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Why the biomass of over-crowded populations of *Galium aparine* L. does not increase during density-dependent mortality? An experimental approach

JAVIER G. PUNTIERI[1] and PETR PYŠEK[2]

Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB
[1] Current address: Departamento de Botánica, Universidad National del Comahue. Unidad Postal Universidad. 8400, Bariloche, Argentina (author for correspondence).
[2] Current address: Botanical Institute, Czech Academy of Sciences, CZ-252 43 Pruhonice, Czech Republic.

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Summary

Biomass accumulation, mortality, growth allometry and size-hierarchy development over time were assessed for an experimental, over-crowded population of *Galium aparine*. Individual plants were labelled according to emergence time and initial size. The allometry of growth of 54-day old *G. aparine* populations at different densities with or without the addition of physical support was analysed for another experiment. The significant decrease in population density over time in the over-crowded population was not accompanied by a significant increase in biomass. The biomass/stem length allometry differed between large and small plants within this population. Initial size had a more clear effect on plant survival and growth than emergence time. The slope of the biomass/length allometric line increased with population density in the second experiment, but was not significantly affected by support availability. The absence of biomass accumulation over time in *G. aparine* populations could be due to the shift in the hierarchy of resource exploitation of the population caused by the progressive increase in elongation of the largest individuals and their subsequent lodging.

Key words: *Galium aparine*, competitive hierarchies, competition, self-thinning, emergence time.

1. Introduction

Both empirical evidence and theoretical models consider self-thinning, i.e. the simultaneous occurrence of population biomass accumulation and density-dependent mortality, the most common outcome of overcrowding in populations of sessile organisms, including plants (YODA et al. 1963, WHITE & HARPER 1970, WELLER 1987). Self-thinning is believed to be preceded by a stage of competitive hierarchy development, during which plant biomass and shape become increasingly variable among neighbour plants (ROSS & HARPER 1972, HARPER 1977, MARKS & PRINCE 1981, MILLER 1987, BENJAMIN 1990). Differences in light conditions tend to make small plants in crowded populations to develop more in stem length than in biomass, compared to large plants. The more pronounced elongation of small plants makes them more prone to structural failure, as they reach a biomass/height relationship incompatible with vertical growth, which decreases their survival probability (HARA 1988, THOMAS & WEINER 1989, KING 1990, WEINER 1990). In self-supporting plants, the biomass/height allometry is subject to two opposing selective forces: whereas competition for light favours the development of a longer stem, gravity favours the development of a shorter and sturdier stem, capable of supporting the biomass of the plant and standing external destabilizing forces such as wind (see KING 1990, GIVNISH 1995).

As long as external support is available, the height growth of climbing plants is less restricted by biomechanical constraints than that of self-supporting plants (DEN DUBBELDEN 1994, GIVNISH 1995). This may have notable effects on the development of competitive hierarchies and the pattern of density-dependent mortality in crowded conditions. Little information concerning the response of climbing plants to crowding is available, despite the importance of many of them as weeds (but see WEINER 1990, KLIMEŠ & KLIMEŠOVÁ 1994). Studies on crowded populations of *Galium aparine* L. (Rubiaceae), a widely distributed annual climbing weed, indicated that although density-dependent mortality takes place as usual, the growth of the surviving plants may not over-compensate for the biomass loss due to mortality (PUNTIERI & HALL 1996). The results of other studies suggest that intra-specific competition has little effect on size differences among neighbour plants in this species (PUNTIERI 1993, PUNTIERI & PYŠEK 1993, 1998). The present study was aimed at analysing the allometric relationship between biomass and stem length in experimentally-grown crowded plants of *G. aparine* and assessing the role of emergence time and post-emergence size on plant success. Additionally, the effect of physical support on the biomass/length allometry at different densities was analysed.

