The effects of nutrient availability and removal of competing vegetation on resprouter capacity and nutrient accumulation in the shrub Erica multiflora

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ABSTRACT

Nutrient availability is increasing in the Mediterranean Basin due to the great number and intensity of fires and higher levels of anthropomorphic pollution. In the experiment described in this paper, we aimed to determine the effects of N and P availability and of the removal of competing vegetation on resprouter capacity, biomass, and nutrient accumulation in Erica multiflora. Plants of the resprouter species E. multiflora were clipped to 0% of aerial biomass in a post-fire Mediterranean shrubland and fertilisation experiments and removal of competing vegetation were established in a factorial design. The resprouting of clipped plants was monitored during the first year after clipping and at the end of the year, all plant resprout populations were harvested and their resprout structure, biomass and N and P content measured. N fertilisation had no significant effect on leaf biomass either at plant level or on the total aerial biomass per stump unit area; however N concentration in resprout biomass did increased. P fertilisation slightly increased resprouting vigour and had a significant effect on P content of the leaf biomass. The removal of competing vegetation increased the ratio between leaf biomass and stem biomass, the lateral expansion of resprout, the hierarchy of resprouts branching, and the P content of stems, above all when P fertilisation was applied. These results show that as a response to decreased competition E. multiflora has the capacity to modify the relative proportions of the nutrients in the aerial biomass. All these characteristics allow E. multiflora to persist in increasingly disturbed Mediterranean ecosystems and contribute to the retention of nutrients in the ecosystem during early resprouting phases.

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1. Introduction

In Mediterranean ecosystems, the high cost of biomass production together with the considerable levels of natural damage (recurrent fires, severe dry periods, and herbivore pressure) are proposed as general explanations for resprouting capacity (Mooney and Dunn, 1970; Lloret et al., 1999). This reproductive strategy enables plants to immediately recover lost ground and has even been considered in ecological theory auto-succession (Hanes, 1971).

In general, Mediterranean ecosystems are considered to be poor in nutrients (Mooney and Dunn, 1970; Ellis and Kummerow, 1989). On the other hand, there is evidence of the role played by nutrients in limiting resprouting capacity (Prevost,
Resprouting capacity should be especially important in nutrient-poor environments and in environments such as Mediterranean ecosystems where there is a great risk of post-fire nutrient losses caused by torrential rainfalls.

Some experiments have demonstrated that resprouting vigour is strongly reduced by the presence of competing vegetation. Resprouting should be stronger when a perturbation has destroyed not only the biomass of a single plant but also that of its neighbours (Vilà and Terradas, 1995a, 1998; Vilà et al., 1998). Less is known about the interaction between nutrient availability and the presence of competing vegetation on patterns of resprouting intensity, on the nutrient capture during resprouting and on the structure of sprouts population of each plant.

In some studies, competition has been considered to have a more relevant role in nutrient-rich than in nutrient-poor environments (Grime, 1977; Reader, 1990); in others, however, competition has been reported to be equally important in rich and poor environments (Tilman, 1982; Wilson and Tilman, 1993). The idea that the intensity of competition depends on resource availability in ecosystems remains controversial (Welden and Slauson, 1988; Peltzen and Kochy, 2001). Most experiments carried out on the interaction between competition and nutrient supply levels have been conducted by removal of competing vegetation. These experiments have been conducted mostly in grassland communities (see Tilman, 1990) and less often in Mediterranean shrublands (Vilà and Terradas, 1995a). Furthermore, two different structural levels can be distinguished in a context of plant competition. The first level is represented by genetic individuals in the population that are the result of sexual reproduction; the second level is found within individual plants and is the result of their modulated growth pattern. At this second level, competition exists between different modules within the same plant (Berstson and Weiner, 1991).

During the last century, the temperature in the Mediterranean Basin showed an overall trend towards warming (Piñol et al., 1998; Peñuelas et al., 2002; Peñuelas and Boada, 2003) and precipitation levels are currently experiencing a long-term downward trend in some Mediterranean areas (Kutiel et al., 1996; Esteban-Parra et al., 1998). This change in climate is occurring simultaneously with changes in nutrient availability in many areas of the Mediterranean Basin. Fire frequency has increased in the eastern part of the Iberian Peninsula in recent decades (Pausas, 2004). Frequent fires may result in cumulative nutrient loss through volatilisation, smoke particles, windblown ashes, soil leaching, and erosion, thereby magnifying the possible limiting role of nutrients. Fire can increase N and P availability in the initial period after fire (Carreira et al., 1996; Gimeno-García et al., 2000). However, this sudden increase in P availability only last for a short time due to the fact that such increases principally occur in soluble P in inorganic soil (Kutiel and Kutiel, 1989; Thomas et al., 1999). Moreover, P losses caused by volatilisation (Soto et al., 1997) or rainfall erosion (Thomas et al., 1999) can often be higher after fire. The capacity of quick absorption of nutrients after a fire event has been suggested as one of the benefits of a resprouting strategy (Specht, 1973; Romanya et al., 2001) and, in this way, the liberated nutrients can easily be retained by the resprouting species following a disturbance. Another driver of change in nutrient availability is the alteration of global biogeochemical cycles by human activities. The global N cycle has now reached the point in which more N is fixed annually by human-driven processes (fertilisers, combustion of fossil fuels, and waste from stock-raising) than by natural processes (Vitousek et al., 1997). Nitrogen inputs and N and P foliar concentrations seem to have increased in some Mediterranean species in the last few decades (Peñuelas and Filella, 2001).

