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Effects of disturbance on the reproductive potential of *Lavandula stoechas,* a Mediterranean sclerophyllous shrub

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Studies on the effects of perturbations on Mediterranean shrub vegetation have most often emphasized the role of disturbance by fire. Here I report on the effects of a relatively mild (as opposed to burning) disturbance on *Lavandula stoechas.* The study was carried out in two adjacent plots, one in which all shrub aboveground biomass had been eliminated mechanically two years before, the other with an intact layer of shrub. Although the study species lacks developed underground organs, root sprouting ensued clearing and average interplant distance at the treated site was indistinguishable from that in the control area. Average percent plant mass accounted for by living branches with leaves was significantly higher for rejuvenated, cleared-plot individuals, which also produced about twice as many flowering heads and seeds per head as their control-plot counterparts, along with heavier individual seeds. Naturally occurring seedlings survived relatively better at the cleared plot, probably as a result of the joint effects of decreased litter cover, increased water availability, and higher growth rates. The average fresh mass of one-year-old seedlings at the open was 243 mg, vs 10 mg of shrub-plot seedlings. No seedling survived the first summer drought out of ca 1000 seedlings that emerged from seed sown in a nearby, intact shrub stand. It is hypothesized that mild, relatively local disturbance elicits competitive release, which has a major effect on both the fecundity of individuals and the demography of this species.

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Fire is probably the most-studied agent of vegetation change in Mediterranean ecosystems. By changing the availability of nutrients in soil or removing allelochemicals, burning of aboveground biomass is accepted to enhance shrub regeneration (e.g., Keeley 1987, Riggan et al. 1988, Swank and Oechel 1991, Trabaud 1990, Tyler and D'Antonio 1995). Many Mediterranean shrub species are adapted to fire, either through basal sprouting or heat-stimulated seed germination (Keeley 1986a,b; see however Mesleard and Lepart 1989, Lopez-Soria and Castell 1992), and it is commonly accepted that shrub communities represent successional stages subsequent to forest destruction by fire.

Fire is unexceptional in Mediterranean ecosystems, but less-devastating, local perturbations such as landslides, tree windthrowing, or intensive trampling by animals also exist in these areas. Man-mediated disturbances like shrub clearing and logging also represent relatively mild perturbations which, albeit more local than most wildfires, represent an opportunity for shrub regeneration and colonization (e.g., Chambers et al. 1990, Clark 1990, Frelich and Lorimer 1991, Young and Hubbell 1991). The effect of such disturbance types on shrublands has been largely neglected, and this may have resulted into regenerative behaviors different from those exhibited by fire-adapted species going totally unnoticed.

Lavandula stoechas (Lamiaceae) is a Mediterranean sclerophyllous shrub that is very common in southern Spanish shrublands either in lowlands or mountain

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ranges. Compared to other sclerophyllous shrub species, the response of *L. stoechas* to fire is very poor, probably because it has no underground organs (Herrera 1987) and because its seeds germinate without heat stimulation (Herrera 1991). Several characteristics of the species' reproductive process are known, including floral biology and phenology, pollination (e.g., Devesa et al. 1985, Duffield et al. 1993, Herrera 1991, 1993), but factors affecting its regeneration and low seedling abundance in the field in spite of copious seed production remain unexplored. Here I report on the response of *L. stoechas* shrubs to a mild (as opposed to burning) perturbation, and investigate the effect that this perturbation may have on the population dynamics of the species.

