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Neighbour effects on *Erica multiflora* (Ericaceae) reproductive performance after clipping

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Abstract – The effect of interspecific competition on resprouting and reproductive success and the relationship between above-ground vegetative biomass variability and reproductive biomass variability were analysed during resprouting after clipping. For this purpose, a field experiment was performed by removing neighbours around individuals of *Erica multiflora* in a Mediterranean shrub community. Removal of neighbours increased the number of sprouts and the above-ground vegetative biomass of target plants. However, it did not decrease plant size variability. Neighbours decreased the likelihood of fruiting and the biomass of fruits. In target plants that had set fruits a simple allometric relationship between above-ground vegetative biomass and the biomass of fruits explained 42 % of the variation in fruit biomass. The probability to set fruits at a given plant size was smaller in plants with neighbours than without neighbours. Presence of neighbours also increased the variability of fruit biomass within the population, because 50 % of target plants with neighbours did not set fruits. This failure to set fruits may be related to shading, the small size of plants with neighbours, as well as a delay in development. © Elsevier, Paris

Multispecific neighbourhood / resprouting / size-dependent reproduction / reproductive variability / size variability

1. INTRODUCTION

Competition affects the reproductive performance of plants [31]. Classical interspecific neighbourhood models predict that competition has a negative effect on fecundity by reducing target plant size [4, 16, 18], because reproductive allocation is often size-dependent [22, 23, 25] and competition make plants smaller [31]. Competition may also reduce reproductive output due to the small size of the plants. Predictions from models have been field tested for annual species [19] and for deciduous forest communities [20]. However, Ellison et al. [10] developed an alternative model and tested it on *Arabidopsis thaliana* illustrating that competition can have direct effects on fecundity independent of its effect on plant size. Competition directly affects fecundity by changing resource allocation within plants [5] and plant morphology [10, 21], and by reducing flowering [12, 26].

The positive correlation between plant size and reproductive allocation suggests that reproductive variability is also related to vegetative size variation. Size variation may influence genetic variation in future generations. If plants are highly variable in size, reproduction may be restricted only to large plants because small ones may fail to reproduce [31, 33]. Size variability does not always increase with competition [32]. For example, competition for nutrients reduces mean plant size but does not affect size variability [30]. Similarly, competing plants can grow in height [9] or decrease branching [11] without increasing size variability. As stated by Ellison et al. [10], we predict that competition may not influence vegetative size variability but might increase reproductive variability. In this paper we field tested Ellison's et al. [10] predictions in a Mediterranean shrubland where target plants are grown in the absence of neighbours and with neighbours present.

Resprouting from subterranean structures is a major feature of several woody Mediterranean species [13] following above-ground biomass removal due to disturbance such as fire, cutting or herbivory. In a previous paper Vilà and Terradas [27] showed that in clipped *Erica multiflora* L. (Ericaceae) removal of neighbours modified the resprouting dynamics of target plants by increasing the number of sprouts and the mean sprout biomass. However, sexual reproduction of such plants was not described, nor the relationship between resprouting and reproductive success.

Here we studied the effect of competition on size and reproductive variability by means of a removal field experiment. *E. multiflora* was chosen as a target plant because of its capacity to resprout after aerial biomass removal. The main aims of our study are: (i) to analyse the effect of competition by multispecific neighbours on plant size and plant size variability of *Erica multiflora* and (ii) to examine the effect of above-ground vegetative biomass and competition on reproductive biomass and the reproductive variability within the population.

2. MATERIALS AND METHODS

2.1. Species and study site

Erica multiflora L. (Ericaceae) is an evergreen shrub that typically occurs on calcareous soils of the Western Mediterranean Basin, where it is a common component of coastal shrubland. In the study area, plants attain less than 1 m in height. *E. multiflora* produces abundant sprouts after aerial biomass removal, either from a stump or shallow roots [15] and flowering does not occur until the second year after biomass removal. Vegetative growth occurs twice a year: in spring (from March to June) and autumn (from September to November).

Flowers are grouped in inflorescences located at the terminal position of branches. Each inflorescence is composed of between one and several hundred flowers. Flowering occurs from mid-September to mid-December. In January, fruiting takes place and almost all seeds mature. Fruits are capsules of less than 3 mm in length and diameter containing on average 25.8 ± 0.48 seeds (mean ± S.E., n = 96) that weigh in average 0.047 ± 0.001 mg each (mean ± S.E., 20 groups of 200 seeds each), (F. Lloret, unpubl. data).

