

Effect of root competition and shading on resprouting dynamics of *Erica multiflora* L.

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Abstract. Resprouting from underground structures is one of the main regeneration strategies of Mediterranean shrubs after aerial biomass disturbance such as fire or clear-cutting to reduce fire risk. In order to study the effect of root competition and shading (simulated shoot competition) on *Erica multiflora*, growth, morphology, flowering performance and sprout size variability during resprouting, a factorial field experiment was conducted in which neighbours around target plants were eliminated and plants were shaded with mesh for two years. Root competition reduced sprout recruitment and sprout density (number of sprouts per unit stump area) more strongly than did shading. The negative effect of root competition on sprout biomass was constant with time, while the reduction due to shading increased with time. There was an interaction between root competition and shading on the biomass of sprouts 22 months after treatment: genets without root competition and shading were four times larger than in any other treatment. Both shading and root competition also decreased percentage branching but did not modify maximum sprout height. Only shading decreased the leaf/shoot biomass ratio and the percentage of flowering genets. One year after resprouting, root competition counteracted the effect of shading on inducing sprout biomass variability within the genet because it decreased sprout density. 22 months after treatment, sprout biomass variability was not affected by any main effect. The results suggest that competition among sprouts within the genet is asymmetric. However, shading by genet neighbours may not always increase sprout biomass variability if root competition is also severe.

Keywords: Ericoid; Plasticity; Removal experiment; Sprout size variability.

Introduction

Ecological experiments have shown that plant competition affects several components of plant performance differently over time and between environments (Connell 1983; Schoener 1983; Goldberg & Barton 1992). However, in natural communities it is difficult to separate the different resources for which a plant competes (Goldberg 1990). For plants, one of the negative effects of the presence of neighbours is simultaneous

competition for soil resources (water and nutrients) and for light. The first experiment that separated and combined the effect of root and shoot competition on plant growth was conducted with grasses in the greenhouse (Donald 1958) and suggested that both above and below-ground competition were operative.

Most studies on plant competition have shown that root competition reduces plant growth more than does shoot competition (see review by Wilson 1988). Shoot competition tends to have a more severe effect on plant biomass with time, while the effect of root competition is constant (Aspinall 1960; Martin & Field 1984), though other experiments have contradicted this trend (e.g. Remison & Snaydon 1980). Usually, plants subjected to both root and shoot competition are disproportionately smaller than expected on the basis of an additive effect of shoot and root competition (but see Martin & Field 1984). There are few studies that have analyzed the effect of root and shoot competition to see if these trends occur under field conditions. Christy (1986) found that trenching increased the productivity of *Tsuga heterophylla* but the creation of gaps did not. Likewise, Riegel et al. (1992) found that the understorey of a *Pinus ponderosa* forest was limited by below-ground competition but not by light. More studies carried out in field conditions are needed to make generalizations about the effect of above vs. below-ground competition in natural plant populations.

Competition also influences plant size variability. Competition for light is said to be asymmetric because a large plant can shade and reduce the growth of a small plant but not the other way round (Weiner 1990). Studies have shown that under controlled conditions and in the absence of density-dependent mortality, shoot competition increases plant size variability (Schmitt et al. 1986; Weiner 1986). In contrast, root competition is referred to as asymmetric because even if it is much more severe than light competition, it reduces growth of both small and large plants and it does not increase plant size variability (Weiner 1990). Competition also influences plant morphology (Tang et al. 1990; Kembell et al. 1992). Weiner et al. (1990) demonstrated that

individuals of crowded populations of *Impatiens pallida* had fewer secondary branches, were taller than individuals from uncrowded populations and competition for light increased plant size variability. These morphological changes would reduce size variability among competing even-aged plants (Geber 1989).

Most plants are modular (clonal plants), composed of a number of similar parts or ramets that are potentially independent of each other. The population dynamics of these plant species is often easier to understand from the analysis at the ramet level rather than at the genet level because plant survival, growth and reproduction are mainly determined by the addition and growth of ramets (Hartnett & Bazzaz 1985a; de Kroon & van Groenendael 1990; Herben et al. 1994). This is the case with tillers from grasses or shoots from woody shrubs from which genetic individuals can hardly be recognized in the field. There is little information on the effects of environmental heterogeneity on clonal growth, specially on the interactions between hierarchical levels (genet and ramet) (Herben et al. 1994), e.g. how genet neighbours can effect both the structure of genets and ramets. Few studies have addressed the question of whether ramets within genets responded to shoot and root competition in the same way as genets within a population.

