

Population density and size inequality in *Galium aparine*

Populační hustota a velikostní hierarchie u *Galium aparine*

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The effects of density and time on the development of size inequality were studied for glasshouse populations of *Galium aparine*. The size of the first-emerging plant in each population was non-destructively measured (individual weight was estimated from height + branches length) and its growth rate was calculated. Destructive harvests were made 45 and 65 days after emergence. The growth rate of the first emerger was significantly affected by the presence of co-specific neighbours as compared with isolated plants. The weight of the first emerger was inversely related to the population density. The inequality of sizes was not affected by density or time but the interaction between these two factors was significant. Kolmogorov-Smirnov two-sample tests (applied on data transformed as a proportion of the maximum value) indicated that other attributes of the size distribution of the populations did change between densities. It is concluded that competition between *G. aparine* plants is a more symmetric process than in most plant species studied. The possible roles of leaf area distribution, shade tolerance and "intra-individual" competition on the degree of symmetry of intraspecific competition are discussed.

Introduction

Differences between individuals in their abilities to capture a limiting resource are expressed under crowded conditions (Weiner et Thomas 1986). Such differences would result in a 'hierarchy of resource exploitation', with a few dominant plants and many suppressed plants (Harper 1977). This dominance-suppression development is usually visualized as a change in the distribution of sizes from normal and with low variability (or inequality) to positively skewed and with high variability (Benjamin 1990). Recent studies, however, recommend that only size variability be assessed, since skewness is a biologically less interpretable feature of a distribution (Weiner et Solbrig 1984, Weiner et Thomas 1986, Benjamin 1990).

Plant density in crowded stands is inversely related to the resource availability for each plant, so that the higher the density the more accentuated the hierarchy of resource use and the higher the size variability are bound to be. Density of co-specific neighbours has generally been found to increase size variability in plant populations (Stern 1965, Salter et al. 1981, Benjamin 1982a, Soetomo et Puckridge 1982).

The development of size hierarchies in plant populations have led some authors to conclude that competition between plants is highly asymmetric (Weiner et Thomas 1986,

Weiner 1990), i.e. that dominant, bigger individuals affect their neighbours but are almost not affected by them. In other words, large plants take up more resources than suggested by their relative size and small plants take up less resources than what their relative size would indicate.

Observations made on both field and experimental populations of the annual species *Galium aparine* suggested that the more crowded the population the more similar neighbours were to one another (Puntieri 1991, Pyšek et Puntieri, in preparation). In the present study, the effect of density on the growth of individual plants and the development of a hierarchy of sizes was analyzed for experimental populations of *G. aparine*. Non-destructive measurements of growth were made for individual plants which, because of their early emergence, were supposed to have an advantage over their neighbours, as shown for other species (Gray 1976, Salter et al. 1980, 1981, Benjamin 1982a, b, 1984a, b, Benjamin et Hardwick 1986).

Materials and methods

G. aparine plants were grown in an unheated glasshouse (Department of Plant Sciences, University of Oxford, England) at four population densities in 9 cm-diameter pots filled with 490 g of sandy loam. Seeds (provided by a seed-supply company) were spread on top of the soil and covered with about one cm of fine sand. Four densities were aimed at: (1) 1, (2) 20, (3) 40 and (4) 80 plants per pot (157, 3144, 6288 and 12575 plants/m² respectively). Two harvests and six replicates per density and per harvest were planned. Unfortunately, the emergence of plants varied considerably between repetitions, particularly at higher densities, so that some of the pots were excluded from the experiment. The resulting mean number of plants for the highest density was 53 plants per pot (8331 plants/m²). The number of replicates for each treatment and each harvest was: six for density 1, four for densities 2 and 3, and three for density 4. Thirty other plants were grown individually at the same time in order to allow the estimation of the variability in sizes of isolated plants. Only those isolated plants of the experiment (six for each harvest), however, were used for measuring individual growth and comparing performances of individuals at different densities. Additional pots with densities of *G. aparine* plants similar to those used in the experiment were prepared; these plants were used to obtain an equation for the non-destructive estimation of the dry weight per plant.

