Oecologia (1995) 102: 64–69

ORIGINAL PAPER

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Sprout recruitment and self-thinning of *Erica multiflora* after clipping

Received: 3 February 1994 / Accepted: 1 November 1994

Abstract Regrowth after clipping and the effect of local competition were studied in a natural population of *Erica multiflora* in a Mediterranean shrubland, by removing neighbours at 1 and 2 m around the target plants during four growing seasons. Removal of surrounding natural vegetation increased the number, the density (number of sprouts per stump area) and the biomass of the sprouts growing from clipped plants. Target plants only interacted with their near neighbours. Target plants had a negative relative increment in the number of sprouts per stump during the 18 months immediately following treatment, but a positive increment thereafter, which suggests that there was a constant or episodic recruitment of sprouts within the stump after clipping. Competition treatment had a non-significant effect on the negative increment of sprouts per stump. The self-thinning trajectory was different for the different competition treatments: there was an allometric negative relationship between density of sprouts and mean biomass of survivors during all sampling periods in genets without neighbours in a 1-m radius; the self-thinning trajectory of sprouts in genets without neighbours in a 2-m radius was short, a net increase in sprouts per stump area was accompanied by an increase in mean sprout biomass 30 months after clipping. During the same period, however, plants with neighbours showed a decline in both the sprout biomass and density.

Key words Continual basal sprouting · Neighbourhood competition · Resprouting · Self-thinning of sprouts *Erica multiflora*

Introduction

In Mediterranean plant communities, most woody plants resprout after disturbance (fire, clear-cutting, herbivory), often from well-defined subterranean structures (James 1984). When a resprouting species loses its aerial biomass, new sprouts develop from these subterranean structures. Resprouting vigour depends on several factors such as plant age (Keeley and Zedler 1978), availability of nutrients (Rubinstein and Nagao 1976), size and depth of the lignotuber (Auld 1990), environmental conditions, such as weather conditions (Riba 1991), and competition.

Disturbance reduces competition among plants and increases resources available at the individual level (Sousa 1984; Wilson and Keddy 1986). Clipping has been used to simulate both the removal of above-ground biomass by disturbance, and different levels of competition–by removal of neighbours. Disturbance and competition have pronounced effects on resprouting, and these effects should not be confused (Mueggler 1972).

Clipping a resprouting species encourages regrowth of many sprouts per genet during the first growing seasons after cutting, thus leading to the development of an even-aged ramet population. Self-thinning describes plant mortality due to competition in crowded even-aged stands (Yoda et al. 1963). Self-thinning has been studied at the population level in terms of the negative density-dependent relationship between mean plant biomass and density of the survivors (Westoby 1984). Our concern is whether this relationship may be applied to the different ramets (sprouts) that compose a single plant during resprouting after clipping. Several ecologists (Harper 1977; Hutchings 1979) suggest that thinning among ramets would only be expected to be observable over a rather narrow range of time

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depending on the degree and nature of physiological integration of ramets within a genet (Novoplansky et al. 1989). Nevertheless, a self-thinning model was applicable to shoots of coppicing *Castanea sativa* (Ford and Newbould 1970) and *Erica arborea* (Riba 1991), although these observations were made on chronosequences of stands of different regeneration age, not by following a population of ramets within a genet through time.

This study deals with the effect of removal of neighbours on the resprouting dynamics after clipping, and with the effect of competition by neighbouring vegetation at the genet and at the ramet level. Our main hypotheses are:

1. Removal of neighbours increases the resource availability at the plant level, and thus the resprouting vigour of target resprouting plants may be enhanced by sprout recruitment and above-ground biomass (Vilà et al. 1994).
2. Lonsdale and Watkinson (1982) found that tillers of *Lolium perenne* self-thinned at high densities; the same was found for *Phragmites australis* (Mook and Van der Toorn 1982). The presence of few dominant sprouts and the mortality of many small ones has been observed in resprouting species (Riba 1991, Giovannini et al. 1992), and this suggests that self-thinning does also occur in a population of sprouts within a stump.
3. Westoby (1984) pointed out that a low "site quality" involves a lower thinning line (reduced intercept but unchanged slope). Removal of neighbours provides better growing conditions, i.e. an increase in sprout recruitment as stated in (1), and therefore we predict that increased sprout density within the stump may generate higher inter-sprout competition; consequently, sprout mortality will be higher when neighbours are removed than when they are present. Sprouts of plants without neighbours may have a higher thinning line than sprouts of plants with neighbours.

Few studies have investigated the role of the presence or absence of neighbours in the dynamics of resprouting. In this paper we present a field experiment in which competition after clipping was reduced by removal of neighbours at different distances from a resprouting target plant in order to test our hypotheses.