2. Materials and methods

2.1. Study species

G. aparine is an annual species with hook-climbing habit. Provided physical support is available, it may reach 2 m in height, although it may complete its life cycle as a prostrated plant. The above-ground portion of each plant consists of a square-section main stem, branches (which start developing from the basal nodes of the main stem), and whorled leaves and leaf-like stipules at each stem node. Both stem and leaves have abundant hooked hairs which fasten the plant to most types of surface it contacts, including other plants. The stem of *G. aparine* does not grow in diameter once it has completed its extension (J. PUNTIERI and P. PYŠEK, unpul. obs.). *G. aparine* is considered native to Europe and Asia but nowadays it has an almost worldwide distribution (MOORE 1975, HOLM et al. 1977). It is a troublesome weed in cultivated fields, woodlands, wastelands, hedgerow ditches and roadside verges (SALISBURY 1942, FALÍNSKI 1986, GRIME et al. 1988, MALIK & VANDEN BORN 1988, BUREL & BAUNDRY 1990, MATTHEI 1995, MAMAROT 1996).

2.2. Experimental design and data record

Two independent experiments were set up in a glasshouse under a natural day/night light cycle (14–16 hs. of daily radiation; Department of Plant Sciences, University of Oxford, UK). Each experimental population consisted of closely packed square pots which simulated the structure of a self-sown, crowded patch of *G. aparine*. This experimental design was considered valid for a study centered on the response of labelled individual plants throughout the growth period. More statistically-sound designs were inapplicable because of the large surface of homogeneous glasshouse space required for setting up independent replicates and the amount of simultaneous measurements that would have been necessary given the equipment and working-force available to the authors.

In both experiments 3.6 cm-side and 4 cm-deep plastic pots filled with sandy loam were the sample units. The soil used was relatively light and well-aerated and proved to be appropriate for the growth of this species in a previous study (PUNTIERI 1993). In experiment 1, very dense *G. aparine* populations were grown. Seeds for this experiment were collected manually from natural populations (roadside, river bank, field margin and hedgerow) in Oxfordshire (UK). Forty seeds were sown in each pot and covered with approximately 1 cm of soil. Because of possible positional effects in the glasshouse, two blocks of pots were arranged. Each of these blocks was surrounded by two guard rows of equally sown pots, so as to minimize border effects and simulate as closely as possible the structure of self-sown populations. The outer guard row of plants was supported by string, so as to make them grow vertically at all times. All pots were watered daily.

Block 1 consisted of 36 pots arranged in a 6 x 6 pot group. Six harvests of six pots were planned. Each pot was randomly assigned to a harvest time. Harvests were limited to four due to the flowering of some plants. The production, and hence shedding, of fruits would induce complicated errors in dry matter assessment. In block 2, 24 pots arranged in a 4 x 6 pot group were prepared, allowing four harvest of six pots each. Harvests were made at the same time as in experiment 1. One of the pots to the fourth harvest was eventually discarded due to the fungal infection and death of all plants rooted in it. The harvests were carried out 58 (29 April 1991), 79, 94 and 124 days after the first emergences for both blocks.

For each block, a group of pots with the same number of pots and a similar sowing density of *G. aparine* was set up in the same glasshouse beside the corresponding block. These pots were used as replacements for those pots that were harvested, so as to avoid creating gaps in the canopy after each harvest.

In this experiment, seedlings were labelled as they emerged, every two days from the day of the first emergences up until the end of the period of massive emergence, and every three days from then on. Labelling was carried out by painting a portion of the base of the hypocotyl with non-toxic plastic paint. Fifteen days after the first emergences, when the emergence of new seedlings had ceased, seedlings were classified into three size categories: plants smaller than 2 cm high (from the soil surface to the apical meristem) were considered small plants, plants between 2 and 3 cm high were considered intermediate-size plants and plants higher than 3 cm high were considered large plants. Two small plants, two intermediate-size plants and two large plants were labelled in each pot of block 1 and in 18 pots of block 2, irrespective of their emergence groups.

At harvest, each individual in each selected pot was cut at soil level and its emergence group, initial-size group, stem length (including the main stem and all branches) and dry weight (after oven-drying at 70°C for 40 hs.) were recorded.

In experiment 2, seeds provided by a seed supplier were sown at four densities (1, 2, 4 and 8 plants per pot). Two groups of 36 pots were prepared for each density. Each group of each density was assigned to each of two treatments: with support or without support. In the middle of each pot of the first of these treatments, a 30 cm long thin wooden stake was inserted. In the pots of the "without support" treatment, plants were supported only by their own tissues and by neighbour plants. Dry weight and stem length of each plant were recorded after 54 days of growth. A more detailed description of the design and preparation of this experiment as well as part of its results are published elsewhere (PUNTIERI & PYŠEK 1993); here we report only the biomass/stem length allometry of these plants.

