Journal of Vegetation Science 5: 145-152, 1994
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Effect of local competition on resprouting of *Arbutus unedo* after clipping

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Abstract. To evaluate the effects of local competition on the growth and size variability of sprouts following disturbance in a natural population of *Arbutus unedo* in Catalonia, plants were cut at the base and a neighbor removal experiment was performed. Removal of neighbors resulted in an increase in the number and biomass of sprouts at 2 and 7.5 months after clipping. Number and biomass of sprouts was also correlated with initial plant size (stump area). Inter-genet competition appeared to be symmetric, and acted to delay the onset of interference among sprouts within a genet. Size variability of sprouts on an individual was positively correlated with their density on the stump, supporting the hypothesis that competition among ramets (sprouts) within a genet is asymmetric. Reduced inter-genet competition from neighbor removal resulted in an increase in the number and biomass of sprouts growing from a stump. This resulted in an increase in the asymmetry of competition among sprouts, and therefore an increase in the size variability of these sprouts.

Keywords: Disturbance; Inter-genet competition; Plant competition; Removal experiment; Size variability.

Nomenclature: Tutin et al. (1964-1980).

Introduction

Competition plays a major role in the structure and dynamics of plant communities (e.g. Keddy 1989; Grace & Tilman 1990). Manipulation experiments are necessary to establish the effect and response to competition in natural conditions. Most manipulation studies have been done by removing the neighbors around a target plant (Aarssen & Epp 1990). While plant competition has been studied with removal experiments in several types of ecosystems, there has been relatively little study of the role of competition in mediterranean vegetation, despite the great amount of research on many other aspects of plant ecology in mediterranean ecosystems including ecophysiology, ecosystem dynamics and fire ecology (Keeley 1988).

In sclerophyllous mediterranean plant communities, most of the plant growth following a disturbance like clipping comes from resprouting, often from subterranean structures (James 1984). Sprouting is a function of (1) plant age (Hobbs & Gimingham 1984), (2) availability of carbohydrate reserves (Jones & Laude 1960), (3) environmental conditions (Laude et al. 1961; Riba 1991), and (4) the size and depth of the lignotuber (Auld 1990). Neighborhood interactions may also influence the extent of resprouting. In the present study we clipped plants of *Arbutus unedo* at ground level and studied influence of neighbors on the growth of sprouts.

There have been few studies of competition among woody plants during resprouting after a disturbance (e.g. Ford & Newbould 1970; Pýšek 1991; Riba 1991), and little is known about the effect of competition by neighboring plants on resprout dynamics (Vilà & Terradas 1992). When plants are clipped, certain responses may result from the physiological and morphological effects of the clipping itself (Jameson 1963), but competition from surrounding vegetation can have a pronounced effect on the outcome of studies involving clipping (Mueggl 1972). Competition can occur among ramets of a genet as well as among genets, and the former may be under the control of the plant to some degree (Hutchings 1979; Berntson & Weiner 1991; Sprugel et al. 1991). Consequently, a full understanding of plant competition will require a mechanistic integration of competition at these two levels. For example, how does competition among ramets of the same genet, which are to some degree physiologically integrated, differ from competition among genets?

Current thinking about local intra- and inter-genet competition lead us to several hypotheses concerning the influence of neighbors on sprout dynamics:

1. Plants without neighbors will be more vigorous and consequently will produce a greater number and a greater biomass of sprouts than plants with neighbors (Vilà & Terradas 1992), i.e., there is competition between resprouting plants.
2. Inter-genet competition is usually asymmetric (Weiner 1990). Therefore, genets with neighbors will show greater size variability than genets without neighbors.
3. Reduced inter-genet competition will increase the number and/or growth of sprouts on a genet. This increase in ramet biomass per unit stump area will increase competition among these ramets for some resources.

If this competition among ramets within a genet is symmetric (Weiner & Thomas 1986), it will reduce or have little effect on size inequality of ramets within a genet. Alternatively, if inter-ramet competition is asymmetric, size variability of ramets will be higher at higher ramet densities resulting from reduced inter-genet competition (de Kroon et al. 1992).

