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Effects of nutrient availability and neighbours on shoot growth, resprouting and flowering of *Erica multiflora*

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Abstract. To test if low soil fertility and competition limit the performance of Mediterranean shrubs, and if the effects of competition on plant performance were modified by soil fertility, we subjected shrubs of *Erica multiflora* to a factorial field experiment of fertilization and removal of neighbours around target plants. After 18 months of treatment, fertilization had stimulated the growth of pre-existent sprouts and biomass allocation into stems to new sprouts, but decreased the frequency of sprout flowering. Removal of neighbours increased the number and biomass of new sprouts, the probability of sprout flowering and the biomass of flowers. Fertilization slightly enhanced sprout recruitment and the probability of sprout flowering when neighbours were removed, but did not modify the other parameters of plant performance. According to our results, both low soil fertility and competition limited plant performance. Competition was slightly more intense in fertilized plants, but only in determining sprout and flowering bud stimulation.

Keywords: Competition; Field experiment; Mediterranean ecosystem; Removal experiment; Soil fertilization.

Introduction

Whether plant competition is stronger in fertile than in infertile soils is still debated. When neighbours are removed, an increase in light, temperature and water availability could modify nutrient dynamics. According to Grime (1979), competition is less intense in infertile soils due to the reduced size and slow growth rate of plants that create less shading than plants in more fertile soils. Instead, in fertile soils, competition would be intense because they support high growth rate and a large biomass with consequent pre-emption of space and light. However, some authors have disputed the generality of this trend (Keddy 1991). Tilman (1982, 1988) predicted that competition for soil nutrients would be intense on unfertile soils because resource limitation is essential for competition to occur. Therefore, field tests should address these contrasting predictions about the interplay of competition and soil productivity on plant performance.

Many mediterranean-type soils are known to have a relatively low fertility (Specht 1981) and it has been postulated that such restricted nutrient availability can limit plant growth. Field trials have emphasized that nitrogen and phosphorus are the two nutrients most likely to limit the growth of evergreen, sclerophyllous, mediterranean shrubs in the Californian chaparral (McMaster et al. 1982), in the Australian jarrah (Dell et al. 1987) and in the South African fynbos (Witkowski et al. 1990). Recently, similar studies in the Mediterranean basin have not found significant responses to fertilization with N, P and K on the growth of *Arbutus unedo* (Castell & Terradas 1994). However, fertilization experiments in *Quercus ilex* forest suggest that N-addition increased the elongation of current-year shoots (Sabaté et al. 1992).

Likewise, some mediterranean-type communities are composed of dense, evergreen shrublands where competition by neighbour plants may also limit plant growth as suggested by neighbourhood and empirical studies. For the Chilean matorral, Fuentes & Gutierrez (1981) reported a positive correlation between the sum of the canopy ground projections and the distance of a target shrub to its neighbour. In chaparral, removal of rooted shrubs enhanced herb establishment (Swank & Oechel 1991). In the same way, in a Catalan garrigue, removal of neighbours increased resprouting of *Arbutus unedo* (Vilà et al. 1994).

Studies of nutrient availability and competition can help clarify aspects of the interaction between soil nutritional status and competition in Mediterranean vegetation, as well as the short-term effect of some current management practices. In some isolated areas of the Mediterranean region, woody shrub vegetation is regularly subjected to clear-cutting (Giovannini et al. 1992) or selective thinning (Vélez 1985) in order to reduce the amount of living and dead fuel to prevent fire risk. We may expect removal of vegetation to influence plant performance as a consequence of modifications in resource availability and reduction of competition. For example, in southern Catalan shrublands, *Erica multiflora* is maintained after selective removal of more fire-prone species such as *Quercus coccifera* and *Ulex parviflorus* (Bladé pers. comm.).

Resprouting is a main feature of some species in these Mediterranean shrublands. Regrowth after aerial biomass removal takes place by recruiting shoots originated in a subterranean structure known as lignotuber or burl. Thus, resprouting species are keystone species in the regeneration after disturbances such as fire, intense herbivory or the management practices described above. In this paper we focus on two questions: (1) are growth, resprouting and reproductive performance influenced by fertilization and competition? (2) do the effects of competition increase when plants are fertilized? For this purpose, we report the plant response of an evergreen, ericoid Mediterranean shrub to an increase in nutrient supply and decreased competition in a field experiment with nutrient addition and neighbour removal around target plants.