Resprouting ericoid species are multistemmed evergreen shrubs which resprout after aerial biomass removal (Le Maitre et al. 1992) from a woody swollen structure at the stem base known as a lignotuber or burl. Ericoids are good models for the study of the effects of shoot and root competition among ramets within the genet, because each sprout is a modular unit that recruits, grows, flowers and dies. Thus, colonization of the habitat, survival and fitness of the genet depends upon seedling recruitment as well as the behaviour of ramets. Inter-ramet competition appears to be asymmetric in the ericoid *Arbutus unedo* because sprout-size variability increased with sprout density (Vilà et al. 1994). Similar patterns have been observed in clonal plants (de Kroon et al. 1992; Hara et al. 1993), although it may depend on the degree of physiological integration among ramets, as well as the nature of the competition with neighbouring genets.

Some Mediterranean resprouting shrubs are long-lived with low seedling recruitment. After a disturbance such as fire, the maintenance of the population depends largely on the number of basal dormant buds and their potential for developing into sprouts. Fire reduces biomass of neighbours, and thus temporally reduces competition with the established vegetation (Vilà & Terradas 1995a). However, there is no information about the extent to which differences in the amount of shoot and root competition are important during the regeneration

stage after disturbance. A wildfire does not burn a site homogeneously. Instead, it creates patches of dead (burned or dried) and live aerial biomass, depending on the nature of the vegetation and the characteristics of the fire. In this scenario, resprouting plants may be surrounded by neighbours from different species that compete for a variety of resources. Competition may be for different resources in different neighbourhood assemblages. In the Mediterranean shrubland studied, clear-cutting and herbivory management practices may also create heterogeneous neighbourhoods and thus change the intensity of shoot and root competition.

In this paper I assess the importance of shoot and root competition on resprouting, flowering, morphology and sprout size variability in the Mediterranean ericoid shrub *Erica multiflora* by neighbour removal and simulating shoot competition by shading. The questions addressed in the present study are: 1. Does the importance of root competition and shading change with time? 2. Is there an interaction between root competition and shading? 3. Does shading change sprout morphology? 4. Does root competition and shading modify sprout size variability as predicted by the symmetric and asymmetric competition models?

Material and Methods

Species and study site

Erica multiflora is an evergreen sclerophyllous shrub which typically occurs on high pH soils in the western Mediterranean Basin, where it is a common component of the coastal shrubland. *E. multiflora* produces abundant sprouts after aerial biomass removal by disturbance from a small lignotuber or from shallow roots. Vegetative growth occurs twice a year: in spring, from March to June, and in autumn, from September to November. Seedling recruitment is fairly low (Lloret unpubl.). *E. multiflora* can grow up to 3 m in height, but in the study area plants rarely attain more than 1 m. Flower buds appear in August-September and flowering occurs from mid-September to mid-December. After disturbance (e.g. fire) flowering occurs two years later.

The study site is a coastal shrubland located on the Serra de les Comes (40° 53' N, 0° 41' E) in El Perelló (Catalonia, Spain) at an elevation of 300 m a.s.l. and 16 km from the Mediterranean coast. The soil is very stony and shallow, classified as Lithic haploxeroll (pers. obs.). The climate is mediterranean; at the nearest weather station (El Perelló), 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 % is due to spring and autumn

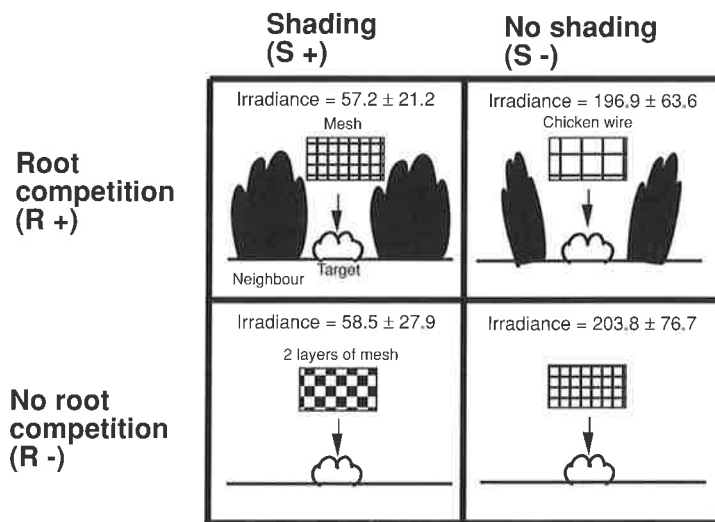


Fig. 1. Schematic representation of competition treatments. Upper values indicate irradiance (mean \pm s.e.) of the photosynthetic active radiation for each treatment. These values measured at the lignotuber surface at midday on six clear, sunny days are given in microeinsteins/m²/s. Note that lignotuber surfaces were covered in different ways in order to achieve consistent treatments within the same shading level (see text for a detailed explanation of competition treatments).