Methods

Study site and species

The study was carried out at the Doflana Biological Reserve, a coastal area near the Gulf of Cadiz, in southern Spain (37° 1'N, 6° 33'W). The area has a Mediterranean climate: January and July being respectively the coldest (9.8°C) and hottest (24.6°C) months. Average rainfall is 537 mm yr', although from 1991 to present it has been < 50% of long-term average. Vast areas in the Reserve (some 100 km') are vegetated by sclerophyllous shrub mixed with *Pious pinea* stands growing on fixed sand dunes (see Rivas-Martinez et al. 1980 for a description of vegetation; plant nomenclature below follows Valdes et al. 1987). Shrub species in the Cistaceae and Lamiaceae dominate this shrub, all of which disperse huge numbers of small seeds each summer and are unable to sprout following fire (Herrera 1987). *Lavandula stoechas (Lavandula* hereafter) is an aromatic shrub up to 1 m high with showy, head-like inflorescences which appear mostly during March and April (Herrera 1986). Being self-fertile (Munoz and Devesa 1987), many-flowered, and heavily visited by a number of bee species (Herrera 1988), seed production is invariably very high. As demonstrated by abortion rates and experimental manipulations, fecundity is strongly resource-limited. Seedlings are only rarely observed in the field (unpubl.).

A vegetation management program started in 1993 at the study area with which it was intended to create a mosaic of varied vegetation types from monotonous extensions of sclerophyllous shrub. Only mechanical procedures were used to clear shrub (e.g., ploughing, hand removal, and/or by harrow), whereas burning was carefully avoided. The effect of disturbance on *Lavandula* was studied in an area vegetated by of a mixture of shrub and *Pinus* where two adjacent 1 ha plots had been created from a single, homogeneous stand of old shrub. In one, all aboveground shrub biomass had been pulled out with harrow and the dead vegetation taken away, which resulted in an extension of mostly open land with a few trees (the `open' plot). Harrow penetrated at most 0.5 m in the soil, therefore many older shrub roots are likely to have survived this treatment, whereas younger plants and seedlings were completely removed. The adjacent area retained the original dense cover of shrubs in all age classes (the `shrub-covered' plot). In addition to shrub removal, *Pinus* treelets 1—3 m tall which occurred at very high densities were thinned to 30 ha^{-1} in both plots. Thus, some disturbance occurred at both sites, with the major difference among these being the layer of shrub. Management took place in December 1993 and data in the present study pertains to the second spring following disturbance.

Plot comparisons

Three 30 m long, parallel linear transects were used to estimate live woody plant canopy cover at each plot using a line-intercept method. Intercepts with dead shrubs that remained standing were also noted. I also stretched out a 2 m long measuring tape and noted if the vertical projection of a fine-pointed pin, set at 5 cm intervals, touched bare sand, dead plant remains (twigs and litter), or living shrubs. The tape was stretched ten times on each plot, and data are reported as average relative frequencies.

To estimate population density, I recorded the number of shrubs within ten 25 m^2 (5 x 5 m) sampling units per plot. Interplant distances were estimated by selecting a number of large plants and registering the distances to the nearest five reproductive (> one flowering head) conspecifics. In optimal, greenhouse conditions, *Lavandula* needs at least two years to flower (unpubl.), so none of the flowering plants in the plots could be from seeds germinated after disturbance. At the open plot, and because all aboveground biomass had been eliminated in December 1993, flowering plants necessarily represented root sprouts.

By the time flowering had finished (late April), the total number of flowering heads produced by 50 medium-sized (0.25—0.50 m of diameter) shrubs was counted at each plot. To check the vigor of shrubs after drought stress, ten additional reproductive, medium-sized shrubs per plot were excavated, their roots clipped, and branches covered with leaves separated from bare dead branches. The proportion of aboveground plant mass accounted for by each component was determined by weighing.

Seed production was determined for 20 (ten per plot) large-sized (> 0.5 m in diameter), randomly-chosen *Lavandula* shrubs which were marked in late April when flowering was past. On each shrub, I counted the total number of heads produced, then bagged ten fruit-developing heads with small individual mesh exclosures which would avoid seed dispersal. When seeds were ripe (early summer), 198 bagged heads remaining were collected and seeds from each head weighed to the nearest 0.1 mg. Seeds were then examined under a microscope to separate filled seed from abortions. From head number and seed production per head I estimated the number of filled seeds produced per plant. Among-plot differences in the mass of individual seeds were investigated by weighing one filled, randomly chosen seed from each of four heads per shrub.