Material and Methods

Description of study species and study site

Erica multiflora (*Ericaceae*) is an evergreen sclerophyllous shrub that typically occurs on basic soils of the western Mediterranean Basin, where it is a common component of the coastal shrubland. After aerial biomass removal *E. multiflora* produces abundant sprouts (defined as shoots physically connected at the base to a moderately enlarged stump or to shallow roots). However, continual basal sprouting has been observed in the absence of any major disturbance. Vegetative growth of sprouts occurs twice a year: in spring (from March to June) and autumn (from September to November). *E. multiflora* can reach 3 m in height, but in the study area plants attain only a height of 1 m. Flower buds appear in August-September and open from mid-September to mid-December.

The study site is located in a coastal shrubland on the Serra de les Comes (40° 53' N, 0° 41' E) in El Perelló (Catalonia, Spain), 9 km from the sea, and at an elevation of 300 m a.s.l. The soil is an extremely stony and shallow Lithic haploxeroll (pers. obs.), reasonably fertile, but with a low phosphorus content (3.5 p.p.m. of extractable phosphorus - Olsen method). The climate is typically Mediterranean. At the nearest weather station (Perelló), the mean monthly temperature ranges from 4.5 °C in January to 29 °C in July; the mean annual temperature is 16 °C. The mean annual precipitation is 591 mm, of which 45 % occurs in the autumn. The area was burned by a wildfire in 1976 and has been lightly grazed recently. The shrubland is dominated by *Rosmarinus officinalis*, *Quercus coccifera*, *Erica multiflora* and *Ulex parviflorus*, which contribute 39, 14, 12 and 8 % of ground cover, respectively. The understorey is dominated by the grass *Brachypodium retusum* which covers 63 % of the ground layer.

Experimental design and data analysis

80 *Erica multiflora* individuals were selected at random in an area of 100 m × 100 m in July 1989. To ensure independence among treatments, target plants were separated by at least 6 m. The height and basal diameter ($\geq$ 0.5 cm) of all sprouts per plant were recorded and three existing sprouts per plant were randomly selected and tagged for subsequent measurements. The experimental design consisted of a two-by-two factorial design with two levels (presence or absence) of both neighbours and fertilization of the soil. The design was randomly replicated 20 ×, with each replicate containing a focal plant of *E. multiflora* with or without neighbours and with or without soil fertilization.

The fertilizer was added only once, after the treatments involving removal of neighbours were applied, i.e. on 17 July 1989. It consisted of a mixture of 21 % ammonium sulfate, 18 % calcium superphosphate and 60 % potassium chloride (Cross industry), in the proportion of 7:12:20 (N:P:K) and in a concentration of 236 kg/ha. The fertilizer was spread by hand on an area of 30 cm radius around the target plant and raked lightly into the soil. The fertilizer treatment is equal to the one used for olive, almond and peach orchards in the area, but was stronger than the ones used in previous fertilization experiments in mediterranean-type soils (e.g. McMaster et al. 1982; Groves 1988).

Elimination of neighbours was carried out by manually removing all vegetation growing in a 1.5 m radius around the target plant. The regeneration of this neighbouring vegetation was maintained to a minimum by manually clipping sprouts and seedlings that appeared, every 2 months during the experimental period.

The biomass of each sprout was estimated before treatment, using an allometric equation which predicted the dry biomass after oven-drying at 80 °C for 96 h, W as a function of sprout length, L measured as the height of the longest branch and the diameter at its base, D:

$$\log W = 1.287 + 0.840 \log L + 1.680 \log D \qquad (1)$$
($r^2 = 0.94$; $n = 35$).

These data were obtained by measuring haphazardly selected sprouts from clipped plants in the plots where neighbours were removed.

In January 1991, the three sprouts tagged per target plant were harvested (subsequently referred to as 'old' sprouts). We weighed the current year's vegetative biomass and the biomass of flowers after separation and oven-drying at 80 °C for 96 h. Mean sprout growth and mean sprout biomass of flowers was estimated by the mean of the vegetative biomass and the biomass of flowers of the three tagged sprouts per target plant, respectively. New sprouts (basal diameter < 0.5 cm) of the target plants were counted and harvested. Leaves and stems in new sprouts were separated and weighed after oven-drying at 80 °C for 96 h.