The capacity to capture nutrients may become a vital part of the ecological strategies of Mediterranean plants in context of a global change, in which a decrease of water availability, more erratic and torrential rainfalls, greater erosion, and increased fires and nutrient deposition may lead to steeper gradients in nutrient supply and thus affect the regenerative capacity of the Mediterranean sclerophyllous ecosystems. This new environmental scenario may challenge the capacity of sprouting strategies and their role in the maintenance of the structure of present-day Mediterranean ecosystems. The capacity to capture nutrients under different levels of competition and nutrient availability may be the key for Mediterranean resprouters to maintain their current areas of distribution and retain nutrients in the ecosystem in the near future.

Erica multiflora is a common evergreen shrub that typically occurs in coastal shrublands on calcareous soils in the western Mediterranean Basin (Orshan, 1989). Its resprout vigour has been studied in light of a number of different disturbances (Lloret and López-Soria, 1993); water stress (Vilà and Terradas, 1998; Llorens et al., 2003), warming (Llorens et al., 2004), competing vegetation (Vilà, 1997) and herbivores (Vilà and Lloret, 1996; Vilà et al., 1998). The current coincidence between climate change and increase in nutrient supplies warrants an investigation of the capacity of dominant Mediterranean shrubs to change their sprout structure and to capture and retain nutrients in their biomass in response to nutrient pulses originating from forest fires or pollution.

In a post-fire shrubland with a history and a structure typical of widespread zones of the Mediterranean Basin, we conducted a factorial design experiment involving nutrient fertilisation and the removal of competing vegetation as way of studying to study the effects of disturbance on E. multiflora, a typical Mediterranean resprouting shrub species. Our aims were to investigate the effects of a sudden increase in N and P supplies and different densities of competing vegetation on (i) resprouting vigour and structure (biomass, number, size, and branching distribution of resprouts at genet level), and (ii) the nutrient content of the resprouts.

2. Materials and methods

2.1. Experimental site

The experiment was conducted in a naturally regenerated post-fire shrubland that was burnt three times in the period 1965–1985. The last fire occurred in summer 1985, 5 years before the experiment started. The study site was located on a
level hill top (slope 0–5%) in the pre-coastal mountain range of central Catalonia at 300 m above sea level (41°37′ N, 1°50′ E). In this area, a Lithic haploxeroll soil associated with Lithic xerothens soils exist over Eocene calcareous-loam rocks of sedimentary origin. The soil has a high pH (8.3 ± 0.2) and high proportions of carbonates (55.9 ± 1.2%) and active lime (12.2 ± 0.5%) (Sardans, 1997). The soil extractable NO$_3^-$ and NH$_4^+$ were 9.59 ± 0.77 and 0.73 ± 0.07 mg kg$^{-1}$ soil, respectively (Sardans, 1997). The bicarbonate-extractable P in soil was low (4.05 ± 0.3 mg P kg$^{-1}$ soil). The climate is Mediterranean with a moderate continental component. The annual average temperature is 14 °C, with the average minimum temperature of the coldest month being –1.9 °C and the average maximum temperature of the hottest month being 31.8 °C. Mean annual rainfall is 517 mm (period 1985–1996) and the summer drought period comprises 3 months from June to September. The vegetation type is a post-fire Mediterranean shrubland (Erico Thymaleetum tinctoreae) with young saplings of Aleppo pine (Pinus halepensis) and small resprouts of interior holm oak (Quercus ilex subsp. rotundifolia). The total plant cover when the experiment started (1990) was 77.5 ± 3.7%. The most abundant species were P. halepensis (29.3 ± 6.1%), Rosmarinus officinalis (15.7 ± 3.7%), Brachypodium rietum (10.1 ± 4.1%), Thymus vulgaris (4.5 ± 1.98%), and E. multiflora (4.1 ± 1.6%).

2.2. Experimental design

We established two different experimental designs in order to study separately the effects of N and P fertilisation. Each of the experimental designs had two factors: N or P fertilisation and the removal of competing vegetation, and consisted of four treatments—C (Control) and R (removal of competing vegetation treatment without fertilisation), N and NR (fertilisation with equivalent doses of 500 kg N ha$^{-1}$ with and without competing vegetation), or P and PR (fertilisation with equivalent doses of 250 kg P ha$^{-1}$ with and without competing vegetation). These designs enabled us to investigate the possible effects of N and P supplies, the competitive pressure within resprouting, and the interactions between N and P and competition. We assigned 21 genets randomly to each treatment. Due to the heterogeneity of the plot area, the design was completely random and a block design was discarded.

Aerial biomass was completely removed from all the plants to simulate a strong perturbation and to allow subsequent resprouting while the subterranean biomass was not altered. The treatments were applied to individual plants. Fertilisation consisted of hand application of doses equivalent to 250 kg P ha$^{-1}$ of calcium phosphate and 500 kg N ha$^{-1}$ of ammonium nitrate. These doses were chosen as they have been employed in several previous experiments using nutrient manipulation and are considered to be of intermediate intensity (Mayor and Rodà, 1994). The fertilisation treatments were conducted in July (the month with the highest frequency of fires). In both cases the fertiliser was dispersed homogeneously in a 1 m$^2$ circle around the target plants. The removal of competing vegetation consisted of the complete removal of all competing aerial biomass in a 1 m$^2$ circle around the target stump. This method has been shown to reduce competition in previous field experiments on shrublands and grasslands and is regarded to be an efficient way of detecting the presence of competition (Aarseen and Epp, 1990). The removal of competing vegetation was continued throughout the experiment in order to completely suppress this pressure. Target plants were kept at least 4 m apart in order to avoid treatment interferences. The average distance between target plants in the field was 6.3 ± 1 (S.E.) m.