To investigate the fate of seedlings under no disturbance, *Lavandula* seed was sown in an untouched shrub area at 1 km from the main study site. Ten 25 x 25 cm sub-plots were randomly distributed over an area of 1 ha, the top five cm of soil removed within each sub-plot and replaced with commercial, sterile pot substrate. On October 1993, I distributed 100 mg (ca 140 seeds) of *Lavandula* seed from the previous fruiting season over each sub-plot, then covered the seeds with a thin layer of substrate. Through the following year, sub-plots were monitored for the number of live seedlings at about monthly intervals.

On April 1995, randomly-chosen seedlings from three common species including *Lavandula* were carefully picked with their roots from the open and shrub-covered plots, taken to the laboratory inside plastic bags and weighed. Shrub clearing (and intensive soil stirring) took place in December 1993, which probaly killed older seedlings at the open plot. Therefore, all seedlings weighed had to be from seed germinated in either the spring or autumn of 1994, or during 1995, and thus at most one-year old. The sample from the undisturbed site, on the other hand, may have included some older seedlings. A 14 yr field experience with shrub seedlings at the site helped me to age seedlings from general appearance and the degree of cotyledon attrition, but even if I made any mistake it would fall on the conservative side of the hypothesis that relatively mild disturbance elicits higher seedling growth rates (i.e., any older seedling from the untreated plot should be expected to be more massive than a younger one from the cleared plot).

The open and shrub-covered plots were scanned for the numbers of seedlings of four dominant species including *Lavandula.* Seedlings from these species can be recognized at very early stages of development, either by a characteristic odour *(Rosmarinus officinalis, Helichrysum picardii)* or appearance *(Halimium halimifolium* and *Lavandula). I* surveyed the sites in spring (when seedlings were expected to be more abundant) and also at the onset of autumn (when a great seedling mortality was expected to have occurred because of summer drought). I counted the number of seedlings within 40 circular, 0.3 m diameter sampling units per plot. These were set in line at 2 m intervals and differed among sampling dates. I attempted to record both live and dead seedlings, but only with great difficulty were the desiccated seedlings distinguished against the dark-grey litter. Therefore, the analysis below deals only with live seedlings which were easily detected.

Data analyses

Site comparisons were made either by independent Student's t-test for means or (if more than one factor was taken into account; i.e., shrub identity) by ANOVA. Computations were performed with procedures in SAS (SAS 1990) and SYSTAT (Wilkinson 1986) statistical packages. Masses and dimensions were log-, and percentages arcsin-square-root transformed (Sokal and Rohlf 1981). Statistical significances are abbreviated as ns (not significant), *($p < 0.05$), **($p < 0.01$), and ***($p < 0.001$). Means are reported + one standard error.

Results

Effects on the vegetative phase

The second spring following shrub removal, the cleared plot had similar species composition as the adjacent area with undisturbed shrub (Table 1). An exception was *Erica scoparia,* represented only on the open plot by an isolated, large plant which presumably sprouted after disturbance. In general, most other species had either comparable or lower cover on the disturbed compared to the undisturbed plot. *Helichrysum picardii,* a low shrub which develops well on mobile sand, was very abundant in the open but relatively scarce at the shrub-covered area. Dead shrubs on the undisturbed shrub plot accounted for 5.8`%% of total cover. In contrast, only living shrubs occurred in the open plot, where cover was about one third that of the control area.

Table 1. The identity and relative cover of sclerophyllous shrub species in two neighbouring plots at Donana, southern Spain. Shrub cover at the open plot was completely eliminated by harrow ca 20 months before this study.

