

## Effects of soil disturbance, fire and litter accumulation on the establishment of *Cistus clusii* seedlings

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### Abstract

*Cistus clusii* is an early successional shrub, the most drought-resistant species of *Cistus* which colonises perturbed areas in the southern Iberian Peninsula and regenerates entirely from seeds after a fire. Some of the factors controlling germination and seedling establishment were examined in a field experiment in which we tested the effect of soil disturbance, fire, and litter accumulation on seedling emergence. In a first experiment, soil disturbance and fire were applied to plots in the field with a factorial design in April 1992. In a second experiment, we measured the effect of adding *C. clusii* litter. The number of seedlings, annual plants and grasses, and the coverage of mosses were recorded in 1993 and 1994.

Soil disturbance increased the number of *C. clusii* seedlings almost seven-fold but did not change the number of grasses, annual plants nor moss cover. Fire significantly increased the number of *C. clusii* seedlings only in combination with soil disturbance, and it did not affect the presence of annuals, grasses nor moss cover. Litter increased the number of *C. clusii* seedlings in the following two years.

Overall, soil disturbance as a single factor had the most significant effect on seedling emergence, though plots disturbed and treated with fire had the highest number of seedlings, implying that germination of *C. clusii* seeds was enhanced by processes that alter the hard seed coat and break the physical dormancy imposed by the testa. In addition, recruitment of *C. clusii* was dependent on rainfall, as drought significantly reduced the number of seedlings appearing in winter.

### Introduction

In Mediterranean ecosystems species are adapted to the periodic removal of standing biomass, and regenerate their populations after recurrent fires either by resprouting from roots and root-stumps or entirely from seeds (Naveh 1974). Whereas some species are capable of using both ways to recover from catastrophic events (facultative resprouters or seeders), others are constrained to one way and are then termed obligate resprouters or seeders (Keeley 1987). Seeds of most seeder species accumulate in large quantities in the soil (Baker 1989) and may reach deep layers where temperature is lower during a fire (Auld 1986; Bradstok & Auld 1995). Seeds of some seeder species need

stimulation by fire to germinate (fire-recruiters *sensu* Keeley 1991), whereas seeds of other seeders germinate regularly in absence of fire. It has been proposed that fire desiccates the seed coat, breaking physical dormancy (Brits et al. 1993) and prompting germination. Otherwise, seeds may remain stored in the soil bank for years. The ability of buried seeds to germinate or to remain dormant depends on traits of the seed, and is further controlled by the soil environment (Baskin & Baskin 1989). In hard-coated seeds, germination is triggered by perturbations which expose seeds to agents such as temperature fluctuations that contribute to alter the seed coat, which is impervious to water. Thus this kind of seeds establish easier after a fire or

terrain movement (e.g., road sides) that bring seeds to the surface than in still soil.

After the seed coat is permeable and imbibed by water litter may influence seed germination because it can modify the spectral composition of light reaching the seeds (Facelli and Pickett 1991) thus inducing a differential germination (Roy & Sonié 1992) which may affect species composition. Litter may also cause physical constraints to seedling emergence (Bergelson 1990; Tilman & Wedin 1991; Moro et al. 1997) and protect soil from direct insolation, creating a better environment for seedling establishment especially in Mediterranean environments (Keeley 1992; Pugnaire et al. 1996).

In this paper we report the results of a field experiment in which we tested the effect of fire, soil disturbance and litter accumulation on germination and establishment of an obligate seeder shrub, *Cistus clusii* Dunal, a species in the Cistaceae which, as all members in the family, are characterised by hard-coated seeds. *Cistus* species are early colonisers adapted to a spectrum of unpredictable disturbances characteristic of Mediterranean ecosystems (Troumbis & Trabaud 1986), in which germination is readily enhanced by fire (Naveh 1974; Montgomery & Strid 1976). The soil seed bank of *Cistus* species is usually large in patches dominated by these shrubs, and population dynamics after catastrophic events is largely dominated by factors controlling seed germination.

We tested the hypotheses that perturbations such as soil disturbance and fire alter the seed hard coat, enhancing germination and establishment of *C. clusii*, and that the protective effect of litter favours seedling establishment.