Mean old sprout growth and mean biomass of flowers on sprouts were analyzed using a two-factor ANCOVA which included competition and soil fertilization as the main effects and the mean of the estimated biomass of the old tagged sprouts before treatment as covariate. The number and biomass of new sprouts and the leaf/shoot biomass ratio were compared by an ANCOVA with competition and soil fertilization as the main effects and estimated biomass of all sprouts before treatment as the covariate. In order to normalize the data, mean sprout growth, mean sprout biomass of flowers, and biomass of new sprouts were square root transformed, while number of new sprouts, mean sprout biomass and estimated biomass of old sprouts before treatment were log transformed. Leaf/shoot biomass ratio in new sprouts was not transformed. The effect of different treatments on the percentage of plants flowering was compared by a G-likelihood test.

Table 1. Effect of fertilization and neighbour removal on the vegetative performance of *Erica multiflora* (± s.e.). Values followed by different lower-case letters are significantly different ($n = 20$).

Treatment	Mean sprout growth (g/year)
Control	0.23± 0.07 a
Fertilization	0.32± 0.05 b
Neighbour removal	0.20± 0.07 a
Fertilization + neighbour removal	0.54± 0.19 b
Treatment	Number of new sprouts per plant
Control	31.10± 6.91 a
Fertilization	20.35± 3.67 a
Neighbour removal	65.21± 15.67 b
Fertilization + neighbour removal	102.89± 19.80 c
Treatment	Total biomass of new sprouts (g)
Control	6.56± 1.33 a
Fertilization	6.49± 1.52 a
Neighbour removal	14.31± 4.36 b
Fertilization + neighbour removal	21.13± 3.90 b
Treatment	Leaf/shoot biomass ratio
Control	1.44± 0.11 a
Fertilization	1.21± 0.10 b
Neighbour removal	1.49± 0.11 a
Fertilization + neighbour removal	1.17± 0.15 b

Results

Fertilization had a positive effect on mean growth of tagged sprouts ($F_{1,72} = 4.23$, $p = 0.04$) but neighbour removal did not ($F_{1,72} = 0.4$, $p = 0.53$) (Table 1). The interaction fertilization × neighbour removal was not significant ($F_{1,72} = 0.002$, $p = 0.963$). This growth was not significantly correlated with biomass of sprouts before treatment. Removal of neighbours increased the number of new sprouts per plant ($F_{1,72} = 21.36$, $p < 0.001$) but fertilization had no significant effect on this variable ($F_{1,72} = 0.01$, $p = 0.93$) (Table 1). The interaction between fertilization and neighbour removal was slightly significant ($F_{1,72} = 4.03$, $p = 0.048$): fertilization enhanced sprout recruitment when neighbours were removed. Removal of neighbours increased the total biomass of new sprouts ($F_{1,69} = 11.003$, $p = 0.001$), but fertilization did not increase this variable ($F_{1,69} = 0.56$, $p = 0.46$) (Table 2). The interaction between both factors was not significant ($F_{1,69} = 9.88$, $p = 0.099$). The number and biomass of new sprouts were positively related to the biomass of the plants before treatment ($F_{1,72} = 11.38$, $p = 0.00$; $F_{1,69} = 9.88$, $p = 0.002$). Fertilization decreased the leaf/shoot biomass ratio in new sprouts ($F_{1,72} = 4.16$, $p = 0.04$) (Table 1).

Fertilization had a negative effect on the percentage of sprouts which produced flowers (G-likelihood test = 4.764, $p = 0.03$). Only 47 % of the sprouts from fertilized target plants with neighbours flowered. However, 90 % of the fertilized target plants without neighbours flowered (G-likelihood test = 24.48, $p = 0.0001$) (Table 2). Removal of neighbours increased the mean biomass of flowers per sprout ($F_{1,72} = 20.36$, $p = 0.0001$) but fertilization did not ($F_{1,72} = 0.76$, $p = 0.39$) (Table 2). The biomass of flowers was positively correlated with the vegetative biomass of the sprout ($F_{1,72} = 11.51$, $p = 0.0001$). Removal of neighbours did not modify this relationship (Fig. 1).

Table 2. Effect of fertilization and neighbour removal on the percentage of flowering old sprouts and the biomass of flowers. Values followed by different lower-case letters are significantly different ($n = 80$).