2.3. Measurements and sampling of biomass

The basal area of stumps was measured at the beginning of the experiment after sprouts had been removed. No differences in the mean size of the individuals assigned to each treatment were detected, thereby assuring the homogeneity and equal distribution of plant sizes across the different treatments.

The number of resprouts from every stump (the resprout number) was measured every two months in order to monitor the evolution of sprouting. One year after the beginning of experiment, resprouts of all the experimental plants were harvested. The following measurements were taken: (1) total number of resprouts of each plant; (2) basal diameter, height and number of lateral branches of each resprout; (3) total biomass, leaf biomass and stem biomass of each plant; (4) N and P concentration in the leaves and stems of the resprouts and (5) N and P content of the total biomass and stem and leaf fractions.

2.4. Chemical analyses

Leaves and stems were dried in an oven at 70 °C for 48 hours until a constant weight was reached. Seven replicates of each biomass fraction per treatment were analysed. Nitrogen concentrations were analysed by the Kjeldhal method in a KJELTEC 1030 autoanalyser (RECATOR, Högänäs, Sweden) after acid digestion (with H$_2$SO$_4$ + Devarda catalyst) conducted in a Tecator digester (TECATOR, Högänäs, Sweden). Phosphorus concentration was analysed by ICP-AES (Atomic Emission Spectroscopy with Inductively Coupled Plasma) (in a spectrophotometer JOBIN YVON JI 38, JOBIN, France) after biacid digestion (HNO$_3$/HClO$_4$, 2:1) in a microwave oven (SAMSUNG, Seoul, South Korea).

2.5. Statistical analyses

The normality distributions of all the variables analysed were tested by the Kolmogorov–Smirnov test (Statistica 6.0, StaSoft Inc., Tulsa, OK, USA). The effects of treatments on leaf, stem and total aerial biomass, on number of resprouts per plant, and on N and P concentration and contents at the end of the experiment were analysed by factorial ANCOVA (with the plant stump area as cofactor). When the cofactor was not significant, a factorial ANOVA was used (Stastview 5.0.1, SAS Institute Inc., Berkeley, CA, USA). When significant differences were detected, a mean contrast between treatments was conducted by the Duncan new multiple range test. When the plant stump area explained a significant part of the variance, the significance of this effect was analysed by a regression analysis. For analyses of the experimental
Factors on the ratio between leaf and stem biomass growth, an ANCOVA with stem biomass growth as a covariable was used, given the possible dependence of the ratio values of the denominator (Jackson et al., 1990; Liermann et al., 2004).

To investigate the competition within plant modules, resprout size and branching distribution in each genet was statistically analysed to determine the effect of treatment on the intra-plant population traits used as an estimation of the structure of the resprout population of each plant. The statistical tests used for this purpose were: the coefficient of variation (CV), the skewness coefficient (g) and the Gini hierarchy coefficient (G). These coefficients were calculated as in Bendel et al. (1989) and have been widely used to analyse the structure of biological populations. CV assesses the deviation value with respect to the mean value while skewness assesses the degree of asymmetry of the distribution around the mean as the difference in the grouping at the two extremes of the distribution. While the skewness coefficient assesses the proportion of the individuals of different sizes, the Gini coefficient assesses the hierarchy of population distribution and has an intuitive significance for ecological studies (Weiner and Solbrig, 1984). For more information on these coefficients, see Sen (1973). The values of the three coefficients in the population distribution of each plant sprout were statistically analysed by ANOVAs in order to detect experimental treatment effects. In all the analyses, the significant level was established below $P = 0.05$.

The intensity (IN) and the importance (IM) of the effects of competition (Welden and Slauson, 1988) on the sprouting biomass and on N and P content were also analysed by the ANOVA results. The following equations were used to calculate these variables:

$$IN = \frac{(NC - C)}{C} \times 100$$

$$NC = \text{Variable mean value of the plants with removal of competing vegetation.}$$

$$C = \text{Variable mean value of the plants without removal of competing vegetation.}$$

$$SC = \text{Variance explained by removal of competing vegetation.}$$

$$ST = \text{Total variance.}$$

To estimate the degree of significance of the values obtained for the importance and the intensity of competition, we conducted an ANOVA analysis within the variable of C with respect to R, of N with respect to NR, and of P with respect to PR.

3. Results

3.1. Resprouting vigour

Removal of competing vegetation had no effect on either total biomass or number of resprouts on each plant although there was an increase in the ratio between leaf biomass and stem biomass in plants when either P ($P = 0.006$) and N fertiliser was applied ($P = 0.046$) (Tables 1 and 2). Stem biomass had a significant effect ($P = 0.028$) on the ratio between leaf and stem biomass in the design of N fertilisation $\times$ Removal of competing vegetation but not in the design $P$ fertilisation $\times$ Removal of competing vegetation (Table 1).

No general effects of N fertilisation on resprouting vigour were observed other than a significant decrease in the ratio between leaf and stem biomass and in mean height of the sprouts of each plant (Table 1). N fertilisation also decreased the number of sprouts in the plants at the end of the first year after clipping ($F = 2.1, P = 0.11$) although not significantly. A negative interaction between N fertilisation and the removal of competing vegetation was detected in leaf, stem and total biomass growth (Table 1). Plant growth under N fertilisation and the removal of competing vegetation was lower than growth under N fertilisation alone, under the removal of competing vegetation alone, and in the controls. The high area had a positive effect on biomass leaf and stem biomass and a negative effect on the growth relative to stump area (Table 1).

