

EFFECTS OF COMPETITION AND DISTURBANCE ON THE  
RESPROUTING PERFORMANCE OF THE  
MEDITERRANEAN SHRUB *ERICA MULTIFLORA*  
L. (ERICACEAE)<sup>1</sup>

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Two field experiments were designed to evaluate the importance of competition, fire, repeated disturbance, and their interactions on the vegetative and reproductive performance of the Mediterranean shrub *Erica multiflora* over a 2.5-yr period. In a burn experiment, fire was applied to the ground-level stumps of previously clipped 13-yr-old plants with a propane torch and competition was diminished by removal of neighboring plants. Fire resulted in a reduction of sprout vigor and biomass of flowers; mature neighbors also reduced *E. multiflora* sprout vigor and flowering. The interaction between fire and competition was nonsignificant. In a stand burned by a wildfire we studied the effects of regenerating neighbors on target plants by removing all neighbors or only *Quercus coccifera*, the most dominant species in the burned stand. In this stand we also simulated herbivory by repeatedly clipping the sprouts of *E. multiflora*. Regenerating neighbors did not affect target plant sprout vigor after the wildfire, but did cause a decrease in the biomass of flowers per plant. Survival decreased after repeated clipping but was not affected by neighborhood treatment. The results suggest that the importance of competition on resprouting vigor was temporally variable. Variables related to plant size rather than species determined competitive superiority: resprouting neighbors did not affect resprouting performance of target plants, but mature neighbors did. In nature, fire may directly reduce vegetative and reproductive biomass by the heating effect. But it may have an indirect positive effect on biomass, by reducing competition among plants. Frequent disturbances that removed aboveground biomass of *E. multiflora* had a detrimental effect on target plant survival independent of neighborhood effect.

Fire is a major factor determining structural and functional characteristics of Mediterranean shrublands (Naveh, 1974). The role of fire as a disturbance in these communities is profound and has been well studied (Mooney and Conrad, 1977). In addition to fire, plants in the western Mediterranean Basin are subjected to frequent disturbances such as heavy livestock grazing and browsing and clearing of brush as a measure to reduce fire hazard (Perevolotsky and Haimov, 1992; Serrada, 1993). Such disturbances reduce survival and growth in some species (Barbour and Minnich, 1990).

The negative effects of neighbors in the competition for resources in Mediterranean shrublands has been less studied, but has been shown to exist among mature shrubs in

the Chilean matorral (Fuentes and Gutierrez, 1981) and in the chaparral (Schlesinger and Gill, 1978), as well as in resprouting species of the Mediterranean Basin (Vilà and Terradas, 1992; Vilà, Weiner, and Terradas, 1994). After a wildfire, plant competition may be reduced compared to competition among mature plants because fire removes vegetation, and neighboring individuals when regenerating are smaller than in a mature community. However, plant performance is more likely to reflect conditions of the immediate neighborhood than those averaged over a larger spatial scale (Tyler and D'Antonio, 1995). Size and developmental stage of neighbors as well as their identity affect plant performance (Goldberg, 1990). After fire some species may be better competitors than others because they have fast resprouting and high cover (Papió, 1988). In the western Mediterranean Basin shrublands, it has been predicted that after fire, there is competition among different species that is based on plant functional and structural attributes (Trabaud, 1983). Malanson (1985) simulated competition between a pair of hypothetical fire-prone shrub species that differed in competitive ability. He found that the strong competitor dominated the community, while the weak competitor did not have an effect on the other species.

Although a community may progressively return to its prefire species composition (Hanes, 1971), some species that resprout from lignotubers have low survival after fire (Bradstock and Myerscough, 1988). To understand the dynamics of these fire-prone communities it is necessary not only to understand the effects of fire, grazing, or other disturbances and competition as individual factors, but also to have information about their interactions. The ways in which competition and fire affect plant com-

<sup>1</sup> Manuscript received 8 November 1994; revision accepted 16 March 1995.

The authors thank J. Pietx, J. Montes, A. Vicens, and M. Pamplona who collaborated in the field work. We thank J. Canadell, L. López-Soria, F. Lloret, and M. Riba for their multiple suggestions on experimental design and data analysis. We kindly acknowledge J. H. Connell, C. M. D'Antonio, B. E. Mahall, J. M. Moreno, J. Raventós, C. M. Tyler, J. Weiner, and two anonymous referees who provided helpful recommendations on various versions of the manuscript. UCSB Plant and Population Ecology Groups provided thoughtful comments on data analyses and early drafts. We are indebted to W. Rehlaender for the detailed editing of the manuscript. We thank the Departament d'Agricultura, de Ramaderia i de Pesca de la Generalitat de Catalunya, for allowing us to use the study site. Financial support was provided as a part of Comissió Interdepartamental de Recerca i Tecnologia (Ajuda a Joves Investigadors AR89), the Fundació Caixa de Barcelona and mostly by the Comissió Interdepartamental de Ciència y Tecnologia (FOR 91-1054 project).