2.3. Data analyses

Because of the low number of plants corresponding to both early and late emergence tails in experiment 1, these plants were pooled with those of the closest more numerous emergence group, leaving three emergence groups for each experiment: early-emerging plants = emergence group A (0–4 days from the first emergences), intermediate emergence-time plants = emergence group B (5–6 days from the first emergences) and late-emerging plants = emergence group C (7–12 days from the first emergences). The number of plants and aboveground biomass corresponding to each emergence group in each harvested pot were obtained. The effects of harvest time (four levels), emergence group (three levels), block (two levels) and the interactions among these factors on number of plants, aboveground biomass (log-transformed) and plant weight (log-transformed), were assessed by means of ANOVA for unbalanced designs (GLM procedure). The variation of the plant dry weight CV per pot with harvest time, block and the harvest time x block interaction was assessed with a two factor ANOVA.

Log-dry weight (Y-variable) vs log-stem length (X-variable) relationships were described by means of linear regressions. Regression slopes were compared by means of F-tests followed by Tukey's HSD paired comparisons (ZAR 1984).

3. Results

3.1. Experiment 1

The total number of seedlings corresponding to emergence groups **A**, **B** and **C** were, respectively: 184, 571 and 284 for block 1 and 44, 112 and 85 for block 2. Plants developed vertically, supporting each other, for the longest part of the experiment. However, the canopy collapsed between the last two harvests in both blocks,

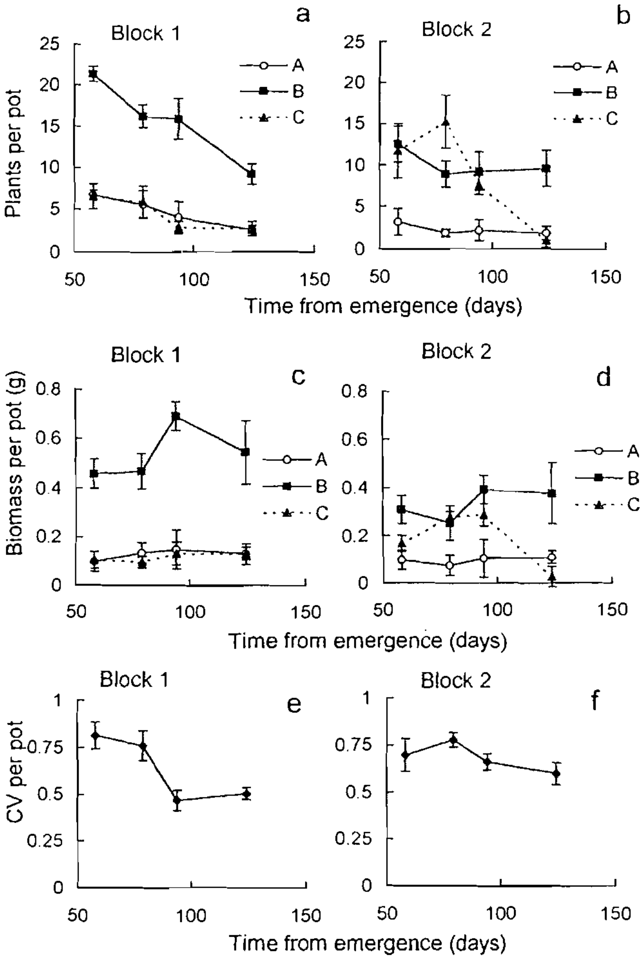

Fig. 1. Mean (± 1 SE) number of plants per pot (a, b), aboveground biomass per pot (c, d) and coefficient of variation (CV) per pot at four harvests (58, 79, 94 and 124 days after emergence) for plants of blocks 1 and 2 of experiment 1. Plants emerged at different times after the first emergences (0–4 days: **A**, 5–6 days: **B** and 7–12 days: **C**) are discriminated in graphs "a" to "d".