The pots assigned to the different treatments were randomly arranged on a bench. The distance between contiguous pots was 30 cm. A row of pots with 15-25 plants of *G. aparine* was placed surrounding the experiment pots, so that the border effect was minimized. A petri dish was placed under each pot in order to allow sub-irrigation. The number of seedlings in each pot was recorded daily during the period of emergence.

The first plant that emerged in each pot (or one of the first seedlings if more than one emerged approximately at the same time) was labelled with a wire ring and its growth was monitored at 3-6 days intervals by measuring its linear size (length of main stem + length of all branches). The dry weight of the labelled plants in each stage of growth was estimated by means of the equation: $\text{WEIGHT (g)} = -0.0538 + 0.0037 \text{ LINEAR SIZE (cm)}$; $r=0.99$; $n=160$. The plotting of residuals indicated that this linear relationship was more suitable for the estimation of the dry weight of *G. aparine* plants for the period of growth encompassed in this study than the more commonly used allometric relationship: $\log(\text{weight}) = a + b \log(\text{linear size})$. Moreover, the variation of this relationship was found

not to be related to the density of the population for the conditions and range of sizes in this experiment (for a sample of 72 plants growing independently at known densities: $F=0.00$ and $p=0.976$ for the regression between weight/linear size and density).

The growth rate of the labelled plant was measured by fitting a regression line between the $\log_e$ -transformed weight (estimated from the linear size, see above) and the $\log_e$ -transformed number of days from emergence. The first two values of weight obtained were omitted from the line-fitting. The inclusion of such values would have implied the fitting of a more complex and less interpretable equation. The regression line explained at least 94% of the variation in $\log_e(\text{weight})$. The slopes obtained for different densities were compared by ANOVA.

Harvests were made 45 days and 65 days after the emergence of the first plants. Each time, all plants present in each pot were cut at soil level. The linear size of each plant was measured before oven-drying for 40 hrs. at 70°C. The labelled plant and the remaining plants in each pot were weighed separately.

The size variability was evaluated by means of the Gini coefficient of inequality for the linear sizes of all plants in each pot¹⁾. The equation for the Gini coefficient is:

$$\frac{\sum_i \sum_j |x_i - x_j|}{2n^2 \bar{x}}$$

where x_i and x_j are the size values of plants i and j , n is the number of plants in the sample and $\bar{x}$ is the mean plant size for the sample. This coefficient, initially used in economics and now applied to ecological studies, varies between 0 (equal values) and 1 (highly variable values) and is highly correlated with the coefficient of variation (Weiner et Solbrig 1984).

The effect of density and time on the biomass and the inequality of sizes of the population, the mean weight per plant and the weight of the labelled plant were evaluated by means of two-way ANOVA (GLM procedure for unbalanced designs). Tukey-Kramer multiple comparisons (Day et Quinn 1989) were also carried out for each variable. Since only one value of the size inequality (between pots) could be obtained for each harvest in the case of isolated plants, the variance of the Gini coefficient for that treatment was estimated using the Jackknife procedure (Sokal et Rohlf 1981). Comparisons between harvests and with the size inequality found for other densities were then carried out by means of paired t-tests.

Comparisons of size distributions between populations at different densities and between harvests were carried out by means of Kolmogorov-Smirnov two sample tests (Sokal et Rohlf 1981). Since my main interest was to compare the shapes of the cumulative distribution curves rather than mean values, linear sizes were transformed using the following equation:

$$x_i' = \frac{x_i}{\max}$$

¹⁾Although the dry weight is a more suitable measure of plant size than the linear size, the strongly linear relationship between linear size and dry weight found for *G. aparine* plants within the range of sizes encompassed in this study means that the same values of the Gini coefficient would be obtained here for either the linear size or the estimated dry weight.

where x_i is the i -th value of one of the groups to be compared and $\max$ is the maximum value for that group. Therefore, after that transformation each of the groups to be compared consisted of proportional values (x_i') ranging from 0 to 1.

