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Effects of disturbance caused by traditional Spanish rural land use on the regeneration of *Cytisus multiflorus*

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Abstract. *Cytisus multiflorus* is a leguminous *matorral* shrub native to the NW Iberian Peninsula, where it is one of the most important species in the extension of matorral at the expense of set-aside agricultural land. Dehesas have traditionally been used for extensive livestock raising and matorral was periodically burnt, cut or pulled out. The two latter practices are now out of use. However, burning is more frequent than in the past. The effects of fire, cutting, and pulling out of *C. multiflorus* on its regeneration was studied in order to ascertain whether the presently increasing distribution of the species relates to fire-stimulated regeneration or to the reduction of other traditional practices.

Three years after treatment two sets of parameters were determined: 1. Plant origin: seedlings and different ramet types (ramets = resprout clumps), density, weight, and biomass as well as the percentage of resprouting. 2. Seed persistence at various soil depths. The possible mechanisms of breaking dormancy and plant emergence in different years after fire were studied in other experiments.

The results suggest that the regeneration mechanism in *C. multiflorus* is stimulated by fire, but it is not an exclusive relationship. Stimulation occurs also after other disturbances leading to the total elimination of aerial biomass. The present expansion of the species does not appear to result from the abandonment of some traditional practices, such as cutting or pulling out, but from frequent fires (resulting in aerial-biomass elimination).

Keywords: Cutting; Fire; Mediterranean shrubland; Pull-out; Ramet; Seed bank; Seedling.

Nomenclature: Tutin et al. (1964-1980).

Introduction

Mediterranean-type ecosystems are characterized by extensive shrubland, for example, the Spanish matorral. Frequent fires in the mediterranean areas have stimulated studies on the response of their plants to fire. On the whole they respond rapidly and the response varies depending on the fire regime (Malanson & O'Leary 1985; Trabaud 1989, 1992; Keeley 1986, 1995; Bond & van Wilgen 1996). The regenerative ability of the dominant species is generally accepted as an 'adaptive strategy' of plants to fire (Margaris 1981) and some species even depend on fire for completing their life cycle (Bond & van Wilgen 1996). However, in contrast to other mediterranean-type regions, human activity in the Mediterranean basin has been very intense and includes not only burning, but also other types of perturbation such as cutting, pulling out, ploughing and grazing. This implies that regenerative ability in some species has not necessarily developed as a selective response to fire although they could effectively regenerate after fire (e.g. Trabaud 1989; Trabaud et al. 1993; Tárrega et al. 1995, 1997; Riba 1997; Gómez-Sal et al. 1999).

After fire many Mediterranean shrub species regenerate by sprouts and/or by seeds. The most frequent vegetative response is resprouting of plants whose above-ground biomass has been destroyed; this is called 'rootstock resprout' in Spain (Casal et al. 1984, 1990; Herrera 1987; Gómez-Gutiérrez et al. 1988; Canadell et al. 1991; Calvo et al. 1992; Lloret & López-Soria 1993; Vilà 1997). Vigorous post-fire resprouting occurs through the stimulation of many dormant buds in the below-ground plant parts, but this stimulation may also result from other disturbances of the above-ground part (Kummerow 1989; Canadell & Zedler 1995; Canadell & López-Soria 1998). In some species the vegetative regeneration after fire also takes place from buried branches or superficial lateral roots (Gómez-Gutiérrez et al. 1988; Fernández-Santos & Gómez-Gutiérrez 1994a). However, sometimes the latter type of resprout is not directly stimulated by fire (Fernández-Santos & Gómez-Gutiérrez 1994a). Sprouting from epicornic stem buds is rare in the Mediterranean basin, only one tree species (*Quercus suber*; Pausas 1997), as is another fire adaptation (serotiny) found in other mediterranean-type ecosystems (Pausas 1999).

Some of the shrub species produce a persistent soil seed bank which plays an important part in their generative regeneration (Fenner 1985; Trabaud 1987; Steele 1993; Hosking et al. 1996). Their seeds often require stimulation to break dormancy, and some of the stimuli are linked to disturbances which eliminate the vegetation cover (Keeley 1977; Pieterse et al. 1988). However, the direct causes triggering seed germination vary greatly, e.g. high temperature (Martin et al. 1969; Trabaud 1987; Doussi & Thanos 1994), charred wood (Keeley 1995) and smoke (Brow et al. 1993; Keeley & Fotheringham 1998) produced by fire; aeration and scarification caused by soil movement (Williams 1981; Baker 1989).

Cytisus multiflorus (White broom), is a leguminous matorral shrub native to the NW Iberian Peninsula. It occurs on sandy soils on the Meseta and in highland regions (Gómez-Gutiérrez et al. 1991). Actually it is one of the most important species in the 'matorralization' of dehesas – i.e. extensive open holm-oak woodland with a pronounced herbaceous layer – and set-aside agricultural land, where it constitutes vast monospecific stands. Dehesas have traditionally been utilized for extensive livestock raising, although they have also been partly cultivated (Gómez-Gutiérrez 1993). Until ca. 20 yr ago it was very common to pull out matorral shrubs for crop growing, or to cut it for fodder and fuel. At present these two practices are out of use; the livestock stocking rate is smaller than in the past and burning occurs more frequently than previously, now every 6 -10 yr. In Spain there has been a strong increase in the annual number of fires and the total land surface burnt, as a consequence of increased land abandonment (Moreno et al. 1998).