storms. The area was burned by a wildfire in 1976. At the time of the study, the vegetation was dominated by *Brachypodium retusum*, *E. multiflora*, *Quercus coccifera*, *Rosmarinus officinalis* and *Ulex parviflorus*. *B. retusum*, *E. multiflora*, and *Q. coccifera* accounted for 79 %, 40 % and 37 % of the total vegetative cover, respectively.

Experimental design

In December 1990, 12 groups of four individuals of *E. multiflora* separated by at least 4 m were chosen at random in an area of 2500 m². Each selected plant was clipped at ground level and the removed sprout biomass was weighed after drying at 80 °C for 96 hours. The two main perpendicular diameters of the lignotuber surface (stump) were measured and the lignotuber area was calculated assuming that it was elliptical in form.

A two factor randomized complete block design was performed. Each of the four individuals per group (block hereafter) were assigned at random to one of the following competition treatments (Fig. 1):

1. Root competition and shading (R+S+)

Vegetation around the target plant was not removed. Target plants were covered by a cylinder of green plastic mesh (net of 1.5 mm diameter) that reduced irradiance by 75 % on the lignotuber surface at midday of a sunny and clear day. Mesh cages were fastened to the soil surface using four steel pins. This reduction in light availability closely approximated natural light reduction by canopies at the ground level at midday on a clear, sunny day (57.2 ± 21.1 microeinstein m⁻² s⁻¹) (see Fig. 1).

2. Root competition (R+S-)

Neighbours of the target plant were tied back using twine to reduce shading by neighbours to target plants without modifying root competition. Irradiance value for this treatment was 196.9 ± 63.6 microeinstein m⁻² s⁻¹. I assumed that target plants were surrounded by neighbour roots after trenching around similar nearby *E. multiflora* individuals and observing that the arrangement of roots was highly intermingled. The target plant was covered by a cylinder of chicken wire mesh in order to prevent herbivory.

3. Shading (R-S+)

All neighbours within a 1.5 m radius around the target plant were removed by clipping. It was assumed that this distance was sufficient to decrease competition by neighbours (Vilà & Terradas 1995c). The potential effect of neighbours that resprouted was mitigated by manual clipping the regenerated vegetation every two months. Trenching would have been impracticable in this study site because (1) the soil was very shallow and stony, and (2) trenching would have injured the root system of the target plant. Target plants were covered by two layers of green plastic mesh to achieve the same light reduction level as in (R+S+) treatment (58.5 ± 27.9 microeinstein m⁻² s⁻¹). This way, both shading treatments were constant despite different root competition treatments and could statistically be considered to belong to the same treatment level.

4. No competition (R-S-)

All neighbours in a 1.5 m radius around the target plant were removed by clipping. As in (3), the potential effect of neighbours that resprouted was mitigated by manual clipping the regenerated vegetation every two

months. Target plants were covered by a cylinder of green plastic mesh in order to produce the same sunlight incidence on the stump surface as in (R+S-) treatment, that is 203.8 ± 76.7 microeinsteins $m^{-2} s^{-1}$. In this way, both unshaded treatments were constant despite different root competition treatments and could statistically be considered to belong to the same treatment level.

Removal of vegetation is the most common neighbour manipulation approach to the study of species interactions in the field (Aarssen & Epp 1990). Removal of above-ground neighbour vegetation has the advantage, in comparison with trenching or introductions of vegetation, of not disturbing the soil; but the disadvantage is that it does not remove neighbour roots and hence, below-ground fragmentation by root occupation may still lead to reduced plant growth (McConnaughay & Bazzaz 1992). Fonteyn & Mahall (1978) used this method and found that target plants of *Ambrosia dumosa* and *Larrea tridentata* without neighbours had higher water potentials than when neighbours were present, indicating that removal of neighbours increased water availability. In the present shrubland, soil P-content in plots without neighbours was also higher after two years than when there were neighbours present, suggesting that elimination of neighbours increased soil P-availability (Vilà & Terradas 1995b).