Table 1. Results of ANOVAs (Fisher's F and error probability, P, are provided) assessing the effects of emergence group (EG), harvest time (HT), block (BK) and their interactions on number of plants, aboveground biomass and mean aboveground plant weight.

	number of plants		plant biomass (log-transformed)		weight per plant (log-transformed)	
factor	*F*	*P*	*F*	*P*	*F*	*P*
harvest time (HT)	16.2	0.001	1.2	0.31	21.6	0.001
emergence group (EG)	67.3	0.001	41.9	0.001	1.9	0.16
block (BK)	3.4	0.07	0.1	0.71	1.7	0.19
EG × HT	2.7	0.02	1.2	0.31	1.1	0.38
EG × BK	19.4	0.001	3.9	0.02	4.9	0.008
HT × BK	0.4	0.77	0.6	0.60	2.8	0.04
EG × HT × BK	4.1	0.001	1.1	0.36	0.4	0.86

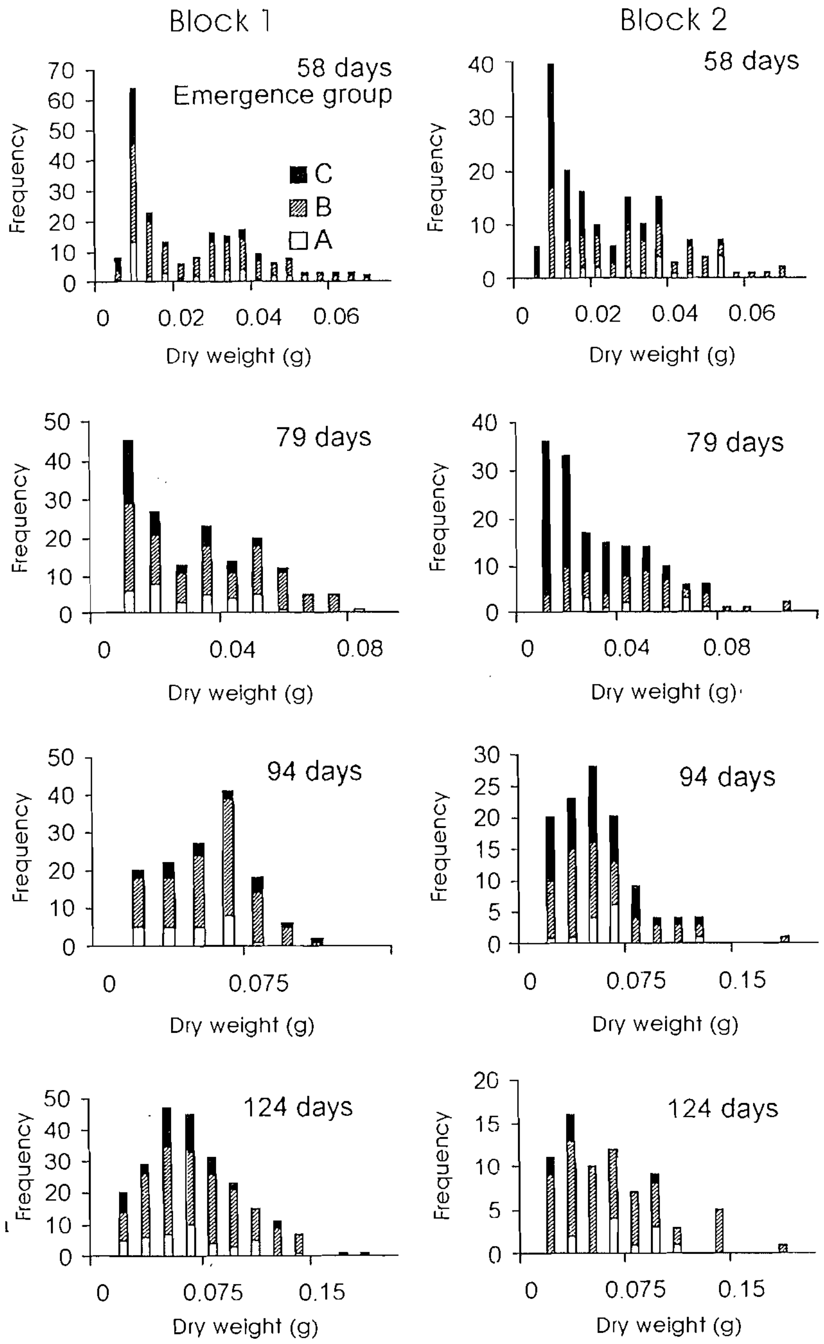

Fig. 2. Frequency distribution of plant dry weights for blocks 1 (left column) and 2 (right column) of experiment 1 at four harvests (58, 79, 94 and 124 days after emergence), discriminated by emergence group (**A**, **B**, and **C**).