Results

By the time of harvest the labelled plants were larger than the average of their neighbours (Table 1). In all repetitions the labelled plant was among the first half of the population in terms of size and in one replicate of each treatment it was the largest plant. The number of days required for the population to reach 50% of the number of plants at harvest was lower and less variable at densities 2 and 3 than at density 4. No density-dependent mortality was observed during the experiment.

The weight of the labelled plant and its growth rate were significantly higher for the isolated plants than for those growing with neighbours; these variables did not change among treatments 2, 3 and 4, although the differences became more notable over time (Tables 1, 2). The total weight of the plants in each pot was significantly lower for the lowest density than for the other three treatments after 45 days of growth but such a difference was non-significant 20 days later. The mean weight of the neighbours of the labelled plant decreased significantly

Table 1. - Mean ($\bar{X}$) and standard error (SE) of variables obtained per pot at mean densities: 1 (density 1), 20 (density 2), 40 (density 3) and 53 (density 4) plants per pot, harvested 45 days after emergence. Means followed by the same letter are not significantly different when compared by Tukey-Kramer multiple-comparison test ($P < 0.05$).

		Density treatment			
		1	2	3	4
Wt 1 ¹	X	1.023 a	0.219 b	0.145 b	0.187 b
	SE	0.211	0.044	0.047	0.065
GR 1 ²	X	3.880 a	1.630 b	1.395 b	1.753 b
	SE	0.181	0.080	0.228	0.162
Total Wt ³	X	1.023 b	2.324 a	2.307 a	2.792 a
	SE	0.211	0.170	0.062	0.106
Wt 2 ⁴	X	—	0.106 a	0.061 b	0.055 b
	SE	—	0.007	0.002	0.004
Dominance ⁵	X	—	0.106 a	0.068 a	0.076 a
	SE	—	0.023	0.023	0.032
Emergence ⁶	X	—	5.75 b	5.25 b	11.00 a
	SE	—	0.25	0.95	2.08
Gini ⁷	X	0.287 a	0.313 a	0.305 a	0.479 a
	SE	0.271 ⁸	0.026	0.033	0.084

¹Weight of the labelled plant (g)

²Growth rate of the labelled plant (regression coefficient of the relationship $\log_e \text{wt}$ vs. $\log_e \text{time}$)

³Total weight per pot (g)

⁴Mean weight of unlabelled plants (g)

⁵Relationship between the weight of the labelled plant and that of its pot neighbours