The shading treatment used in this experiment tried to simulate shading at the ground level due to shrub and grass canopies. Irradiance measurements were checked at midday during six sunny, clear days at two months intervals following treatments using a sunfleck integrating ceptometer (Li-Cor® Decagon Devices Inc.) set at the lignotuber surface. Mean irradiance values for each of the four treatments are presented in Fig. 1.

The period of treatment covered four growing seasons – two springs and two autumns. In January and November 1992, the number of sprouts per stump and the number of branches per sprout were counted. The length of each sprout was also measured as the distance from the stump surface to the top of each sprout. In November 1992, above-ground biomass was harvested and vegetative biomass was separated from flowers. Material was weighed after drying at 80 °C for 96 h.

The biomass of each sprout was estimated using an allometric equation which predicted sprout dry biomass Z as a function of sprout length X measured as the length of the longest branch per sprout and number of branches per sprout Y :

$$\ln Z = -5.21 + 1.39 \ln X + 0.37 \ln Y \quad (1)$$

($r^2 = 0.92$, $n = 60$ for January 1992)

$$\ln Z = -5.10 + 1.38 \ln X + 0.43 \ln Y \quad (2)$$

($r^2 = 0.93$, $n = 30$ for November 1992)

Data for these allometric equations were obtained measuring randomly selected sprouts collected from adjacent *E. multiflora* plants subjected to clipping to cover the entire existing range of sprout sizes as in the experiment. Allometric relationships and shoot basal area can change with crowding (Weiner & Thomas 1992). However, because of the small diameter of sprouts (> 5 mm) and their crowded arrangement on the stump; measurements with a caliper would have been very tedious, with chances of damaging the sprouts.

Statistical analyses

The effect of the competition treatment on sprout number, biomass and density (number of sprouts per unit of stump area) 12 and 22 months after treatment was analyzed with a two-factor analysis of covariance (ANCOVA) which included the biomass of the plant before clipping as the covariate. This covariate explained more of the variance in several sprout parameters than stump area did (Lloret & López-Soria unpubl.). Maximum height (length of the longest sprout per stump) and number of branched sprouts 12 and 22 months after treatment, and leaf/shoot biomass ratio at the end of the experiment were also evaluated by an ANCOVA which included the density of sprouts as the covariate. Before proceeding with ANCOVA, the assumption that separate regression slopes of the groups did not differ was previously tested. To improve homogeneity of variances, the sprout biomass of the plant before clipping, maximum sprout height per stump, leaf/shoot biomass ratio and number of branched sprouts per stump were \log_{10} transformed; all other variables were square-root transformed. Percentage of flowering plants among treatments was compared by a G-test.

The size variability of the sprout population was calculated as the coefficient of variation (CV) for the estimated biomass of sprouts within each stump. The effect of root competition and shading on the CV of the estimated biomass of sprouts within each stump was analyzed with an ANOVA.

Results

Mean above-ground biomass of target plants before the experiment was 115.11 g and only 10.53 and 17.86 g 12 and 22 months after the experiment. The above-ground biomass of the target plant before treatment had a positive significant effect on the biomass of sprouts per stump 12 and 22 months after treatment and the number and density of sprouts per stump 22 months after treatment (Table 1).

12 months after treatment, target plants with root competition had on average 43 sprouts per stump while target plants without root competition had 107 (Fig. 2). This increase in number of sprouts in target plants without root competition doubled sprout biomass per stump. One year after treatment, shading also reduced the biomass of the sprouts per stump without decreasing the number of sprouts (68 sprouts, 8.96 g in shaded stumps; 82 sprouts, 12.1 g in unshaded stumps). The interaction between root competition and shading was significant on the sprout biomass per stump 22 months after treatment (Table 1): biomass of sprouts per stump was four times greater in unshaded target plants without competition than in any other competition treatment (Tukey-test, $p < 0.001$) (Fig. 2). At that time shading decreased the number of sprouts per stump (56 in shaded stumps, 72 in unshaded stumps). Root competition also reduced significantly the number of sprouts per stump (38 with root competition, 90 with no root competition). Root competition also reduced the number of sprouts per stump unit area by a factor two. Shading did not change sprout density at any time (Table 1; Fig. 2). In summary, the relative importance of the negative effect of shading on plant growth increased with time: it accounted for 7% of the variation in sprout biomass 12 months after treatment and for 26% after 22 months. However, the effect of root competition was fairly constant with time: it explained 19% and 16% of the variation in sprout biomass 12 and 22 months after treatment respectively.