We designed a field manipulation experiment to test these hypotheses by comparing the resprouting behavior of a common mediterranean shrub with and without neighbors.

Material and Methods

Species and study site

Arbutus unedo is a perennial, semi-sclerophyllous shrub, commonly found in the Mediterranean Basin maquis on neutral and acidic soils. It shows resprouting behaviour after aerial biomass removal due to fire or clipping. The sprouts emerge from a ligneous structure that, due to its histological features, is considered a lignotuber (Abril 1988). Seedlings are observed infrequently in these communities.

The study site was located in the Collserola Mountains, about 6 km north of the city of Barcelona, northeast Spain, 41° 26' N, 2° 8' E). The study was performed at an altitude of 350 m a.s.l on a 20° north-facing slope. The soil is a Lithic Mollic Xerorthent (Ballbé et al. 1988). In this Mediterranean area, the main annual temperature is 14 °C and the annual rainfall is 614 mm (68-year averages from the Fabra Observatory located near the study site). The vegetation in the study area is a dense homogeneous maquis (mean shrub height 1.2 m; $n = 100$) dominated by *Erica arborea* with 5611 ind./ha and 40.7 % cover, and *Arbutus unedo* with 1666 ind./ha and 25 % cover. The area was burned by a wildfire 10 years before this study.

Experimental design

In April 1989 we selected two 50 m × 50 m blocks. To evaluate possible effects of site heterogeneity, one block was located at the top of a slope and the other at the bottom. The bottom block appeared to have somewhat deeper soil than the upper block. 20 *Arbutus unedo* individuals were chosen in each block. We clipped each plant at ground level. We then randomly chose 10 of these individuals per block and cleared all the vegetation within a 3-m radius around the subject plant. We removed all regrowth in the blocks (except the subject plant) monthly. The remaining 10 individuals per block were used as controls.

We measured the two major perpendicular diameters of the lignotuber stump and estimated the surface area assuming that the surface was elliptical. All the stumps were covered by a cylindrical mesh in order to prevent herbivory. In July 1989 and January 1990, we measured the height and basal diameter of sprouts on each plant at ground level.

The variables used to assess the growth of sprouts were sprout number and estimated sprout biomass at 2 and 7.5 months after treatment. The biomass of each sprout was estimated using a regression model that predicts above-ground dry mass of a sprout, W as a function of its height h and basal diameter d. The model was fit to data from 29 nearby randomly-selected sprouts after 7.5 months of regeneration.

$$\log W = 0.606 + 0.689 \log (hd^2) \quad r^2 = 0.95 \qquad (1)$$

Analyses

Normality of the data was judged by a Kolmogorov-Smirnov test and homogeneity of variances was tested by the F-max test. Because the distributions of sprout growth variables were positively skewed in almost all cases, the number, density (number of sprouts per unit stump area) and estimated biomass of sprouts were transformed. Square-root transformation was used because it gave the best approach to normality and homogeneity of variances.

Effects of competition were evaluated with two-factor covariance analysis (ANCOVA) which included block position and competition treatment as the categorical independent variables. The dependent variables were the number of sprouts on a stump, the estimated total biomass of the sprouts on a stump, and, to study the effect of competition on the size structure of populations of sprouts, the Coefficient of Variation (CV) of the estimated biomass of individual sprouts from each stump (Weiner 1988). The stump area was the covariable for the analysis of sprout growth, and the sprout density (number of sprouts per unit stump area) was the covariable for the analysis of size variability. Both covariables were square-root transformed before treatment. CV was also calculated for the estimated biomass of genets and CVs were compared using 1000 paired 'bootstrapped' estimates (Dixon et al. 1987).