The total biomass of resprouts of the plants fertilised with P was higher ($8.12 \pm 1.39$ g) than in the unfertilised plants ($5.63 \pm 0.77$ g), but this difference was not significant ($F = 2.8, P = 0.12$). P fertilisation had no effect on the other variables affecting resprouting vigour (Tables 1 and 2). No interactions were observed between the removal of competing vegetation and P fertilisation.

No trends were found in the importance and intensity of competition due to N or P fertilisation other than in the ratio between foliar and stem biomass (comparison between C and R: 0.05% importance in control plots versus 12.6% in P-fertilised plants, $P = 0.018$ in the ANOVA). Thus, the percentage of the total variability accounted for by the removal of competing vegetation increased when P fertilisation was applied (Table 3). The effects of competition on the biomass of the plant resprout population decreased when P fertilisation was applied, but tended to increase when N fertilisation was applied (Table 3). A decrease in biomass of the resprout plant was observed when N fertilisation was applied without the removal of competing vegetation.

Neither fertilisation nor the removal of competing vegetation had any significant effect on branching number of the plant sprouts (Table 2). No interactions were observed between N fertilisation and removal of competing vegetation or between P fertilisation and the removal of competing vegetation on number of sprouts or on the branching number of plant sprouts (Table 2).

3.2. Population structure of the resprouts of each genet

The mean number of resprouts per plant was 35.4 ($\pm 3.2$ S.E.). Removal of competing vegetation significantly increased the three coefficients CV, g and G for the number of branches when P but not N was applied (Table 4). The removal of competing vegetation did not significantly change any of the three coefficients CV, g and G for the distribution of height and basal diameter in the resprout population of each plant (Table 4). These results show an increase in dispersion around the mean together with a higher hierarchy of the distribution of the sprout branches in an individual plant sprout population. No significant differences in these coefficients were detected as a response to N or P fertilisation (Table 4). There was a positive correlation between the basal diameter of the resprout and the number of the ramifications on these resprouts under all treatments ($r = 0.8, P = 0.001, n = 21$). No
effects on nutrient concentration (Fig. 1). When P fertiliser
removal of competing vegetation had no other significant ef-
when neighbours were removed (Fig. 1 and Table 5). The re-
had a greater positive effect on P concentration principally
was applied, the importance and intensity of competition in-
treatment (Table 5). No interactions between treatments were ob-
the factorial ANOVA design for each dependent
variable are given in the final three columns. (Nf = N fertilisation, R = Removal of competing vegetation, Pf = P fertilisation).

If an ANCOVA was used, it is indicated by the P value of the cofactor (stump area or stem biomass)

Table 1 – Leaf, stem and total aerial biomass of the plants (g; mean ± S.E.), the mean height of the resprouts of each plant
(mm; mean ± S.E.), leaf, stem and total aerial biomass of the plants per stump area of the plant, and ratio between leaf biomass and stem biomass of all plant sprouts in the different experimental factors in the factorial designs experiments. All the variables are represented by the values reached after a year of clipping and fertilisation. Significant differences
(P < 0.05) between treatments are highlighted in bold type. Different letters in brackets indicate significantly different
values. The significant levels (P) of the two factors and their interaction in the factorial ANOVA design for each dependent

<table>
<thead>
<tr>
<th>Variable</th>
<th>Design: N fertilisation · Removal of competing vegetation</th>
<th>Design: P fertilisation · Removal of competing vegetation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P stump area C R N NR P for R P for Nf P interaction</td>
<td>P stump area C R P PR P for R P for Pf P interaction</td>
</tr>
<tr>
<td>Leaf biomass</td>
<td>3.22 ± 0.55 (a) 3.56 ± 0.51 (a) 3.96 ± 0.81 (a) 2.44 ± 0.59 (a) 3.69 ± 0.85 (a) 0.691 0.100 0.027</td>
<td></td>
</tr>
<tr>
<td>Stem biomass</td>
<td>1.88 ± 0.33 (a) 2.15 ± 0.49 (a) 1.55 ± 0.40 (a) 1.97 ± 0.50 (a) 0.759 0.206 0.049</td>
<td></td>
</tr>
<tr>
<td>Total biomass</td>
<td>5.15 ± 0.86 (a) 6.10 ± 1.30 (a) 4.02 ± 1.00 (a) 5.41 ± 1.34 (a) 0.711 0.142 0.032</td>
<td></td>
</tr>
<tr>
<td>Mean height of the resprouts of each plant</td>
<td>135 ± 11 (a) 134 ± 11 (a) 90 ± 9 (b) 111 ± 11 (a) 0.902 0.043 0.749</td>
<td></td>
</tr>
<tr>
<td>Leaf biomass/stump area</td>
<td>0.0007 0.071 ± 0.011 (a) 0.100 ± 0.026 (a) 0.059 ± 0.022 (a) 0.053 ± 0.011 (a) 0.716 0.081 0.006</td>
<td></td>
</tr>
<tr>
<td>Stem biomass/stump area</td>
<td>0.0002 0.040 ± 0.006 (a) 0.059 ± 0.015 (a) 0.037 ± 0.016 (a) 0.031 ± 0.007 (a) 0.948 0.292 0.015</td>
<td></td>
</tr>
<tr>
<td>Total biomass/stump area</td>
<td>0.121 ± 0.017 (a) 0.170 ± 0.041 (a) 0.096 ± 0.039 (a) 0.084 ± 0.170 (a) 0.714 0.141 0.032</td>
<td></td>
</tr>
<tr>
<td>Leaf biomass/Stem biomass</td>
<td>0.028 1.63 ± 0.17 (a) 1.93 ± 0.12 (a) 1.11 ± 0.19 (b) 1.43 ± 0.20 (b) 0.046 0.001 0.962</td>
<td></td>
</tr>
</tbody>
</table>

C = control, without N fertilisation and without removal of competing vegetation; N = with N fertilisation and without removal of competing vegetation; R = without N fertilisation and with removal of competing vegetation; Pf = with P fertilisation and without removal of competing vegetation; NR = with N fertilisation and removal of competitive vegetation; P = with P fertilisation and without removal of competing vegetation; PR = with P fertilisation and with removal of competing vegetation.

