Effects of *Rosmarinus officinalis* neighbors on resprouting of *Erica multiflora* individuals

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Abstract

To study the effects of competition in Mediterranean shrubland regeneration following disturbance, we used a neighborhood approach to assess the influence of mature *Rosmarinus officinalis* neighbors on the resprouting of *Erica multiflora* individuals after clipping. Sprout biomass of target plants 2 years after clipping was regressed against various measures of neighbor abundance within a 2 m radius around target *E. multiflora* individuals in which all vegetation except *R. officinalis* had been removed. The largest single influence on the biomass of sprouts produced was the previous biomass of the resprouting plant. The abundance of *R. officinalis* neighbors had a weak but detectable effect on resprouting of *E. multiflora*. Abundance of neighbors within 60 cm from target plants was the best predictor of regrowth. At this distance, two simple measures of neighbor abundance within the neighborhood, the number of neighbors and the sum of their heights, were significant in accounting for variation in resprouted biomass. None of the combinations of neighbor variables performed significantly better than single variables. The best models accounted for around 24 percent of the variation in resprout biomass. As in other studies, angular dispersion of neighbors never had a significant effect on performance of target plants. The weak but significant response of resprouting to variation in *R. officinalis* abundance suggests that the intensity of competition in the experiment was low because of the removal of other species.

Introduction

The role of plant-plant interactions in structuring Mediterranean-plant communities has received little attention. Most ecological studies have focused on the role of disturbances (Cowling 1987), such as fire (Naveh 1974) or vegetation clearing in order to enhance tree species growth and/or to reduce fire risk (Rico et al. 1981; Herrera 1997; Lloret & Vilà 1997). Disturbance reduces competition through a reduction in plant density and an increased availability of resources for those plants that survive the disturbance (Noble & Slatyer 1977). However, competition during the recovery following disturbance may be important in regeneration processes in Mediterranean plant com-

munities (Tyler & D'Antonio 1993). The presence of thick, evergreen shrubland stands with high plant density and resultant considerable canopy overlap in many Mediterranean shrublands suggests that competition may be strong relatively soon after disturbances.

Resprouting is a very common regeneration strategy after disturbance, and most of the vegetation growing after a disturbance in many plant communities, especially Mediterranean vegetation, comes from resprouting of below-ground structures. The extent of resprouting by an individual is a function of intrinsic factors such as age (Hobbs & Gimingham 1984), storage of resources in subterranean structures (Jones & Laude 1960), and pre-disturbance plant size (Lloret & López-Soria 1993), as well as environmental con-

ditions such as disturbance intensity (Canadell et al. 1991) and, as shown in removal experiments, competition from neighbors (Vilà et al. 1994; Vilà & Terradas 1995a, b).

Because plants are sessile and their resources do not diffuse quickly over long distances, competition is inherently local (Stoll & Weiner 1998). One way to investigate competition in the field is though 'neighborhood' competition models in which the performance of individual plants is studied as a function of the local abundance of neighbors. In monospecific stands, neighborhood models have been largely used to relate yield of a target plant to several parameters of neighborhood performance (Benjamin & Hardwick 1986), such as distance to target plant (Cody 1986), spatial distribution (Mack & Harper 1977), crown cover (Wagner & Radosevich 1991), biomass (Gaudet & Keddy 1988) or composite measures of neighbor abundance (Waller 1981; Weiner 1984; Grace & Platt 1995). Plants in nature are usually surrounded by several species which often differ in their growth form, age, and spatial arrangement, making multispecies neighborhood models difficult to test with realistic sample sizes. Sometimes a single species in the community could explain much of the neighborhood effects (Firbank & Watkinson 1987) and this may be the simplest way to begin to understand local competition in multispecies stands.