Species (family)	Plot	
	Open	Shrub-covered
Cistus libanotis (Cistaceae)	0.1	4.9
Erica scoparia (Ericaceae)	0.2	0
Halimium commutatum (Cistaceae)	0.1	0.5
Halimium halimifolium (Cistaceae)	1.8	4.5
Helichrysum picardii (Asteraceae)	1.2	0.4
Lavandula stoechas (Lamiaceae)	0.2	0.3
Rosmarinus officinalis (Lamiaceae)	0.6	3.2
Stauracanthus genistoides (Fabaceae)	0.4	0.3
Overall living shrub cover	4.6	14.1
Overall dead shrub cover	0	5.8
Open ground	*95.4*	*85.9*

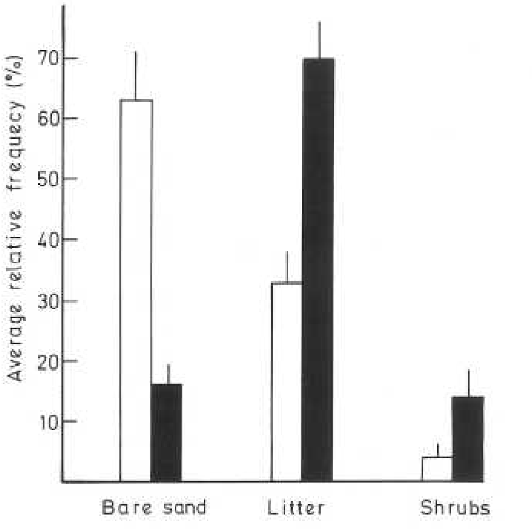

Fig. 1. The relative abundances of bare sand, areas covered by dead plant remains, and living shrubs at the study plots. Vertical lines span two standard errors of the mean.

Live shrubs were about three times more frequent at the shrubby (14%) than at the cleared plot (4%), based upon the point frame method (Fig. 1), which is consistent with values provided by line intercepts (Table 1). A large proportion of ground covered by dead matter was found, which accounted for 70% of hits on the undisturbed plot. This includes both dead, standing shrubs and dry shrub fragments on the ground. The occurrence of this nearly continuous and thick layer of twigs and litter resulted in low (15%) bare sand. In contrast, where shrubs had been eliminated bare sand was dominant (63`/) and litter less abundant (33° o).

The density of the *Lavandula* population was significantly higher at the shrub-covered plot, although the species also occurred on the open plot (Table 2). Few older, reproductive shrubs inhabiting the place prior to disturbance appeared to be killed as a result of harrow, as evidenced by interplant distances being statistically undistinguishable from those at the undisturbed plot. Furthermore, individuals growing in the open were greener and apparently more vigorous than those at the adjacent shrubby plot, which had a significantly lower proportion of mass accounted for by young, healthy branches with leaves in their canopies.

Flowers and seeds

Lavandula shrubs in the open plot produced more than twice as many flowering heads as those in the shrubby plot (Table 3). Also, the flowering heads of open-plot shrubs set complements of seeds that were on average 2.5 heavier than those of their counterparts at the shrub-covered plot, which was due in part to many more filled seeds being produced per head (84 vs 36 on average), but also to individual seeds being heavier than those produced by plants at the control area.

The proportion of aborted seeds was also significantly lower for individuals growing in the cleared area, and the average number of filled seeds produced per shrub accordingly larger (Table 3). Because only large plants were chosen for this comparison of seed output (91.7 + 11 heads plant $^{-1}$ for the open-site, 90.6 + 10 heads plant $^{-1}$ for the shrubby-site sample), the analysis fails to reflect substantial among-plot differences that existed in absolute head number (Table 2). In other words, the relative fecundity of open-plot shrubs was 2.5 times greater, but since they also produced on average twice as many heads as individuals growing within the shrubby area, their absolute fecundity was probably around five times higher.

Seedlings

The dynamics of seed germination and seedling fate in the absence of disturbance is shown in Fig. 2. At the unmanaged, dense shrub site where *Lavandula* seeds were experimentally distributed, nearly complete germination occurred soon after release into the soil: ca 140 seeds/sub-plot were sown, and nearly 100 seedlings appeared on average only sixteen days later. From then onwards, seedling numbers decreased progressively through the winter likely as a result of desiccation, then dropped precipitously during spring and summer. Herbivory was observed only rarely. No seedlings survived for the whole year out of ca 1000 seedlings for all ten sub-plots.