### Study site and species

We carried out the experiment in the Dehesa del Generalife Park (Granada, Spain, 37°12' N, 3°40' W, 780 m elevation), in a mixed evergreen oak forest of *Quercus rotundifolia* Lam. (González-Hernández et al. 1992). The understorey is dominated by *Cistus clusii*, *Ulex parviflora*, and *Lavandula stoechas*, though scattered individuals of *Retama sphaerocarpa* are also present. Annual species grow from winter to early summer, but perennial herbs, grasses, and mosses dominate small patches between shrubs and trees. The shrub community is typical of early successional stages after fire (Carreira et al. 1991). Soil is an orti-calcic luvisol (FAO 1988) well developed over a unsorted, calcareous con-

glomerate of polygenic origin on an eroded plateau with imperfect drainage (Aguilar et al. 1977). Climate is Mediterranean with cool, moist winters (mean 6 °C in December) and hot, dry summers (mean 26 °C in July). Annual rainfall in this area is irregular, averaging 475 mm distributed mainly in spring and autumn, with peaks in March and November.

*Cistus clusii* is a multi-branched shrub of up to 1 m-tall, with white flowers and narrow leaves found in dry calcicolous regions of the southern Iberian Peninsula with a high frequency of fires. It is the most drought-resistant species of *Cistus* (Polunin & Smithies 1973), and usually colonises eroded soils. *C. clusii* is a fast-growing species with a high concentration of nitrogen in its leaves (Carreira et al. 1991). Seeds are small (average of 0.32 mg, Thanos et al. 1992) and accumulate in high numbers in the soil. The lack of morphological adaptations to dispersal suggests that *Cistus* have a restricted spatial dynamics (Trabaud & Oustric 1989; Carreira et al. 1993), though dispersal by herbivores could be significant (Malo & Suárez 1996). Like other species in the genus, *C. clusii* is an obligate seeder, and populations recover entirely from seeds after adult plants are killed by fire. Size and thickness of seed coat in *Cistus* indicate that they have been selected for persistence and longevity in the soil (Troumbis & Trabaud 1986).

### Methods

Experimental plots were established in April 1992 within an area occupied by *C. clusii* and along three parallel transects separated 5 m each. Above-ground biomass of shrubs and herbs was cut with scissors in 0.5 × 0.5 m plots placed at 1 m intervals along the transects. Biomass was removed to avoid interference of the shrub canopy with treatments. In the first experiment we tested the effect of fire and soil disturbance on seedling establishment. Soil was disturbed by digging with a shovel the ~3 upper cm of soil. Soil disturbance and fire treatments were assigned randomly to the plots in a factorial design with three replicates. The fire treatment was applied with a propane torch for two-minute periods throughout the plot. Such treatments render soil temperatures which simulate a medium-intensity fire (Canadell et al. 1990). In plots with both treatments, fire was applied after soil was disturbed. Plots had a variable, and generally small, amount of litter which was not removed before the treatments were applied. A second experiment was performed at the

same time to assess the effects of litter on seedling emergence. We applied  $800 \text{ g m}^{-2}$  of *Cistus* litter collected in the surroundings of our experimental site to  $0.5 \times 0.5 \text{ m}$  plots randomly distributed in the same area as the above experiment. Treatment and control plots ( $n = 6$ ) were all cleared of above-ground biomass. The amount of litter applied was an intermediate value between the maximum found just underneath the shrub canopy and the absence of litter on bare ground between shrubs.

The field site was visited every two months to monitor germination, and in January 1993 we recorded the number of seedlings of *C. clusii* and of annual plants and grasses at the  $0.25 \times 0.25 \text{ m}$  central core of each plot, as well as the percentage of moss cover. In the same plots we counted in late March 1994 the number of *C. clusii* seedlings that appeared the preceding winter (1993–1994), those which had survived from the previous year (1992–1993), the number of individual herbs present in the inner core of the plots (annuals and grasses) and the percent moss cover. On both sampling dates we also measured seedling densities underneath and between the canopy of mature plants using  $0.25 \times 0.25 \text{ m}$  quadrats. Shrub density in the area was assessed on five  $10 \times 10 \text{ m}$  plots. Canopy cover was determined using the intercept method along six-5 m random transects.

Statistical analysis of log-transformed data was performed by two-way ANOVA using the GLM procedure of the SAS statistical package (SAS 1989), with soil disturbance and fire as factors. Differences between means in other comparisons were assessed by *t*-tests.