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munities have usually been studied separately, if at all. The purpose of this study was to study the interaction among the effects at fire, simulated herbivory, and neighbors of different developmental stages (plants regenerating and at maturity) in a Mediterranean shrubland where both fire and grazing are a common occurrence.

The ericoid growth form is common, in fire-prone Mediterranean communities of the Old World (Good, 1974). Ericoids are multistemmed evergreen shrubs, some of which resprout after aerial biomass removal, such as after fire (le Maire, Jones, and Forsyth, 1992). These species constitute a low to mid-high closed shrubland in soils with high C content, low pH and rich in fine particle fraction (Cowling, 1992). In the western Mediterranean Basin shrublands, *Erica multiflora* relies almost entirely on vegetative regeneration for persistence after fire because seedling recruitment is poor. In addition, *E. multiflora* is grazed by both sheep and goats, which appear to impact negatively its survival. Because of its heavy dependence on vegetative regeneration for recovery after disturbance, *E. multiflora* may be particularly impacted by the presence of more vigorous regrowing neighbors. *Quercus coccifera* is an example of the latter. We hypothesized that mature neighbors have a greater negative effect on target plants than regenerating neighbors. Also, we suppose that after a wildfire the negative effects of neighbors are intensified by the presence of the vigorous *Q. coccifera*.

The specific objectives of this study were: (1) to document the effects of fire and competition by mature neighbors on resprouting vigor and flowering of *E. multiflora* over a 2-yr period; (2) to analyze the effect of regenerating neighbors after a wildfire on the resprouting vigor and flowering of this species; and (3) to investigate the effects of repeated clipping and presence of neighbors on plant survival after a wildfire.

## MATERIALS AND METHODS

**Study sites and species description**—There have been described up to 700 species of the genus *Erica*, of which over 600 are confined in the Cape Region of South Africa (Good, 1974). These ericoids constitute one of the major fire-prone plant communities of the Southern Africa fynbos (Cowling, 1992). Other species of *Erica* are distributed in the east side of Africa, across the Mediterranean and into Europe. *Erica multiflora* L. (Ericaceae) is an erect, short-leaved resprouting shrub 1 m high distributed in the lowlands of the northwestern Mediterranean Basin. This species co-occurs with *Quercus coccifera* L. (Fagaceae), a monoecious highly branched shrub. Both species are common components of the type of vegetation known as "matorral" and "garrigue." Postfire floristic development and community structure of these Mediterranean communities have been described by Malanson and Traub (1987). These species resprout from underground organs after aboveground biomass removal. *E. multiflora* resprouts from a small stump or from superficial roots (Lloret and López-Soria, 1992). For *Q. coccifera* new sprouts develop from buds located in a root sucker, and it is difficult to distinguish among different genets (Malanson and Traub, 1988).

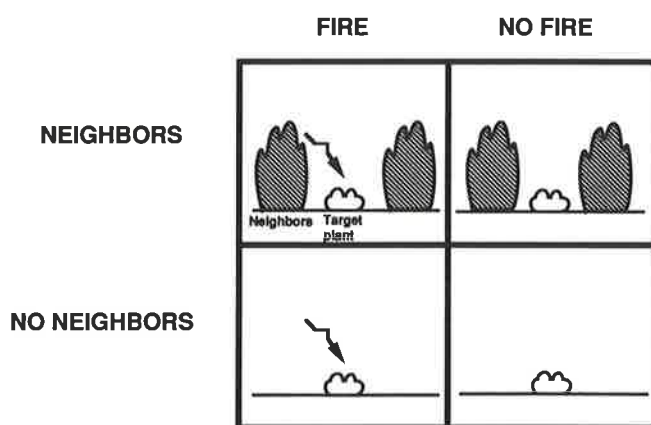


Fig. 1. Diagrammatic representation of the burn experiment. See text for a detailed explanation of the fire and neighbor removal treatments.

Because we were interested in comparing the competition effects of mature neighbors vs. regenerating neighbors we qualitatively compared the effects of neighbors in target plant resprouting by removal experiments at two sites: a mature 13-yr-old vegetation and a postfire 3-month-old vegetation. Experimental sites were two Mediterranean coastal shrublands in Catalonia, Spain. One of the study sites was located on the Serra de les Comes (40°53'N, 0°41'E) at El Perelló; this site was burned by a wildfire in 1976. The woody vegetation was dominated by the evergreen shrubs *Rosmarinus officinalis* L. [(Lamiaceae) (10,190 kg/ha)], *E. multiflora* (1,170 kg/ha), *Ulex parviflorus* L. [(Fabaceae) (4,400 kg/ha)] and *Q. coccifera* (2,770 kg/ha), which accounted for the 73.4% cover. In this study area, plants attained 1 m height. The second site was located 10 km from El Perelló in the Tivissa mountains (41°0'N, 0°41'E) and burned in a lighting fire caused in July 1989. Three months later, when we set up the experiment, *Q. coccifera* sprouts accounted for >50% of ground cover, (1,590 kg/ha), and sprouts barely attained 15 cm height. The geologic substrate was composed of calcareous rocks of the late Jurassic or early Cretaceous. The soil at both sites was extremely rocky and shallow with clay texture. It was rich in organic matter and low in available P. We classified it as a Lithic haploxeroll. The climate is Mediterranean; at the nearest weather station (Ginestar) mean monthly temperatures range from 3.5 C in January to 33 C in July, and annual precipitation is 474 mm, of which 45% occur in spring and autumn, mostly as thunderstorms. The driest months are July and August, also the period during which most wildfires occur.