Some neighborhood studies have assumed that the effect of a neighbor will decrease with its distance from a target plant (Weiner 1984), whereas other models have simply measured some aspect of neighbor abundance, e.g., biomass (Goldberg & Werner 1983) or simply the number of neighbors (Silander & Pacala 1985), within a neighborhood around the plant. The most successful competition indices for predicting target plant performance usually involve a cut-off distance beyond which competition is not detectable (Wagner & Radosevich 1991). It has also been suggested that since there is also competition among a target plant's neighbors, the overall effect of some neighbors on a target plant may be null or even positive due to indirect effects (Fowler 1984).

A neighborhood approach to the study of plant competition has seldom been used in Mediterranean shrublands because this method is difficult to apply in mixed stands (Fuentes & Gutierrez 1981; Bond et al. 1984) unless all species of neighbors are lumped together. In the present study we analyzed the effect of the abundance of the most dominant neighbor, *Rosmarinus officinalis* L., on the resprouting vigor of the co-occurring species *Erica multiflora* L. after a selective clearing where *R. officinalis* was left undisturbed and *E. multiflora* aboveground biomass was removed. The specific questions addressed are:

(1) Do resprouting plants respond to variation in the abundance of one of the dominant species of neighbors?

(2) Over what distance do neighbors interfere with resprouting?

(3) Which measures of neighbor abundance are the best predictors of competitive effects?

Material and methods

Description of study site and species

The study site was a coastal shrubland located on the Serra de les Comes (40°53′ N, 0°41′ E) in El Perelló (Catalonia, Spain), 16 km from the Mediterranean coast at an elevation of 300 m. The soil is extremely stony and shallow, classified as *Lithic haploxeroll*. The climate is typically Mediterranean. At the nearest weather station (Perelló), mean annual temperature is 16 °C. The mean low temperature is 4.5 °C in January and the mean high is 29 °C in July. Mean annual precipitation is 591 mm, of which 45% results from spring and autumn storms. The area was burned by a wildfire in 1976. The dominant species in the shrub vegetation are *Rosmarinus officinalis* L. (4890 individuals ha^{-1} and 11% cover) and *Erica multiflora* L. (15277 individuals ha^{-1} and 40% cover). Other common shrub species include *Quercus coccifera* L. and *Ulex parviflorus* L. The understorey layer is dominated by the rhizomatous grass *Brachypodium retussum* (Pers.) Beauv. with 79% cover.

Erica multiflora (Ericaceae) and *Rosmarinus officinalis* (Lamiaceae) are two common erect evergreen shrubs which typically occur in coastal shrublands on calcareous soils of the Western Mediterranean Basin (Orshan 1989). *Erica multiflora* can measure 3 m in height, but in the study area plants are less than 1 m tall. Leaves are linear and sclerophyllous, about 8 mm long and 1 mm wide and live almost 4 years. After aerial biomass removal, this species produces abundant sprouts from a moderately enlarged stump or from shallow roots. Vegetative growth occurs twice a year: in spring (from March to June) and autumn (from September to November). *Rosmarinus officinalis* is a non-resprouting species which can reach up to 2 m in height, but in our study area plants are

less than 1 m. *Rosmarinus officinalis* leaves are linear and semi-sclerophyllous, about 15 mm long and 3 mm wide, bright green above and white-tomentose beneath. Vegetative growth takes place from January to August.

Beside being a dominant species, *R. officinalis* was selected for the study for two other reasons. First, it does not resprout and thus it is possible to distinguish genetic individuals and to measure size at the individual level. Second, when selective clearings are conducted at this area, *R. officinalis* is almost always left undisturbed, while *E. multiflora*, *U. parviflorus* and *Q. coccifera* aboveground biomass is removed (V. Bladé, personal observation).

Neighborhood manipulation and sampling

In December 1990 sixty *E. multiflora* plants located at least 6 m apart were randomly selected. All sprouts were clipped to ground level and weighed after drying at 80 °C for 96 hours. Each target plant was covered by a chicken wire mesh in order to prevent herbivory by rabbits. All vegetation within 2 m of target plant except for *R. officinalis* was also clipped at ground level. Since root removal would have been a major soil disturbance for non-removed plants, we took the approach of limiting soil disturbance by removing only above-ground biomass. Previous removal experiments showed that aboveground biomass removal of all neighbors increased target *E. multiflora* biomass of sprouts by 40% (Vilà 1997). In the present study, growing vegetation around target plants was removed every two months to reduce competition by species other than *R. officinalis*.