Materials and methods

Species and study site

Erica multiflora (Ericaceae) is an evergreen shrub that typically occurs on basic soils of the western Mediterranean Basin, where it is a common component of coastal shrubland. *E. multiflora* produces abundant sprouts after aerial biomass removal, either 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). In the study area, plants attain less than 1 m in height.

The study site was located in the coastal shrubland Serra de les Comes (40° 53′ N, 0° 41′ E) at El Perelló (Catalonia, Spain) at an elevation of 300 m above sea level and 9 km from the sea. The soil is extremely stony and shallow, classified as *Lithic haploxeroll*. The climate is typically Mediterranean characterised by summer drought. Mean monthly temperature ranges from 4.5° C in January to 29° C in July. The mean annual temperature is 16° C. Mean annual precipitation is 591 mm, of which 45% occurs in the spring and autumn, mostly as thunderstorms. The area was burned by a wildfire in 1976. At present, the shrubland vegetation is dominated by *Rosmarinus officinalis*, *Quercus coccifera*, *E. multiflora* and *Ulex parviflorus*, which contribute 39, 14, 12 and 8%, respectively, of ground cover. The understorey is dominated by *Brachypodium retusum*, which covers 63% of the ground.

Experimental design

In July 1989, 60 *E. multiflora* individuals were randomly selected in an area of 2 ha; 20 plants of *E. multiflora* were randomly chosen for each of the following three competition treatments: (1) all neighbours within a 2-m radius of target plant were removed at ground level; (2) as in (1), but within a 1-m radius; (3) control: neighbourhood was not modified. The plots where all target plant neighbours within 2- and 1-m radius were removed were maintained in these conditions during the experiment by clipping regrowing neighbour vegetation every 2 months.

The sprouts of the target *E. multiflora* were clipped at ground level and the area of each stump was estimated, assuming that the stump surface was elliptical, by measuring the longest diameter and the diameter perpendicular to it. Each target plant was covered with a metallic mesh to prevent herbivory by rabbits and sheep.

Since a long-term study of shrub growth requires a non-destructive measure of biomass, the biomass of each sprout per target plant was estimated using a different allometric equation for each data sampling which predicted sprout dry biomass (Z) as a function of sprout length (X) measured as the height of the longest branch and of the number of branches per sprout (Y):

$\ln Z = A + B \ln X + C \ln Y$ ($0.824 < r^2 > 0.96$, $31 < n > 51$).

At the first sampling, these data were obtained measuring haphazardly selected sprouts collected from nearby plants subjected to clipping, but from July 1990, we decided to choose deliberately selected sprouts from nearby plants subjected to clipping to cover the entire existing range of sprout sizes.

In January 1990, July 1990 and January 1991 all the sprouts of each target plant were counted, and their length and the number of branches per plant were measured. In January 1992, above-ground biomass of target plants was harvested. Material was weighed after drying at 80° C for 96 h.

Sprout mortality within the stump between two consecutive sampling dates $t-1$ and t was estimated by the relative increment of sprouts per stump: $(r_t - r_{t-1})/r_{t-1}$, with r_t = number of sprouts per stump at time t and r_{t-1} = number of sprouts per stump at time $t-1$. The self-thinning trajectory of sprouts was determined for each competition treatment by plotting the relationship between the log of mean sprout biomass and the log of the number of living sprouts per stump area on the four sampling dates.

Statistical analysis

The effect of the competition treatment (0, 1 and 2-m clearing radius) on the total number and total biomass of sprouts from each stump of *E. multiflora* 6, 12, 18 and 30 months after treatment was statistically analysed by an ANCOVA which included competition treatment as the main factor and the area of the stump as the covariate. Density of sprouts (number of sprouts per stump unit area) and relative increment of sprouts per stump was statistically analyzed by an ANOVA. To normalize errors, the number of sprouts and the area of the stump were square-root transformed, while all other variables were log-transformed. Pairwise comparisons among the three levels of competition treatment were performed by a Scheffé F-test. Growth curves were tested for goodness of fit of regression lines by checking the assumptions made in a linear-regression model (Rosner 1995).

Results

All target plants produced a great number of sprouts in the first growing season after clipping. Individuals without neighbours had more sprout recruitment than the controls over all the periods sampled (Fig. 1). However, there were no statistically significant differences in sprout number between target plants without neighbours within 1 and 2-m radius (Scheffé test, $P < 0.05$).