**Burn experiment**—In October 1989, two plots of 2,500 m<sup>2</sup> each were selected at El Perelló. Forty target plants of *E. multiflora* were randomly selected in each plot and clipped at ground level. Each plant was at least 4 m away from any other target plant. The experimental design was a factorial combination of two variables, fire and competition. Ten target plants per site were randomly assigned to each of the four combinations of the two treatments: with and without fire, with and without neighbors (Fig. 1).

Fire was applied to the stumps with the flame of a

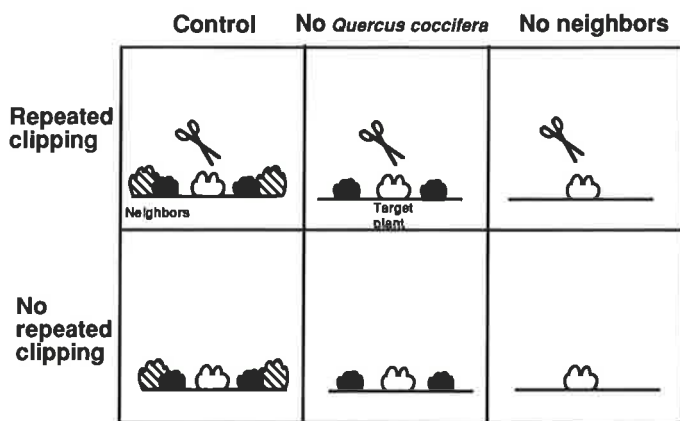


Fig. 2. Diagrammatic representation of the wildfire experiment. See text for a detailed explanation of the selective neighbor removal treatments and repeated clipping of target plant sprouts.

propane torch, using the method previously described by Lloret and López-Soria (1992). The range of temperature (350–550 C for 3 min) was chosen according to measurements estimated from field data from wildfires in Mediterranean shrublands (Trabaud, 1979), and represented a medium-intensity fire. Competition was eliminated by clipping at ground level all the vegetation growing within a 1.5 m radius around the target plants. A previous study (Vilà and Terradas, 1992) suggested that a 1.5 m radius was greater than plant root lateral elongation, and that this removal treatment increased growth of target plants. Any regrowing vegetation in the neighbor removal treatments was removed every 2 mo by manual clipping at ground level. Each target plant was covered by a chicken wire meshing in order to prevent herbivory by rabbits and sheep.

The length of all target plant shoots was measured from the stump surface and the number of branches on each shoot counted in three consecutive growing seasons (July 1990, January 1991, and July 1991). In January 1992 we harvested the plants, separated the vegetative from the reproductive structures (flowers), and weighed these parts after drying at 80 C for 96 hr.

**Wildfire experiment**—In October 1989, two plots of 2,500 m<sup>2</sup> each were selected at Tivissa in a stand burned by a wildfire in July 1989. In each plot, we randomly chose 30 *E. multiflora* that had resprouted. Each selected plant was located at least 4 m from another selected plant. Ten plants per plot were randomly assigned to each neighborhood removal treatment as follows (Fig. 2): 1) Control: unmodified neighborhood vegetation, which was mainly dominated by *Q. coccifera*; 2) No *Q. coccifera*: we clipped at ground level all *Q. coccifera* sprouts in a 1.5 m radius around the target plant; 3) No neighbors: we clipped at ground level all the vegetation in a 1.5 m radius around the target plant.

As in the previous experiment, each target *E. multiflora* genet was enclosed by a metallic mesh in order to prevent herbivory by rabbits and sheep. All *Q. coccifera* sprouts growing from the no *Q. coccifera* treatment, and all vegetation from the treatments without neighbors were eliminated every 2 mo by manual clipping.

The length of shoots of all target plants was measured and the number of branches per shoot counted in January 1990, July 1990, and January 1991. In January 1992 we harvested the plants, and separated and weighed their vegetative and reproductive biomass (flowers) after drying at 80 C for 96 hr.

In order to assess the influence of repeated clipping on plant survival, aboveground biomass was clipped from half of the target plants ( $N = 30$ ) by randomly selecting five plants per treatment and plot in January 1990, 6 mo after the wildfire. The same plants were clipped every 6 mo for 2 yr. The remaining 30 target plants were left as controls. Mortality of clipped and control target plants was recorded in July 1990, January 1991, July 1991, and January 1992.