Shading decreased the percentage of flowering target plants (G -test = 9.10; $p = 0.004$). Only 4.2% of the shaded target plants flowered as compared to 37.5% of the unshaded target plants. Root competition did not have a significant effect on flowering (G -test = 0.51; $p = 0.48$).

Neither root competition nor shading had a significant effect on maximum sprout height per stump (Table 2). 22 months after the treatment, this parameter was density-dependent ($F_{1,30} = 0.75$; $p = 0.01$). At that time plants were in average 32.10 cm in height. 20% of the sprouts were branched 12 months after treatment and branching increased from 20 to 45% 22 months after treatment. Shading decreased the number of branched sprouts per stump from 26% to 14% 12 months after treatment ($F_{1,31} = 11.76$; $p = 0.001$) and from 51% to 38% 22 months after treatment ($F_{1,31} = 5.47$; $p = 0.03$). Root competition had a significant negative effect on branching only 22 months after treatment (37% with root competition, 52% with no root competition) ($F_{1,31} = 7.01$; $p = 0.013$). The density of sprouts increased the number of branched sprouts per stump 22 months after treatment ($F_{1,31} = 9.14$; $p = 0.005$). Shading decreased leaf/shoot biomass ratio 22 months after treatment from 1.12 to 1.44 ($F_{1,31} = 15.36$; $p = 0.0001$). Root competition had a nonsignificant effect on this parameter ($F_{1,31} = 2.31$; $p = 0.14$) (Table 2).

The main effects of root competition and shading on the coefficient of variation (CV) of sprout biomass within a stump were nonsignificant. However, the interaction between root competition and shading was significant 12 months after treatment ($F_{1,32} = 3.36$; $p = 0.07$): shading increased the CV of sprout biomass only in the target plants without root competition (Fig. 3). 22 months after treatment, neither root competition nor shading had a significant effect on the CV of sprout biomass. At that time, in plants with root competition the increase in density of sprouts per unit area of stump increased sprout biomass variability within the stump ($r^2 = 0.35$, $p < 0.0001$) (Fig. 4). However, the relationship was not significant for plants without root competition.

Table 1. Analysis of covariance of the effect of root competition and shading on (a) number of sprouts per stump, (b) density of sprouts and (c) biomass of sprouts per stump in *Erica multiflora*. The covariate, sprout biomass of the plant before clipping, was log-transformed and the dependent variables were square root transformed to normalize errors; m0 = months; SS = sum of squares. Significance levels: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns = non significant. See text for a detailed explanation of treatments.

Source	DF	Number of sprouts		Density of sprouts		Biomass of sprouts	
		12 mo SS	22 mo SS	12 mo SS	22 mo SS	12 mo SS	22 mo SS
Block	11	42.65 ns	85.37 ns	48.38 ns	72.84 ns	11.44 ns	11.54 ns
Root competition (R)	1	138.02 ***	71.96 ***	90.90 ***	38.61 *	15.28 ***	31.88 ***
Shading (S)	1	15.28 ns	34.41 *	5.92 ns	15.73 ns	5.58 *	53.65 ***
S × R	1	8.58 ns	24.01 ns	2.65 ns	10.64 ns	1.29 ns	24.45 **
Plant biomass	1	25.77 ns	53.20 *	14.05 ns	32.02 *	7.55 *	10.40 *
Residual	32	205.04	238.64	167.46	187.21	37.89	71.00

