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The effects of physical support and density on biomass production and size hierarchies of Galium aparine populations

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We assessed the growth and size inequality of experimental populations of *Galium aparine* at different densities with and without physical support. Those plants for which support was provided gained more weight than those unsupported. The presence of support increased the relative growth rate of the plants and reduced mortality at the highest densities. The biomass of the population was also higher in the case of supported plants. The size inequality of the population was not affected by the support-treatment but varied with density. Since density-dependent mortality took place at higher densities, and the variation of the relative growth rate increased with density, dominance-suppression could be assumed. This was not, however, reflected in an increase in size inequality before the period when mortality occurred, which suggests that size is not necessarily a good predictor of the use of resources by individuals of this species.

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The terms dominance-suppression and size hierarchy (Harper 1977, Begon 1984, Weiner and Thomas 1986) were proposed to describe an increase in size inequality (or between-plant size variation) thought to affect the ability of each individual to capture the available resources. The development of size hierarchies is considered a driving force in the process of density-dependent mortality of plant populations (White and Harper 1970, Watkinson 1985, McFadden and Oliver 1988, Oliver and Larson 1990). Much emphasis has been given recently to the idea that the development of size hierarchies occurs due to the asymmetric character of competition between co-specific neighbours: bigger individuals would be more efficient in making use of the available resources, particularly when light is the limiting factor (Begon 1984, Weiner and Thomas 1986, but see Turner and Rabinowitz 1983, Ellison 1987). Since the intensity of competition increases with the density of the population, dominance and suppression would take place sooner at higher densities.

Galium aparine L. is a climbing annual species which grows densely in scrub (Salisbury 1942) as well as in cultivated areas throughout the world (Malik and Vanden Born 1988). Artificial communities in which physical support by other plant species allows *G. aparine* to grow in height (e.g. hedgerows) seem to be particularly favourable for this species (Burel and Baundry 1990). Since mutual support between co-specific individuals would allow them to grow taller and therefore increase their chances to reach low branches of shrubs and trees, growing in crowded conditions without size hierarchy development may be advantageous for this species. We tested three hypotheses by means of a glasshouse experiment: (1) the development of size hierarchies in this species is not hastened in more crowded populations, (2) physical support represents an important resource

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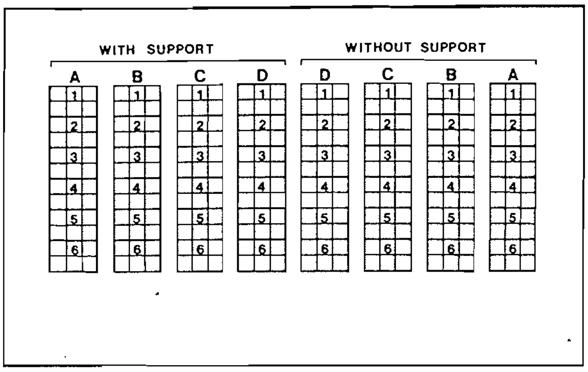

Fig. 1. Experimental design, which included two support treatments (with and without support) and four densities (A–D). Each of the six blocks of each treatment (1–6) consisted of six plots (small quadrats). The blank area surrounding the experimental pots was occupied by guard pots.

for *G. aparine* and consequently (3) the availability of physical support affects the development of size hierarchies in this species.

Materials and methods

The experiment was set up in an unheated glasshouse (Dept of Plant Sciences, Univ. of Oxford, U.K.) on the 3rd of August 1991. Seeds of *G. aparine* were sown in 3.6 cm-side and 4 cm-depth square pots partly filled with sandy-loam and then covered with a 1 cm layer of that soil. One 4 mm-diameter bamboo stick was inserted centrally within each pot down to the pot base. Such sticks only reached the surface of the soil and occupied the space in which longer sticks to provide support were to be placed in the support-treatment pots. After the bulk of emergence, pots were thinned to four densities: one, two, four and eight plants per pot (further termed as A, B, C, and D), trying to keep the initial size heterogeneity within and between pots as low as possible. The pots were divided into two support-treatment groups, all four densities of seedlings being represented in each group. Each support treatment × density combination consisted of six contiguous blocks each of which included six pots (Fig. 1); these blocks were treated as independent samples for the statistical analyses. Pots with the same number of seedlings as those of the experiment were arranged surrounding each treatment in order to reduce the border effect (guard pots). This design may be considered inappropriate from the statistical viewpoint, but the number of guard pots and space that would have been necessary had a random design been used (considerably increased by the support provided and the tendency of *G. aparine* plants to attach to one another) were impractical. Because of the relatively restricted area occupied by the group of experimental pots, any effect of the position of either support-treatments was considered to be unlikely. However, since the probability of making a type I error when judging the effect of the support-treatment could have been increased by the design chosen, the error probability considered as significant for the statistical tests was $P < 0.025$.