After fire, *Cytisus multiflorus* behaves as a facultative resprouter, and the vegetative regeneration takes place from rootstock and from superficial lateral-roots (Fernández-Santos et al. 1992). Mature plants also produce a great number of seeds, that are dispersed both explosively (up to 3 m) and by ants (Moreno-Marcos et al. 1992). These seeds are characterized by innate dormancy and an impermeable seed coat (Moreno-Marcos 1992), as is frequently the case in leguminous species (Bossard 1993; Doussi & Thanos 1994). Their dormancy can be broken by scarification (100 % germination) or high-temperature treatment (Añorbe et al. 1990).

We aim to ascertain whether the presently increasing spread of *Cytisus multiflorus* relates to fire-stimulated regeneration or to the reduction of other traditional practices. Moreover, we aim to obtain information which would enable restraining the expansion of this species. Another species of this genus, *C. scoparius,* shows similar characteristics of seed production and dispersal (see Bossard 1990, 1993; Smith & Harlen 1991; Paynter et al. 1996) and is regarded as a pest in some Mediterranean regions (Parson & Cuthbertson 1992; Parker 1997). This paper examines the effect of burning, cutting and pulling out treatments on the regeneration of *Cytisus multiflorus* and compares its population structure, three years after treatment, with mature populations. We examined plants emerging after each type of perturbation for their origin (seedlings and different ramet types), density, weight, and biomass. Furthermore, we studied mortality and dormancy in the soil seed bank.

Methods

Study area

The study was carried out in a dehesa situated in the NW of the province of Salamanca (40° 00' N, 7° 45' W). The region forms part of the North Meseta and is slightly undulating. Soils are sandy and acidic, with a predominance of Cambisols, on granitic bedrock. The climate is Mediterranean with a mean annual precipitation of 600 mm and a pronounced summer drought, with only 23 % of the annual rainfall and a high evapo-transpiration from May to September. The vegetation is a typical 'dehesa', i.e. open *Quercus rotundifolia* woodland with herbaceous layer encroached by matorral dominated by *Cytisus multiflorus*. The dehesa is used as traditional pasture for cattle and sheep, and the matorral is burnt frequently in small patches (one to several hectares).

Seedlings and ramets

In the first experiment the effect of different types of disturbance was monitored in an area in which *Cytisus multiflorus* was the only woody species. The matorral was evenly distributed throughout the selected area, with 60 % cover of *Cytisus*; it had been burnt seven years before. An experimental area of 50 m × 14 m was fenced in order to protect it from the livestock effect. This area was divided into four plots, 10 m × 10 m each, with a similar plant cover and structure, separated by 2-m wide paths which were cleared of matorral. Three plots were treated in mid-June in one of the following ways: controlled burning; cutting back; and pulling out; the fourth plot remained undisturbed and acted as a control. *Burning* was carried out following the local practice of the farmers, i.e. setting fire with matches directly to the plants and preventing it from spreading to other plots; as a result all above-ground plant biomass was totally burned locally. *Cutting* was done manually to ground level. *Pulling out* of plants was preceded by roughly disturbing the soil with a mattock to a depth of 15 - 20 cm in order to facilitate the manual pulling; around larger plants the soil was disturbed to a greater depth.

Three years after treatment the following parameters were determined: Regeneration mode, plant density (seedlings and different types of ramets – i.e. sprout clumps), dry weight of each plant (aerial part) and of the total aerial biomass per area unit. These parameters were studied in four, 1 m × 10 m, replicates under each treatment. Each plot was divided into 10 such rectangles and the four inner adjacent ones were sampled; these were carefully excavated in order to distinguish seedlings from different ramet types. In the burned and cut rectangles the proportion of rootstock was also determined. The undisturbed plot (control-1) was 10 m^2 in size; here the origin of the plants present was determined only for the small plants (approximately less than 50 g dry weight). The category 'seedlings' included all plants originated from seeds, even if they were 2 or 3 yr old. Dry weight was always determined after drying plants at 80 °C for 24 hours.

In order to compare the three types of disturbance, analysis of variance (ANOVA) was applied followed by pairwise comparisons using Tukey tests. Differences at $P < 0.05$ were considered significant.

An additional study was carried out in two recently (one to two years ago) burnt neighbouring areas, in order to evaluate the same parameters in younger *C. multiflorus* populations. Both pre-burn populations were similar to those in the first experiment: 8 - 9 yr old, with a 60 % matorral cover, and burnt by farmers in summer. No livestock grazing occurred after the fire. The parameters were studied in a 5 m × 2 m rectangle in each population using the same methods as described above.

Seed bank

In the first experiment the effect of treatments on the soil seed bank, namely on seed density, vertical distribution, viability, and dormancy was determined. Three years after the treatment, 20 quadrats, 20 cm × 20 cm, were randomly chosen in each fenced plot; 100 soil samples were taken from each plot at depths 0 - 2.5, 2.5 - 5, 5 - 10, 10 -15, and 15 - 20 cm.