Results

Number and biomass of sprouts

Stand position (block) or its interaction with competition had no statistically significant effect on any of the growth variables studied; therefore, the interaction block × competition variation was pooled in the analysis (Sokal & Rohlf 1969). Individuals with neighbors produced significantly fewer sprouts and less total biomass than individuals without neighbors (Fig. 1, Table 1). Competition from neighbors resulted in a 73.9 % decrease in sprout number and a 83.8 % decrease in sprout biomass after two months and a 29.5 % decrease in sprout number and a 55.9 % decrease in sprout biomass after 7.5 months (Fig. 1). At 2 months presence versus absence of neighbors accounts for more than the half the variation in sprout number and biomass. At 7.5 months competition has less of an effect, but it still accounts for 12.9 % of variance in sprout number and 26.8 % of the variance in estimated total biomass of sprouts.

Lignotuber stump area had a statistically significant positive effect on the number and estimated biomass of sprouts (Table 1; Fig. 2).

Table 1. Analysis of covariance of (a) number of sprouts and (b) estimated biomass of sprouts of *Arbutus unedo* on competition (factor) and stump area (covariate), at 2 and at 7.5 months after treatment. The dependent variables and the covariate are square-root transformed.

(a) Number of sprouts

	2 months		7.5 months	
	F	*p*	*F*	*p*
Block	0.126	0.725	0.0002	0.988
Competition	26.033	0.0001	6.792	0.015
Stump area	17.727	0.0003	14.745	0.0007

(b) Sprout biomass

	2 months		7.5 months	
	F	*p*	*F*	*p*
Block	0.399	0.533	0.565	0.459
Competition	29.932	0.0001	14.355	0.0008
Stump area	17.868	0.0002	33.613	0.0001