after which all plants developed slanted or horizontally, leaning on the guard-pot plants. In both blocks, a large proportion of plants consisted of an unbranched main stem. Some plants, which comparised an increasing proportion of the population in successive harvests, developed one or two branches from the axillary buds of the cotyledons and, occasionally, smaller branches from the most basal whorl of normal leaves. Nevertheless, by the time of the last harvest, most of the smallest plants, many intermediate-size plants and even some large plants were still unbranched. In many large individuals the presence of dead branches at the time of the last harvest indicated that die back had taken place. Unfortunately, the extent of die back in each plant could not be quantified due to the drop of dead branches before and during harvest.

Table 2. Mean and standard deviation of regression coefficients relating plant dry weight and stem length (both variables log-transformed) for plants of each size peak of blocks 1 and 2 of experiment 1 harvested 58, 79, 94 and 124 days after emergence. The coefficient of determination (R^2) is indicated for each regression.

		weight distribution peak	regression coefficient		R^2	N
			mean	st. dev.		
Block 1						
	58 days	first	0.942	0.065	70.2	89
		second	2.977	0.183	69.1	119
	79 days	first	0.931	0.101	59.5	55
		second	2.055	0.085	83.9	113
	94 days	first	0.846	0.192	69.7	9
		second	1.788	0.074	82.1	128
	124 days	first	1.517	0.352	57.5	14
		second	1.641	0.071	69.3	234
Block 2						
	58 days	first	0.828	0.082	60.6	67
		second	3.090	0.199	69.4	107
	79 days	first	0.818	0.110	51.0	53
		second	1.800	0.075	84.7	105
	94 days	first	0.698	0.146	60.9	15
		second	1.542	0.072	81.9	102
	124 days	first	–	–	–	–
		second	1.516	0.099	77.5	69

For both blocks, the number of plants per pot decreased over time after the period of emergence (Table 1; Fig. 1 a, b). Plant number per pot depended very significantly on emergence group, harvest time and the emergence group x block interaction (Table 1). Less significant effects on plant number per pot were found for the emergence group x harvest time and the emergence group x block x harvest time interactions. Plants corresponding to emergence group **B** were, on average, more numerous and included more biomass than those corresponding to the other emergence groups throughout the experiment (Fig. 1). Biomass per pot did not vary significantly between harvests but was significantly affected by emergence group and (less significantly) by the emergence group x block interaction (Table 1; Fig. 1c, d). Mean plant weight per pot increased over time, and was significantly affected by the interactions between emergence group and block and harvest time and block

Table 3. Mean and standard deviation of the regression slope relating plant weight and stem length (log-log transformed) for plants of experiment 1 labelled according to initial size and harvested 58, 79, 94 and 124 days after emergence. The coefficient of determination (R^2) and the number of plants in which each regression was based are indicated.

initial size	mean	st. dev.	R^2	N
small	0.962	0.082	78.2	39
intermediate	1.519	0.081	81.2	82
large	1.218	0.077	71.9	99

Table 4. Mean and standard deviation of the regression slope relating plant weight and stem length (log-log transformed) for plants grown at different densities with or without physical support (experiment 2). The coefficient of determination (R^2) and the number of plants in each condition (N) are indicated. Mean regression coefficients sharing a similar letter (a–c) are not significantly different (Tukey's HSD test).

initial density	treatment	mean	st. dev.	R^2	N
1 plant per pot	without support	0.290a	0.064	36.0	36
	with support	0.455ab	0.133	23.3	36
2 plants per pot	without support	0.847b	0.071	67.1	71
	with support	0.876ab	0.143	34.4	71
4 plants per pot	without support	0.956abc	0.096	41.7	137
	with support	1.259bc	0.176	27.4	134
8 plants per pot	without support	1.296bc	0.130	30.3	226
	with support	1.429	0.110	38.0	276