In a third study the soil seed bank was sampled immediately after disturbance in order to determine the effect of treatment on seed germination and/or destruction. The study was conducted in a mature 10-yr-old stand within the dehesa, with an 80 % matorral cover while it was burnt at the beginning of August. The fire was very intense due to the high temperature and dry conditions. The control and digging-treatment plots were established in an adjacent unburnt area. 20 randomly chosen soil quadrats (20 cm × 20 cm at five depths, as in the first experiment) were taken from each treatment on the next day after fire, in order to determine seed numbers, vertical distribution, and state (viability and dormancy).

Seeds were separated from the soil by drying soil samples, breaking soil aggregates, sieving through a 2.5 mm and 1 mm mesh, collecting the intermediate fraction and extracting seeds by having them floating in carbon tetrachlorate. The collected seeds were tested for dormancy and viability in 30 replicates of 50 seeds in each. They were washed in a 3.5 % sodium hypochlorite solution (bleech) and placed in Petri dishes (Puentes 1984), then kept in a dark cool place (Añorbe et al. 1990). Every two days, germinated and rotted seeds were counted and removed. Seeds were considered germinated when the radicle extended > 1 mm (Vigna et al. 1983). Seeds that germinated within one month were recorded as non-dormant (Añorbe et al. 1990; Holmes 1989). The remaining dormant seeds were scarified mechanically by hand to facilitate imbibition. Those that germinated within another month were regarded as viable and the rest as non-viable (Moreno-Marcos 1992).

Comparisons were carried out using two ways ANOVA methods (treatment and depth), followed by pairwise comparison, as mentioned above.

Results

Types of regeneration in Cytisus multiflorus

Three years after the treatment (experiment 1) and 1-2 yr after the fire, seedlings and ramets were sampled in all plots (Fig. 1). In the burnt and cut plots resprouts originated from rootstocks or superficial lateral roots – either thick roots growing from the below-ground parts of a former plant (Type-1) or thin ones originating from a new ramet (Type-2). Type-1 were usually large ramets and near to the rootstocks which had not resprouted. No Type-2 ramets were found in 1-yr and 2-yr old populations after fire. In the pull-out plot there always remained some pieces of the extended lateral root system, from which resprouting took place. In this plot seedlings with a small swelling (about 1.5 cm in diameter) in the root/stem-link area were found.

Seedling and ramet density

Plant density (seedlings + ramets) was higher in all plots three years after treatment than in the control plot (10-yr-old) (Table 1). Among the treatments density was significantly higher in the pull-out plot than in the burnt or cut plots. We did not find significant differences between the two latter treatments.

There were more seedlings than ramets in all populations, except in the older ones (control-1) where few seedlings were found (Table 1). Their number was particularly high three years after pull-out and significantly higher than three years after burning or cutting. Among the latter treatments there were no differences. If we took account of weight-age classes, built according to the mean and maximum weights for seedlings in 1-yr, 2-yr and 3-yr old populations (Fig. 2, Table 2), seedling density of any weight-age class was higher in the pull-out plot than in the others, except for the 3-yr-old individuals; in the latter class differences were not significant. We did not find significant differences between the cut and burnt plots in either of the weight-age classes considered.

Ramet density varied less than seedling density in the

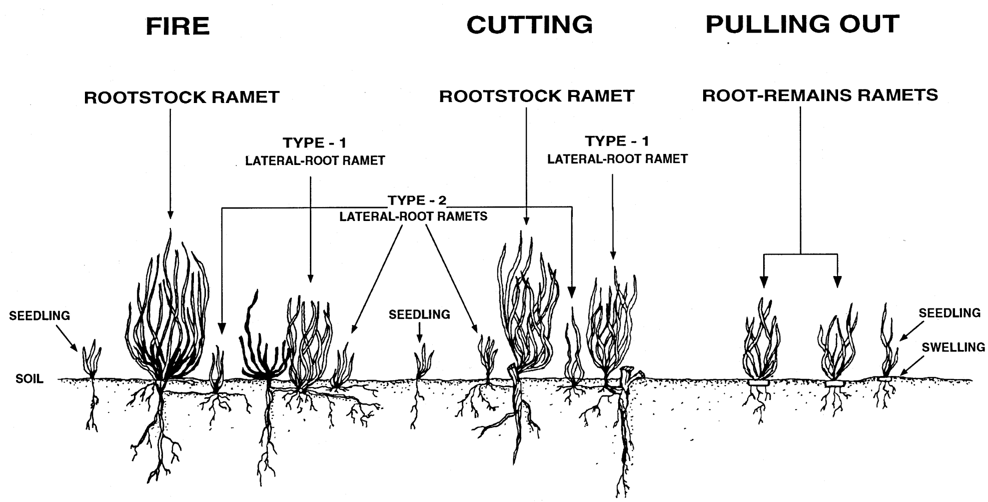


Fig. 1. Regeneration of *Cytisus multiflorus* following fire, cutting or pulling out: seedlings and different ramet types (resprout clumps). Burned parts in black.