**Data analysis**—Some of the target plant tags of the burn experiment were accidentally lost and some target plants were used for another experiment (not described in this paper) in the third and fourth sampling periods; these plants were not included in the analysis. The sprout biomass was estimated using an allometric equation that predicted sprout dry biomass ( $Z$ ) as a function of sprout length measured as the length of the longest branch per sprout ( $X$ ) and the number of branches per sprout ( $Y$ ) at each sampling date:

$$\ln Z = A + B \ln X + C \ln Y$$

$$(0.824 < r^2 > 0.96, 31 < N > 51).$$

At the first sampling date, data for the allometric equation were obtained by measuring haphazardly selected sprouts collected from nearby plants subjected to clipping. But as the experiment progressed, we deliberately chose sprouts taken from some nearby plants to cover the entire range of sprout sizes that target plants had. Since the parameters of such a power function vary over the course of sprout development, a different allometric equation was applied for each experiment, plot, and sampling period.

For the burn experiment the number of sprouts [ $\log(x + 1)$  transformed] and the biomass of sprouts [ $\log(x + 1)$  transformed] were examined with a three-factor ANOVA, which included plot as a random effect and competition and fire as fixed effects. The effects of competition and fire on the flower biomass of the plants that had flowered (log transformed) were evaluated by a three-factor ANCOVA with the vegetative plant biomass (log transformed) as the covariate.

For the wildfire experiment, the number of sprouts (log transformed) and biomass of sprouts (log transformed) were examined with a two-factor ANOVA, which included plot as a random effect and the neighborhood treatment as a fixed effect. Pairwise comparisons among the three levels of neighborhood treatment were performed with a Scheffé  $F$ -test. The effects of the removal of neighboring plants on the flower biomass of the plants that had flowered (log transformed) were calculated with a two-factor ANCOVA, with vegetative plant biomass as the covariate.

The effects of different treatments on the percentage of plants flowering and survival of target plants subjected to the repeated clipping were each compared by a log-likelihood test.

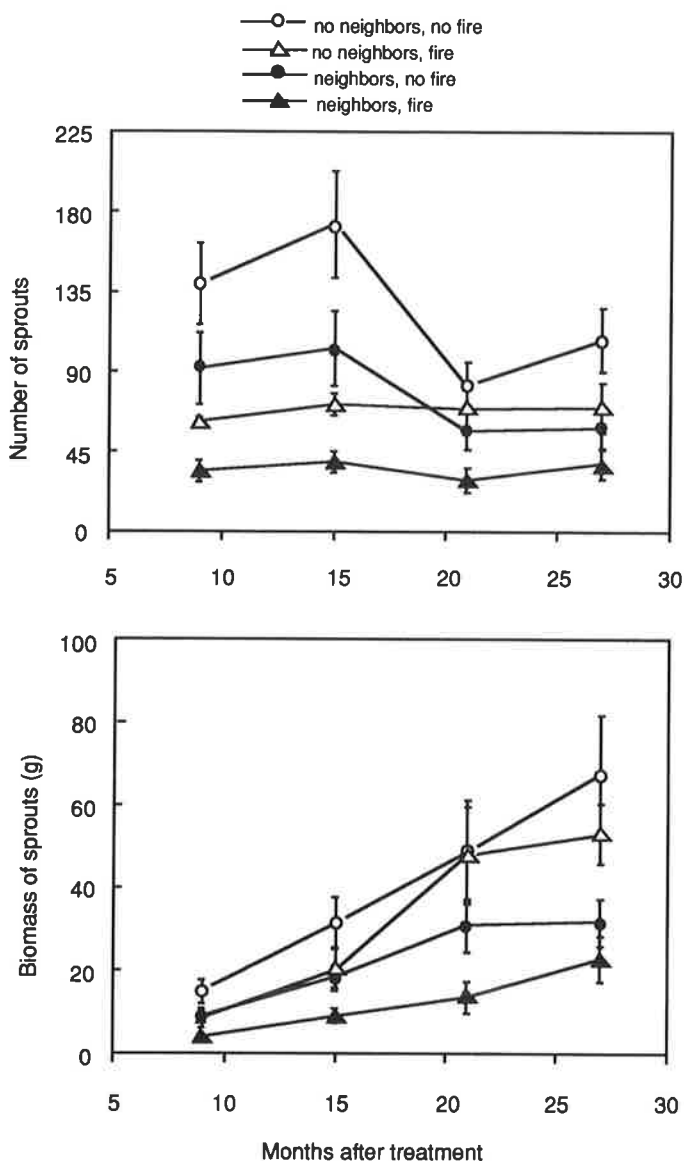


Fig. 3. Effect of fire and competition on the number and estimated biomass of sprouts per stump of *Erica multiflora* 9, 15, 21 and 27 mo after treatment in the burn experiment. Numbers are means  $\pm$  1 SE ( $N = 20$ ). The release from competition consisted of the removal of the surrounding vegetation in a 1.5 m radius. The fire treatment was applied by the flame of a propane torch (350–500 C for 3 min) onto the plant stump.