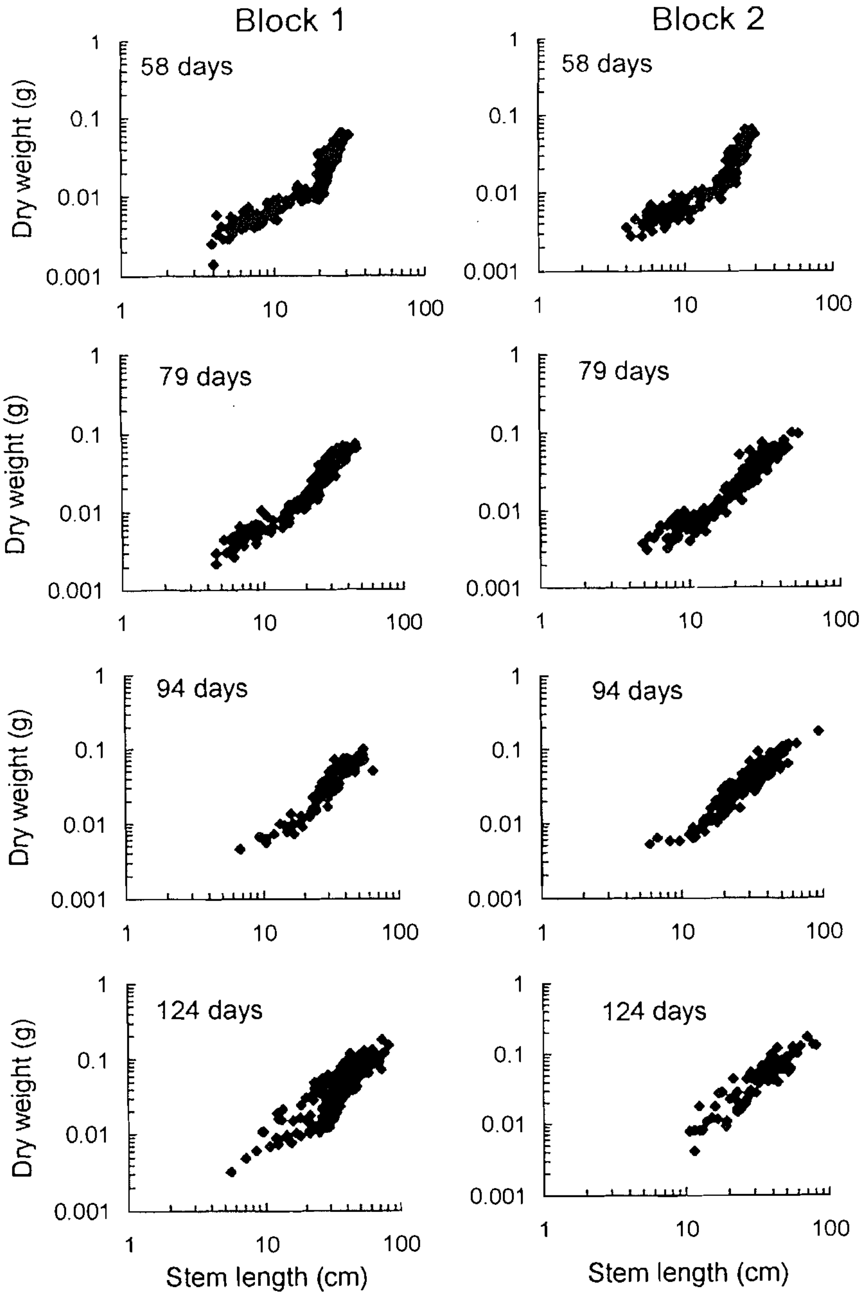

Fig. 3. Relationship between plant dry weight and stem length (log-log scale) after 58, 79, 94 and 124 days of growth for blocks 1 (left column) and 2 (right column) of experiment 1.

(Table 1). The CV of the dry weight per plant decreased significantly over time ($F = 8.1$, $P < 0.001$; Fig. 1 e, f). Non-significant effects of block ($F = 1.2$, $P = 0.09$) and of the block x harvest time interaction ($F = 2.3$, $P = 0.28$) on the CV per pot were found.