studied populations, mainly rootstock ramets (Table 1). The lowest ramet number was found in the pull-out plot and these ramets were of a different type than in the other populations. In burnt and cut plots, ramet density was similar to that found in the control plot. These treatments did not differ significantly in ramet number (Table 1), but differences were found in the vegetative response if ramet types were taken into account. The number of burned or cut plants was 21.7 ± 1.4 (standard error) and 20.5 ± 1.2 plants/ $10m^2$, respectively , and the proportion of rootstock ramets was 46.5% in the burned plot and 27% in the cut one; quite frequently (mainly after cutting) a lateral-root ramet type-1 was found next to a rootstock which did not resprout. Among the main results we mention (Fig. 3): (1) in the burnt plot the number of rootstock ramets was significantly greater than that of lateral-root type-1 ramets, whereas in the cut one it was the reverse; (2) the number of rootstock ramets was significantly greater in the burnt than in the cut plot, whereas that of lateral-root type-1 ramets was highest in the cut one; (3) the number of lateral-root type-2 ramets was similar in both. This last type of ramet began to appear three years after burning or cutting and continued to be present (young ramets) in 10-yr-old populations (control-1).

Seedling and ramet weight and aerial biomass

We found that in the pull-out treatment the aerial biomass was significantly lower than in the other plots (Table 3). Its mean value in the burnt plot did not differ significantly from that in the cut plot, and was 26 % of that in the control-1 one (10-yr-old). Some results are different from those in the previous paragraph since we found that mean-weight values corresponding to each plant type (according to their origin) were very different (Table 2).

Generally, in each population seedling weight was much lower than that of ramets, hence their contribution to the aerial biomass was low; 0.1 % in the control-1 plot and less than 5 % in the burned or cut ones. In the pull-out plot seedlings had a mean-weight and contribution to the total aerial biomass which were significantly higher than in burnt or cut plots; however resprouts were also larger than seedlings and their contributions to the total aerial biomass was similar. We did not find significant differences between the burnt and cut plots.

Among ramets, the rootstock ones were the biggest in all populations; they accounted for more than 85% of the aerial biomass in burnt plots. In the cut plot the proportion was less (59%), owing to their lower numbers, and

Table 1. Number of different plant types per 10 m^2, differentiated according to their origin, three years after fire, cutting and pulling out (mean values ± 95% confidence interval; $n = 4$), and in the control-1 plot (10-yr-old). Results of comparison in each group ($P < 0.05$ for a different letter). R.R . = Rootstock ramets; L-R.R.1 = Lateral-root ramets type-1; L-R.R.2 = Lateral-root ramets type-2; R-R.R. = Root-remains ramets. * R.R.+L-R.R.1, without differentiation. Means with a different letter are significantly different.

Population	Total	Seedlings	Ramets	R.R.	L-R.R.1	L-R.R.2	R-R.R.
Control-1	19	5	14	12	*	2	- - -
Fire	57.2 ± 15.8 a	40.0 ± 16.8 a	17.2 ± 2.0 a	10.0 ± 2.1	3.2 ± 2.4	4.0 ± 1.9	- - -
Cutting	50.2 ± 7.2 a	31.2 ± 5.1 a	19.0 ± 3.2 a	5.8 ± 2.0	9.0 ± 2.9	4.2 ± 1.6	- - -
Pulling out	98.8 ± 18.3 b	89.2 ± 16.5 b	9.6 ± 1.9 b	- - -	- - -	- - -	9.6 ± 1.9

Table 2. Dry weight (g) of different plant types, according to their origin, three years after treatment: fire, cutting and pulling out, and in populations of different age after fire (F): 1-yr, 2-yr, 10-yr (control-1 plot). Mean values ± 95% confidence interval, and results of comparison in each group ($P < 0.05$ for means with a different letter). R.R. = Rootstock ramets; L-R.R.1 = Lateral-root ramets type-1; L-R.R.2 = Lateral-root ramets type-2; R-R.R. = Ramets from root-remains . * R.R.+L-R.R.1 without differentiation.

Population	Plants	Seedlings	R.R.	L-R.R.1	L-R.R.2	R-R.R.
1-yr after fire	15.6 ± 8.1 a	0.4 ± 0.1 a	74.2 ± 36.7	11.3 ± 3.3	-	-
2-yr after fire	8.5 ±.3.4 a	1.2 ± 0.3 b	147.6 ± 35.5	31.4 ± 10.3	-	-
3-yr after:						
Fire	56.2 ± 23.7 b	3.7 ± 0.9 c	278.0 ± 107.4	82.3 ± 16.8	4.8 ± 5.0	-
Cutting	52.8 ± 17.8 b	3.1 ± 1.2 c	270.6 ± 142.8	107.0 ± 32.8	5.1 ± 4.8	-
Pulling out	10.8 ± 6.5 a	6.5 ± 1.5 d	-	-	-	50.9 ± 48.6
10-yr after fire	597.8 ± 350.1 c	3.3 ± 6.1 abcd	943.4 ± 453.4	*	10.0 ± 25.4	-

the compensation by a higher proportion of lateral-root ramet type-1; we did not find significant differences between burnt or cut plots in ramet aerial biomass. Lateral-root ramets showed variable weight; type-1 similar to that of rootstock ramets, although lower, and type-2 similar to that of seedlings. This last ramet type represented less than 1 % of the aerial biomass in each plot. In the pull-out plot there were also different types (weight) of resprouts which reached a higher weight the larger the root remains were.