Those plants growing at a density of two per pot were labelled with coloured plastic rings located at the base of the stem in order to identify individuals sharing the same pot. With the same objective, all plants at densities of four and eight per pot were labelled with a dot of water-resistant non-toxic plastic paint on one cotyledon. Both 8 and 15 d after the bulk of emergence the size of each plant was assessed by measuring its linear size (height + length of all branches). A sample of plants taken from populations contiguous to the experimental pots set up for that purpose showed that dry weight could be predicted accurately from certain linear dimensions (WEIGHT = $-0.58 + 0.31\,(\text{HEIGHT})^2 + 6.71$ (COTYLEDON LENGTH × COTYLEDON WIDTH) $- 0.46$ DENSITY, $n = 54$, $R^2 = 74.8$ for the first measurement; WEIGHT = $1.89 + 2.78$ LINEAR SIZE, $n = 40$, $R^2 = 94.5$ for the second measurement).

After 15 d of growth the short sticks were replaced by 50 cm-long sticks in all pots of one of the support-treatment groups and in all guard pots surrounding that treatment. A grid made out of a similar kind and number of sticks was placed over the pots without support-sticks in order to make the light environment of both support treatments more alike. The grid was supported in its corners by sticks inserted in guard pots and its height over the plants was kept to a minimum and varied as the plants grew taller, so that none of them touched the grid.

Watering was carried out from above with a watering can (rose no. 0). All pots received NPK fertilizer (Phostrogen 437 p.p.m. (N: 10%, P: 4.4%, K: 22.4%, Mg: 1.3%, Fe: 0.4%)) supplied every four d in the water.

All the plants were harvested 54 d after emergence by cutting them at soil surface level. The height and length of branches of each plant were recorded and the plants were dried at 70°C for two d and weighed to the nearest 0.1 mg.

The effect of support treatment, density and their interaction on the mean weight/plant, total weight and size inequality (measured here as the coefficient of variation, CV) were assessed by taking the mean value of each of these variables for each block (so that six replicates were used for each support treatment × density combination). The individual relative growth rate (RGR) was calculated by means of the equation: $\text{RGR} = (\log \text{wt}_2 - \log \text{wt}_1)/(t_2 - t_1)$, where wt_1 and wt_2 are the estimated plant weight at times 1 (t_1) and 2 (t_2) (Květ et al. 1971). The RGR was obtained for the period between both non-destructive measures and for the period between the second non-destructive measure and the harvest. The RGR was compared between support

Table 1. Values of Fisher's F-statistic and significance (P) when assessing the effect of the support treatment, density and the interaction between these factors on traits obtained for populations of *G. aparine* after (A) 15 and (B) 54 d of growth.

Variable	N	Support		Density		Interaction	
		F	P	F	P	F	P
A							
weight/plant	48	0.38	ns	1.47	ns	3.47	ns
total weight	48	5.37	ns	484.55	***	5.03	**
CV	48	0.12	ns	3.34	ns	1.63	ns
RGR	160	0.49	ns	23.68	***	1.57	ns
B							
weight/plant	48	19.2	***	1114.6	***	4.0	*
total weight	48	18.6	***	11.5	***	4.5	**
CV	48	0.09	ns	24.7	***	3.4	ns
RGR	164	7.3	**	142.4	***	2.0	ns

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.025$, ns $P > 0.025$.

treatments and densities, but, unlike the other measures, the number of replicates used for the RGR between the second record and the harvest depended on the number of plants for which the recognition of the paint label at harvest (at densities C and D) was possible (the complete degradation of the cotyledons made that impossible for many of the plants). In order to use a similar number of samples for each density when comparing the RGR, 20 random samples (without replacement) were taken from each of the block at densities A and B. Similarly, the RGRs between both non-destructive harvests were compared after randomly selecting 20 RGRs from each support treatment. All comparisons were carried out by standard methods (Sokal and Rohlf 1981).