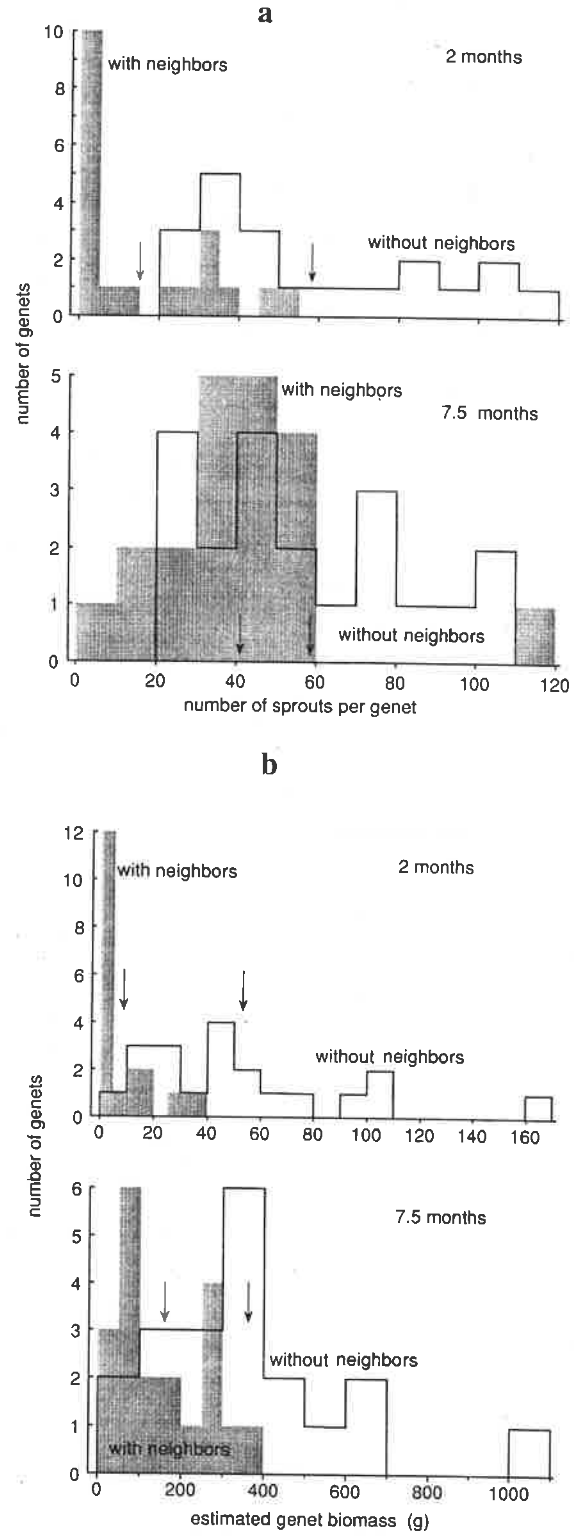


Fig. 1. Distributions of (a) number of sprouts per genet and (b) estimated sprout biomass per genet ($n = 20$) for the *Arbutus unedo* plants. Arrows represent means for plants with (left) and without (right) neighbors after 2 (above) and 7.5 (below) months treatment.

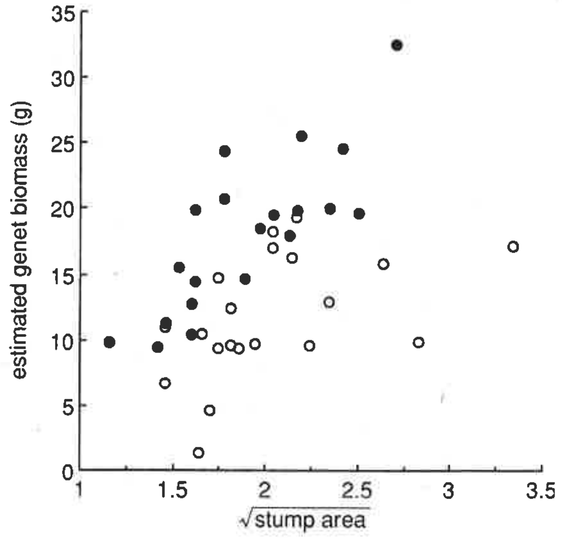


Fig. 2. Relationship between stump area (cm^2; square-root transformed) and estimated biomass (g) on *Arbutus unedo* plants with neighbors (o) and without neighbors (•), 2 months after treatment.

Table 2. Effect of competition (factor) and density of sprouts per unit stump area (covariate; square-root transformed) on size variability (Coefficient of Variation of estimated biomass) of sprouts from each stump of *Arbutus unedo* at 2 and 7.5 months after treatment.

	2 months		7.5 months	
	F	*p*	*F*	*p*
Block	0.536	0.470	8.134	0.008
Competition	3.217	0.084	2.478	0.124
Density of sprouts	0.160	0.692	24.986	0.0001