Comparing mean weight and density of each plant type between populations of different ages after fire and control-1 (10-yr-old) (Tables 1, 3), it becomes clear that the weight of rootstock ramets and lateral-root ramets type-1 increased with population age, while their density was steady. Probably these resprout types occur only during the first year after fire, and their survival is high. Conversely, young lateral-root ramets of type-2 were found in the control-1 plot. Hence the confidence interval for their mean weight is very wide. The latter resprout type, as well as some seed germination, continue to occur for quite some years after fire.

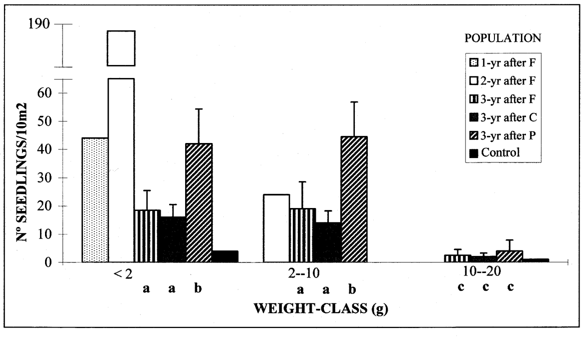


Fig. 2. Number of seedlings of each weight class (g dry weight) per 10 m^2 found three years after treatment: fire (F), cutting (C), pull-out (P), and in populations of different ages after fire: 1-yr, 2-yr and 10-yr-old (control-1). Mean values ± 95% confidence interval ($n = 4$). Results of ANOVA (2 factors) followed by pairwise comparisons ($P < 0.05$ for means with different letters).

Soil seed bank

The seed number found immediately after treatment (third study) and the results of the comparison are shown in Fig. 4. A high seed number was found in the topmost soil layer in the control-2 plot. The majority of which could have been produced in the same year, since the samples were collected soon after seed dispersal. Seed number decreased significantly with soil depth. Nevertheless, 381 seeds/m^2 were found between 2.5 - 20 cm soil depth, which points to the importance of the soil seed bank in *C. multiflorus* apart from the annual seed dispersal. In the burned plot a considerable decrease in seed number, 23.5 %, was found as compared to the control. This decrease was significant only in the topmost soil layer. On the other hand total seed number in the pull-out plot did not differ significantly from the control. Furthermore seed distribution was strongly affected in that the soil seed bank was deepened resulting in its homogenization.

Results of seed dormancy and viability test are shown in Table 4. Fire seems to be very effective in stimulating seed germination, even at a soil depth of 2.5 - 5 cm.

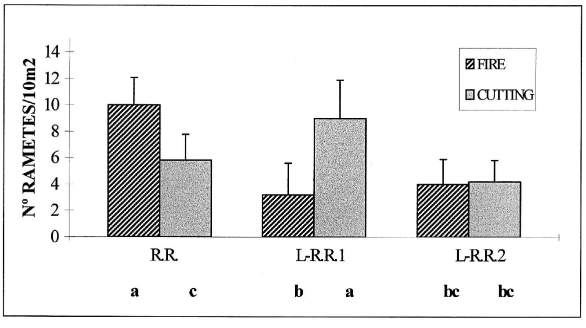


Fig. 3. Number of rootstock ramets (R.R.), lateral-root ramets type-1 (L-R.R.1), and lateral-root ramets type-2 (L-R.R.2) per 10 m^2 found three years after fire or cutting. Mean values ± 95% confidence interval ($n = 4$). Results of ANOVA (two factors) followed by pairwise comparisons ($P < 0.05$ for means with a different letter).

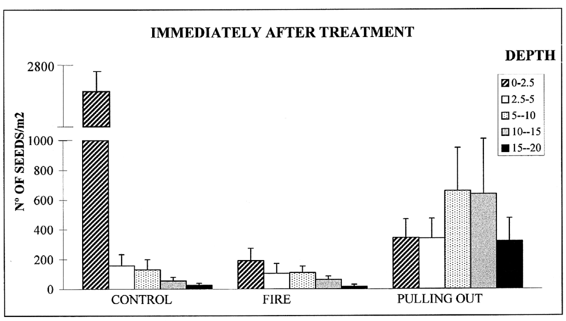
Table 3. Aerial biomass (g dry weight) per 10 m^2, according to plant origin, found three years after fire, cutting and pulling out (mean values ± 95% confidence interval; $n = 4$), and in control -1 plot (10-yr-old). Results of comparison in each group. R.R. = Rootstock ramets; L-R.R.1 = Lateral-root ramets type-1; L-R.R.2 = Lateral-root ramets type-2; R-R.R. = Ramets from root-remains . * R.+L-R.R.1, without differentiation. Different letters indicate significant ($P < 0.05$) differences between means.