## RESULTS

**Burn experiment**—The number of sprouts increased until 15 mo after treatment and then decreased in the no-fire treatments. New, but small, sprouts appeared between 21 and 27 mo after treatment. Removal of neighbors increased the number of sprouts only at 9 and 21 mo after treatment. However, fire decreased the number of sprouts in all sampling periods (Fig. 3). Removal of neighbors increased the biomass of sprouts in all sampling periods, but fire only decreased it at 9 and 15 mo after treatment, being nonsignificant afterwards (Fig. 3).

The variance explained by neighbors in the effect on sprout biomass increased through the study period. The

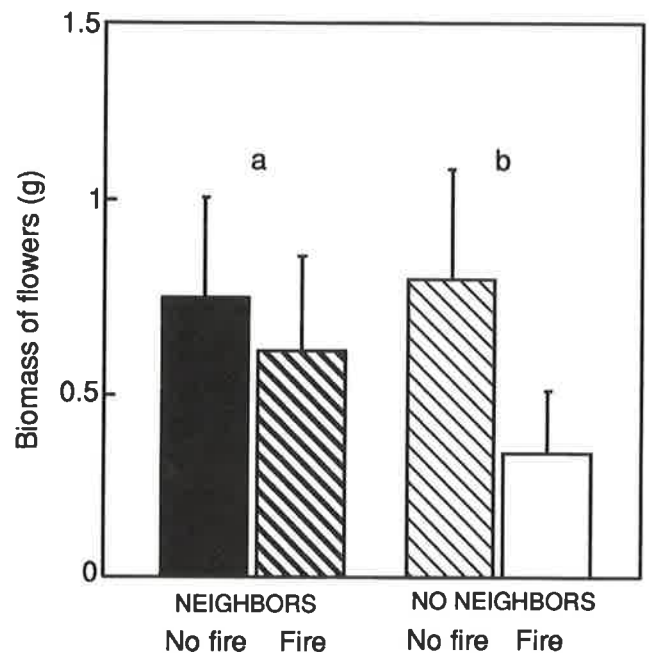


Fig. 4. Effect of fire and competition on biomass of flowers ( $+1$  SE) of *Erica multiflora* 27 mo after treatment in the burn experiment. Bars with different lowercase letters indicate significant different values ( $P < 0.05$ ). See Fig. 3 for treatment description.

presence of neighbors explained only 9% of the variance in the earlier months after treatment, but explained 23% at 27 mo after treatment. In contrast, the importance of the effect of fire on sprout biomass decreased with time. Fire explained 19% of the variance of sprout biomass 9 mo after treatment and only 3% after 27 mo (Table 1).

Removal of neighbors had a positive effect on the percentage of plants flowering ( $G = 5.476$ ,  $P < 0.05$ ). Only 52% of the plants with neighbors flowered compared to 81% of the plants without neighbors. However, whether or not a plant flowered was independent of fire treatment ( $G = 1.342$ ,  $P = 0.248$ ). Fifty-nine percent of the burned plants flowered, while 73% of the nonburned plants did.

Removal of neighbors did not affect the biomass of flowers ( $F_{1,72} = 0.06$ ,  $P = 0.80$ ), but fire significantly reduced the biomass of flowers ( $F_{1,72} = 5.98$ ,  $P = 0.02$ ) (Fig. 4). Biomass of flowers was independent of the vegetative plant biomass ( $F_{1,72} = 0.58$ ,  $P = 0.56$ ).

**Wildfire experiment**—Target plants without neighbors increased the number of sprouts with time, while target plants with neighbors only increased the number of sprouts during 15 mo after treatment, decreasing afterwards. However, all target plants increased biomass with time (Fig. 5). Neighbor removal had a nonsignificant effect on the number and biomass of sprouts (Table 2).

Flowering was observed in more than half of the target plants, and it was independent of the neighborhood removal treatment ( $G = 0.052$ ,  $P = 0.974$ ). Fifty-five percent of the target plants with neighbors (control) flowered, while the same percentage of target plants without neighbors and 60% of the ones with only *Q. coccifera* neighbors did.

Removal of neighbors had a significant effect on the

TABLE 1. Analysis of variance of the effect of neighbors and fire on (a) the number of sprouts and (b) estimated biomass of sprouts per stump of *Erica multiflora* in a burn experiment. To normalize errors, the number and biomass of sprouts were natural log ( $x + 1$ ) transformed. See Fig. 1 for neighbor and fire treatment descriptions.

Source	9 mo			15 mo			21 mo			27 mo		
	df	SS	P	df	SS	P	df	SS	P	df	SS	P
a) Number of sprouts												
Plot	1	0.07	0.800	1	0.51	0.510	1	0.01	0.929	1	0.32	0.621
Neighbors	1	5.91	0.025	1	4.94	0.434	1	7.31	0.009	1	3.47	0.107
Fire	1	22.87	0.000	1	19.99	0.000	1	4.84	0.031	1	5.37	0.047
Neighbors × fire	1	0.50	0.509	1	0.01	0.991	1	1.35	0.246	1	0.34	0.609
Residual	75	84.44		75	87.79		50	49.09		49	63.14	
b) Estimated biomass of sprouts												
Plot	1	0.03	0.815	1	0.00	0.965	1	0.00	0.988	1	0.00	0.969
Neighbors	1	4.10	0.013	1	5.52	0.010	1	10.52	0.002	1	9.70	0.002
Fire	1	8.73	0.000	1	8.08	0.002	1	3.69	0.057	1	1.23	0.256
Neighbors × fire	1	0.09	0.713	1	0.39	0.487	1	2.83	0.094	1	0.67	0.403
Residual	74	46.90		73	58.37		50	48.67		46	42.85	