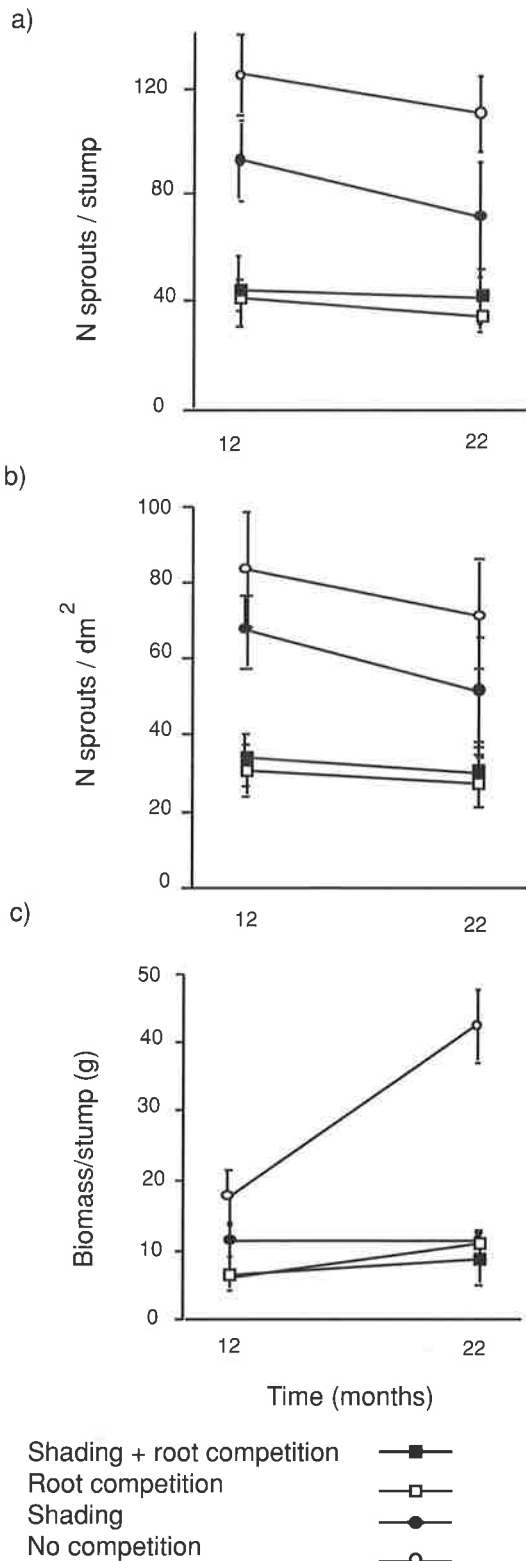


Fig. 2. Number of sprouts per stump (a), density of sprouts (b), biomass of sprouts per stump (c) (\pm S.E.) 12 and 22 months after treatment ($n = 12$). (See text for a detailed explanation of treatments and data analyses.)

Table 2. Effect of shading and root competition on the morphology of *Erica multiflora* (\pm S.E.). Values followed by different lower-case letters are significantly different within one period.

Treatment	Maximum sprout height (mm)	
	12 months	22 months
Shading + root competition	16.98 \pm 1.68 a	30.12 \pm 3.90 a
Root competition	19.91 \pm 1.99 a	28.75 \pm 3.39 a
Shading	19.54 \pm 1.25 a	33.04 \pm 3.12 a
No competition	21.86 \pm 2.22 a	36.51 \pm 2.39 a

Treatment	Branched sprouts (%)	
	12 months	22 months
Shading + root competition	14 \pm 4 a	29 \pm 6 a
Root competition	24 \pm 4 b	46 \pm 5 b
Shading	14 \pm 3 a	47 \pm 5 b
No competition	28 \pm 3 b	57 \pm 3 c

Treatment	Leaf/shoot biomass ratio
	22 months
Shading + root competition	1.01 \pm 0.05 a
Root competition	1.36 \pm 0.05 b
Shading	1.24 \pm 0.11 a
No competition	1.52 \pm 0.08 b

Discussion

Resprouting performance, flowering and sprout morphology

Although internal conditions of the plant determine sprout recruitment and growth (Taylor et al. 1982), environmental conditions such as competition can also influence resprouting dynamics in *E. multiflora*. Root competition and shading decreased resprouting vigour. Root competition was more important than shading in determining biomass of sprouts and the relative importance of the negative effect of shading increased with time. Other field experiments that have examined both root and shoot competition agree that root competition is generally more important than shoot competition in natural communities (Christy 1986; Riegel et al. 1992; Wilson 1993). The results of the present experiment suggest that short-term resprouting after aerial biomass removal (e.g. disturbance) is primarily dependent on underground resources needed to develop dormant buds in the lignotuber. Light may not be a limited resource until later, when some amount of above-ground biomass has re-established (Eagles 1972). In the present study, the interaction found showed that plants without root and shoot competition had the greatest sprout biomass. The interaction between root competition and shading suggests a positive feedback between a release from root and shoot competition. In reality, the interaction is