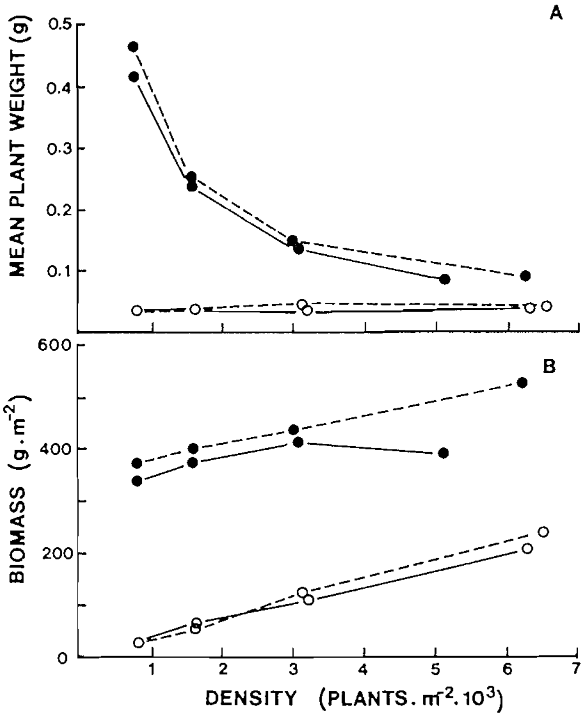

Fig. 2. Weight/plant (A) and biomass per m^2 (B) of *G. aparine* at different densities with (– – –) and without (——) support after 15 (○) and 54 (●) d of growth.

Results

After 15 d of growth (before the supporting sticks were set up) the effects of side, density and the interaction between these two factors on the mean weight/plant were not significant (Table 1A, Fig. 2A). The total weight per unit area, on the other hand, increased significantly with density but was unaffected by side; the interaction between density and side was significant (Table 1A, Fig. 2B). The CV of the mean weight/plant was not affected by density, side or their interaction (Table 1A, Fig. 3A). The RGR between the first and the second non-destructive measures was not significantly affected by side but decreased significantly with density (Table 1A, Fig. 3B). The CV of the RGR was similar for all densities at both support treatments (Fig. 3C).

By the time of the harvest (after 54 d of growth) most plants were growing actively. The support treatment affected notably the way in which plant development was taking place. The main axis of those plants for which support was provided was growing almost vertically, whereas that of those plants lacking support was growing mostly horizontally. The effects of support treatment, density and their interaction were significant both on the weight of individual plants and on the total weight of the population (Table 1B, Fig. 2A,B). The biomass production of *G. aparine* without support increased between densities A and B but was similar for densities B, C and D. For supported plants there was a considerable increase in biomass between densities C and D.