The removal of competing vegetation significantly increased (F = 6, P = 0.017) the P concentration in stems, above all when P fertiliser was applied. A significant interaction was observed between P fertilisation and removal of competing vegetation (F = 32, P < 0.0001) in the sense that P fertilisation had a greater positive effect on P concentration principally when neighbours were removed (Fig. 1 and Table 5). The removal of competing vegetation had no other significant effects on nutrient concentration (Fig. 1). When P fertiliser was applied, the importance and intensity of competition increased the concentration of P in leaf and stem (Table 5). These effects were not observed as a response to N fertilisa-

3.3. N and P concentrations and contents

The addition of N fertiliser significantly increased the concentration of N in leaves (F = 4.7, P = 0.036) and stems (F = 6.2, P = 0.013). N fertilisation had no significant effect on P concentrations (Fig. 1). The addition of N fertiliser and the removal of competing vegetation tended to decrease N and P contents in the plant leaves and stems, although these effects were not statistically significant (Fig. 2).

Addition of P fertiliser significantly increased (42%) concentration P in leaves (F = 9.7, P = 0.0003), but not in stems (F = 1.15, P = 0.381) (Fig. 1). The highest concentrations of P in leaves were found when P fertilisation was accompanied by the removal of competing vegetation (Fig. 1). These results denote an interaction between P fertilisation and removal of competing vegetation that was only marginally significant (F = 2.78, P = 0.10) in the ANCOVA test. Fertilisation with P had no significant effect on N concentration (Fig. 1) but sig-
significantly increased the N and P contents of plant leaves and stems (up to 50% in leaf P content; Fig. 2). In all of the statistical analyses of N and P contents of leaf and stem, the stump area accounted for a significant part of the variance. A negative interaction between N fertilisation and removal of competing vegetation was observed in N and P content. This interaction was significant in leaf, stem, and total biomass P content (Fig. 2).

4. Discussion

Resprout recruitment in the first year after thinning occurred gradually rather than suddenly. New sprouts were produced throughout the year of monitoring. This trend was observed in all treatments and resprout recruitment did not stop in any treatment. This behaviour agrees with previous studies in which successive appearance of resprout cohorts has been observed (Vilà and Terradas, 1995b). The recruitment of successive resprout cohorts has also been observed in other resprouter species: Arbutus unedo (Mesléard and Lepart, 1989), Salvia leucophylla and Artemisa californiac (Malanson and Westman, 1985) and Eucalyptus sp. (Holland, 1969).

The removal of competing vegetation did not produce important changes in resprouting vigour, although it did have effects on individual resprout structure and on branch distribution within the plant resprout population. Increases in the proportion of leaf biomass with respect to stem biomass and in the number of branches in the resprouts, especially when P fertilisation was applied, indicate a trend towards lateral expansion to compete with competitors for space. Greater resprout growth in the P-fertilised plants, especially when the competing vegetation had been removed, could have increased branching of the resprouts to take advantage of the greater availability of light and water.

The increase in the Gini coefficient for the number of resprout branches at plant level was a sign of an increase in the hierarchy of branching in the sprout population after a decrease in competitive pressure. Although no significant interaction was detected in the ANOVA test (P = 0.29) regarding the hierarchy of the number of ramifications in the plant sprout population, P fertilisation was the only factor that tended to increase this hierarchy when competing vegetation was removed. This effect is probably due to the lack of

### Table 2 — Total number of sprouts per plant, number of sprouts per stump area, and the mean number of sprout ramifications in the plant for the different treatments one year after clipping. The values of each treatment of the different variables are represented. (Different letters a, b, c indicate statistically significant differences between different treatments). Numbers are means ± S.E. Significant differences (P < 0.05) between the treatments are highlighted in bold type. The significant levels (P) of the two factors and their interaction in the factorial ANOVA design are given in the final three columns. (Nf = N fertilisation, Pf = P fertilisation, R = Removal of competing vegetation). If ANCOVA was used, it is indicated by the P value of the cofactor (stump area)

<table>
<thead>
<tr>
<th>Variable</th>
<th>P stump area</th>
<th>C</th>
<th>R</th>
<th>P for R</th>
<th>P for Nf</th>
<th>P interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sprout number</td>
<td>—</td>
<td>44 ± 8 (a)</td>
<td>33 ± 4.3 (b)</td>
<td>35.3 ± 7.9 (a)</td>
<td>41.4 ± 8.0 (a)</td>
<td>0.961</td>
</tr>
<tr>
<td>Sprout number cm⁻²</td>
<td>0.0016</td>
<td>0.985 ± 0.184 (a)</td>
<td>0.928 ± 0.155 (a)</td>
<td>0.904 ± 0.431 (a)</td>
<td>0.761 ± 0.180 (a)</td>
<td>0.756</td>
</tr>
<tr>
<td>Sprout branches</td>
<td>—</td>
<td>2.02 ± 0.25 (a)</td>
<td>2.25 ± 0.32 (a)</td>
<td>1.98 ± 0.44 (a)</td>
<td>2.55 ± 0.49 (a)</td>
<td>0.301</td>
</tr>
</tbody>
</table>