The study site was located in a coastal shrubland on the 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. Shrubs cover was less than about 1 m high with on average densities 19 005 shrub individuals per ha. The soil is stony and shallow, classified as lithic haploxeroll. The climate is typically Mediterranean, characterized by summer drought. Mean monthly temperatures 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 shrub vegetation is dominated by *Rosmarinus officinalis* L., *Quercus coccifera* L., *Erica multiflora* L. and *Ulex parviflorus* L. which contribute 39, 14, 12 and 8 % of ground cover, respectively. The understorey is dominated by the grass *Brachypodium retusum* (Pers.) Beauv. which covers 63 % of the ground layer.

2.2. Experimental design

Sixty plants of *Erica multiflora* were randomly selected in July 1989. Twenty plants were randomly assigned to each of the following treatments: (i) all neighbour shoots within a 2 m radius of the target plant were removed at ground level; (ii) as in (i), but within a 1 m radius; (iii) control: neighbourhood was not modified. In (i) and (ii) the regrowing shoots were clipped every 2 months to maintain the experimental conditions during the study.

Removal of vegetation is the most common neighbour manipulation approach to the study of species interactions in the field [1]. Removal of above-ground neighbour vegetation has the advantage, in comparison with trenching, of not disturbing the soil; but the disadvantage that it does not remove neighbour roots and hence, below-ground competition may still reduce plant growth [17]. In a previous study, Vilà [26] showed that removal of above-ground biomass of neighbours as a way to reduce competition increased target plant growth.

The sprouts of *E. multiflora* were clipped at ground level and the area of each stump was estimated by measuring the longest diameter and the diameter perpendicular to it, assuming that the stump surface was elliptical. Each target plant was covered with a metallic mesh to prevent herbivory by rabbits and sheep. In January 1992, the number of sprouts per *E. multiflora* plant was counted and target plants were harvested. Above-ground vegetative biomass was separated from reproductive biomass (fruits) and weighed after drying at 80 °C for 96 h. One of the best estimates of reproductive success is plant seed set. However, in the plant system studied this value could not easily be directly measured because of the large production of fruits per plant and the small size of individual seeds. For this reason, and because there is not much variation in the number of seeds set per fruit, we used the biomass of fruits (B) as a measure of the reproductive success because it is dependent on the number of fruits (N): $B = 2.41 + 0.26\ N$; $r^2 = 0.879$, $n = 100$ [F. Lloret, unpubl. data].

2.3. Statistical analysis

The effect of different competition treatments (0, 1 and 2 m clearing radius) on the number and above-ground vegetative biomass of sprouts was statistically analysed by an ANCOVA which included competition treatment as the main factor and the area of the *E. multiflora* stump as the covariate. A previous study had shown that sprouting vigor after disturbance was positivelly correlated to Ericaceae stump area [2]. Likelihood of plant fruiting was compared by a log-likelihood test (*G*-test) and the fruit biomass of the