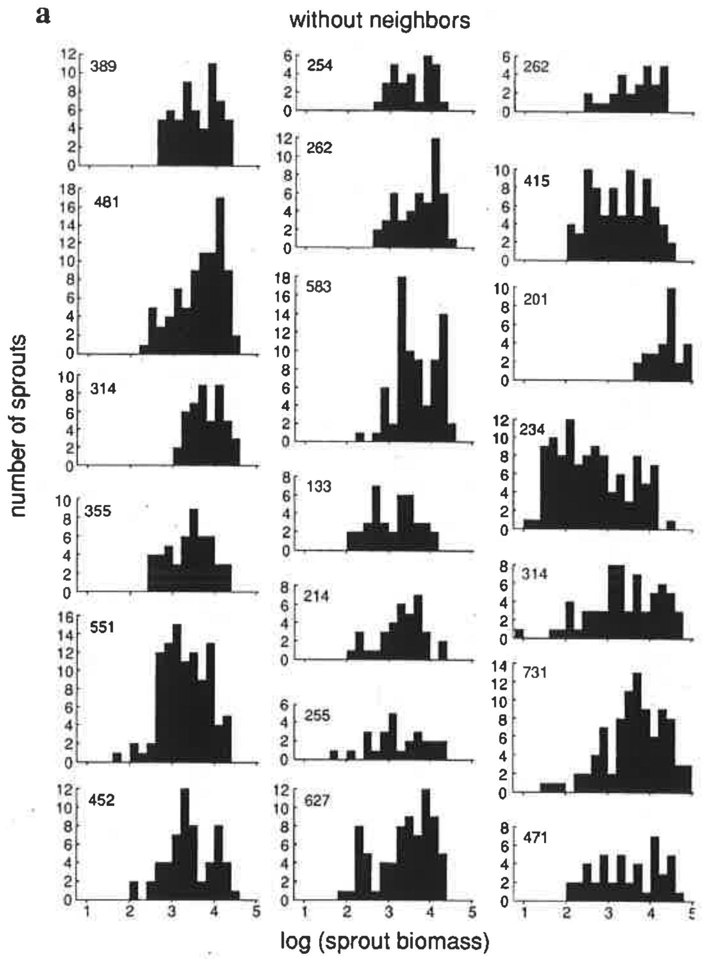


Fig. 3. Size distributions of estimated biomass (log-transformed) of sprouts from each stump (a) without neighbors and (b) (overleaf) with neighbors, 7.5 months after treatment. Stump area (cm^2) is in the upper left corner of each histogram.

Variability in sprout (ramet) and genet size

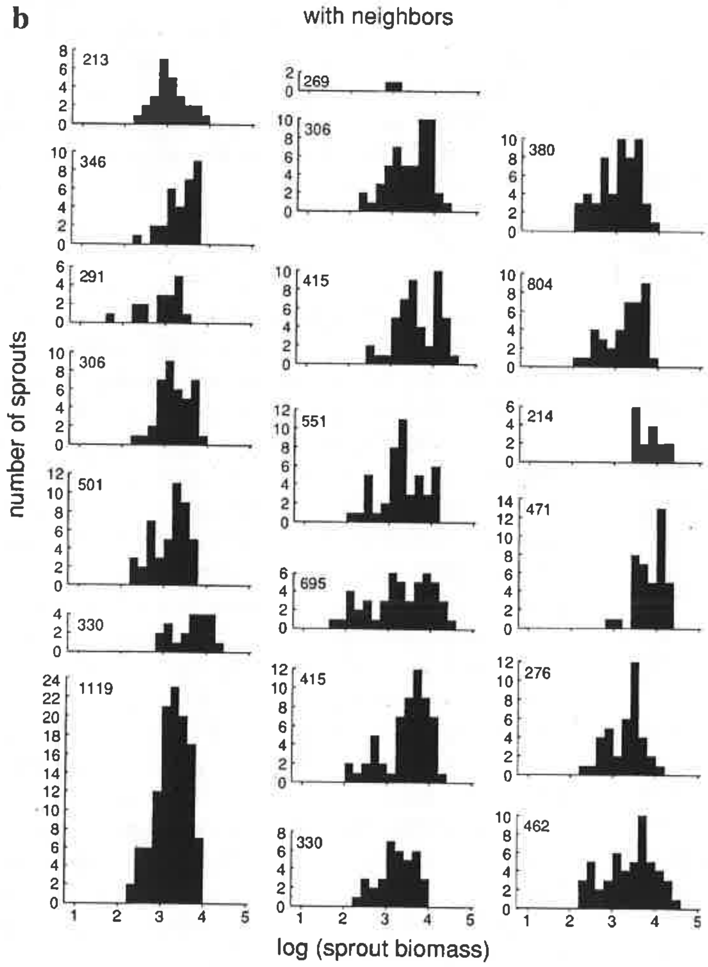
The biomass distributions of both genets within the population (Fig. 1) and sprouts on a stump (Fig. 3; note log scale) were highly skewed and unequal in both treatments and at both time periods. There was a significant effect of sprout density on sprout size variability after 7.5 months but not after 2 months. However, competition or density × competition interaction had a non significant effect on the size variability of sprouts on a stump (Table 2). Size inequality of sprouts from a stump was higher when neighbors were present after 7.5 months (Fig. 4).