The following variables were measured for all *R. officinalis* neighbors within a 2 m radius of the target plant: (1) distance to the target plant, (2) compass orientation relative to target plant, (3) height of the longest branch, (4) plant cover estimation, assuming that the canopy was elliptical, by measuring the longest diameter and the diameter perpendicular to it (5) basal diameter 5 cm above ground. Previous removal experiments demonstrated that a 2 m radius exceeded the neighborhood competition radius of *E. multiflora* in this study area (Vilà & Terradas 1995b). In January 1992 all sprouts of the target plant were counted, harvested and weighted after drying at 80 °C for 96 hours.

Statistical analyses

A regression approach (Sokal & Rohlf 1981) was used to assess the potential influence of neighboring plants on the target plants after taking the previous sprout biomass of the target plants into account. Thus, the final sprout biomass (b_1) of the target plants served as a dependent variable which was regressed against the previous sprout biomass (b_0) and various neighbor variables: number, height, basal diameter, crown diameter of neighbors and combinations of those variables, summed over the cutoff distance (which varied from 0.1 to 2.0 m). Various distance decay models were also tested but none of them were successful in predicting the performance of target plants. Therefore, they are not included in the results. The angular dispersion (Zar 1974; Mack & Harper 1977; Waller 1981; Weiner 1984), a measure of how clumped ($d = 0$) or evenly dispersed ($d = 1$) the neighbors are, was also used as an independent variable in the regressions. For the interpretation of the relationship between the variables in the model, we calculated partial correlation coefficients as measures of 'effect sizes' = $\sqrt{(t^2/(t^2 + \text{d.f.}))}$ where $t = t$-value of the variable effect in the regression model and d.f. = residual degree of freedom. t-values were the estimates out of the multiple regressions divided by their standard errors. The significance of the partial correlation coefficient was calculated based on the given t-values (Cohen 1977).

The previous and final sprout biomass of the target plants was log transformed and plant height square-root transformed in order to achieve a normal distribution of the residuals and to ensure homoscedasticity.

Results

Overall, target plants produced 148 ± 12 (mean ± s.e.) sprouts that weighed 18.61 ± 1.1 g. There were no significant differences between sprout biomass of target plants with no neighbors (18.76 ± 2.39 g, $n = 14$) and those with one or more neighbors (18.56 ± 1.25 g, $n = 46$). Previous target plant sprout biomass accounted for 14.8% of the variability in final sprout biomass.

Rosmarinus officinalis density ranged from 0 to 67 individuals within the 2 m radius around target plants, reflecting the natural degree of variation in local *R. officinalis* crowding. The mean number of *R. officinalis* plants closer than 40 cm was only three and their effect on target plant growth was not significant. Number of

Table 1. Regression analysis of the effect of several measures of local *Rosmarinus officinalis* abundance (x) on sprout biomass of *Erica multiflora*. Previous target plant sprout biomass was included in the regression model: log (sprout biomass) = $a + c$ log (previous biomass) $+d$ x. Neighborhood distance was 60 cm and values have 42 degrees of freedom. R_{part} = partial correlation coefficient or 'effect size' calculated as $\sqrt{(t^2/(t^2 + d.f.))}$ where t = t-value of variable effect. v.a. % = percentage of variance accounted for by the regression model. bdm = neighbor basal diameter 5 cm above-ground; dc1 = neighbor crown length; dc2 = neighbor crown width; ht = $\sqrt{\text{(neighbor height)}}$.