⁶Days for 50% emergence in a pot

⁷Gini coefficient of size inequality

⁸Jackknife estimation of the variance

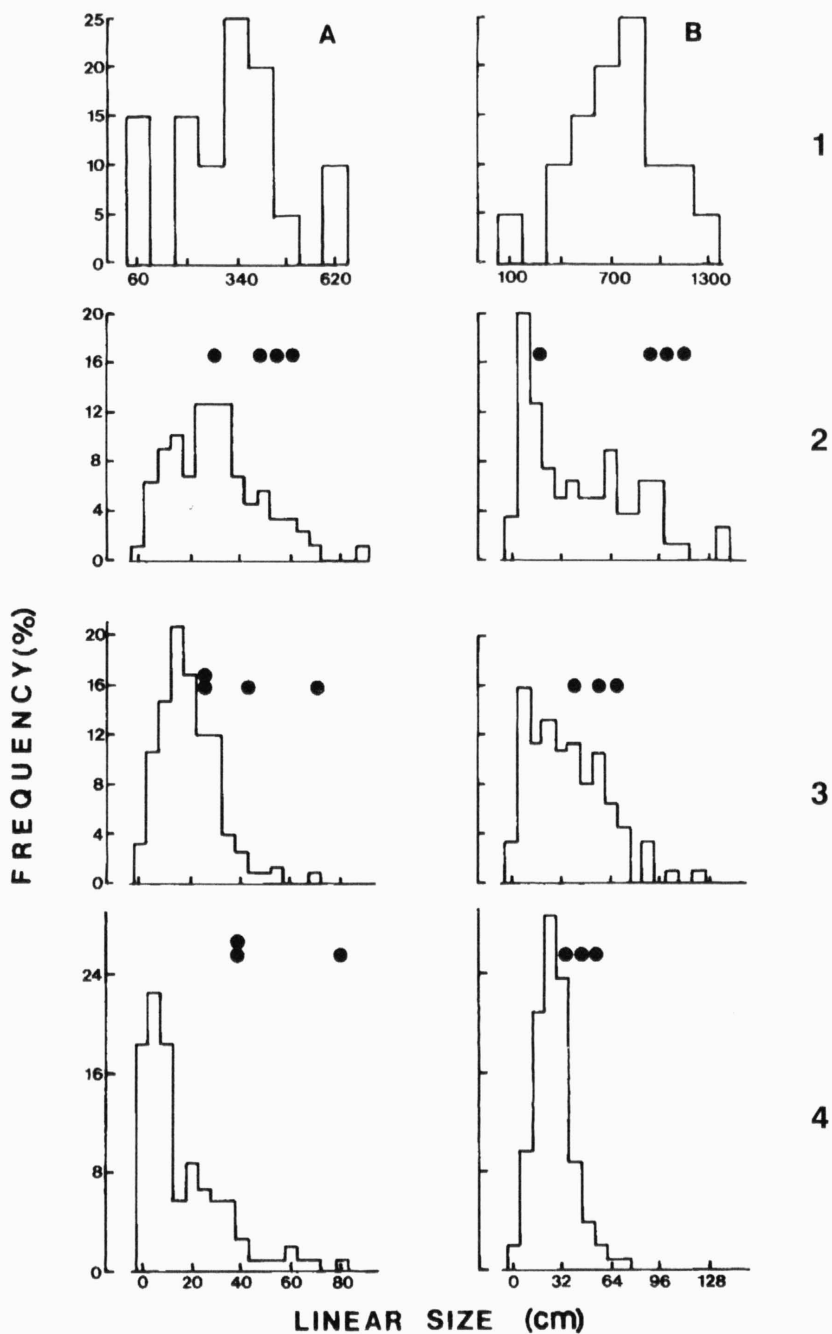


Fig. 1. - Size distribution for plants of *G. aparine* growing at different densities(1-4) 45 (A) and 65 (B) days after emergence. All replicates for each density (indicated on the right side of the diagram) are pooled in each histogram. The dots on top of each histogram represent the approximate position of the first-emerging plants of all replicates.

with density. The weight of the labelled plant did not vary between harvests, although the total weight per pot increased significantly between harvests (Table 3).

The inequality of sizes varied independently of the population density and the harvest time. However, the interaction between these two factors had a significant effect on that coefficient. The relationship between the weight of the labelled plant and the total weight of the other plants in the pot (a measure of the degree of dominance of the labelled plant) varied with density (it was significantly higher for density 2 than for densities 3 and 4).

Table 2. - Mean (X) and standard error (SE) of variables obtained per pot at mean densities: 1 (density 1), 20 (density 2), 40 (density 3) and 53 (density 4) plants per pot, harvested 65 days after emergence. Means followed by the same letter are not significantly different when compared by Tukey-Kramer multiple-comparison test (P). See Table 1 for details on the parameters considered.

		Density treatment			
		1	2	3	4
Wt 1	X	2.549 a	0.356 b	0.180 b	0.103 b
	SE	0.376	0.057	0.033	0.024
GR 1	X	3.772 a	1.520 b	1.418 b	1.247 b
	SE	0.156	0.222	0.153	0.172
Total Wt	X	2.549 a	2.903 a	3.638 a	3.567 a
	SE	0.376	0.784	0.169	0.271
Wt 2	X	-	0.141 a	0.097 b	0.069 b
	SE	-	0.034	0.005	0.003
Dominance	X	-	0.111 a	0.053 b	0.029 b
	SE	-	0.012	0.010	0.005
Emergence	X	-	5.25 a	6.25 a	7.00 a
	SE	-	1.03	0.48	1.00
Gini	X	0.207 ab	0.390 a	0.370 a	0.261 b
	SE	0.2665	0.017	0.018	0.036

Table 3. - Value of Fisher's statistic (F) for the effects of density, harvest time and the interaction between both factors on the variables measured on experimental populations of *G. aparine*. The results for the last five variables correspond to comparisons among densities 2, 3 and 4. * P<0.05, ** P<0.01, *** P<0.001, ns P>0.05. See Table 1 for details on the parameters considered.