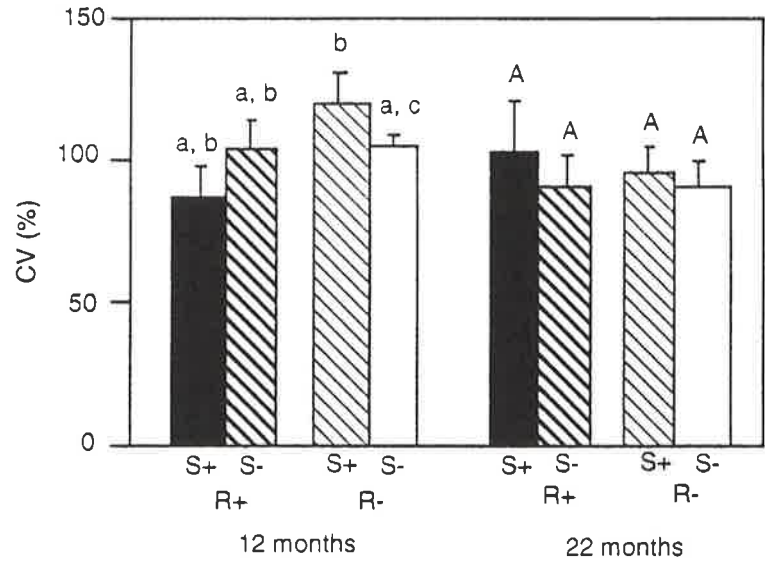


Fig. 3. Coefficient of variation (\pm s.e.) of the estimated biomass of individual sprouts per stump 12 and 22 months after treatment. Significant differences over all competition treatments within a sampling date are indicated by different lower-case letters (12 months) and upper-case letters (22 months). R+ = root competition, R- = no root competition, S+ = shading, S- = no shading. (See text for a detailed explanation of competition treatments.)

not just for two resources, but for two groups of resources: light has both a qualitative and a quantitative component (Dale & Causton 1992), and there are various relevant soil resources.

The importance of light for plant development is not only restricted to photosynthesis. Some life history processes can be regulated by light quality via the phytochrome (Mohr 1972; Schmitt & Wulff 1993). Shading reduced flowering of *E. multiflora*. This effect could be related to a decrease in the amount of light necessary for flowering induction and also to a decrease of the amount of available carbohydrates due to a decrease in photosynthetic rates. When there is a decrease of light incidence, carbohydrates may be mainly reallocated to vegetative growth at the expense of reproductive investment. The experiments of Pfitsch & Pearcy (1992) and Iason & Hester (1993) in perennial plants, also show

that a diminution in light decreased allocation of resources to reproductive structures.

Competition also modified sprout morphology. Root competition and shading decreased sprout branching but only shading reduced the leaf/stem ratio. Sprout height increased with sprout density. These results suggest that a decrease in light availability decreases resource allocation to photosynthetic tissues resulting in etiolated sprouts. A decrease in the red/far red light ratio that induces a shift in the phytochrome form could be one of the causes of growth plasticity (Kasperbauer 1971) by increasing the length of support structures and reducing leaf area (Skálová & Krahulec 1992). Ballaré et al. (1988) observed that *Datura ferox* seedlings subjected to shading increased resource allocation to shoots, which allowed leaf position in the upper layers of the canopy to intercept light.

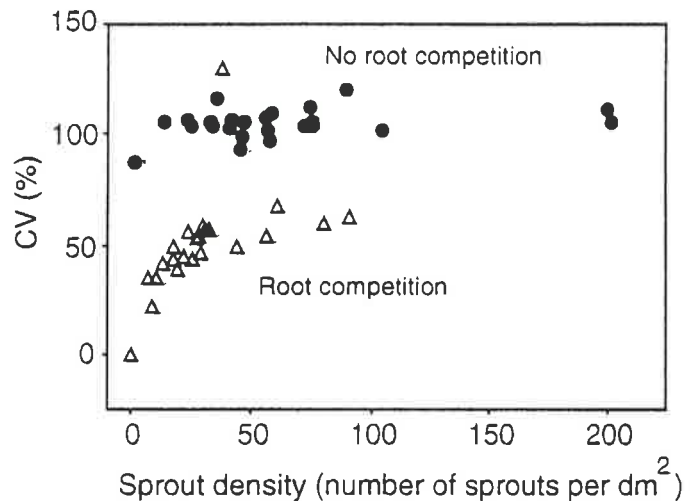


Fig. 4. Relationship between density of sprouts (number of sprouts per stump area) and coefficient of variation of the estimated biomass of sprouts 22 months after treatment in plants with and without root competition. (See text for a detailed explanation of competition treatments.)