Independent variable	t-value	p-value	R_{part}	%v.a.c.
log (previous biomass)	3.51	0.001	0.476	
number of neighbors	−2.07	0.045	0.304	22.49
log (previous biomass)	3.57	< 0.001	0.482	
$\sum$(height)	−2.18	0.035	0.319	23.3
log (previous biomass)	3.44	0.001	0.468	
$\sum$(bdm)	−1.95	0.058	0.288	21.7
log (previous biomass)	3.16	0.003	0.438	
$\sum$(dc1*dc2)	−1.22	0.229	0.184	17.5
log (previous biomass)	3.39	0.002	0.464	
$\sum$(bdm*ht)	−1.74	0.089	0.259	20.3
log (previous biomass)	3.10	0.003	0.431	
$\sum$(dc1*dc2*ht)	−0.92	0.363	0.140	16.2

Table 2. Summary of measure of *Rosmarinus officinalis* abundance within 60 cm of *Erica multiflora* individuals. bdm = neighbor basal diameter 5 cm above-ground; dc1 = neighbor crown length; dc2 = neighbor crown width.

Measure	n	Mean	Min	Max	s.d.
Angular dispersion	46	0.34	0	0.78	0.26
Number of neighbors	60	4	0	25	5.88
$\sum$(height) [m]	46	5.15	0.54	16.11	4.27
$\sum$(bdm) [cm]	46	12.80	1.78	43.05	8.58
$\sum$(dc1*dc2) [m^2]	46	0.65	0.15	1.98	0.38
$\sum$(bdm*height) [m^2]	46	0.92	0.11	3.28	0.57
$\sum$(dc1*dc2*height) [m^3]	46	0.52	0.11	1.81	11.30

ficinalis neighbor abundance on resprout biomass decreased with cutoff distances greater than 65 cm, and was no longer significant at cutoff distances greater than 80 cm from target plant (Figure 2). None of the other independent variables tested (basal diameter, canopy diameter and combinations) had a significant effect on target plant biomass. Angular dispersion of *R. officinalis* neighbors never contributed significantly in accounting for variation in regrowth, but inclusion of angular dispersion in the regression models increased the significance of measures of neighbor abundance and neighbor height slightly.

R. officinalis neighbors within cutoff distances from 45 to 65 cm from target plants had a negative effect on target plant sprout biomass (Figure 1). In a two variable regression with initial sprout biomass and number of neighbors within 60 cm from target plant as independent variables, the model accounted for 22% of the variation in resprout biomass (t-value = −2.07, p = 0.045). The effect size of number of neighbors was 30% (Table 1). Within that neighborhood radius, the number of *R. officinalis* plants ranged from 0 to 25. There was also a large variation in several other measures of neighbor position and size (Table 2).

In a two variable regression with initial sprout biomass and sum of neighbor heights within 60 cm as independent variables, the model accounted for 23% of the variation in resprout biomass (t-value = −2.18, p = 0.035). The partial correlation coefficient for this negative effect of total neighbor height on final biomass of target plants was 32%. Effect of total neighbor height was strongest when the cutoff distance was 40 to 65 cm from the target plant. The effect of *R. of-*

