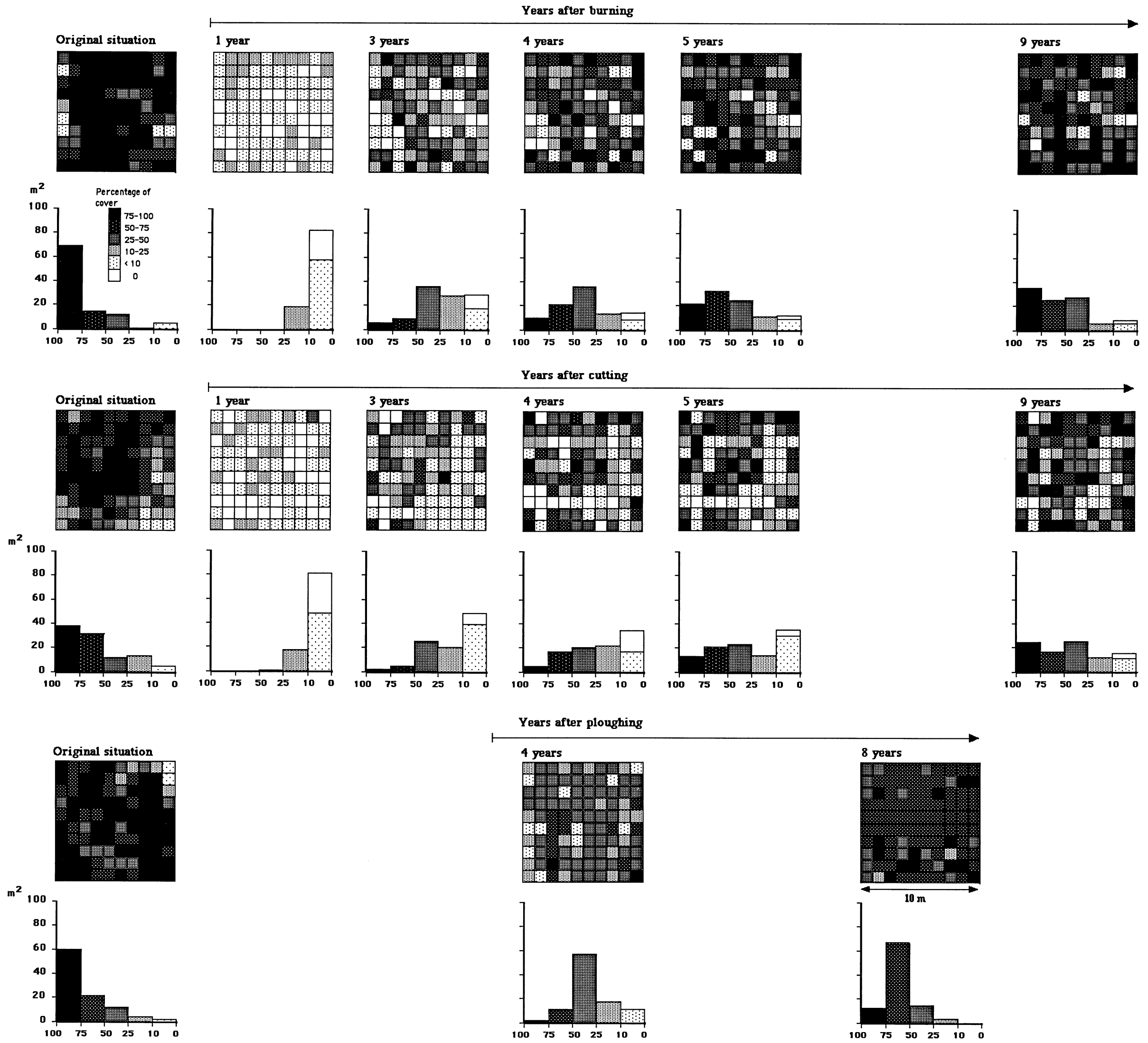

Figure 1. Spatial-temporal dynamis of cover and frequency of cover of *Erica australis* in area C.I. originally and after the experimental treatments

Recovery after ploughing

Recovery is slower after ploughing (Figures 1 and 2). Recovery was initiated in the second-third year, but with very low cover values. Due to this poor recuperation data were not taken in area P.R. until the third year and in C.I. until the fourth year. The original state was not attained in area P.R. during the nine-year follow-up (Figure 3), although the increase is very small from the fifth year and does not show any significant differences either compared to the original situation or successive years (Table 5). Recovery is much slower in area C.I., although cover attained during the eighth year is very high. There are significant differences throughout the study period (Table 5).