Treatment	% flowering plants
Control	78.2 a
Fertilization	47.4 b
Neighbours removal	83.0 a
Fertilization + neighbour removal	90.2 a
Treatment	Mean biomass of flowers per sprout (g)
Control	0.72 ± 0.20 a
Fertilization	1.04 ± 0.27 a
Neighbours removal	1.58 ± 0.40 b
Fertilization + neighbour removal	2.20 ± 0.41 b

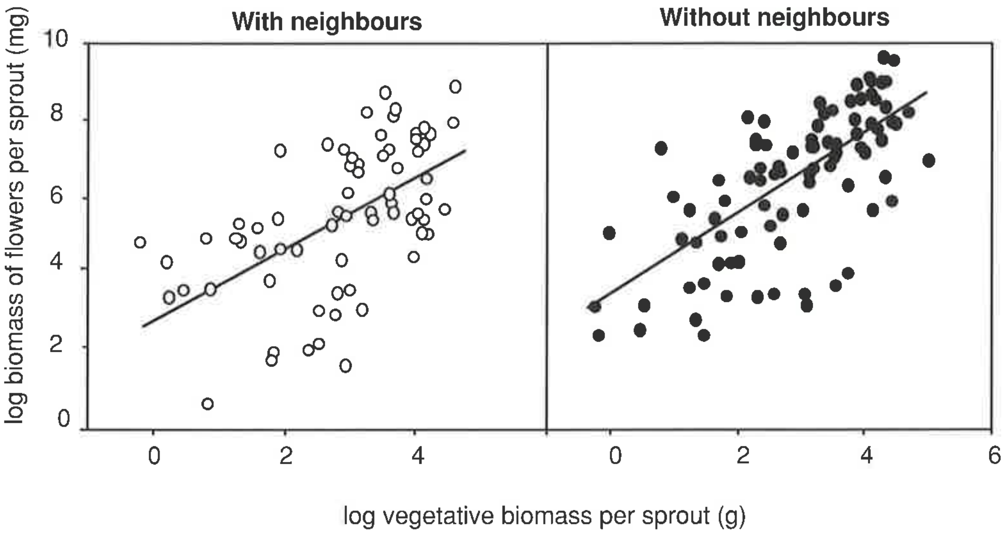

Fig. 1. Relationship between the biomass of flowers and the vegetative biomass per sprout in *Erica multiflora* with neighbours (open circles) and without neighbours (solid circles).

Discussion

Fertilization and neighbour removal increased the performance of *Erica multiflora* . Responses to fertilization were similar to those reported in previous studies on mediterranean shrubs. For instance, fertilization with N and P increased growth in the chaparral species *Adenostoma fasciculatum* and *Ceanothus greggii* (McMaster et al. 1982); N and P, added separately or together, also increased growth in the fynbos species *Leucospermum parile* and *Phylica cephalantha* (Witkowski et al. 1990) and in *Eucalyptus diversicolor* trees in karri (Groves 1988). In the present study, growth of old sprouts was enhanced by fertilization but not by removal of neighbours, indicating that nutrients limited the growth of *E. multiflora.*

However, recruitment of a new cohort of sprouts was limited by competition with neighbours. Continual basal sprouting in mediterranean species has been observed in the absence of any identifiable disturbance in *Erica arborea* and *Arbutus unedo* (Mesléart & Lepart 1989), *Salvia leucophylla* and *Artemisia californica* in chaparral (Malanson & Westman 1985), and in Australian *Eucalyptus* spp. (Holand 1969). The fact that resprouting occurs in the absence of disturbance suggests that it also serves as a mechanism of genet expansion which has the effect of maintaining species populations that are long lived but have low reproduction (Keeley 1992). Nevertheless, some authors argue that continual basal sprouting could be a consequence of non-observed micro-disturbances (Riba 1991), micro-environmental differences such as sprout senescence (Jones & Raynal 1987), or loss of apical dominance (Blake & Carrodus 1970). Resprouting of mature genets could be a rapid response to local disturbance and release from competition, as has been shown in clonal plants (Schmid & Bazzaz 1990). Although genet expansion is limited in resprouting species as compared to clonal plants, this behaviour could be especially important in this species because sprouts can be recruited at the edge of the plant from shallow roots allowing it to explore adjacent soil microsites, as well as to increase its cover area and subsequently to extent the access to light.