After the first 2 months the CV of genet size of plants with neighbors (142.8 %) was significantly higher than for plants without neighbors (75.3 %; $p < 0.05$; paired bootstrapped estimates) although this was primarily due to the fact that many of the stumps with neighbors had no sprouts (Fig. 1a). After 7.5 months the variability in genet size was similar for plants with and without neighbors (67.7 % and 65.3 % respectively; Fig. 1b).

Discussion

The lignotuber can be considered as a bank of dormant buds and as a storage organ for carbohydrates and nutrients (James 1984). Lignotuber size influenced the process of resprouting: larger stumps produced more sprouts and more total biomass (Table 1; Fig. 2). A positive relationship between genet size and number of sprouts has also been observed in other *Ericaceae* species, *Erica multiflora* (Vilà & Terradas 1992) and *E. arborea* (Riba 1991).

There is large size variation within plant populations, and competition is one factor which has been shown to influence this variation (Weiner 1988). A genet is composed of a population of ramets (in this case sprouts) whose size distribution changes over time. A resprouting *Arbutus unedo* individual consists of many small sprouts and few large ones, the latter of which contribute most to the total plant biomass. The population has a hierarchical structure: the population consists of a distribution of genets of different sizes, and each



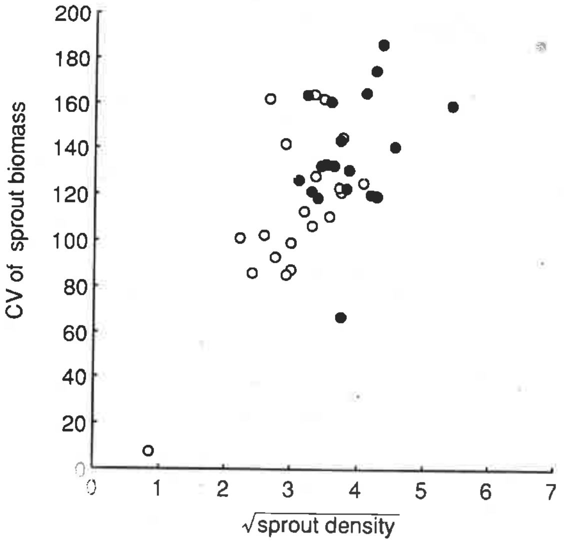


Fig. 4. Relationship between the sprout density (number of sprouts per unit stump area) and the coefficient of variation of estimated sprout biomass of *Arbutus unedo* plants with neighbors (o) and without neighbors (•), 7.5 months after treatment.

genet consists of a distribution of ramets of different sizes (Berntson & Weiner 1991). Competition occurs at both levels: among whole genets and among ramets of a genet (de Kroon et al. 1992). The mechanism of competition may be the same or different at the two levels, and the lower level may be fundamentally different because ramets on a genet may be integrated to a greater or lesser extent, giving the plant some control over competition amongst its ramets (Hutchings 1979).

Competition from neighboring plants appears to delay resprouting and decrease the amount of resprouting in *Arbutus unedo*. Resprouting genets which interact with neighboring vegetation have fewer and smaller sprouts than those with neighboring plants (Vilà & Terradas 1992). Contrary to our hypothesis that inter-genet competition would be asymmetric, our results suggests that inter-genet competition is symmetric, and may fit the 'altered-speed' model (Morris & Myerscough 1984), i.e. inter-genet competition slows the rate of development of genets that have neighbors, but not the form of this development. For example, there was no increase in the number of sprouts from lignotubers without neighbors over the period from two to 7.5 months following clipping, suggesting that a resprouting lignotuber without neighbors produces a certain number of sprouts (depending on its size) over a relatively short period of time. These sprouts grow and interact but additional sprouts are not initiated. The number of sprouts on genets with neighbors, on the other hand, increased from two to 7.5 months, although there were still fewer than on plants without neighbors. Thus, the process of resprouting was much slower when neighbors were present. Symmetric plant competition may often be a result of competition for soil resources, while plant asymmetric competition may usually be for light (Weiner 1990). In the months following clipping, competition among genets may be for soil resources. Significant shading of genets by other genets may not occur until much later when they become quite large.