Recovery after the three treatments

On comparing the three treatments in both areas (Figures 1-3) the cover values attained by this species follow an increase pattern contrary to the original situation. The original values in area C.I. were high but not surpassed during the nine-year study. In area P.R. the original cover values were small and had already been surpassed by the fourth year. This is due to the fact that once interspecific competition is eliminated,

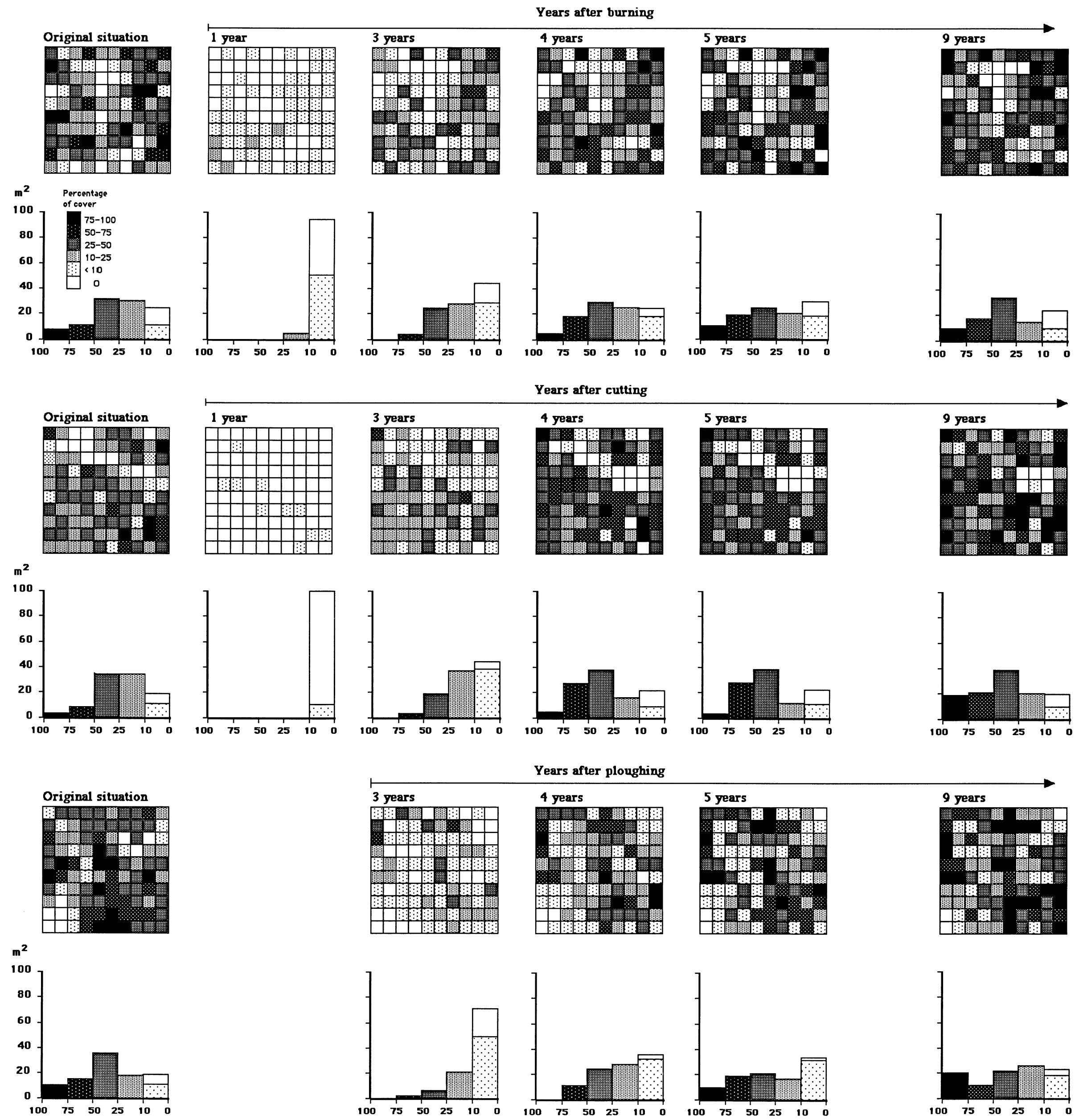

Figure 2. Spatial-temporal dynamics of cover and frequency of cover of *Erica australis* in area P.R. originally and after the experimental treatments

the dominant species occupies the greatest area during the first few years of the secondary succession process. The cover distribution frequency histograms show that the frequency distribution does not tend to a similar state to the original after disturbances in C.I. area, but tends rather towards a more homogeneous one. This is not so clear in the P.R. area.