### Table 3 — Intensity and importance of the competition between the plants with and without removal of competing vegetation treatment (R) within the same fertilisation situation: No fertilisation (C and R), N fertilised (N and NR), and P fertilised (P and PR) on variables of sprouting vigour. The significance level of the difference between the variable values of C respect to CR, N respect to NR, and P respect to PR calculated in an ANOVA are given in the final three columns

<table>
<thead>
<tr>
<th>Variable</th>
<th>Competition intensity (C, R)</th>
<th>Competition intensity (N, NR)</th>
<th>Competition intensity (P, PR)</th>
<th>P ANOVA (C,R)</th>
<th>P ANOVA (N, NR)</th>
<th>P ANOVA (P, PR)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf biomass</td>
<td>22.85</td>
<td>41.34</td>
<td>-18.59</td>
<td>1.37</td>
<td>2.20</td>
<td>0.002</td>
</tr>
<tr>
<td>Stem biomass</td>
<td>13.89</td>
<td>26.73</td>
<td>-12.87</td>
<td>0.005</td>
<td>1.13</td>
<td>0.01</td>
</tr>
<tr>
<td>Total biomass</td>
<td>18.57</td>
<td>34.63</td>
<td>-16.07</td>
<td>0.009</td>
<td>1.69</td>
<td>0.006</td>
</tr>
<tr>
<td>Leaf biomass cm⁻²</td>
<td>54.91</td>
<td>-0.10</td>
<td>12.84</td>
<td>4.61</td>
<td>0.001</td>
<td>0.005</td>
</tr>
<tr>
<td>Stem biomass cm⁻²</td>
<td>47.46</td>
<td>-16.23</td>
<td>-10.80</td>
<td>3.72</td>
<td>0.003</td>
<td>0.003</td>
</tr>
<tr>
<td>Total biomass cm⁻²</td>
<td>53.22</td>
<td>-12.52</td>
<td>3.11</td>
<td>4.32</td>
<td>0.003</td>
<td>0.0003</td>
</tr>
<tr>
<td>Leaf biomass/stem biomass</td>
<td>18.79</td>
<td>28.86</td>
<td>30.01</td>
<td>0.05</td>
<td>3.37</td>
<td>12.60</td>
</tr>
</tbody>
</table>
external competition accelerating the resprout growth, intraplant competition among resprouts, and asymmetrical lateral branching. The positive effects on resprouting vigour after removal of competing vegetation and fertilisation when the nutrient is a limiting factor have been observed in other studies (Reader, 1990; Vilà and Terradas, 1995b), although not in all (see Matlack et al., 1993). Although it does not provide any direct evidence (Hara, 1988), the Gini coefficient is strongly influenced by competition and usually rises when competition increases (Hutchings, 1986). The positive correlation observed between the height of resprouts and their corresponding branch numbers indicates that resprout branching increases when resprouts reach certain heights. The removal of competing vegetation allows dominant resprouts at plant level to reach this height faster and in this way the hierarchy of the ramification process in the resprout populations increases.

The Gini coefficient and the skewness coefficient varied in different ways according to the variable and experimental factor studied. These differences, which have also been observed in other experiments (Weiner, 1985), call for caution when choosing which coefficient to use in the analysis of the effects of experimental factors on the distribution values of the population variables. An increase in the hierarchy of the distribution of one variable does not necessarily imply a parallel increase in the skewness or in the CV.

The P content in the aerial sprouting biomass increased in response to addition of P. This capacity for accumulation of a limiting nutrient such as P can provide a competitive advantage during future growth. These results fit the hypothesis of resprouting advantage providing the capacity to quickly absorb resources after perturbations in response to pulses in nutrient supplies (Schmid and Bazzaz, 1990; Kroon and Schieving, 1991). The capacity to increase nutrient content in biomass during resprouting events coinciding with similar nutrient increases in soils is a trend that might help prevent nutrient losses during the first regeneration phase after a disturbance and help increase water-use efficiency (Sing et al., 2000; Mohammad and Zuraigi, 2003). Such a capacity would enable E. multiflora to resist current and future environmental changes since it allows more efficient use of available nutrients and improves use of water, which global circulation models (GCMs) and ecophysiological models predict will become scarcer in the Mediterranean region (IPCC, 2001; Sabaté et al., 2002; Peñuelas et al., 2004).

The lack of effect of N fertilisation on resprouting vigour and on nutrient content contrasts with previous reports, in which N fertilisation increased resprouting vigour and nutrient content in E. multiflora (Vilà and Terradas, 1995a) and in other resprouting species (Di Tommaso and Aarseen, 1995a) and in other resprouting species (Di Tommaso and Aarseen, 1995b) and in other resprouting species (Di Tommaso and Aarseen, 1995c). This result is especially important because levels of available N in habitat soil are low compared to current values reported from natural soils (Malhi et al., 2003; Dorland et al., 2003), even though the high proportion of nitrate with respect to ammonium indicates high rates of

Table 4 – Means (± S.E.) of the CV (CV, %), the skewness coefficient (g) and the hierarchy coefficient (G) for stem basal diameter, the height and number of branches of each sprout in the sprout populations of the plants treated and not treated for each experimental factor. (Different letters a, b, c indicate statistically significant differences between different treatments). Significant differences (P<0.05) between the treatments are highlighted in bold type. The significant levels (P) of the two factors and their interaction in the factorial ANOVA design are given in the final three columns. (Nf = N fertilisation, Pf = P fertilisation, R = Removal of competing vegetation)