biomass of flowers per plant ( $F_{2,8} = 6.09$ ,  $P = 0.02$ ). Plants without neighbors had more biomass of flowers than plants with neighbors (Fig. 6), but there were nonsignificant differences between plants without *Q. coccifera* neighbors or with neighbors (Scheffé-test,  $P < 0.05$ ). Biomass of flowers per plant was independent of the aerial vegetative biomass ( $F_{1,8} = 1.83$ ,  $P = 0.21$ ).

The severe effect of the repeated clipping treatment on target plants prevented us from including this factor in the overall analysis of this experiment. Two clippings in a 6-mo interval caused 80% plant mortality and after four clippings all 30 plants had died. None of the 30 control plants died (Fig. 7).

## DISCUSSION

*E. multiflora* showed a plastic response to competition and fire through alteration in the number and biomass of sprouts. Mallik and Gimingham (1983) reported that several Ericaceae species are able to resprout quickly after cutting or burning because they invest belowground photosynthates in aboveground growth. Fire probably damages the meristematic tissue of the stump (Zammit, 1988). Fire had a negative effect on the number of sprouts until  $> 2$  yr after the fire treatment was applied. This continued response could be due to a delayed reactivation of meristematic tissues, and because buds that survive are deeper

in the soil and sprouts from them take longer to reach the surface (Moreno and Oechel, 1991). However, the effect of fire on the biomass of the sprouts diminished with time, possibly because the initial growth was due to an increase in resource availability at the plant level when the plant had few sprouts.

Competition with mature plants decreased the resprout vigor of *E. multiflora*. Vilà and Terradas (1992) previously showed that competition with mature neighbors decreases the number and biomass of resprouts of this species after experimental clipping. However, after a wildfire when all plants were burned, resprouting vigor was not affected by the presence of neighbors. Moreover, even though we previously suspected that fast-growing species such as *Quercus coccifera* might decrease growth of our target plant, we did not find this to be the case. Comparison between the results of the two experiments makes it reasonable to think that the importance of competition increases as stand development proceeds. Schlesinger and Gill (1980) found evidence for competition for water and light during the development of pure stands of the chaparral shrub *Ceanothus megacarpus*. In our study, competition by regenerating plants compared by mature ones (13-yr-old regeneration stand), even if some of the same species were involved, was not important because the small plants of the regeneration stand would cause less shading and less soil resource depletion than large indi-

TABLE 2. Analysis of variance of the effect of neighbors after a wildfire on (a) the number and (b) estimated biomass of sprouts per stump of *Erica multiflora* in a wildfire experiment. To normalize errors, both dependent variables were natural log transformed. See Fig. 3 for neighbor treatment descriptions.

Source	6 mo			12 mo			18 mo			30 mo		
	df	SS	P	df	SS	P	df	SS	P	df	SS	P
a) Number of sprouts												
Plot	1	3.97	0.013	1	1.13	0.101	1	1.21	0.043	1	1.80	0.042
Neighbors	2	0.25	0.834	2	0.04	0.965	2	0.03	0.986	2	0.88	0.498
Neighbors × plot	2	1.27	0.331	2	0.98	0.302	2	1.77	0.053	2	0.87	0.344
Residual	24	13.11		24	9.31		24	6.37		21	8.12	
b) Estimated biomass of sprouts												
Plot	1	6.60	0.016	1	1.79	0.001	1	4.74	0.008	1	3.11	0.036
Neighbors	2	0.15	0.962	2	0.11	0.953	2	0.13	0.965	2	0.47	0.620
Neighbors × plot	2	3.64	0.179	2	2.31	0.172	2	3.46	0.068	2	0.77	0.546
Residual	24	23.62		24	14.63		24	13.76		19	11.67	