The competition treatment had a non-significant effect on the density of sprouts per stump 6 and 12 months after treatment (Fig. 2). But 18 months after treatment, removal of neighbours 1 m around target plants increased the density of sprouts per stump, while 30 months after treatment positive effects on the density of sprouts were observed in both the 1- and 2-m-radius treatments. Differences in the density of sprouts between target plants without neighbours within 1 and 2 m were non-significant (Scheffé test, $P < 0.05$).

Growth curves for *E. multiflora* genets under different competition treatments were linear and had different slopes (Fig. 3). Linear regression accounted for more than 90% of the variance in biomass over time for plants without neighbours in 1- and 2-m-radius treatments and controls. The slope of the regression for plants without neighbours (both 1- and 2-m-radius treatments) was steeper than for control plants. Competition effect on above-ground biomass per stump was not statistically significant until 18 months after treatment. Plants with neighbours had less sprout biomass than plants without neighbours in 1 and 2 m radius. There was no significant difference in sprout biomass between the two neighbour removal treatments (Scheffé test, $P > 0.05$).

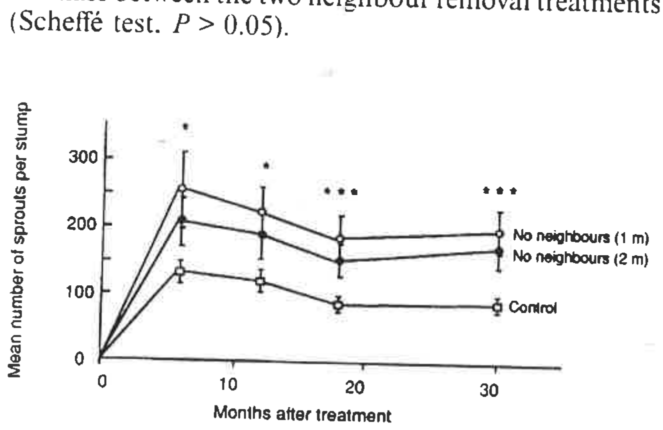

Fig. 1 Effect of competition treatment on the mean number of sprouts (±SE) per stump (n = 20) for *Erica multiflora*. *No neighbours (2 m)*: we clipped the vegetation at ground level within a 2-m radius from the target plant. *No neighbours (1 m)*: we clipped the vegetation at ground level within a 1-m radius from the target plant. *Control*: target plants surrounded by undisturbed local vegetation

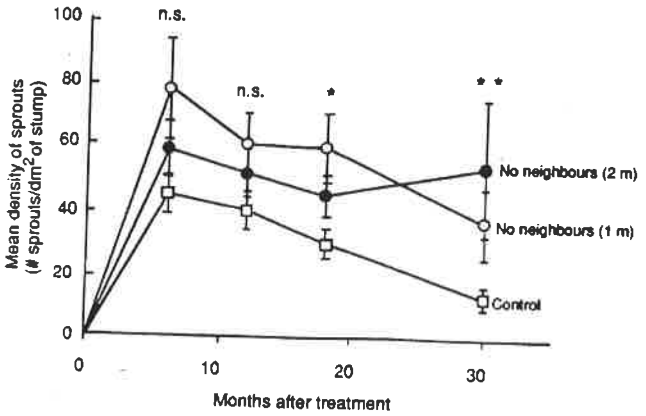

Fig. 2 Effect of competition treatment on the mean density of sprouts (±SE) per stump (n = 20) for *E. multiflora*, calculated as the number of sprouts per unit area of stump. See Fig. 1 for competition treatment description

There was a decrease in the relative increment of sprouts per stump from 6 months to 18 months after treatment. However, this increment was positive during the last resprouting interval measured (18–30 months) (Fig. 4). Competition treatment had a non-significant effect on the relative increment of sprouts per stump during the period sampled.

Visual fitting of the self-thinning trajectories of sprouts were different under different competition treatments (Fig. 5). Sprouts of the genets without neighbours followed the lowest thinning line (the intercept was reduced) until 18 months after clipping. At that moment a zero slope trajectory was caused by a sharp decline in sprout density (Fig. 2) and there was no accumulation of biomass (Fig. 3). Target plants without neighbours in a 1-m radius showed a self-thinning trajectory throughout the data sampling: a decrease in the sprout density in the stump, together with an increase in mean sprout biomass. Finally, target plants with neighbours removed in a 2-m radius self-thinned during an 18-month period following treatment, although they subsequently achieved a net increase in the density of sprouts per stump, together with an increase in mean sprout weight.