## Results

The shrub understorey was widely dominated by *C. clusii*, with densities ranging from 15 000 to 50 000 plants  $\text{ha}^{-1}$  with an average of  $45\,000 \pm 1000$  plants  $\text{ha}^{-1}$  and a canopy cover of  $62 \pm 2\%$ . Seedling emergence began in December 1992, seven months after the treatments were applied. The first half of the summer of 1992 was unusually cold and moist, but the drought season began in mid-July, and was persistent, with no appreciable rainfall until February 1993. Summer temperatures were very high, reaching  $>43 \text{ }^\circ\text{C}$  in late July. By the time of seedling counting in January 1993, a high percentage were already dying probably due to lack of water but were still observable. Rainfall was very low during 1992 and 1993, with totals of 287 and 214 mm (60% and 45% of average), respectively.

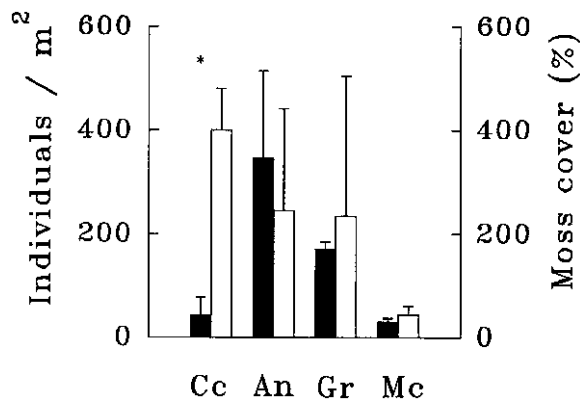


Figure 1. Number of *Cistus clusii* (Cc), annual plants (An) and grass (Gr) seedlings, and percent moss cover (Mc) in control plots (solid bars) and in plots added with litter (clear bars) in January 1993. Data are mean value of individuals per square metre ( $\pm 1 \text{ SE}$ ). Significant differences ( $p < 0.05$ ) are indicated by \*.

The number of *Cistus* seedlings underneath the shrub canopy in 1993 was  $224 \pm 36 \text{ m}^{-2}$ , more than four-fold the number outside the canopy. In untreated experimental plots (control) the average number of *Cistus* seedlings was  $42.7 \text{ m}^{-2}$ , a value similar to between-canopy gaps.

In our experiment, the main factor affecting seedling emergence after the treatments were applied was soil disturbance. Remotion of the upper soil layer significantly ( $p < 0.01$ ) increased *C. clusii* recruitment almost seven-fold (Table 1), but did not increase the number of grasses and annual plants above the control level.

Though plots in which fire was applied tended to have a number of *C. clusii* seedlings higher than control plots (Table 1), the effect was not statistically significant ( $p = 0.12$ ), mostly due to a wide range of variation caused by plot heterogeneity. By the same reason, and although fire reduced the number of both annual and grass seedlings (Table 1), differences with the control were not statistically significant. The highest germination rate, though, was found in disturbed plots treated with fire (Table 2), which reached almost  $700 \pm 150$  seedlings  $\text{m}^{-2}$  ( $\sim 7 \times 10^6 \text{ ha}^{-1}$ ).

The percentage of moss cover was unaffected by the treatments (Table 1). Adding litter significantly ( $p < 0.05$ ) increased the establishment of *C. clusii* seedlings but did not affect the number of annual species, the number of grass seedlings nor moss cover (Figure 1).

Temperatures throughout the summer of 1993 were mild, reaching  $40 \text{ }^\circ\text{C}$  for only a few days in August. Nevertheless rainfall decreased to 45% of the average,

Table 1. Effect of soil disturbance and fire treatments on the number of *C. clusii*, annual plants and grass seedlings, and percent moss cover in January 1993. Data are mean value of individuals per square metre ( $\pm 1$  SE). The interaction was not significant.

Factors	<i>Cistus</i> seedlings	Annuals	Grasses	Moss cover
Disturbance				
Control	88 $\pm$ 35	205 $\pm$ 135	131 $\pm$ 27	19 $\pm$ 2
Disturbed	560 $\pm$ 106	237 $\pm$ 89	144 $\pm$ 41	16 $\pm$ 9
<i>p</i>	0.002	0.85	0.79	0.79
Fire				
Control	235 $\pm$ 59	336 $\pm$ 144	173 $\pm$ 33	22 $\pm$ 8
Fire	413 $\pm$ 107	107 $\pm$ 21	101 $\pm$ 29	12 $\pm$ 7
<i>p</i>	0.12	0.19	0.18	0.40

Table 2. Combined effect of soil disturbance (D<sup>+</sup>, control D<sup>-</sup>) and fire (F<sup>+</sup>, control F<sup>-</sup>) treatments on the number of *Cistus*, annual plants and grass seedlings, and percent moss cover in January 1993. Data are mean value of individuals per square metre ( $\pm 1$  SE).