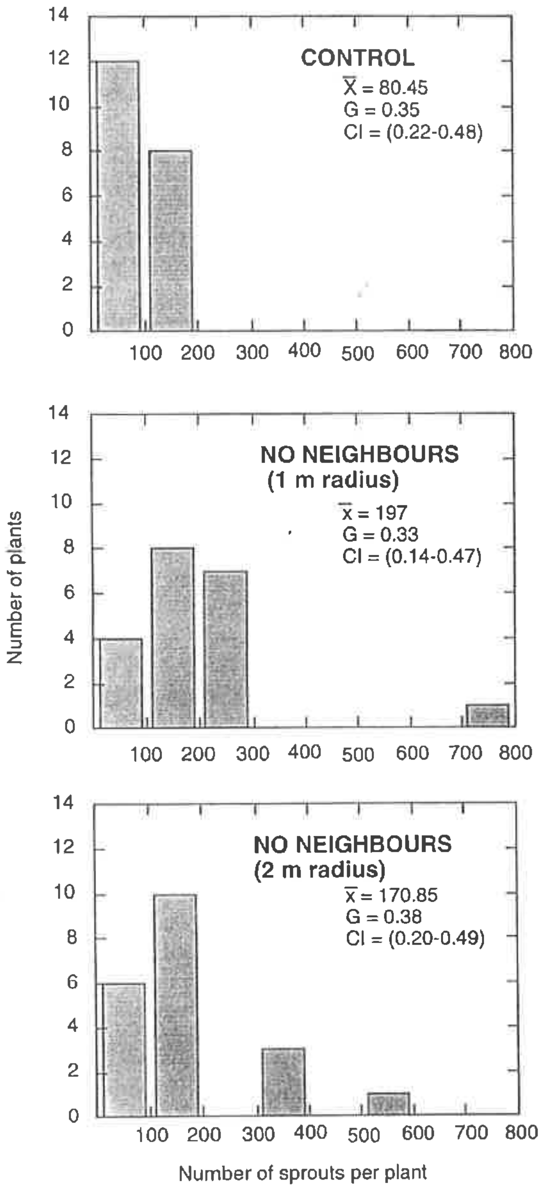

Figure 1. Distributions of number of sprouts per plant of *Erica multiflora* after three competition treatments: Control: all neighbours present; no neighbours (1 m): all neighbours within 1 m removed; no neighbours (2 m): all neighbours within 2 m removed. Mean sprout number, Gini coefficient (G) and 99 % bootstrap confidence intervals (CI) are given for each treatment.

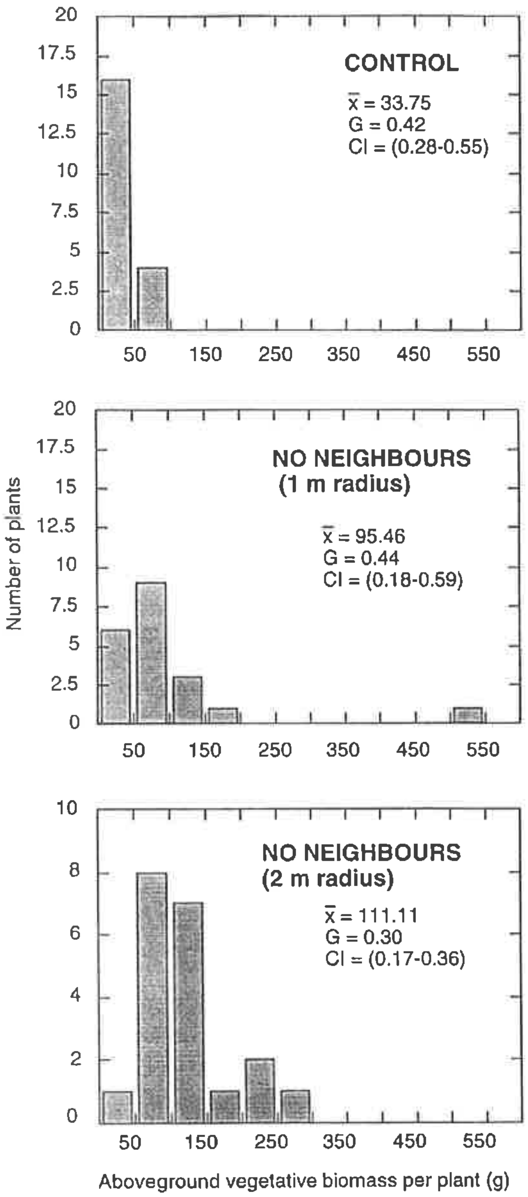

Figure 2. Distributions of above-ground vegetative biomass per plant of *Erica multiflora* after different competition treatments. Mean vegetative biomass, Gini coefficient (G) and 99 % bootstrap confidence intervals (CI) are given for each treatment. (See *figure 1* for competition treatment description).

plants that had flowered was also evaluated by an ANCOVA which included above-ground vegetative biomass of the plants as the covariate. To normalize errors, the area of the stump was square root transformed, while all other variables were log transformed. Pairwise comparisons among the 3 levels of competition treatment were performed by a Scheffé *F*-test [34].