Intra-genet competition actually begins before resprouting, viz. as competition among buds, growing or not growing into shoots. In some species the density of ramets produced by a genet is tightly regulated so that competition among ramets is limited, but this does not seem to be the case in *A. unedo*. On the other hand, there are clearly many buds on the lignotuber which could sprout but do not, suggesting that sprouting controlled to some degree by the genet, and our results show that inter-genet competition slows the process of sprouting.

Although competition among genets appears to be symmetric, the data are consistent with the hypothesis that competition among ramets of a genet is asymmetric. The evidence here is the correlation between density of ramets (sprouts) per unit genet area and the size inequality of these ramets (Fig. 4). A positive relationship between density and size variability is consistent with the hypothesis of asymmetric competition, in which large ramets diminish the growth of small ones in a disproportionate way (Weiner & Thomas 1986). Two possible mechanisms for this asymmetry seem most reasonable:

First, asymmetric competition between plants is usually associated with competition for light (Weiner 1990). Unlike competition between whole genets, sprouts on a stump are very close together and shading can begin soon after resprouting begins. Large sprouts will shade small ones and the asymmetry of this interaction will increase size variability before the onset of self-thinning of sprouts. In this view ramets are seen as relatively autonomous, competing for light as if they were independent shoots growing at the same density.

Alternatively, apical dominance mediated by hormones could result in a suppression of the recruitment and growth of small sprouts by the first sprouts that emerged (Blake & Carrodus 1970). Since the shoots of one individual may be integrated, we might expect the plant to exert some control over competition among its parts (Novoplansky et al. 1989; Berntson & Weiner 1991). But integration will not necessarily make the competition among integrated parts more symmetric. If it is better for a genet to develop into a shrub with a few large shoots rather than one with many smaller shoots, then natural selection will favor genets in which some sprouts dominate and suppress others. Apical dominance represents such a mechanism, and it could be an evolved response to selection for intra-genet competitive asymmetry. In addition to suppressing completely the growth of some buds, apical dominance may represent a more efficient way for a genet to practice "asymmetric competition" among its ramets than just allowing them to compete for light.

Whether the proximate mechanism of asymmetric competition between sprouts is shading or apical dominance, it appears that we do not need to invoke a direct effect of competition from neighboring genets on the size variability of sprouts within genets. The effect of neighbors occurs indirectly through the size and density of sprouts on a genet. In the early stages of resprouting, genets without neighbors had a large density of sprouts. This gives rise to greater variability in sprout size on a genet later on.

Our conclusions that inter-genet competition is symmetric whereas intra-ramet competition is asymmetric during the early months of regeneration mirrors recent conclusions by de Kroon et al. (1992) from their experimental studies on competition within and among clones in monocultures of *Brachypodium pinnatum* and *Carex flacca*. Our results suggest that this relationship between intra- and inter-genet competition may not be restricted to clonal plants. The mechanisms of competition within and among genets, and the evolution of modular integration may be more important than clonal growth *per se*.

The negative effects of neighboring plants on resprouting are evidence that competitive interactions among and within individuals play a major role in the resprouting dynamics within this Mediterranean vegetation. Competition among resprouting genets delays the onset of resprouting, reduces sprouting of individual plants, and changes the interactions of sprouts on plants.

Acknowledgements. We thank the Corporació Metropolitana de Barcelona for permission to use the study site in Parc de Collserola. J. Canadell, F. Lloret, L. López-Soria and M. Riba helped with data analyses and commented an earlier version of the manuscript. The critical comments from H. de Kroon, R.K. Peet, L. Aarssen and two anonymous reviewers were very helpful. Financial support was provided in part by the Comisión Interministerial de Ciencia y Tecnología (FOR91-1054 project), and the Comissió Interdepartamental de Recerca i Innovació Tecnològica (Ajuts a Joves Investigadors).

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Received 31 December 1992;
Revision received 14 July 1993;
Accepted 20 July 1993.