Discussion

Neighborhood studies usually report low values for the correlations between target plant and neighborhood performance even in monocultures. Waller (1981) reported that 5–59% of the variation in the number of leaves in several violet populations was accounted for by neighborhood indices. Fowler (1984) also found weak negative effects in a population of *Linum grandiflorum var. rubrum* in a common garden experiment. Neighborhood predictors perform best in low-cover communities where the number of neighbors is low such as deserts (Cody 1986), sand dunes (Mack & Harper 1977) or low density shrublands (Fuentes & Gutierrez 1981). In our study, less than 24% of the variation on *E. multiflora* final sprout biomass could be explained by the number or sum of the heights of *R. officinalis* neighbors. In the present study we removed other species to investigate the effects of one species of neighbor. The removal of other species represented a great release from competition (Vilà 1997) that may
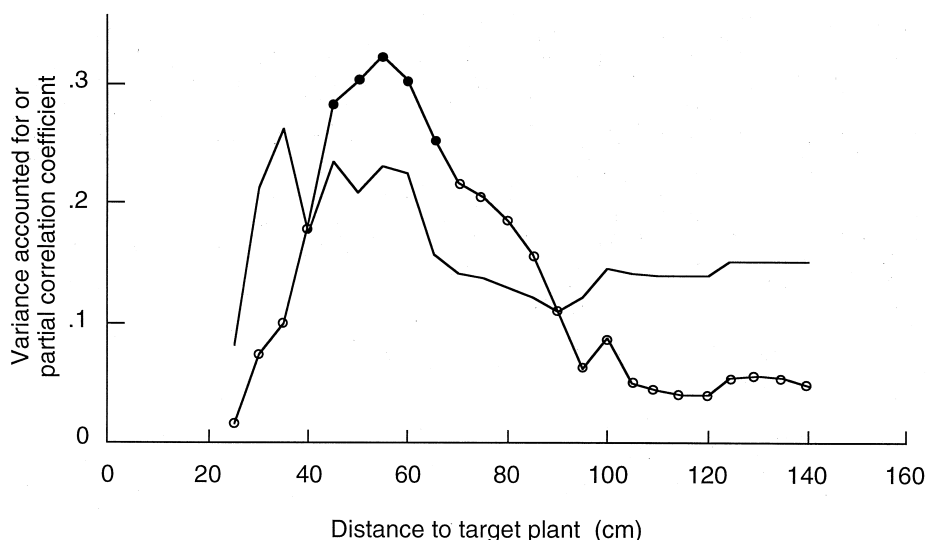
Figure 1. Variance in biomass of sprouts accounted for (line only) and partial correlation coefficient (line with symbols) for the number of *Rosmarinus officinalis* neighbors within different distances from *Erica multiflora* in the regression log (sprout biomass) = a log (previous biomass) $+c$ (number of neighbors), where a and c are parameters. Filled symbols show significant ($p < 0.05$) partial correlation coefficients.

have masked the more subtle effect of variation in abundance of one species.

The relationship between target plant performance and neighbor performance may not be linear, making neighbor effects more difficult to detect. In a sward of *Festuca rubra*, Liddle et al. (1982) found that the relationship between tiller production and several measures of neighborhood abundance was not usually linear. In many cases the response of plants to neighbor abundance is hyperbolic (Weiner 1984; Wagner et al. 1989; Silander & Pacala 1985) or triangular: target plants with few/small neighbors can be large or small (presumably because other factors beside neighbors can also limit size), but plants with many/large neighbors are almost always small (Goldberg 1987; Stoll & Weiner 1998).

Plants competed only with relatively near neighbors. Neighbors located more than 80 cm from target plants did not appear to have a negative effect on the biomass of target plants. The statistical model fit best when the cutoff distance for the neighborhood was 60 cm. It would be reasonable to consider this to be an estimate of neighborhood size for this species in this community. Other studies on herbaceous vegetation have also found that individuals only compete with their closest neighbors (Fowler 1984; McConnaughay & Bazzaz 1987).

Combinations of neighborhood variables were not better than simple measures of neighbor abundance in predicting the target plant performance. This can be

seen as encouraging to the modelling of neighborhood competition, because models can be based on easily-measured quantities such as the number of neighbors (Silander & Pacala 1985). As in several other studies (Weiner 1984; Wagner & Radosevich 1991), angular dispersion of neighbors never had a significant effect on target plant performance, although the inclusion of angular dispersion in the statistical model increased the significance of neighbor abundance slightly, suggesting that angular dispersion may have an effect, but that we did not have the statistical power to demonstrate this. Models in which the effect of a neighbor within the neighborhood decreased with distance from the target plant performed much more poorly than simple neighborhood models in which distance within the neighborhood is ignored. Models without a cutoff distance below 2 m also performed very poorly. In other words, when neighbors beyond a certain neighborhood distance are ignored, the effect of neighbors within the neighborhood does not seem to decreases with distance from the target plant. This is one of the simplest approach in neighborhood competition modelling (e.g., Silander & Pacala 1985).