Population	Total	Seedlings	Ramets	R.R.	L-R.R.1	L-R.R.2	R-R.R.
Control-1	11 357	16.5	11 341	11 321	*	20.1	-
Fire	3213 ± 1599 a	148 ± 74 a	3065 ± 1525 a	2782 ± 1384	264 ± 131	19 ± 10	-
Cutting	2652 ± 633 a	97 ± 23 a	2554 ± 610 a	1570 ± 375	963 ± 230	22 ± 5	-
Pulling out	1067 ± 383 b	578 ± 207 b	489 ± 175 b	-	-	-	489 ± 175

However, among the seeds in the top 2.5 cm, apparently not destroyed by fire, the proportion of those that rotted during the study of germination was very high (53%), as compared to less than 2 % for the rest of the plots and depths. Thus, both seed destruction and stimulation were limited to the top 5 cm soil layer. No significant differences were found between the pull-out and control plots.

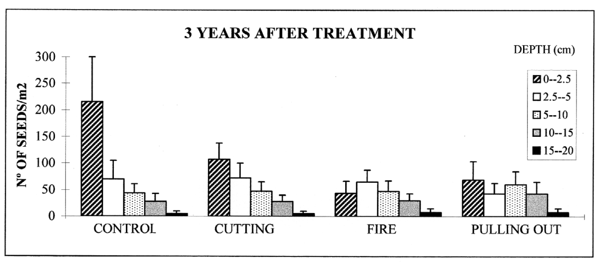
Seed number and vertical distribution found three years after treatment (experiment 1) are shown in Fig. 5. In control-1 plot (10-yr-old) a high seed density was found in the top 2.5 cm soil layer, and the number decreased significantly with soil depth, up to the density of 5 seeds/m^2 at a soil depth of 15 - 20 cm. When comparing the cut plot with the control-1, no significant differences were found either in the vertical distribution of seeds or in the seed number. However, there was a significant decrease in seed number in the topmost soil layer of the burnt plot as compared to the control-1 or the cut one, while at other soil depths there were no differences among these treatments. The soil seed bank found in the pull-out plot showed no vertical structure and was deeper than in the other ones as a direct result of the treatment. No significant differences were observed in seed number, except for the level 0 - 2.5 cm in the control-1.

The mean viability index was 99 % and the dormancy index between 96 - 98 % in all the plots. We did not find significant differences in these indices either between treatments or soil depths. Both viability and dormancy indices were very high and the soil seed bank was barely depleted by application of the different treatments. These values are the major determinants of long seed persistence in the soil. One should bear in mind that this soil seed bank had not been renewed during the preceding three years.



	0 - 2.5	2.5 - 5	5 - 10	10 - 15	15 - 20	TOTAL
Control	ag	b	bc	cd	d	g (2052 ± 999)
Fire	be	bc	bc	cd	d	f (482 ± 144)
Pulling out	ef	ef	fa	fa	ef	g (2298 ± 1030)

Fig. 4. The direct effect of treatment on the *Cytisus multiflorus* soil seed bank. Mean number of seeds per m^2 ± 95% confidence interval ($n = 20$), at five different soil depths, immediately after treatment. Results of ANOVA (2 factors) followed by pairwise comparisons ($P < 0.05$ for a different letter). TOTAL = sum of seeds at five depths.



	0 - 2.5	2.5 - 5	5 - 10	10 - 15	15 - 20	TOTAL
Control	a	be	bc	cd	d	f (362 ± 100)
Cutting	ae	be	bc	cd	d	fg (260 ± 65)
Fire	bc	b	bc	cd	d	g (197 ± 52)
Pulling out	be	bc	be	cd	d	fg (221 ± 75)

Fig. 5. Seed number and vertical distribution in the soil seed bank three years after treatment. Mean number of seeds per m^2 ± 95% confidence interval ($n = 20$), at five different soil depths. Results of ANOVA (2 factors) followed by pairwise comparisons ($P < 0.05$ for a different letter). TOTAL = sum of seeds at five depths.

Table 4. Treatment effects on *Cytisus multiflorus* seeds at four different soil depths (except in the pulling-out treatment). Mean proportion (%) of germinated seeds ± 95% confidence interval immediately after treatment. Number of tested seeds in parentheses. Results of ANOVA (two factors) followed by pairwise comparisons. *Seeds that became rotten were not included in the counting. Different letters indicate significant ($P < 0.05$) differences between means.

Treatment	Depth (cm)				
	0 - 2.5	2.5 - 5	5 - 10	10 - 20	TOTAL
Control 2	2.3 ± 1.0 (200) a	2.2 ± 1.6 (120) a	2.4 ± 1.9 (100) a	2.8 ± 2.1 (60) a	2.4 ± 1.5 (480) a
Fire	19.1 ± 6.9 (150) b	27.4 ± 14.3 (80) bc	2.1 ± 1.8 (80) a	1.9 ± 0.9 (50) a	14.8 ± 6.6 (360) b
Fire*	43.2 ± 11.3 (67) c	”	”	”	19.3 ± 7.5 (277) b
Pulling out	-	-	-	-	3.0 ± 1.8 (400) a