<table>
<thead>
<tr>
<th>Design: N fertilisation Removal of competing vegetation</th>
<th>Variable and coefficient</th>
<th>C</th>
<th>CR</th>
<th>N</th>
<th>NR</th>
<th>P for R</th>
<th>P for NF</th>
<th>P interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal diameter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CV</td>
<td>46.2 ± 3.1 (a)</td>
<td>48.2 ± 3.4 (a)</td>
<td>55.1 ± 3.8 (a)</td>
<td>44.8 ± 4.5 (a)</td>
<td>0.37</td>
<td>0.52</td>
<td>0.22</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>1.07 ± 0.16 (a)</td>
<td>0.88 ± 0.18 (a)</td>
<td>1.06 ± 0.32 (a)</td>
<td>0.81 ± 0.17 (a)</td>
<td>0.28</td>
<td>0.84</td>
<td>0.55</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>0.248 ± 0.016 (a)</td>
<td>0.259 ± 0.018 (a)</td>
<td>0.270 ± 0.025 (a)</td>
<td>0.231 ± 0.023 (a)</td>
<td>0.60</td>
<td>0.84</td>
<td>0.14</td>
<td></td>
</tr>
<tr>
<td>Height</td>
<td>46.0 ± 3.2(a)</td>
<td>47.2 ± 2.1 (a)</td>
<td>50.5 ± 4.9 (a)</td>
<td>45.6 ± 2.1 (a)</td>
<td>0.66</td>
<td>0.69</td>
<td>0.53</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>0.760 ± 0.129(a)</td>
<td>0.525 ± 0.103 (a)</td>
<td>0.599 ± 0.140 (a)</td>
<td>0.651 ± 0.153 (a)</td>
<td>0.40</td>
<td>0.95</td>
<td>0.85</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>0.294 ± 0.019 (a)</td>
<td>0.255 ± 0.010 (a)</td>
<td>0.275 ± 0.026 (a)</td>
<td>0.241 ± 0.014 (a)</td>
<td>0.41</td>
<td>0.91</td>
<td>0.39</td>
<td></td>
</tr>
<tr>
<td>Branches</td>
<td>140 ± 6 (a)</td>
<td>159 ± 10 (a)</td>
<td>155 ± 16 (a)</td>
<td>134 ± 12 (a)</td>
<td>0.41</td>
<td>0.60</td>
<td>0.96</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>1.48 ± 0.12 (a)</td>
<td>1.65 ± 0.18 (a)</td>
<td>1.84 ± 0.24 (a)</td>
<td>1.60 ± 0.26 (a)</td>
<td>0.98</td>
<td>0.54</td>
<td>0.06</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>0.657 ± 0.018 (a)</td>
<td>0.693 ± 0.028 (a)</td>
<td>0.654 ± 0.043 (a)</td>
<td>0.604 ± 0.046 (a)</td>
<td>0.97</td>
<td>0.15</td>
<td>0.39</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Design: P fertilisation - Removal of competing vegetation</th>
<th>Variable and coefficient</th>
<th>C</th>
<th>PR</th>
<th>P</th>
<th>PR</th>
<th>P for R</th>
<th>P for NF</th>
<th>P interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal diameter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CV</td>
<td>46.2 ± 3.1 (a)</td>
<td>48.2 ± 3.4 (a)</td>
<td>48.0 ± 2.5 (a)</td>
<td>50.1 ± 2.9 (a)</td>
<td>0.39</td>
<td>0.67</td>
<td>0.63</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>1.07 ± 0.16 (a)</td>
<td>0.88 ± 0.18 (a)</td>
<td>0.83 ± 0.14 (a)</td>
<td>1.09 ± 0.12 (a)</td>
<td>0.77</td>
<td>0.93</td>
<td>0.33</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>0.248 ± 0.016 (a)</td>
<td>0.259 ± 0.018 (a)</td>
<td>0.248 ± 0.012 (a)</td>
<td>0.266 ± 0.016 (a)</td>
<td>0.27</td>
<td>0.94</td>
<td>0.06</td>
<td></td>
</tr>
<tr>
<td>Height</td>
<td>46.0 ± 3.2 (a)</td>
<td>47.2 ± 2.1 (a)</td>
<td>50.4 ± 2.8 (a)</td>
<td>49.5 ± 2.8 (a)</td>
<td>0.88</td>
<td>0.28</td>
<td>0.74</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>0.76 ± 0.13 (a)</td>
<td>0.53 ± 0.10 (a)</td>
<td>0.39 ± 0.14 (a)</td>
<td>0.45 ± 0.11 (a)</td>
<td>0.47</td>
<td>0.08</td>
<td>0.89</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>0.254 ± 0.019 (a)</td>
<td>0.255 ± 0.010 (a)</td>
<td>0.268 ± 0.014 (a)</td>
<td>0.277 ± 0.015 (a)</td>
<td>0.59</td>
<td>0.28</td>
<td>0.23</td>
<td></td>
</tr>
<tr>
<td>Branches</td>
<td>140 ± 6 (a)</td>
<td>159 ± 10 (ab)</td>
<td>146 ± 12 (ab)</td>
<td>172 ± 11 (b)</td>
<td>0.03</td>
<td>0.34</td>
<td>0.41</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>1.48 ± 0.12 (a)</td>
<td>1.65 ± 0.18 (ab)</td>
<td>1.57 ± 0.20 (ab)</td>
<td>1.88 ± 0.17 (b)</td>
<td>0.02</td>
<td>0.30</td>
<td>0.62</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>0.657 ± 0.018 (ab)</td>
<td>0.693 ± 0.028 (ab)</td>
<td>0.626 ± 0.044 (a)</td>
<td>0.726 ± 0.023 (b)</td>
<td>0.04</td>
<td>0.98</td>
<td>0.29</td>
<td></td>
</tr>
</tbody>
</table>
Fig. 1 – N and P concentration (mg g⁻¹) (mean ± S.E.) in the resprout leaves and stems of the plants of the two experimental designs (different letters indicate statistically significant differences between different treatments). C = control, without N fertilisation and without removal of competing vegetation, N = with N fertilisation and without removal of competing vegetation, R = without N fertilisation and with removal of competing vegetation, NR = with N fertilisation and removal of competitive vegetation, P = with P fertilisation and without removal of competing vegetation, PR = with P fertilisation and with removal of competing vegetation.