The size and (presumably) the growth rates of *Lavandula* seedlings changed dramatically following disturbance, and the same was true for other co-occurring species (Table 4). Among-plot differences were particularly striking for *Lavandula,* however, whose seedlings were 24 times heavier at the open. Site-specific effects on seedling mass were even larger (MS = 25.24) than effects due to species identity (M = 0.72, Table 4). Note that all seedlings weighed were < 1 yr-old (as indicated by general appearance and the degree of cotyledon attrition).

Study plots differed in the abundance of 1 yr-old seedlings (Table 5). The spring survey at the open plot yielded 107 seedlings in all four species considered, whereas only 48 were detected at the shrubby area (only ten and five, respectively, were *Lavandula* seedlings). The autumn survey yielded only three *(Halimium halimifolium)* seedlings at the shrub-covered plot, as opposed to 51 in the open (of which five were *Lavandula).*

Table 2. Population and individual characteristics of *Lavandula stoechas* at the study plots. Means are followed by standard errors (in parentheses). Values of the Student's test for mean comparisons are also given.

Variable	Plot				T, p
	Open		Shrub-covered		
	(SE)	N	X (SE)	N	
Density (plants 25 m^{-}-)	3.9 (1)	10	6.9 (1)	10	2.39, *
Distance among reproductive plants (m)	2.3 (0.2)	65	2.2 (0.1)	80	0.40, ns
% plant mass accounted for by branches with leaves	69.4 (3)	10	41.8 (5)	10	4.82, ***
Flowering heads per shrub	62.4 (7)	50	30.6 (4)	50	4.1, ***

Table 3. A comparison of reproductive output of *Lavandula stoechas* shrubs in the study plots. ANOVAs including plot and individual plant identity (nested under plot) as the main effects were performed for the first four variables, of which only the value of F for the plot effect is reported.

Variable	Plot				Mean comparison
	Open		Shrub-covered		
	X (SE)	N	t (SE)	N	
Mass of seeds head^{-1} (mg	81.5 (3)	98	32.5 (3)	100	F = 16.1, * **
Number of filled seeds head'	83.8 (5)	50	35.8 (4)	50	F = 179.4, ***
% aborted seed head^{-1}	20.7 (2)	50	29.3 (2)	50	F = 8.6,
Mass of individual seed (mg)	0.78 (0.02)	40	0.69 (0.02)	40	F = 9.2, **
Estimated mass of seeds plant -' (g)	7.7 (1)	10	3.1 (1)	10	T = 3.1, **
Estimated number of seeds plant- '	8082 (1672)	10	3495 (1035)	10	T = 2.9, **

Discussion

Competitive root-to-root interactions may determine spacing, size, and fecundity in plants from arid habitats (e.g., Farmer 1984, Cody 1986, Manning and Barbour 1988, Kadmon and Shmida 1990, Reichenberger and Pyke 1990, Mahal and Callaway 1992). In accordance with this, the increase in reproductive capacity of *Lavandula* shrubs following clearing probably originated from decreased competition with neighbors for nutrients and/or water. Because shrub seedlings are particularly sensitive to competitive interactions (Swank and Oechel 1991, Tyler and D'Antonio 1995), differences in seedling size of *Lavandula* among the open and shrubby plots may also have resulted from competitive release.

In general, well developed root systems are essential for seedlings to survive the first summer drought and become established in seasonal habitats (Frazer and Davis 1988, Reichenberger and Pyke 1990). The small seedlings of *Lavandula,* however, seem unable to reach this threshold size and complete their first year of life unless removal of older shrubs elicits relatively high growth rates. Recruitment might also occur episodically only in unusually rainy years. However, the observation that at least some seedlings in the open plot endured summer during the dry year of this study suggests that precipitation alone is not responsible for lack of establishment. Rather, evidence suggests that recruitment is rare in *Lavandula* as a result of extremely low growth rates due to root competition with adult shrubs.