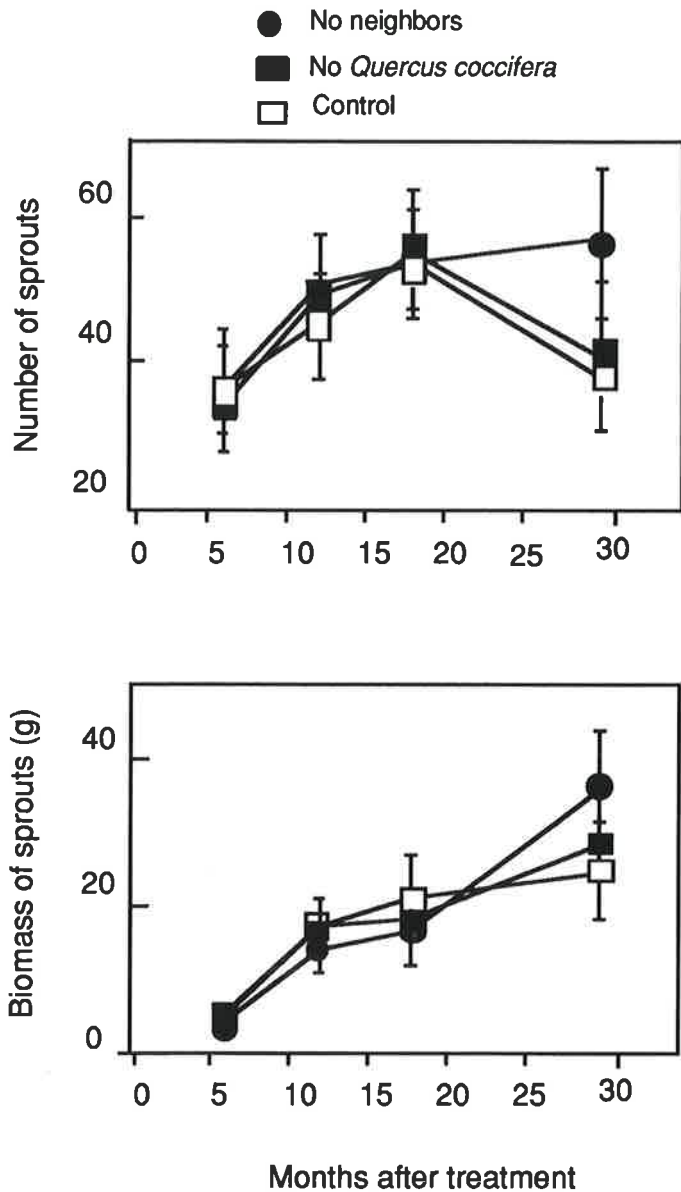


Fig. 5. Effect of competition on the number and estimated biomass of sprouts per stump of *Erica multiflora* 6, 12, 18 and 30 mo after a wildfire. Numbers are means  $\pm 1$  SE ( $N = 10$ ). The release from *Quercus coccifera* competition consisted in the removal of its sprouts on a 1.5 m radius around the target plant. The no neighbors treatment consisted in the removal of the surrounding vegetation on a 1.5 m radius.

viduals of the mature stand. While protected underground structures of several herbs and shrubs persist after fire, soil resource requirements at early postfire stages might be lower as compared to those of mature stands. Moreover, the ground at this study site was very rocky and patchy, suggesting that seedlings from both short-lived fire ephemeral and long-lived plants may occupy different ground microsites, avoiding belowground competition among neighbors.

These results agree with the models of hierarchy of competition (Weiner, 1990). When neighbors are larger than target plants, and this would be the case of the target plants surrounded by mature plants (burn experiment),

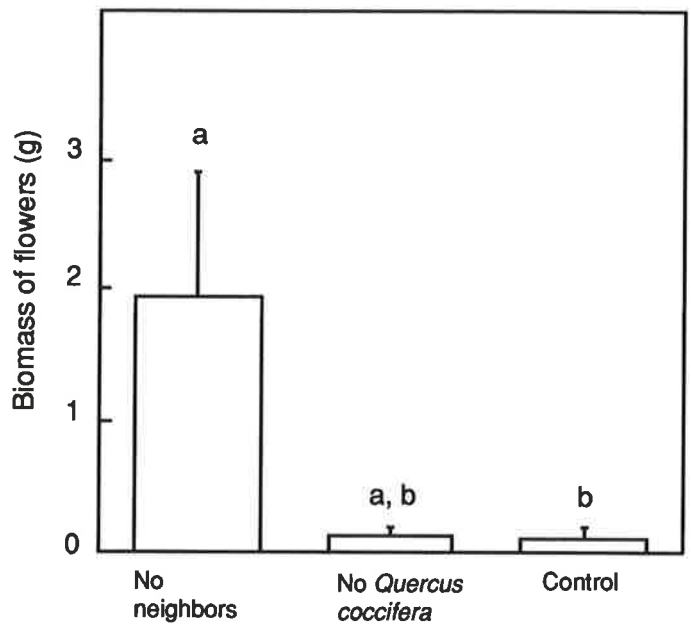


Fig. 6. Effect of competition on the biomass of flowers ( $+1$  SE) of *Erica multiflora* 30 mo after a wildfire. Bars with different lowercase letters indicate significant different values ( $P < 0.05$ ). See Fig. 5 for treatment description.

competition might be one-sided because neighbors encroach on the zone of influence of resprouting target plants by overtopping them and interfering in resource uptake. In this situation, neighbors might have a disproportionately negative effect on small target plants. However, after a wildfire (wildfire experiment), neighbors are mainly the same size as the target plants (i.e., resprouters) or even smaller (i.e., some seeders that appeared the second season after fire). Competition, if it exists then at all, would be two-sided, meaning that the competition effect is pro-