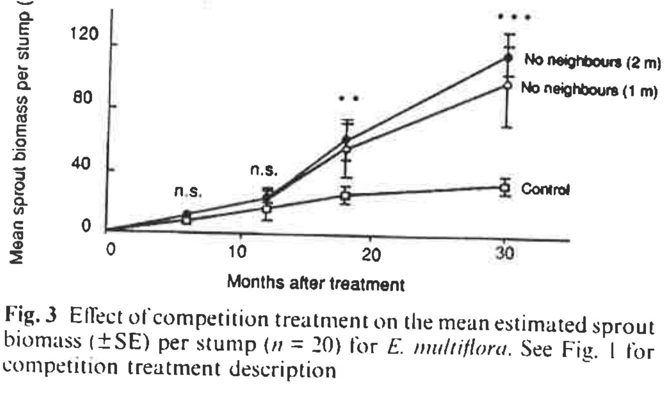

Fig. 3 Effect of competition treatment on the mean estimated sprout biomass (±SE) per stump (n = 20) for *E. multiflora*. See Fig. 1 for competition treatment description

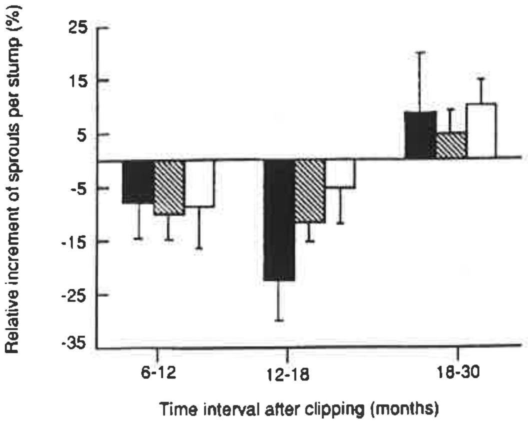

Fig. 4 Effect of competition treatment on the relative increment of sprouts (+SE) per stump ($n = 20$) for *E. multiflora*, calculated by the number of sprouts at time t minus the number of sprouts at time $t-1$ and divided by the number of sprouts at time t multiplied by 100. *Solid bars* no neighbours (2 m), *shaded bars* no neighbours (1 m), *open bars*: control. See Fig. 1 for competition treatment description

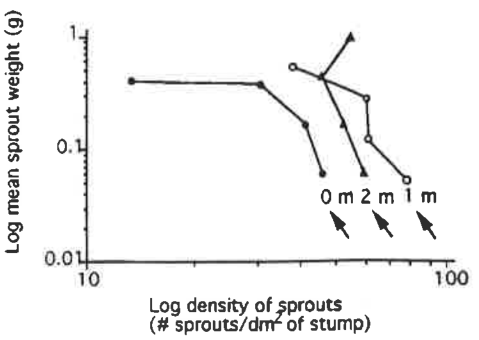

Fig. 5 Relationship between mean sprout weight (calculated by dividing the total sprout weight per stump by the number of living sprouts) and the sprout density (number of living sprouts per unit of stump area) for *E. multiflora* (log-log plot). *Arrows* show the starting point of the thinning trajectory 6 months after clipping for the three different treatments: control (*black circle*), no neighbours in a 1-m radius (*white circle*) and no neighbours in a 2-m radius (*black triangle*). Each point represents a consecutive data sampling and the mean of 20 replicates. See Fig. 1 for a more detailed competition treatment description

Discussion

The presence of neighbours greatly reduced sprout vigour after clipping, by decreasing the number of sprouts and the final above-ground biomass. Growth of biomass was linear in plants with and without neighbours during the 2 years after clipping. Nevertheless, the growth of plants with neighbours was very slow. The assumption that growth in plants is sigmoid, with an early exponential phase, a linear phase and a final levelling-off phase (Hunt 1982), would imply that, during the period studied, *E. multiflora* plants are in the middle phase of the growth curve where the function is approximately linear, as has also been found in a competing population of *Impatiens pallida* (Thomas and Weiner 1989).

Plants react not to the density but rather to the proximity of neighbours (Harper 1977). The fact that there was no difference in resprouting vigour between the two treatments with neighbours removed to different distances indicates that *E. multiflora* competes only with its closest neighbours and not with those slightly further away. Fowler (1984) also found that individuals of *Linum grandiflorum* var. *rubrum* compete with "first order" neighbours. The same trend was described for some herbaceous vegetation (McConnaughay and Bazzaz 1987). Our results suggest that only so much area can be used, and genets only interacted with near neighbours, as was demonstrated for even-aged greenhouse populations of *Lapsana communis* (Mithen et al. 1984).