In general it can be seen that cover values attained in the three treatments are similar in area P.R. after five years with no significant differences (Figure 3, Table 6). However, in C.I. there are significant differences between cutting and the other two treatments, with the smallest cover both in the original state as well as in the last sampling (9 years after burning and cutting and 8 after ploughing). Although the initial re-

Table 4. Results of comparison using the Scheffe test based on Repeated Measures Analysis of Variance of mean cover of *Erica australis* after cutting treatment in both areas

	1st year	3rd year	4th year	5th year	9th year
Cota Isestil					
Original	91.023*	52.45*	28.395*	19.906*	6.234*
1st year		5.282*	17.741*	25.796*	49.616*
3rd year			3.662*	7.732*	22.52*
4th year				0.752*	8.02*
5th year					3.861*
Palacios de Rueda					
Original	27.204*	5.807*	0.074*	0.42*	2.900*
1st year		7.873*	30.117*	34.382*	47.867*
3rd year			7.193*	9.349*	16.914*
4th year				0.141	2.047
5th year					1.113

* = Significant differences.

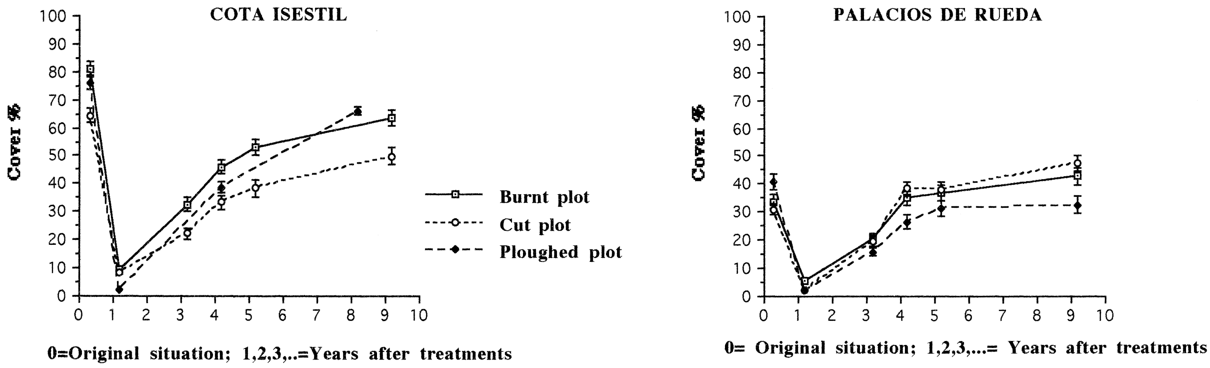

Figure 3. Cover percentage (and standard error) of *Erica australis* in both areas after treatments

cuperation after ploughing was slower, at the end of studied period the cover values were higher than in the other plots in C.I. but not in P.R.

Modifications in average maximun height

The most pronounced increase in height occurs once the plants have occupied practically all the space they originally had and this happens from the fourth year on.

The height attained after burning is greater than that reached after cutting and uprooting in both areas (Figure 4). Height increases in area C.I. throughout the study period shows significant differences between the three treatments. The heights attained in area P.R. after burning and cutting show no significant differences. After ploughing the increase is smaller, although mean maximum height of *Erica australis* is very similar in the three treatments in the ninth year.

As occurred with cover values, the average maximum height values in area P.R. surpassed the original values in the fourth year after burning, cutting and uprooting. The increase is very pronounced temporally, with significant differences (Table 7) in maximum heights after burning and ploughing. The increase after cutting is smaller after the fifth year and shows no significant differences. Original heights are not reached in any case in area C.I. There were only significant differences after the fifth year (Table 7).

Table 5. Results of comparison using the Scheffe test based on Repeated Measures Analysis of Variance of mean cover of *Erica australis* after ploughing treatment in both areas

	4th year	8th year
Cota Isestil		
Original	112.946*	7.797*
4th year		61.394*

Palacios de Rueda					
	1st year	3rd year	4th year	5th year	9th year
Original	51.7*	29.225*	5.158*	0.431	0.196
1st year		3.184*	24.197*	42.694*	58.27*
3rd year			9.827*	22.56*	34.214*
4th year				2.608*	7.368*
5th year					1.209

* = Significant differences.