	Density		Harvest		Interaction	
Wt 1	16.13	***	2.48	ns	2.81	ns
GR 1	101.47	***	1.77	ns	0.62	ns
Total Wt	4.83	ns	11.25	**	0.50	ns
Wt 2	7.64	**	4.53	*	0.26	ns
Total Wt 2 ¹	1.29	ns	41.13	***	0.53	ns
Dominance	4.39	*	1.33	ns	0.75	ns
Emergence	6.77	*	1.99	ns	2.98	ns
Gini	0.34	ns	0.74	n	9.24	**

¹Total weight of the unlabelled plants (g)

The Gini coefficient measured for isolated plants of *G. aparine* did not vary significantly between harvests ($t=0.394$; $P>0.1$). In neither of the two harvests did the Gini coefficient of isolated plants differ significantly from that of the pots at higher densities ($t<1.0$ for all paired comparisons).

The results of the comparisons between proportional-size distributions by Kolmogorov-Smirnov tests appear in Table 4 (see also Fig. 1). In general terms, the distributions were similar between densities 2 and 3 at both harvests and differed between all other pairs of densities.

Discussion

This study shows the effect of neighbourhood density on the development of individual plants of *G. aparine*. As in other species, the position of an individual within the sequence of emergence of a population of *G. aparine* does not necessarily reflect its position in the hierarchy of sizes that will develop in that population. Nevertheless, it appears that the first-emerging plant is likely to be among the largest plants of the population (at least under the conditions imposed in this experiment). Despite that emergence advantage, the weight developed by the labelled plant after 45 days was inversely proportional to the density of its neighbours, as generally found for the mean individual weight in plant populations (see Harper 1977), i.e. those plants of *G. aparine* that, because of their size, appear to dominate in a population, are also affected by their neighbours.

The fact that the weight of the labelled plant growing with pot neighbours did not increase between both harvests (i.e. between 45 and 65 days from emergence) despite the significant increase of both the mean weight of the remaining plants and the total biomass per pot could have two explanations. On the one hand, the competitive pressure on the size class in which the labelled plant belonged may have been higher than that on other size classes. Cases in which the effect of competition seems to be higher on larger rather than smaller individuals have been found for tree stands (e.g. Brand et Magnussen 1988, McFadden et Oliver 1988). On the other hand, those plants in the size class of the labelled plants may have been growing at a lower rate than other plants in the population simply because of their more advanced stage of development, as shown for other species (South et Mason 1991). Additional data about the emergence time and the growth of each plant in the population would be necessary in order to reject any of these hypotheses.

Table 4. Results of Kolmogorov-Smirnov two-sample tests comparing the cumulative distribution of linear sizes of plants at mean densities: 20 (density 2), 40 (density 3), 53 (density 4) and isolated plants after transformation into proportional values. *** $P<0.001$, ns $P>0.05$.

Harvest 1 (45 days from emergence)				Harvest 2 (65 days from emergence)			
Isolated	2		3	Isolated	2		3
2	0.393***			2	0.575***		
3	0.467***	0.170 ns		3	0.581***	0.121 ns	
4	0.558***	0.393***	0.357***	4	0.561***	0.301***	0.255***

The variation in size inequality over time differed between densities (Table 3): at the highest density the Gini coefficient tended to decrease between harvests, whereas at densities 2 and 3 it tended to increase over time (paired comparisons between harvests indicated non-significant variations, $t=1.29$, 0.86 and 1.38 for densities 2, 3 and 4 respectively). The latter pattern corresponds with the results obtained for other annual species in high-density populations (Weiner 1988, 1990). The relatively high size inequality found for the highest density for the first harvest was probably due to the notably long time for 50% emergence in two of the three pots. This is corroborated by the significant correlation between time to 50% emergence and size inequality found here ($r=0.74$; $P<0.001$). Factors other than density should be taken into account when assessing the size inequality of a plant population; genotype (Buford 1989, Govindaraju 1989a, b), herbivory and pathogens (Weiner 1988) and, as shown here, emergence time, may play major roles in the size inequality of a population.