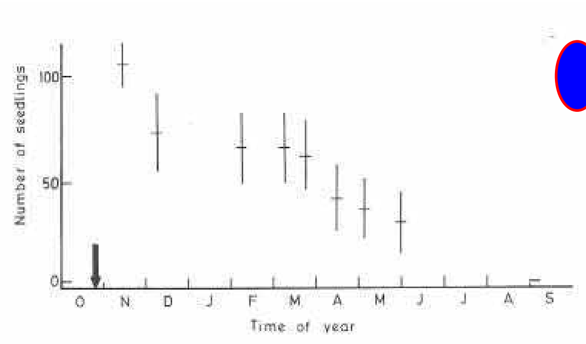

Fig. 2. Changes in the average number of living seedlings at ten experimental plots placed in an unmanaged site with closed scrub. Vertical lines span two standard errors of the mean (horizontal line). The arrow over the abscissa indicates the date of seed sowing.

Table 5. The numbers of one-year-old seedlings of four shrub species at the study plots. Bivariate (site and date) Yates corrected chi-square of independence is $y^2 = 12.68$, DF = 1, $p < 0.001$.

Site	Date	Shrub species (1)			
		HH	HP	RO	LS
Open	Spring	29	48	20	10
	Autumn	11	26	9	5
Shrub-covered	Spring	20	19	0	9
	Autumn	3	0	0	0

(1), HH, *Halimium halimifolium; HP, Helichrysum picardii;* RO, *Rosrnarinus officinalis;* LS, *Lavandula stoechas.*

Litter can have a strong effect on recruitment of prairie as well as forest plant species, the major deleterious effect for seedlings being often light interception. At the site of this study light is unlikely to be a limiting factor for seedling growth, but the extensive layer of twigs and litter at the shrub-covered plot was thick enough to act as a crust that intercepted any but the more intense precipitations (unpubl.). Furthermore, negative effects of litter on seedling growth through allelopathy cannot be ruled out (Vokou and Margaris 1986).

The effect of neighbor removal on *Lavandula* shrubs was so dramatic that even seed size was influenced and open-plot shrubs produced significantly heavier seeds than their counterparts from the undisturbed plot. Variations in seed size at the species (Harper et al. 1970, Silvertown 1981, Armstrong and Westoby 1993), population (Agren 1989, Winn and Gross 1993), and individual levels (for example, Andersson 1990, Antonovics and Schmitt 1986, Nakamura 1988, Rocha and Stephenson 1990) have received considerable attention, whereas intraspecific variations arising from local changes in the intensity of competition have been reported only rarely (Matthies 1990). Since larger seeds often result in larger and/or more competitive seedlings (e.g., Armstrong and Westoby 1993, Schaal 1984, Stanton 1984, Weller 1985, Westoby et al. 1992, see however Hendrix et al. 1991, Stock et al. 1990), increased survivorship of *Lavandula* seedlings in the cleared area may also be explained in part by seed size differences.

Shrub species included in most studies of regeneration are typically those displaying spectacular post-disturbance responses (for example, Gratani and Amadori 1991, Izhaki et al. 1992, Keeley 1986a, 1986b, 1987, Moreno and Oechel 1993). This may overemphasize the role of fire in shrub dynamics and extend the notion that burning is an absolute necessity for vegetation regeneration in Mediterranean ecosystems. In *Lavandula,* however, new stems can be formed from stumps

Table 4. The sizes (in mg of fresh mass) of one-year-old seedlings from three shrub species at the open and shrub-covered study plots. Results of a two-way ANOVA are also reported in which species identity and plot were the main factors.

	Seedling mass (mg)			
	Open plot		Shrub-covered plot	
	(SE)	N	(SE)	N
Halimium halimifolium	421 (99)	10	26 (5)	10
Helichrysum picardii	169 (28)	10	19 (8)	10
Lavandula stoechas	243 (43)	18	10 (1)	18

ANOVA table

Source	Type III SS	DF	MS	F	P
Plot	25.2	1	25.24	238.6	***
Species	1.4	2	0.72	6.8	**
Site x species	0.1	2	0.05	0.5	ns
Error	7.4	70	0.11	0	

and contribute to genet survival provided that disturbance is relatively mild and roots survive the perturbation. Coupled to fast seed germination and enhanced seedling recruitment following neighbor removal, this would encourage regeneration under moderate disturbance regimes.

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