The CV of the weight/plant at harvest was signif-

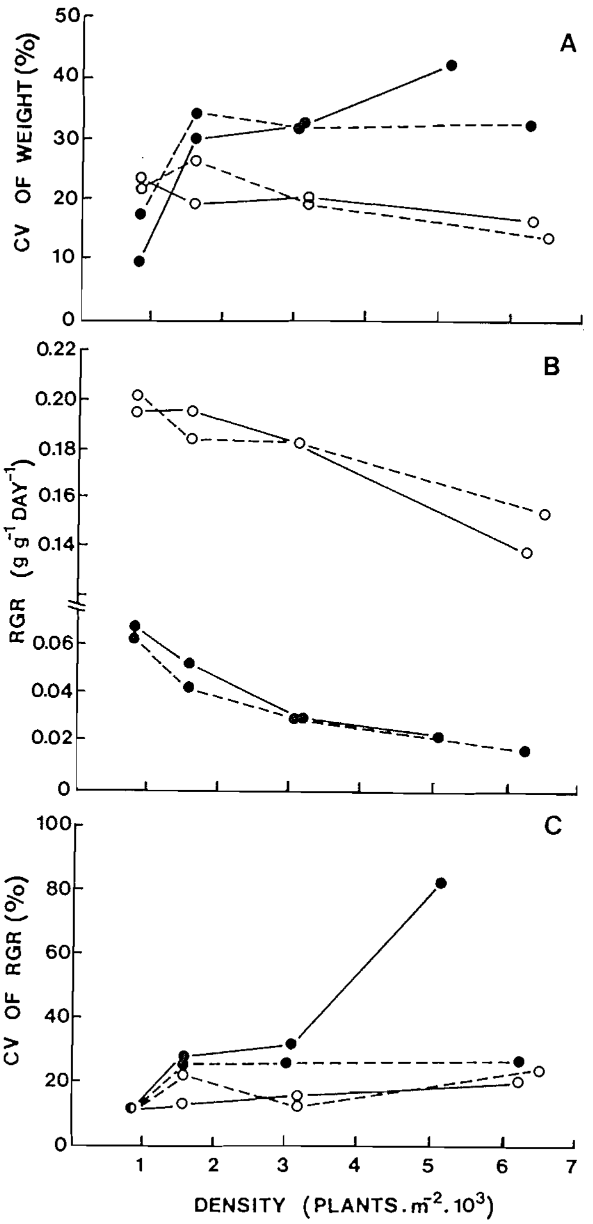

Fig. 3. Coefficient of variation (CV) of the mean weight/plant (A), mean relative growth rate of individual plants between two measures (RGR, B) and CV of the mean RGR (C) of *G. aparine* at different densities with (– – –) and without (——) support. Values 15 (○) and 54 (●) d after emergence are shown.

icantly affected by density (CV higher for densities B, C and D than for A) but not by the support treatment or by the interaction between density and support (Table 1B, Fig. 3A).

The RGR of individual plants between the second non-destructive measure and the harvest was significantly affected both by the support treatment (higher for supported plants) and by density (higher at lower densities) (Fig. 3B). The CV of the RGR increased from density A to B in both support treatments and from density C to D in the control pots (Fig. 3C). In order to assess the statistical probability of obtaining a CV of the RGR as high as that obtained for density D of the control, 500 random samples of plants were taken from the total data set for that support treatment and the CV of the RGR measured for each of them. The actual CV was significantly higher ($P < 0.001$) than 100% of the values obtained for the random samples. The RGR was negatively correlated with the initial weight of the plant (weight after 15 d of growth); the significance of the regression between RGR and initial weight decreased with increasing density for both the control and the support treatment (Table 2).

Some mortality took place at densities B, C and D in pots either with or without support. At the highest density the difference in mortality between support treatments was proved to be significant by the G-statistic for percentages (Sokal and Rohlf 1981; $G_{adj} = 5.131$; $P < 0.025$) (Fig. 4). Since neither disease nor herbivory seemed to have taken place in those pots where mortality was found, density-dependent mortality can be assumed.

Discussion

Both internal forces (e.g. genotypic variation in RGR, intraspecific competition) and external forces (e.g. interspecific competition, herbivory, disturbance) may play important roles in the development of size hierarchies in a plant population (Benjamin and Hardwick 1986, Weiner 1988, Benjamin 1990). In crowded populations, competition may be expected to be the most important of these factors. The results reported here suggest that in early stages of growth (about 15 d from emergence) the size inequality of *G. aparine* populations is not affected by density; in later stages of growth (about 54 d from emergence), however, the inequality of sizes increases with density up to a point and remains fairly constant at higher densities. This supports, to some extent, the first hypothesis proposed in the introduction. The generalized idea of the positive relationship between size inequality and density (Hara 1988, Weiner 1988, 1990) appears to be debatable.

Although the effect of the supporting structures on the size inequality of the population was not significant, the presence of support affected differentially the performance and mortality of *G. aparine* plants, especially at the highest density (Fig. 4), which would support hypothesis (3). Since lower resource capture ability is usually associated with smaller size (but see Thomas and Weiner 1989), an increase in the size inequality of the population is expected before density-dependent mortality takes place (Schmitt et al. 1987, Weiner and

Table 2. Slope of the regression line between the RGR (dependent variable) and the initial weight (independent variable) obtained for each density (A–D) and support treatment (control and support) and for both support treatments pooled. The significance of the slope is indicated. Slopes in the same column sharing the same letter (a–c) are not significantly different from each other when compared by t-test. Significant differences between slopes for both support treatments at the same density (t-test) are indicated by an underline.