The Gini coefficient (G) was used as a measure of the degree of variability. A single Gini coefficient was calculated for each treatment and variable (number of sprouts, above-ground vegetative biomass and reproductive biomass per plant). Differences in Gini coefficient among treatments and among variables were tested for significance by comparing paired bootstrapped confidence intervals of the Gini coefficient based on 1 000 iterations. Because the sample size of the data set used to calculate each G coefficient was small (20 individuals per treatment), 99 % instead of 95 % confidence intervals were used for this purpose [7].

3. RESULTS

Neighbours reduced the number of sprouts per plant ($F_{2,55}$=8.80, P=0.0005) (*figure 1*). There was no significant difference in the number of sprouts between target plants without neighbours within 1 and 2 m (Scheffé-test, P=0.44). Sprout number per plant varied significantly with stump size ($F_{1,55}$=64.60, P=0.0001). A larger stump had more sprouts than a small one ($y = 3.42 + 0.72x$, $r^2 = 0.49$, $P<0.0001$). Plants with neighbours had less above-ground vegetative biomass than plants without neighbours ($F_{2,55}$=19.96, P=0.0001) (*figure 2*). There was no significant difference in this parameter between the two neighbour removal treatments (Scheffé-test, P=0.28). Stump area also had a positive significant effect on above-ground vegetative biomass ($y = 3.34 + 0.46x$, $r^2 = 0.19$, P=0.0025).

The number of sprouts per plant and above-ground vegetative biomass distribution of target plants were skewed and unequal in all treatments (*figures 1* and *2*). The size distributions show that the experimental population was composed mainly of target plants with few sprouts and small biomass, and a few plants with a large number of sprouts and large biomass. There was an overlap between 99 % bootstrapped coefficient intervals for each population, thus competition treatment had no significant effect on size variability (*figures 1* and *2*).

Mean biomass of plants with fruits was larger (94.62 g) than that of plants without fruits (49.25 g) and the difference was significant (t-test=5.34, P=0.0001). Removal of neighbours decreased the percentage of plants with fruits (G-test=9.84, P=0.006). By the time of the final harvest, only 50 % of the plants with neighbours had produced fruits, compared to 90 % and 85 % of the plants without neighbours within a 1 and 2 m radius, respectively (*figure 3*). The probability to set fruits was not only dependent on a plant size threshold because plants without competition set fruits at smaller sizes than plants with neighbours (*figure 3*).

Of the variation in the log of the biomass of fruits, 42 % could be accounted for by differences in the log above-ground vegetative biomass ($F_{1,41}$= 10.34, P=0.002), (*figure 4*). The presence of neighbours decreased fruit biomass ($F_{2,41}$=7.01, P=0.002). Pairwise comparisons show that removal of an increasing number of neighbours results in large biomass of fruits (*figure 3*).

The distribution of fruit biomass within the population was highly skewed, especially in the plants with neighbours (*figure 5*). Although fruit biomass range for plants with neighbours was smaller than for plants without neighbours, the Gini coefficient of fruit biomass for plants with neighbours was significantly greater (0.91) than the plants without neighbours

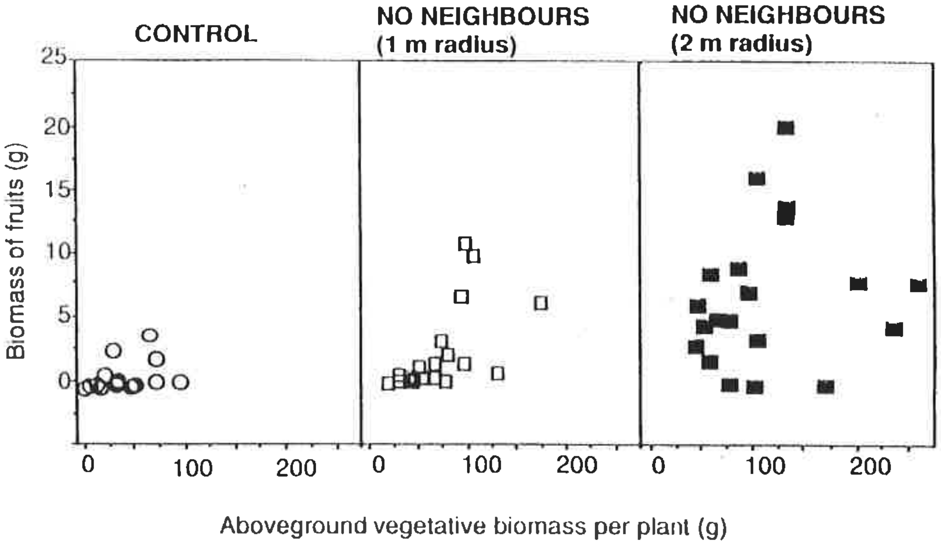

Figure 3. Relationship between above-ground vegetative biomass and biomass of fruits of *Erica multiflora* (see *figure 1* for competition treatment description).