Treatments	<i>Cistus</i> seedlings	Annuals	Grasses	Moss cover
D <sup>-</sup> F <sup>-</sup>	43 $\pm$ 35 <sup>a</sup>	347 $\pm$ 267 <sup>a</sup>	171 $\pm$ 14 <sup>a</sup>	30 $\pm$ 6 <sup>a</sup>
D <sup>-</sup> F <sup>+</sup>	133 $\pm$ 53 <sup>a</sup>	64 $\pm$ 16 <sup>a</sup>	91 $\pm$ 44 <sup>a</sup>	8 $\pm$ 6 <sup>a</sup>
D <sup>+</sup> F <sup>-</sup>	427 $\pm$ 105 <sup>ab</sup>	325 $\pm$ 178 <sup>a</sup>	176 $\pm$ 72 <sup>a</sup>	15 $\pm$ 15 <sup>a</sup>
D <sup>+</sup> F <sup>+</sup>	693 $\pm$ 166 <sup>b</sup>	149 $\pm$ 14 <sup>a</sup>	112 $\pm$ 48 <sup>a</sup>	17 $\pm$ 14 <sup>a</sup>

and plants were strongly stressed by lack of water until the first rains began in Autumn. As a consequence, all *Cistus* seedlings germinated in the 1992–1993 winter season in our plots had died by March 1994, and newly germinated seedlings (in the winter of 1993–1994) in the understorey of *C. clusii* averaged  $113 \pm 25 \text{ m}^{-2}$ , accounting for only approximately 50% of those germinated the preceding season. There were no statistically significant differences caused by soil disturbance or fire treatments in 1994 (Table 3), though disturbed soils had slightly more *Cistus* seedlings and annuals than control soils. Two years after the treatment was applied, litter still significantly increased the number of *Cistus* seedlings (Table 3) but had no effect on annuals and mosses.

## Discussion

Soil disturbance was the main factor affecting seedling establishment in our experiment, increasing the number of *C. clusii* seedlings by enhancing seed germination. Thompson & Grime (1979) noted that germination in many species that form persistent seed

banks is inhibited by darkness, though most seeds with impermeable seed coats germinate equally well in light and darkness over a range of temperatures after the seed coat becomes permeable. Baskin & Baskin (1994) concluded that factors other than darkness associated with the burial environment prevent germination of seeds with permeable testa, an effect attributed to improper aeration (Bibey 1948) and the presence volatile products of anaerobic respiration (Holm 1972). In *C. clusii*, though, germination is most likely prevented by the presence of an impervious seed coat, which may indirectly be altered by soil remotion as disturbance brings seeds into light and increases soil aeration. In our case, the fact that plots disturbed and heated had the highest number of *C. clusii* seedlings (Table 2) shows that light had little effect, since seeds exposed to light were most likely killed by fire. However, when seeds are brought to the soil surface (or near it) they are in a different temperature environment than they had been, i.e., they receive a higher amplitude of daily temperature fluctuations at or near the soil surface than they do while deeply buried. In some hard-seeded species this change in amplitude of daily temperature fluctuations has been shown to promote germination (Vázquez-

Table 3. Effect of soil disturbance and fire on the number of *C. clusii* and annual plants seedlings, and percent moss cover in March 1994. Litter was applied in a different set of plots on the same date. Data are individuals per square metre (mean  $\pm$  1 SE).

Treatments	<i>Cistus</i> seedlings	Annuals	Moss cover
Disturbance			
Control	56 $\pm$ 28	445 $\pm$ 241	29 $\pm$ 14
Disturbed	154 $\pm$ 69	526 $\pm$ 97	20 $\pm$ 13
<i>p</i>	0.24	0.77	0.66
Fire			
Control	144 $\pm$ 50	473 $\pm$ 140	27.7 $\pm$ 10.3
Fire	136 $\pm$ 48	682 $\pm$ 336	27.6 $\pm$ 8.1
<i>p</i>	0.31	0.87	0.78
Litter			
Control	24 $\pm$ 8	680 $\pm$ 480	44.0 $\pm$ 26.0
Litter	88 $\pm$ 24	145 $\pm$ 45	42.5 $\pm$ 37.5
<i>p</i>	0.03	0.49	0.78

Yanes 1981; Vázquez-Yanes & Orozco-Segovia 1984; Baskin & Baskin 1984).