Fertilization increased sprout recruitment when neighbours were removed. Reader (1990) found an increase of rosette recruitment in *Hieracium floribundum* when plants were fertilized and neighbours removed, suggesting that in natural conditions competition would not be important because growth would be constrained by the low nutrient supply *per se*. This was not the case in our study: unfertilized *E. multiflora* was also negatively affected by the presence of neighbours in unfertilized plots, but fertilization amplified the positive effect of removal of neighbours. The fact that sprout recruitment was enhanced more by removal of neighbours in fertilized than in unfertilized plants suggests that competition for nutrients limits continual basal sprouting.

In the same way, a decrease of the leaf/shoot ratio as found is usually associated with an increase in height growth and competition for light. A decrease of the leaf/shoot ratio was also found in experimentally shaded *Erica multiflora* plants after clipping (Vilà unpubl. data), suggesting that light availability decreases resource allocation to photosynthetic tissues.

Removal of neighbours had a positive effect on sprout flowering only when nutrients were added, but fertilization alone decreased flowering. These results suggest that fertilization would enhance vegetative growth to the detriment of floral bud induction when there is competition. A similar result was obtained by Carpenter & West (1988), who found a greater biomass allocation to vegetative structures than to reproductive ones after irrigation and N-fertilization in *Artemisia tridentata* ssp. *vaseyana*.

Biomass of flowers per sprout was also increased by removal of neighbours. This result is consistent with those obtained in a number of other species exposed to a range of intensities of competition (Weiner 1988). The biomass of flowers was positively related to vegetative sprout biomass, but this relationship did not depend on the presence or absence of neighbours. However, Schmid & Weiner (1993) concluded that the relationship between vegetative and reproductive biomass depends on extrinsic factors such as competition by neighbouring plants. One possible reason that the presence of neighbours did not modify this relationship in our study is that sprouts are semi-autonomous functional units connected to the genet stump; it is possible that the relationship between vegetative biomass of the sprout and the biomass of flowers depends more on inter-ramet competition than on inter-genet competition. Hartnett & Bazzaz (1985a) pointed out that interconnected ramets of the clonal plant *Solidago canadensis* were less sensitive to increased inter-genet competition than individuals growing from seeds, suggesting that ramet performance was regulated by the dependence among interconnected ramets (Hartnett & Bazzaz 1985b) and on the combination of both genet and ramet competition.

Our study does not clarify which soil resources limit the growth of *E. multiflora* and which are the underlying mechanisms of competition. The extractable P-content in the soil around non-fertilized target plants with neighbours was lower (3.85 ± 0.25) than that around target plants without neighbours (4.80 ± 0.26) (Vilà unpubl.), indicating that they may compete for P. Otherwise, plant growth in mediterranean-type ecosystems is likely to be water-limited since summer drought is a characteristic trait of mediterranean-type climates (Castell & Terradas 1994). Further studies on the nutrient contents of both soil and plant are required to determine the precise mechanism of competition that limits *E. multiflora* growth.

E. multiflora exhibits plasticity in vegetative growth and biomass allocation as a response to nutrient addition and removal of neighbours. According to the present study, nutrient limits the plant's vertical growth; while the presence of neighbours limits lateral growth of the plant by reducing sprout recruitment. Our results indicate that *E. multiflora* responds to the removal of neighbours through management practices by increasing the recruitment of new sprouts, maybe as diminished competition for soil nutrients and shading. The difference in opinion between Grime and Tilman on the effect of soil fertilization in competition is mainly based on studies on herbaceous plants. Our results show that studies of woody species may be more complex, and hence are not suitable to support their theories. We have observed that the stimulation of sprout and flower buds increases with the removal of neighbours and this effect is enhanced when the soil has been fertilized. However, removal of neighbours and fertilization had an additive effect on the biomass of these structures. Thus, the extent to which competition is stronger in fertilized than in unfertilized soils depends on the measure of performance considered. In *E. multiflora*, the effect of competition on the probability of sprout flowering and sprout recruitment was greater when the soil was fertilized than in natural conditions, supporting Grime's (1979) idea. However, the effect of competition in determining sprout flower biomass and new sprout biomass was independent of the fertilization treatment, supporting Tilman's (1982) point of view.

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