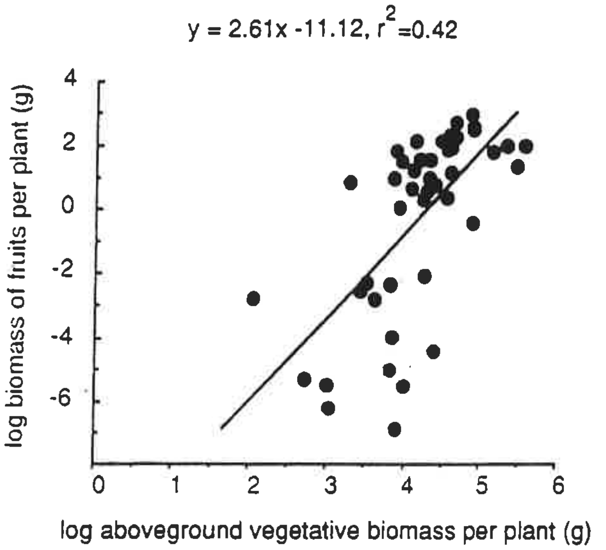

Figure 4. Relationship between above-ground vegetative biomass and biomass of fruits of fruiting plants of *Erica multiflora*. All treatments were pooled.

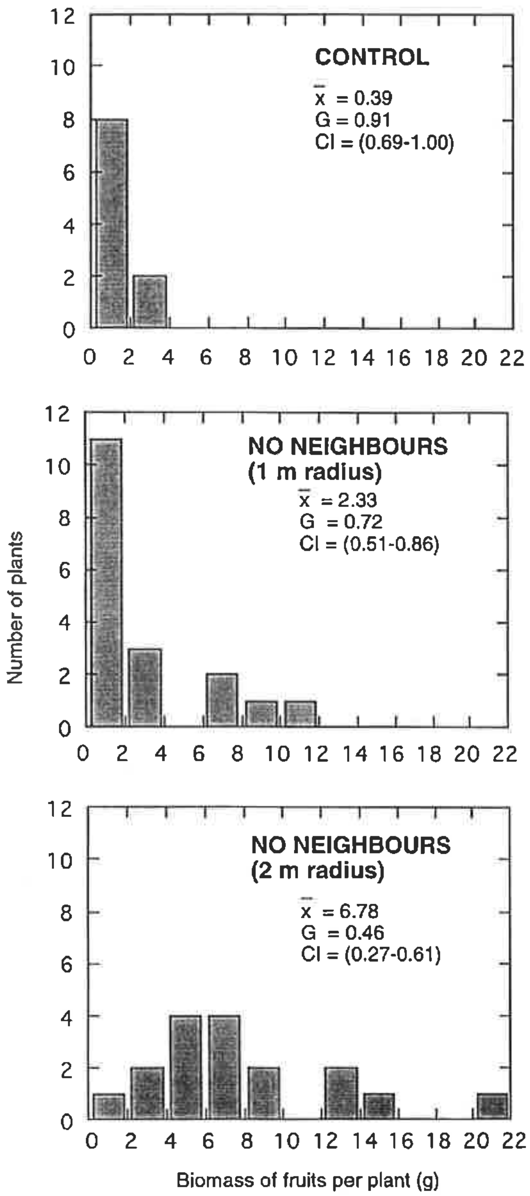

Figure 5. Distributions of fruit biomass per plant of *Erica multiflora* after different competition treatments. Mean fruit biomass, Gini coefficient (G) and 99 % bootstrap confidence intervals (CI) are given for each treatment. Percentage of plants with fruits for control, no neighbours (1 m) and no neighbours (2 m) was 50 %, 90 % and 85 % respectively. (See *figure 1* for competition treatment description).

within a 1 and 2 m radius (0.72 and 0.46 respectively) (*figure 5*). As 99 % bootstrapped confidence intervals overlapped for plants without neighbours within 1m and 2 m radius (CI = 0.51-0.86 and 0.27-0.61 respectively) reproductive variability was not significantly different.