	N	Control			N	Support			Both treatments		
		slope				slope			slope		
A	36	−0.653	***	a	36	−0.641	***	a	−0.647	***	a
B	72	−0.876	***	b	72	−0.795	***	b	−0.862	***	c
C	18	−0.692	**	a	15	−1.444	*	c	−0.742	**	b
D	22	−0.367	ns		29	−0.634	ns		−0.464	ns	

*** $P<0.001$, ** $P<0.01$, * $P<0.05$, ns $P>0.05$.

Whigham 1988, Weiner 1990). In the present study no such increment in size inequality was detected at the highest density of the unsupported treatment after 15 d of growth (Fig. 3A) despite the fact that significant density-dependent mortality appeared to have occurred later on. Moreover, the decrease in size inequality usually expected after asymmetric competition eliminates the small-size end of the size distribution (Weiner 1990), was not found here. These results might be justified if mortality affected a range of plant sizes rather than just the smallest individuals of the population. Unfortunately, many of the labels used to identify individuals at the highest densities (C and D, where most mortality took place) were lost, so that a precise identification of the individuals that died during the period of study was not possible. In addition, the non-significant correlation found between the size inequality before mortality and the degree of mortality for each of the groups of pots at higher densities (C and D, in which mortality was more significant) ($r = -0.026$, $N = 24$), suggests that in this species mortality is not preceded by an increase in size inequality, as generally accepted (Westoby 1984, Firbank and Watkinson 1990). The significant increase in the variation of the RGR in those pots with higher mortality gives further evidence for the idea that some plants were being more affected by competition than others, so that a hierarchy, in terms of resource use efficiency rather than size, was indeed developing. Apparently, intraspecific competition in this species does not restrain exclusively the growth of the smallest individuals of the population and, consequently, size inequality alone ought not to be used as an indication of the variation in resource capture ability between plants.

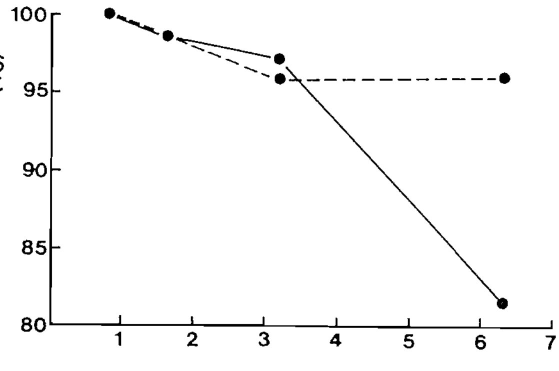

Fig. 4. Survivorship of *G. aparine* with (– – –) and without (——) support 54 d after emergence.

It has been pointed out that a positive correlation between RGR and plant size within a crowded population provides evidence in support of competitive asymmetry (Weiner 1990). Since that correlation was either negative or non-significant in the present study, a symmetric competition pattern could be assumed. However, this result needs to be taken carefully: the ontogenetic drift of the RGR of plants associated with their sigmoidal growth may produce a similar effect on the RGR/size relationship. Such an effect was, presumably, reduced in this case due to the short time of emergence of plants.

It is probable that due to the climbing habit of this species and the associated relative lack of support tissues, the absence of supporting structures could affect the RGR of plants of different sizes according to their position in the canopy after the biggest plants fall over due to gravity, rain or other physical forces. The reduction in the RGR of plants, and their eventual mortality due to competition, irrespective of their sizes has been found in more "self-supporting" species (Thomas and Weiner 1989).

The results of the present study suggest that physical support not only affects the relationship between density and the development of dominance and suppression but also, more remarkably, increases the relative growth rate of individual plants and, to some extent, the biomass production of the population (especially in more crowded populations), thus partially supporting hypothesis (2). Support might then be considered as another resource that *G. aparine* needs in order to achieve full development.

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