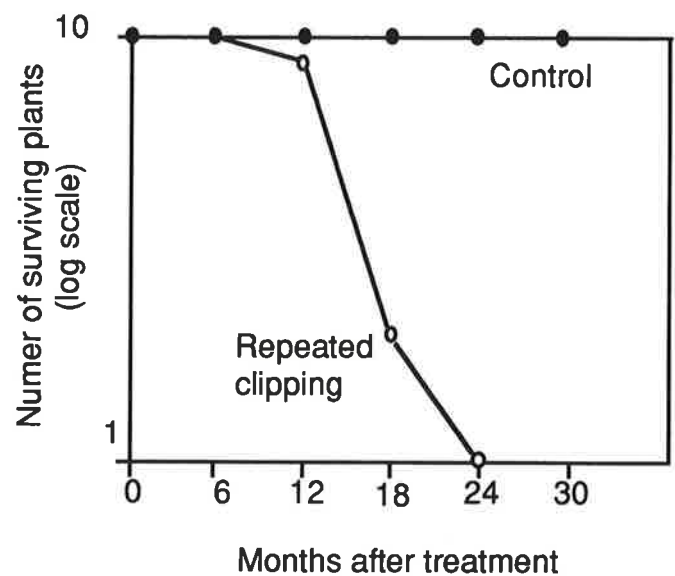


Fig. 7. Survival of *Erica multiflora* subjected to repeated clipping and controls after a wildfire. The repeated clipping treatment was done every 6 mo during 2 yr ( $N = 30$ ).

portional to the size of the competitors. In this situation, competition between target plants and neighbors may be reciprocal for both aboveground and belowground resource uptake.

Competition reduced the percentage of *E. multiflora* plants flowering. This could be related to a light threshold needed for flowering as has been shown in shading experiments (Vilà, 1993). Mature neighboring plants would reduce the quantity and quality (reduction of red:far red ratio) of available light needed for flowering (Ballaré et al., 1988). Fire also reduced the biomass of flowers. We suggest that the main cause was that the cost of regeneration of the vegetative structures was high and reduced the allocation of biomass to reproductive structures. The reduction in initiation of flowering and in the biomass of flowers as a response to competition and fire, respectively, could have negative consequences for population maintenance of this species, which already has low sexual reproduction.

Reproductive output is size dependent (Samson and Werk, 1986). Nevertheless, in our experiments, biomass of flowers per plant was independent of aboveground vegetative biomass. There are several possible reasons for this lack of relation. 1) Biomass of flowers might be related to belowground structure (lignotuber and roots) size and storage rather than to aboveground structure biomass (about which we have no information). 2) Allocation to reproductive structures might be related to genet age (data of which is unattainable). 3) Flowering might be determined by growing conditions of the previous year. 4) Allocation to the lignotuber due to meristematic reactivation could constrain biomass allocated to flowers. 5) Flowering might be determined by ramet (sprout) size rather than by genet size.

Mortality of resprouting genets after frequent fires has been reported in other Mediterranean climate plant communities: in the Greek phrygana (Papanastris, 1980), in the California chaparral (Zedler, Gautier, and McMaster, 1983), in the Australian heath (Bradstock and Myerscough, 1988) and in the South African fynbos (le Maitre, Jones, and Forsyth, 1992). All of these studies provide evidence for a sudden and relatively permanent population change due to short recovery time between fires. Population structure also could be affected by other disturbances such as herbivory (Moreno and Oechel, 1992). The repeated clipping done in our experiments, which could simulate herbivory, negatively influenced plant survival. Obviously, our experimental design simulated an extremely severe situation of herbivory or repeated clearings, but the results make the point that when intervals between aerial biomass removal are very short, there may be a depletion of the bud bank (Zammit, 1988). Restoration of carbohydrate storage and recovery of damage to the meristematic and cambial tissues also would limit vegetative aerial growth. According to Hobbs and Mooney (1985), restoration of belowground structures (e.g., fine roots) would limit vegetative aerial growth in these situations. We have not found that competition affected this result. The vigorous resprouter *Q. coccifera* did not accelerate the detrimental effect of frequent clipping, suggesting that the presence of neighbors or their identity was negligible as compared with the disturbance effect of aboveground biomass removal.

In conclusion, competition and fire both had negative effects on vegetative vigor and flowering of *E. multiflora*. A wildfire might have an indirect effect on resprouting performance by reducing competition. Thus, the competitive effects of a neighbor on individual plant performance show a temporal variation proportional to the size of the cohabiting plants: while mature and bigger neighbors than target plants had a negative effect on resprouting of the target plant, regenerating neighbors of similar size and regeneration stage as the target plant had a null effect. We suggest that during regeneration after fire, the effects of neighbors on target plants are less important than in a mature stand because there may be differences among plants in their regeneration niche (Bond, Cowling, and Richards, 1992), those with microsite heterogeneity (e.g., soil patchiness) may avoid competition among neighbors. The mortality due to repeated clipping found in the present study also questions the resilience of this resprouting shrub to successive disturbances. Mortality is more likely to be caused by frequent and cumulative disturbances than by competition with neighboring plants alone.

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