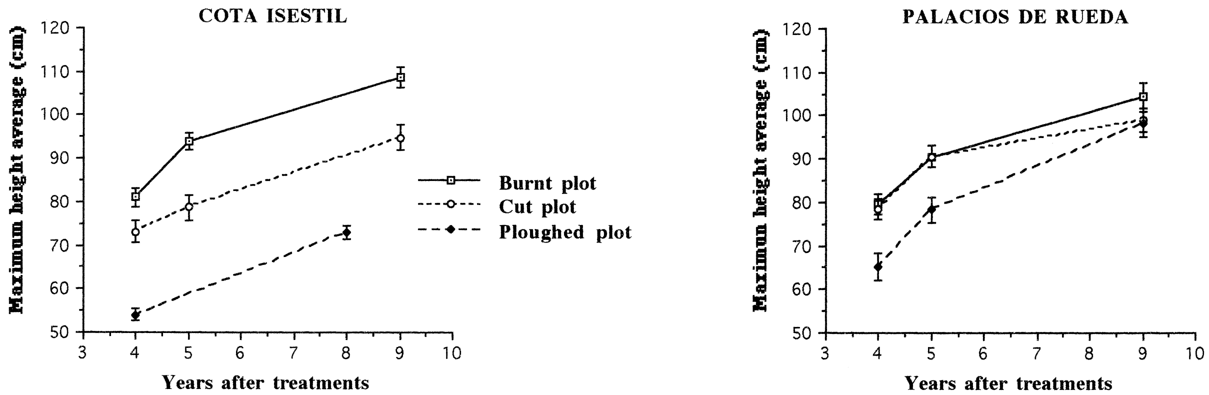

Figure 4. Mean (and standard error) of maximum heights of *Erica australis*.

Discussion

Vegetation developement after different disturbances tends the community to return to an initial stage and thus the beginning of autosuccession depends on the nature of recolonization. When seeds are the main source, the process is often slower than when vegetative regeneration takes place (Forgeard 1990). It is also obvious that vegetation structure in autosuccession processes will be more similar to the original when the recovery mechanism is vegetation resprouting. Keeley & Zedler (1978) and Malanson (1985) stated that germinative strategy is favoured in unusual disturbance conditions, i.e., intervals of 40 years, in shrubs on the Californian coast after fires whilst vegetative resprouting is favoured by shorter intervals of 20 years. In the heathland studied, the frequency with which they have suffered fires is relatively high. However, it can be observed that species with both reproductive traits coexist, though vegetative resprouting is favoured more (Calvo 1993).

Both mechanisms are favoured in the dominant species of these heathlands, *Erica australis*. Germination is greatly stimulated by fire as it causes the mechanical breaking of the seed cover, inactivation of inhibitors present in the soil or activation of the phytochrome system (Ariatnoutsou-Faraggitakki 1984; Keeley & Parker 1990; Menges & Kohfeldt 1995). Vegetative resprouting is also favoured as it keeps the roots intact and has the capacity to benefit

Table 6. Results of comparison using two way ANOVA with repeated measures of mean cover of *Erica australis* in the three treatments (comparison using the Scheffe test)

Cota Isestil

Two ways ANOVA of repeated measurement

Source	df	Sum of squares	F-test	P value
Treatments (A)	2	34849.309	13.453	1.0×10^{-4}
Subjects W. groups	297	384719.957		
Repeated measured (B)	2	138856.242	211.071	1.0×10^{-4}
(AB)	4	9268.164	7.044	1.0×10^{-4}
Bx subjects W. groups	594	195385.593		

Results of application of Scheffe-test

	Original	5th year[1]	9th year[1]
Burnt-Cut	10.891*	8.405*	7.158*
Burnt-Ploughed	1.042	7.868*	0.238
Cut-Ploughed	5.196*	0.008	10.004*

[1] 4th and 8th for ploughed plot.