Table 5 – Intensity and importance of the competition between the plants with and without neighbours (R) within the same fertilisation situation: no fertilisation (C and R), N fertilisation (N and NR), and P fertilisation (P and PR) on N and P concentration. The significance level (P) of the difference between the variable values of C respect to R, N respect to NR, and P respect to PR calculated in an ANOVA are presented in the last three columns

<table>
<thead>
<tr>
<th>Variable</th>
<th>Competition intensity</th>
<th>Competition importance</th>
<th>P ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(C, R)</td>
<td>(N, NR)</td>
<td>(P, PR)</td>
</tr>
<tr>
<td>N in leaves</td>
<td>6.66</td>
<td>4.13</td>
<td>1.84</td>
</tr>
<tr>
<td>N in stems</td>
<td>-5.22</td>
<td>1.59</td>
<td>5.12</td>
</tr>
<tr>
<td>P in leaves</td>
<td>-3.90</td>
<td>4.22</td>
<td>19.12</td>
</tr>
<tr>
<td>P in stems</td>
<td>12.52</td>
<td>-8.72</td>
<td>27.19</td>
</tr>
</tbody>
</table>
Nevertheless, in accordance with other experiments conducted at this same site that have not observed any effects of N fertilisation on growth and nutrient content of other species, this lack of effect of N fertilisation is probably the result of rapid mineralisation of N in these calcareous soils (Sardans et al., 2004). Additional N supply increased N concentration in the leaves and in the stems of the resprouts, but slightly reduced the total biomass of the popu-

Fig. 2 – Total N and P content of leaf, stem and aerial portions (mg per, mean ± S.E.) of plant resprout population (different letters indicate statistically significant differences between different treatments). C = control, without N fertilisation and without removal of competing vegetation, N = with N fertilisation and without removal of competing vegetation, R = without N fertilisation and with removal of competing vegetation, NR = with N fertilisation and removal of competitive vegetation, P = with P fertilisation and without removal of competing vegetation, PR = with P fertilisation and with removal of competing vegetation.
lation of the plant sprouts. The overall effect was that the N and P contents of the plants fertilised with N did not change. This slight reduction in growth in response to N fertilisation is not an exceptional event and has been observed previously in other studies. For example, high levels of N fertilisation (400 kg ha$^{-1}$) in a soil already rich in N decreased the growth of Zea mays, even though this species typically grows in nutrient rich soils (Pozo et al., 1992). Similarly, in a fertilisation experiment with stands of Picea abies, an additional supply of N and P had a negative effect (~10%) on radial growth (Picard et al., 1999). However, the suggested reason for the negative effect of increased nitrogen availability, the increased growth of the competing vegetation (Skrindo and Okland, 2002), does not stand in this case given our experimental conditions (the continuous “clearing” of a 1 m$^2$ circle surrounding the plants).

Thus, further research into this question is warranted in order to gain better understanding of this phenomenon.

E. multiflora showed only a small capacity to increase production of new resprouts and general resprout vigour as a response to fertilisation. Stronger effects were observed in nutrient content. Plants fertilised with N and P increased their concentrations of these nutrients in resprout biomass, although only in plants fertilised with P were these increases translated into increases of absolute P content in biomass. The positive effects of P fertilisation on P content were principally due to P concentration increases and, to a lesser extent, to the effects of sprout vigour during the first year after fertilisation. The removal of competing vegetation increased the lateral expansion of the plant resprout population and increased allocation to photosynthetic structures when P was applied. The removal of competing vegetation increased P concentrations in stems and had a positive effect on biomass and nutrient content. These results show a capacity to increase nutrient capture in response to changes in nutrient supplies during the first stages of resprouting, an ability that is modulated by the presence of competing vegetation. Nevertheless, a single year after clipping may not be long enough to detect the full effects of nutrient addition and the removal of competing vegetation on resprouting vigour. These trends in resprouting and regeneration capacity may be critical for specific persistence in Mediterranean forests and shrublands in the near future in light of continued disturbance. Steeper nutrient gradients (Peñuelas and Filella, 2001), together with warming trends (Piñol et al., 1998; Peñuelas et al., 2002) and a downward trend in precipitations (Esteban-Parra et al., 1998), will play a significant role in the capacity of Mediterranean plant species to capture and use nutrients. In fact, in an altitudinal gradient it has been found that the growth of plants of the genus Erica is more correlated to nutrient availability than to climatic conditions (Hicks et al., 2000).

Acknowledgements

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