Discussion

The results obtained in this study show that *Cytisus multiflorus* regenerated after burning, cutting, and pulling out in a similar way, qualitatively speaking. Following the three treatments, it regenerated by resprouting and seed germination. Some species of the same genus in the Mediterranean basin are also facultative resprouters after fire, notably *C. balansae* (Debussche et al. 1980; Gómez-Gutiérrez et al. 1988) and *C. scoparius* (Tárrega et al. 1992) – species that also resprout after cutting (Debussche et al. 1980; Calvo 1993). *C. scoparius* behaves as obligate seeder in other Mediterranean-type ecosystems where it has been introduced (Parker 1997; Rees & Paynter 1997). *C. multiflorus* resprouts from rootstock and superficial lateral roots, but after pull-out it can resprout only from loose root remains. That would support our idea to regard resprout clumps as ramets (Harper 1977).

The occurrence of a swelling in the root/stem-link area of plants we observed in other burned populations of this species. These swellings were similar to those found in *C. balansae* (Fernández-Santos 1991). Their existence in the fenced-off area excludes the possibility of their being due to livestock treading, as was suggested for other species (Mallik & Gimingham 1983, 1985). Furthermore their existence in the pulled-out plot has led us to suppose that repeated burning might not be the only condition triggering this morphological response which has been discussed in the literature as regards larger swellings such as lignotubers or burls (Lacey 1983; Malanson & Westman 1985; Mesleard & Lepart 1989; Canadell & López-Soria 1998).

The other similarities between treatments were that after three years the generative response of *C. multiflorus* was greater than the vegetative one in terms of plant density. However, the vegetative response was stronger in terms of aerial biomass, specifically after burning and cutting. On the whole, seedling dry weight was lower than that of ramets, because the latter maintained their root system from before the burning or cutting treatment, which probably favoured their growth, development, and survival. This has been observed and reported for other species (Hanes 1981; Keeley 1986; Desouza et al. 1986; Thomas & Davis 1989; Calvo et al. 1998) and is very pronounced in *C. multiflorus,* even if only small root pieces remain in the soil – as occurs after pulling out. Ramets were found to be the larger the closer they were to the rootstock, and after pulling out the bigger were the root remains. It was also observed in other woody species of the Mediterranean basin, that resprouting vigour may be positively related to the size of below-ground structures (Fernández-Santos & Gómez-Gutiérrez 1994 a; Vilà et al. 1994), which in its turn is related to the occurrence of a starch source and a bud bank (Canadell et al. 1991; Canadell & López-Soria 1998).

Furthermore, ramet density varied little in populations of different ages after fire, mainly the rootstock one. This would reinforce the importance of the below-ground structures in ramet growth and development and probably in their survival rate as was found in *C. balansae* (Fernández-Santos & Gómez-Gutiérrez 1994 a). The presence of type-2 lateral-root ramets was similar 3 yr after burning and cutting. We did not find such ramets in younger populations after fire, but new individuals did appear in mature populations. Thus this type of resprout is not directly related to regeneration after perturbation, but rather is a vegetative regeneration mechanism favouring the colonization of new areas as was noted in *C. balansae* (Fernández-Santos & Gómez-Gutiérrez 1994 a).

In the generative response the high number of seedlings reflects the persistence of a soil seed bank following the three disturbances. During these three years no new seeds had been formed, because *C. multiflorus* plants do not start to produce seeds before they have reached 3 - 4 yr of age (pers. obs.), like *C. scoparius* (Smith & Harlen 1991), and also the distance to mature plants was greater than the distance covered by their explosive dispersion (earlier 3 m) (Moreno-Marcos et al. 1992). Nevertheless, the soil seed bank seems not to be affected by treatments as regards the number of viable seeds in relation to seedling number.

Furthermore, there are no big differences in the soil seed bank without treatment. The seed number in the top 2.5 cm of the soil in the mature plot (control-1) is somewhat higher than in the other plots. The difference is small considering that the seed contribution to the soil of the mature plots has continued during these three years and also considering the high seed number found in the topmost layer of experiment 3 (control-2), in which samples were collected soon after seed dispersal. The annual seed production as regards the number of seeds accumulated in the soil seems to be of relative importance, because presumably many seeds had been lost from the soil through the above-ground insect and rodent activity immediately after seed dispersion (Moreno-Marcos et al. 1992), and degradation (Lonsdale 1993). Similarly Paynter et al. (1996) found in *C. scoparius* that vertebrate seed predation was very high for seeds on the soil surface.

The different types of ramet and seedling establishment varied quantitatively depending on the kind of disturbance. Rootstock ramets were larger in number following burning than following cutting. This would indicate that, during a fire, dormant buds at the rootstock base in *C. multiflorus* are directly stimulated, which was reported in other species (Kummerow 1989; Canadell et al. 1991). However, such stimulation does not seem to be strong following this type of fire. Rootstock resprouts are also induced by other indirect stimuli, as was observed by Kummerow (1989) and Canadell & López-Soria (1998) in other species. We propose that resprouting in *C. multiflorus* could be simply caused by the elimination of aerial cover and the presence of an active root system (either accumulating nutrients and water or facilitating their absorption). This could explain the larger number of large type-1 lateral-root ramets following cutting, compensating in this way the lower number of rootstock ramets. It could also explain the resprouting from root remains following pulling out.