Ramet size variability

Sprout size variability was little modified by competition with neighbouring plants. Shading increased sprout size variability only when there was no root competition. Root competition would suppress or compensate for the effect of competition for light because it reduced sprout density within the stump. Thus, the present study suggests that the response of a given sprout to neighbours is dependent upon the conditions of the interconnected sibling ramets (Hartnett & Bazzaz 1985b). Those environmental conditions that modify sprout density within the stump would be the ones that would indirectly determine sprout size and survival.

After 22 months of growth, shading did not increase sprout size variability. There are two plausible causes that may prevent an increase in size variability under shading. First, changes in morphology may prevent an increase in size variability (Geber 1989). Shading decreased sprout branching and leaf/stem ratio, which may result in a more diffuse canopy and consequently less light interception (Ballaré et al. 1988). In the present system model, the phenotypic plasticity of *E. multiflora* sprouts may prevent an increase of size variability within sprouts, even under shading conditions because sprouts are sparsely-branched and have few small leaves. This result would be supported by Ellison's (1989) findings that plant geometry determines self-thinning of natural plant populations.

Alternatively, sprouts are interconnected within the stump and may exchange resources. This explanation is supported by the lowered self-thinning trajectory line of sprouts because a decline of the density of sprouts was not followed by an increase in mean sprout biomass when competing with genet neighbours (Vilà & Terradas 1995c). As suggested by diffusion models, small shoots can be supported by larger-sized-shoots (Suzuki 1994). Surviving sprouts may share assimilates (Marshall 1990) reducing inter-ramet competition. The present results are consistent with the studies of Hartnett & Bazzaz (1983). The authors found that in periods of light limitation, ramets of *Solidago canadensis* shared assimilates enabling genets to integrate local heterogeneity in resource availability. Whether the reason that shading alone did not increase sprout size variability is due to morphological plasticity or physiological integration among sprouts remain tentative, and neither cause is mutually exclusive.

Competition among *E. multiflora* sprouts was asymmetric because an increase in sprout density increases sprout biomass variability, but a decrease in light availability did not always increase ramet size variability. Since sprouts within the stump are interconnected, apical dominance could determine sprout size variability buff-

ering environmental adversity and minimizing competition among its parts. The causes of size variability in ramet populations may be more complicated than in genet populations. The degree of ramet size asymmetry will depend on phylogenetic constraints that determine plant allometry and canopy structure (Suzuki 1994). Further studies should involve detailed manipulations at the ramet level in order to investigate which factors other than light availability may modify sprout size variability.

Concluding remarks

At the genet level, below-ground competition may have a long-lasting effect on plant resprouting, while above-ground competition might be more important when a certain aerial biomass is achieved and soil resources are not in short supply. Vilà & Terradas (1995c) confirmed that ramet self-thinning within a single genet of *E. multiflora* is not fixed, but it can be modified by competition with neighbours. In the present study, it has been shown that sprout size variability increases with sprout density. Thus, environmental factors that affect sprout density may indirectly regulate sprout size.

Proliferation and persistence of *E. multiflora* depend both on the development of sprouts and on the recruitment of seedlings. As the number of sprouts increases within a genet, the probability of genet persistence is increased. Fire may kill some *E. multiflora* genets. However, the integration of sprouts may allow genets to overcome small-scale heterogeneity such as the presence or absence of dead and alive neighbours after fire. Thus, genet decline does not imply population decline because sprout density within a genet may increase leading to population persistence even if genets are very old. Furthermore, all sprouts are capable of flowering, thus plant fitness may be dependent on the number and size of sprouts.

Acknowledgements. I thank M. Pamplona and A. Vicens for their assistance in the field work and for their company. J. Canadell, F. Lloret, J. Terradas, J. Weiner, J.B. Wilson and three anonymous reviewers provided helpful suggestions on experimental design, data analysis and critical discussion of earlier versions of the manuscript. The Agné family offered their land as a study site. Financial support was provided by the Comisión Interministerial de Ciencia y Tecnología (FOR 91-1054 project), and the Comissió Interdepartamental de Recerca i Innovació Tecnològica (Ajuda a Joves Investigadors AR89).

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Received 22 January 1996;
Revision received 7 Juni 1996;
Accepted 25 June 1996.