It could be argued that features of the size distribution of a population other than the variability may change due to competition. For example, bimodality is known to develop in crowded populations of some species (Ford et Diggle 1981, Huston 1986, Huston et De Angelis 1987). Some differences in size distribution were visualized in the populations of the present study after pooling all repetitions of each density treatment (Fig. 1). Although the mean size inequality did not change between densities, significant differences were detected between size distributions as shown by Kolmogorov-Smirnov tests. It appears that at the highest density the size distribution became more normal over time, whereas at density 2 the size distribution became slightly bimodal between harvests. These results seem not to comply with those of other studies in which deviations from normality in size distributions develop as a result of more intense competition between neighbours (White et Harper 1974, Ford et Diggle 1981, Gates 1982, Higgins et al. 1984, Westoby 1984).

The results of this experiment support the idea that competition between *G. aparine* plants in crowded populations is more symmetric than in other species, i.e. there is some effect of small plants on large plants. Other studies have shown a similar kind of interaction, which has sometimes been related to the morphology of the species: species with leaf area evenly distributed along a vertical axis (like grasses and *G. aparine*) seem to be more likely to show symmetric competition and consequently less pronounced dominance-suppression development (see Rabinowitz 1979, Turner et Rabinowitz 1983, Brand et Magnussen 1988, Ellison 1989). However, competition between shoots in two grass species has been found to be asymmetric (de Kroon et al. 1992). Given the relative shade tolerance of *G. aparine*, evidenced by its profuse growth in forested areas and hedgerows (see Holm et al. 1977, Malik et Van den Born 1988, Burel et Baundry 1990), it is possible that those plants shaded by bigger ones are not growing in a less favourable environment than their bigger neighbours. Kembell et al. (1992), on the other hand, found that a shaded branch of a *G. aparine* plant is not sustained by the unshaded portions of that plant. It could then be argued that branches of the same plant in a population may be competing with each other as separate plants. Since the larger plants in a *G. aparine* population are much more branched than the smaller ones, competition may affect the growth of the first group more severely than that of the latter. Studies on a number of species with a range of morphological (leaf shape and arrangement) and physiological features (physiological integration and shade tolerance) are needed if the underlying causes of symmetric and asymmetric competition are to be unveiled.

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Souhrn

Vliv denzity na vývoj velikostní hierarchie v průběhu vegetační sezóny byl sledován na experimentálních skleníkových populacích *Galium aparine*. Velikost první vzešlé rostliny v populaci byla stanovena nedestruktivně (odhad byl proveden na základě regrese mezi vahou a výškou a délkou větví), což umožnilo měřit její růstovou rychlost. Destruktivní odběry byly provedeny po 45, resp. 65 dnech růstu populace.

Růstová rychlost prvních vzešlých rostlin v populaci byla, ve srovnání s izolovanými rostlinami, průkazně ovlivněna přítomností sousedů a jejich hmotnost klesala se vzrůstající hustotou populace. Velikostní hierarchie (inequalita) nebyla ovlivněna denzitou ani časem, byla však zjištěna průkazná interakce mezi těmito dvěma faktory. Kolmogorovův-Smirnovův test odhalil, že se ostatní atributy distribuce velikostí měnily s denzitou.

Na základě prezentovaných výsledků lze konstatovat, že vnitrodruhová kompetice mezi rostlinami *Galium aparine* je symetričtější proces, než je obvyklé u většiny dosud studovaných druhů. Práce dále diskutuje, jaký vliv má na symetrii kompetice rozložení listového aparátu v prostoru, tolerance vůči zastínění a „vnitroindividuální“ kompetice.

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