Seedling density of all age classes was much higher after pulling out than after burning or cutting. This difference occurred in spite of the lack of a direct germination stimulus by scarification, which was unlikely given the thick seed coat (Tran & Cavanagh 1984). Nevertheless, such scarification has been reported in *C. scoparius* (Williams 1981). The higher density of seedlings of 1, 2, and 3 yr could, therefore, be due to a stronger indirect stimulation and/or greater survivorship because of weaker resprout competition. Furthermore, fire did not seem to have an initial positive effect on the direct stimulus of germination. The increase in the proportion of non-dormant seeds was significant, possibly as a consequence of high temperature (Añorbe et al. 1990). We cannot rule out, though, other possible factors related to fire, such as charred wood or smoke. However, many seeds were destroyed. In fact, one year after fire seedling density was lower than two years following fire, and three years after treatments we did not find significant differences between the burn and cut treatments in either of the weightage classes considered. It seems that seed germination in *C. multiflorus* is determined by an indirect stimulus, as a consequence of the modified environment caused by the elimination of aerial parts of the vegetation cover and by soil movement. This has also been reported for other species (Hill & Stevens 1981; Rundel et al. 1986; Lonsdale 1993), possibly due to the effect of light, high temperature, temperature fluctuations, ventilation and soil micro-organisms on bare soil. A larger modification of the environment, e.g. ploughing, would imply a greater stimulus of seed germination. Furthermore, the predominance of 2-yr-old seedlings in all treatments leads us to believe that *C. multiflorus* seeds need more than 1 yr to germinate, as Keeley (1987) has suggested for other species.

Plant and seedling density three years after treatment was much higher than in mature population (control-1). Thus it seems that fire as well as cutting or pulling out favour *C. multiflorus* regeneration by allowing rejuvenation of its populations. The regeneration of aerial biomass is more rapid after burning or cutting than after pull-out. Similar results have been obtained for other matorral species in Spain, such as *Erica australis* (Calvo et al. 1992, 1998), *Cistus ladanifer* and *C. laurifolius* (Tárrega et al. 1995, 1997). Therefore, *C. multiflorus*, like these other species, is not a genuine pyrophyte but forms part of the group of the heliophilous pioneer species which colonize disturbed areas, free of aggressive competitors (Trabaud 1987, 1995). This would support the view that in areas with long and intense human impact, like Spain or in general the Mediterranean basin, probably the role of fire has not been so important in the evolution of the flora as in other Mediterranean-type ecosystems (Pausas 1999).

If *C. multiflorus* were not subsequently burnt, perhaps the extension of its stands would be reduced over the years, since in mature populations new individuals hardly appear and larger plants cannot survive for more than 20 years (Fernández-Santos & Gómez-Gutiérrez 1994 b). Other species of the same genus, such as *C. scoparius* have an average life expectancy of 10 - 12 yr in native habitats (Europe; Waloff & Richards 1977; Rousseau & Loiseau 1982), and more than 17 - 20 yr in 'exotic' habitats (Australia and USA; Smith & Harlen 1991; Smith 1994; Bossard & Rejmánek 1994; Rees &

Paynter 1997). The regeneration of *Cytisus* from the seed bank following plants senescence and death, has not been reported (Smith 1994) unless disturbance creates large gaps in the *Cytisus* canopy (Hosking et al. 1996). Nonetheless, *C. multiflorus* could persist in the absence of disturbance, even over a long period of time, owing to several factors, for instance the prolific seed production and seed dispersal by ants (Moreno-Marcos et al. 1992), the formation of a persistent soil seed bank with an appreciable proportion of non-dormant seeds, and the regeneration of lateral-root type-2 ramets. In another species of the same genus, *C. balansae*, we did not find seedlings following plant senescence and death, but we did find young lateral-root ramets (Fernández-Santos & Gómez-Gutiérrez 1994 a). It seems, thus, that species of this genus are rather difficult to eliminate once they have occupied an area. The utmost care should be taken so as not to introduce them into exotic habitats, since like *C. scoparius* (Parker 1997) they could become a noxious pest.

However, in our study we have also observed that outside the fenced area (experiment 1) livestock seemed to slow down the growth of plants. Plants were smaller than in the control-1 plot and hence the aerial biomass accumulation was less. Many plants were eaten or bitten at the top and some of their shoots were broken. Therefore, maybe by managing grazing and applying an adequate livestock stocking rate, one could control an area occupied by *Cytisus* species, or at least the accumulated biomass – which is directly relevant for the major problem of fire control in the region.

In conclusion, the regeneration mechanism in *Cytisus multiflorus* is stimulated by fire, but not only by fire. Regeneration occurs after any disturbance involving the total elimination of aerial biomass. The present expansion of the species does not appear to be due to the abandonment of some traditional practices, such as cutting or pulling out, but to the more frequent burning. In order to reduce the extension of *C. multiflorus* it seems advisable not to burn but to study other possible treatments, for example the effect of managed grazing and that of an optimal stocking rate.

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