Palacios de rueda

Two ways ANOVA of repeated measurement

Source	df	Sum of squares	F-test	P value
Treatments (A)	2	1571.51	0.462	0.6307
Subjects W. groups	295	502196.88		
Repeated measured (B)	5	349551.124	274.897	1.0×10^{-4}
(AB)	10	15268.698	6.004	1.0×10^{-4}
Bx subjects W. groups	1475	375113.345		

Results of application of Scheffe-test

	Original	3rd year	4th year	5th year	9th year
Burnt-Cut	0.352	0.142	0.435	0.038	0.712
Burnt-Ploughed	2.281	8.936*	1.523	0.042	0.0505
Cut-Ploughed	4.426	6.826*	3.586*	0.017	0.674

rapidly from nutrients incorporated in the soil after the first rains. In this way this species, as many other Ericaceae, uses vegetative resprouting as its main recovery mechanism (Mallik & Gimingham 1983; Calvo 1993; Menges & Kohfeldt 1995). Valbuena (1995) only found resprouts and not seedlings in the post-fire recovery in a similar *Erica australis* heathland. Keeley (1987) stated that the seeds of some species, like Ericaceae, need more than two years to germinate and this must occur under favourable conditions. Because of this recovery is basically attributable to vegetative resprouting (Malanson & O'Leary 1982; Oustric 1984; Forgeard 1990). This allows a fast spatial and quantitative recovery during the first few years; however,

Table 7. Results of comparison using the Scheffe test based on ANOVA of repeated measures of mean maximum heights after the three treatments in both areas

Burnt plot					
Palacios de Rueda			*Cota Isestil*		
	4th year	5th year		4th year	5th year
5th year	3.523*		5th year	0.782	
9th year	2.011*	7.327*	9th year	4.437*	8.945*

Cut plot					
Palacios de Rueda			*Cota Isestil*		
	4th year	5th year		4th year	5th year
5th year	6.142*		5th year	1.08	
9th year	15.554*	1.787	9th year	16.51*	9.145*

Ploughed plot				
Palacios de Rueda			*Cota Isestil*	
	4th year	5th year		4th year
5th year	8.629*		8th year	139.41
9th year	52.153*	18.354*		

the increase in height will be more pronounced than in cover after the fifth year.

The cutting mechanism, whose effect on biocoenosis is limited to destruction of the aerial biomass of the shrub but without altering the base and root portions guarantees the survival of *Erica australis* as vegetative resprouting is the main recovery mechanism. The role this mechanism plays in seeds seems to be nil as germination conditions are not modified in any important way neither as far as nutrient supply nor the possibility of altering the state of seeds present in the bank are concerned (Casal 1985). However, this mechanism causes an increase in the amount of light that reaches the lower parts of the ground and this, together with the elimination of competition, allows recovery of herbaceous species present in the area, as *Lotus corniculatus*, *Aira caryophyllea*, *Avenula marginata* . . . (Calvo, 1993).

The behaviour of this species after both treatments, burning and cutting, is similar, due to the fact that it uses vegetative regeneration as the main recovery process.

However, it is important to emphasize that the cover values attained after burning and cutting follow an increase pattern opposite to the original one. Recovery is comparatively lower in area C.I., where there was no strong interspecific competition than in P.R. *Erica australis* is a shrub species living in frequently disturbed habitats with degraded soils, which can resprout rapidly and take advantage on other shrub species as *Calluna vulgaris* and *Erica umbellata*, which usually can not resprout in these areas. These species employed mainly germinative response, and they reduced their cover after disturbances (Calvo 1993). Thus, on eliminating the competition *Erica australis* surpassed the initial values from the fourth year.

From the edaphic point of view this difference in recovery can be justified by slight variations in chemical parameters in the soil (Table 1). That is to say, the area (P.R.) has higher organic matter values, which means a slight increase in total nitrogen and certain cations Ca^{+}, K^{+} and Mg^{+2} and greater humidity in the soil. These slight differences can favour faster recovery in this species.

An increase in maximum height is observed once spatial occupation has occurred and cover increase has been stabilized after cutting in the same way as after burning.

On analyzing ploughing the response is much slower than to the other two. In this case the only recovery mechanism that these species can use is seed germination using either seeds present in the bank or those from nearby areas that have not been disturbed. This means that the time needed to begin regeneration is longer, although the situation is similar to that of the other treatments from the fourth year on in area P.R. However, the values are close to initial ones in area C.I. after eight years.

To summarize, it can be specified that *Erica australis*, which uses vegetative resprouting as its main recovery mechanism, occupies all the available surface spatially one year after burning and cutting. However, interspecific competition influences the capacity to attain and, in some cases, to surpass initial cover values. Once the increase in cover has stabilized a significant increase in height is observed. Ploughing results in recovery beginning more slowly as the only recovery mechanism is germination. Nevertheless, after the fourth-fifth year the situation is similar to the original one as far as cover percentage is concerned.

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