Reproductive variability of control plants was always greater (0.91) than plant size variability, measured as the Gini coefficient of both the number of sprouts per plant (0.35) and the above-ground vegetative biomass per plant (0.42) within the population. Reproductive variability for target plants without neighbours in a 1 m radius was also significantly greater (0.72) than number of sprouts variability (0.33).

4. DISCUSSION

Neighbours reduced *Erica multiflora* sprouting vigour but did not reduce size variability. The intermingled root system of the species that composes this stand could have induced below-ground competition, which may be responsible for the observed decrease in the number and in the biomass of sprouts in plants with neighbours. In a related study, Vilà and Terradas [28] observed that there was a decrease in the soil P content when neighbours were present compared to when neighbours were removed, indicating that competition for P may occur in this stand. Furthermore, the summer drought which occurs in this Mediterranean community may also cause competition for water [3]. Additionally, shading by neighbours may decrease ramet recruitment as shown in *Festuca rubra* [24] or in *Calluna vulgaris* [12] and thus reduce plant biomass.

They may be two plausible reasons for the non-increase of vegetative size variability due to competition. First, neighbour morphology is a determining factor which influences plant size variability because it affects competition for light differently [11]. In the present study, although neighbours were larger than clipped target plants, the heterogeneous architecture of the neighbourhood would not shade target plants enough to produce variability in target plant vegetative growth [6]. Alternatively, as *E. multiflora* is a slow-growing woody species, it could be that the length of the experiment (2.5 years) represented a short period of growth to induce vegetative size variability. Similarly, at the population level, Edmeades and Daynard [8] did not find any relationship between density and plant size variability for an annual species grown from seeds for less than 44 days.

Competition had a negative effect on biomass of fruits and there was also a simple allometric relationship between the biomass of fruits and above-ground vegetative biomass of target plants that had fruited. The study shows that size-dependent reproductive biomass is not linear as in most other experiments but logarithmic [14, 29]. This allometric relationship would be consistent with the modular growth of *E. multiflora*, in which an individual continues to increase its size by adding new sprouts and by enlarging old ones, all of which are potentially reproductive.

However, as modelled by Ellison et al. [10], the probability to set fruits was not only dependent on a plant size threshold because plants without neighbours set fruits at smaller sizes than plants with neighbours. It is plausible that shading by reducing the red-far red ratio of light decreased reproductive allocation. This result may be supported by several studies that found allocation shifts mediated by a reduction of the red-far red ratio. Iason and Hester [12] found that a reduction of the red-far red ratio inhibited flowering of the congener *Calluna vulgaris*. Similarly, Vilà [26] found that artificial shading decreased flowering in *E. multiflora*. One additional mechanism for the effect of neighbours on fecundity independent on plant size is a shift in morphology due to crowding [10] that may reduce flowering. In *E. multiflora*, each sprout is capable of flowering. Neighbours reduced sprout recruitment and thus the probability of flowering.

Reproductive variability was higher than vegetative variability. The presence of neighbours did not reduce the survival of plants during the census; nor did it modify the size variability of plants. However, it increased the reproductive differences among plants: 50 % of the plants with competition failed to set fruits whereas more than 80 % of the plants without competition did set fruits. Pfitsch and Pearcy [21] found that shading reduced reproduction size more than vegetative size in *Adenocaulon bicolor* suggesting that reduced carbon gain is allocated to storage necessary for regrowth at the expense of investment in sexual structures.

In conclusion, even if size variability was not modified by competition, the variability of reproductive biomass was increased. The study of the factors that determine such variability is an important part of the study of the evolution in natural populations, because it could contribute to variation of fitness. In the case studied, even though all control target plants were alive, some failed to set fruits; consequently, sexual reproduction, if it occurred, might be restricted to only some of the individuals in the population. Our results therefore support the alternative hypothesis proposed by Ellison et al. [10] that competition can reduce reproduction allocation independent of plant size. We suggest that neighbourhood models should consider that other plant traits besides plant size can have a direct influence in reproductive allocation.

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