The amount of resprouting depended more on the size of the plant before clipping than on neighbor abundance. Above-ground biomass is correlated with below-ground biomass. Larger stumps may hold more buds that will become sprouts and have higher carbohydrate levels and nutrient supplies (Canadell & López-Soria, in press). *Erica multiflora* underground
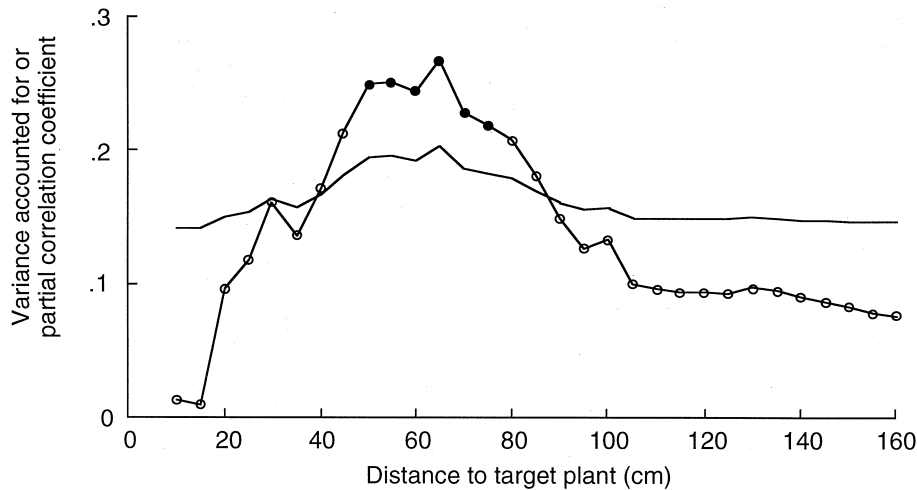
Figure 2. Variance in biomass of sprouts accounted for (line only) and partial correlation coefficient (line with symbols) for sum of *Rosmarinus officinalis* heights within different distances from *Erica multiflora* in the regression log (sprout biomass) = a log (previous biomass) $+c$ (sum of neighbor heights) where a and c are parameters. Filled symbols show significant ($p < 0.05$) partial correlation coefficients.

structures remained intact after clipping and storage of resources or ability to obtain more resources from soil allowed a successful regeneration of the above-ground structures. Size of the plant before clipping, including underground structures, is the result of many previous years of growth influenced by internal and external factors. The history of an individual before disturbance, which determines the number of living buds and the amount of stored reserves available for resprouting, is the primary determinant of post-disturbance regrowth. During the early regeneration stages, growth may depend more on intrinsic factors than by the site quality or competition from neighboring plants. Competition will be weakest immediately following disturbance, but will become more important as biomass increases (Vilà & Terradas 1995a).

Natural variation in competition from one dominant species of neighbor does not seem to be a major contributor to variation in the performance of *E. multiflora* following disturbance. This could be because:

(1) Competition is not a major influence in community development soon after a disturbance. Our results emphasize the role of recent history: how much an *E. multiflora* resprouts after disturbance is primarily a function of how big it was before the disturbance.

(2) Competition is important in community regeneration, but natural variation in a single species does not reflect variation in the diffuse competitive regimes that resprouting plants face. Since all other species were removed, almost all plants in our study had been released from competition. In such a situation competition from one species at its natural abundance did not limit growth in many cases.

We have shown that competition from a single species occurring at its normal abundance after selective clearing is weak but can be detected. The degree of local crowding by undisturbed *R. officinalis* individuals after clearing of other vegetation has a negative effect on the regeneration of *E. multiflora*. Thus, the negative effect of removal of above-ground parts on *E. multiflora* will be reinforced by competition with individuals that have not been removed. We can only speculate about the mechanisms of competition. The observation that neighbor height was a better predictor of target plant regrowth than other measures of neighbor size suggests that competition for light may be important as demonstrated by shading experiments (Vilà 1997), but further studies will be needed to determine the mechanisms involved.

Acknowledgements

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