Self-thinning of sprouts did occur during a short period of regrowth after clipping. However, whereas the relative rate of sprout increment decreased during the early period of regeneration, it increased 18 months after clipping. This result suggests that although mortality of sprouts occurs, the losses incurred are compensated by constant or episodic sprout recruitment. It has been observed that some Mediterranean woody resprouting species produce sprouts not only immediately after aerial biomass removal but also more or less continuously in the absence of major disturbance (Malanson and Westman 1985; Mesléard and Lepart 1989). This recruitment of new sprouts may be a consequence of mortality of the previous sprouts, which would modify microsite environment by an increase in stump space, a decrease of shading, and changes in the hormone content of sprouts which would stimulate bud development. The presence of different cohorts of sprouts in a single stump will ensure genet survival after main-shoot damage by fire, trampling, or herbivory, and by climate-related factors, such as drought or cold and during fire-free intervals. Continual basal sprouting might be more associated with a growth form than with major disturbances (Mesléard and Lepart 1989).

While the relative increase in sprouts during the last period sampled occurred in all competition treatments, only when neighbours were eliminated in a 2-m radius did we observe a net increase in sprout density in the stump. These target plants achieved an increase in the biomass through the multiplication of sprouts, as well as by an increase in mean sprout weight. This trend is represented by the interruption of the self-thinning trajectory, which then takes the opposite direction. Continuous or episodic flux recruitment of new sprouts that accompained sprout mortality might mask the self-thinning trajectory.

We predicted that competition would modify the self-thinning trajectory of sprouts within the genet by decreasing sprout crowding. In the experiment reported here, the self-thinning line of target plants with neighbours was lower in the 1st year after clipping. Moreover, the subsequent decrease in sprout density was not followed by an increase in mean sprout weight, which suggests that the environmental conditions created by neighbours reduced the biomass which can be supported by a given volume of space. Sprouts are interconnected within the stump and may exchange resources (Marshall 1990). In our study, it is likely that during density-dependent mortality, sprouts that survive may share assimilates, thereby reducing differences in sprout growth.

In the intermediate competition treatment, target plants without neighbours within a 1-m radius show a constant self-thinning line supporting an allometric increase in mean sprout biomass as the density of sprouts decreases at the stump. We have observed that *E. multiflora* genets expand by multiplication of ramets, as well as by increasing the size of those previously existing. From this perspective, it would be of great interest to know the relationship between the self-thinning of sprouts and the frequency distribution of ramet sizes. For example, does size distribution of ramets become more uniform and less variable as self-thinning progresses, as has been observed in some genet populations (Weiner and Whigham 1988)? It is possible that ramet populations follow the same trend as genet populations if we assume that sprouts compete for light or that apical dominance takes place (Vilà et al. 1994). It may be reasonable to expect that both shading and apical dominance lead to the mortality of small sprouts. Further studies should include analyses such as the changes in ramet size variability which occur with self-thinning, and the effect of inter-genet competition on this relationship.

As shown, our results confirm that the degree of ramet autonomy in a single genet might not be fixed, but might change according to environmental conditions created by the presence or absence of neighbours. Physiological independence, which may induce some sort of ramet competition (e.g. apical dominance), and ramet integration, which may facilitate the sharing of resources, could occur in different ramets within a single genet, as has been shown among different parts of the clonal plant *Glechoma hederacea* (Price and Hutchings 1992). Also, physiological and anatomical organization of ramets may change during the development of the plant according to environmental conditions, e.g. defoliation (Price and Hutchings 1992) or light (Hartnett and Bazzaz 1983).

In the experiment reported here, we have observed that individual plant response to clipping is modified by the removal of natural surrounding vegetation, even though all target plants had the same regeneration age. Clipping of neighbours increased the resprouting vigour of target plants. Our results suggest that competition among sprouts is modified by competition among genets. Competition by intact neighbourhood lowered the self-thinning line of sprouts due to a decline in the density of sprouts and a non-accumulation of sprout biomass. This result may support the "altered speed" model proposed by Morris and Myerscough (1984), which suggests that plant development is slow when neighbours are present and does not "catch up" with the non-competing genets. In the opposite situation, sprouts of target plants with no near neighbours show a disruption of the self-thinning trajectory because the biomass growth of the genet is a result of both, a net increase in the density of sprouts per stump and their individual growth.

Acknowledgements We gratefully acknowledge the constructive criticism of J. Canadell and M. Riba, J. Weiner who provided helpful comments on experimental design and data analyses, and F. Lloret and two anonymous referees reviewed earlier versions of the manuscript. We are grateful to the Departament d'Agricultura, de Ramaderia i de Pesca de la Generalitat de Catalunya for permission to use the study site. Financial support was provided by the Comisión Interministerial de Ciencia y Tecnologia (FOR 91-1054 project), and the Comissió Interdepartamental de Recerca i Innovació Tecnològica (Grants for Young Researchers).

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