Emergence of *C. clusii* seedlings was positively affected by fire, as it increased the number of seedlings emerging in fire-treated plots in both disturbed and undisturbed plots (Table 2). Fire is another factor that can cause impermeable seeds to become permeable. But fire did not increase the number of annuals nor grasses, showing a differential response of shrub seeds to fire. This response would enable *C. clusii* to establish populations from seeds early after a fire, taking advantage of conditions such as higher space availability and lower competition for resources that follow a fire. The stimulating effect of high temperatures on the germination of *C. clusii* and other species in the genus has been demonstrated in laboratory and field experiments (Arianoutsou & Margaritis 1981; Troumbis & Trabaud 1986; Thanos & Georgiou 1988; Valbuena et al. 1992). Thanos et al. (1992) found that *C. clusii* had a natural germination rate of 30–40% which was increased to >90% if treated with heat (100 °C for 5 min).

The mechanism by which fire enhances seed germination is unclear. While high temperatures during short pulses increase germination, longer periods of time at lower temperatures may have the opposite effect (e.g., Ortiz et al. 1995). Thus, destruction of temperature-labile substances that cause physiological dormancy (Baskin & Baskin 1994) and seed coat alterations that break physical dormancy may be the

outcome of exposure to fire (Brits et al. 1993). Since dormancy in *Cistus* species seems to be exclusively caused by the impermeable seed coat (Arianoutsou & Margaritis 1981; Thanos et al. 1992), the main effect of fire would be the alteration of the testa which allows water to enter the seed. Alteration of the seed coat may be caused also by large fluctuations in temperature, a regime enhanced by the removal of the canopy cover by fire which stimulates germination of some species (Ivens 1978; Brits 1986). For instance, in *Leucospermum cordifolium*, a fire-recruiter fynbos species, Brits et al. (1993) have shown that oxygen exclusion by the testa imposes dormancy on the embryo, but the effect of the hard coat is removed when successive desiccation – caused by fire – and wetting episodes break its surface. Baskin & Baskin (1989) have proposed that temperature fluctuation is the most important environmental factor regulating the timing of breakdown of the seed coat, of which fire is the most extreme example.

Differences in the establishment rate of 1993 and 1994 (Tables 1 and 3) suggests that most *C. clusii* seeds germinated during the first year in treated plots, remaining few seeds available the second year, though drought (total rainfall less than 50% of the mean) may have decreased seed production and germination in 1993.

Fire did not increase germination of grasses and other annual species, as it suppressed seed production in these plots and may have killed other viable seeds on the soil surface. Ne'eman et al. (1992) have

shown that seeds of most annual species germinate and seedlings establish outside the burned canopies of pine trees. In our plots, seed dispersal after the treatments were applied should account for the number of annuals found, only slightly less than in the control. Fire also killed a proportion of mosses, which were able to recover their initial level in one year.

The addition of litter increased the number of *C. clusii* seedlings (Figure 1) but did not change the number of grasses, annuals, or moss cover. It is known that litter has a major role in the dynamics of plant communities because of its physical and chemical effects (Facelli & Pickett 1991). Litter may have enhanced specifically the germination of *C. clusii* seeds, by changing the quality of light reaching the soil (Roy & Sonié 1992), while inhibiting germination of other seeds, an effect which may drastically alter the composition of species (Bergelson 1990; Tilman & Wedin 1991). It is worth to note the significant effect of litter in increasing germination of *C. clusii* two years after its addition, which could be interpreted as maintaining a higher soil moisture level. A personal observation in March 1995 showed that not a single *C. clusii* seedling had established in our plots since the experiment began in April 1992.

In conclusion, *C. clusii* is an early coloniser which germination is enhanced by disturbances that expose seeds to factors such as temperature fluctuations able to break the physical dormancy imposed by the hard coat. In absence of disturbance, seeds in the soil bank remain dormant. This, along with other seed characteristics such as a small size, the presence of hard coat, and a long persistence in the soil, make *C. clusii* a typical pioneer species in Mediterranean environments (Thanos et al. 1992). Indirectly, our data also show that water is a major factor controlling seedling establishment in this environment.

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