Plant dry weights were bimodally distributed at the time of the first harvest for blocks 1 and 2 of experiment 1 (Fig. 2). Bimodality was repeatedly found for the plants in each pot, so that it was not related to between-pot differences in plant weight (data available upon request). For both blocks, the frequency distribution of dry weights became unimodal in successive harvests (Fig. 2).

Plant survival in experiment 1 depended on initial seedling size: the percentages of seedlings corresponding to the small, intermediate and large initial size classes that survived after 124 days of growth were, respectively, 5.6%, 38.9% and 67.6%.

For experiment 1, the log-dry weight to log-stem length relationship had two-slope pattern for the first

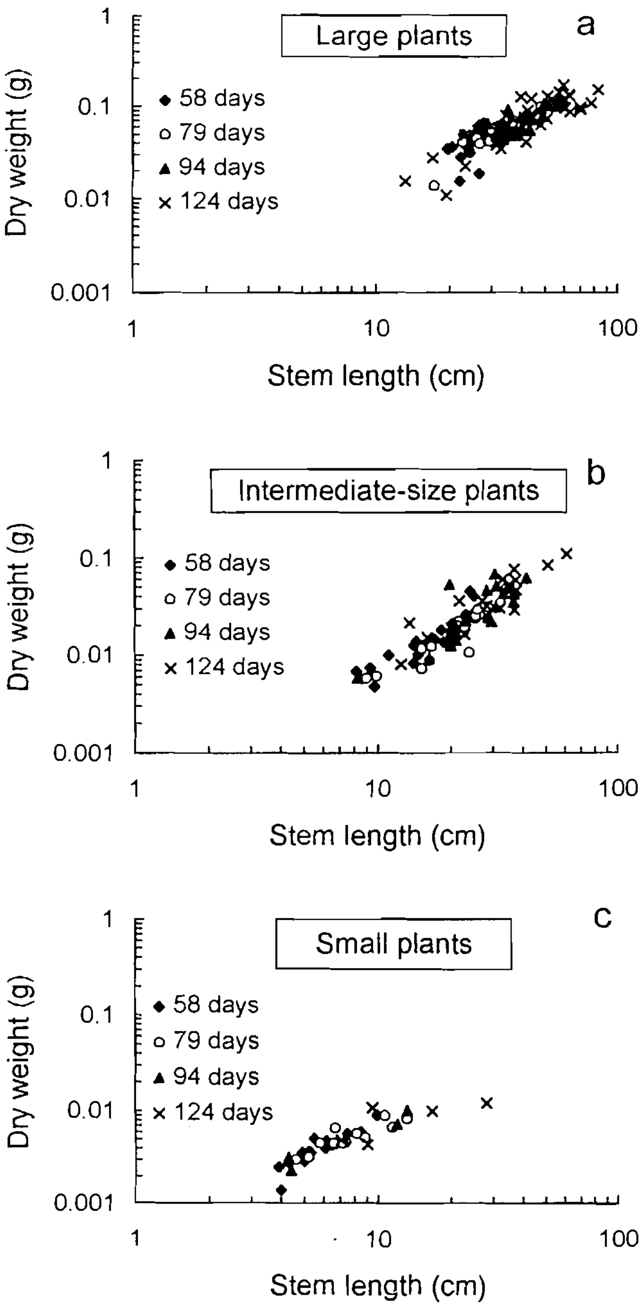

Fig. 4. Relationship between plant dry weight and stem length (log-log scale) for plants labelled as large plants (a), intermediate-size plants (b) and small plants (c) at the beginning of experiment 1, and harvested 58, 79, 94 and 124 days after emergence.

two harvests: a less steep slope was found for small plants than for large plants (Fig. 3; Table 2). This relationship became linear in successive harvests, as the size distributions became unimodal; its slope at the last harvest was less steep than that for the largest plants of the first harvest of experiment 1 (Table 2).

The slope of the allometric biomass/length relationship was low for those plants that were among the smallest plants after emergence, intermediate for large individuals after emergence and high for intermediate-size plants after emergence (Table 3, Fig. 4). For the latter two size groups, the ranges of both plant biomass and length were high and similar for the first and the last harvests (Fig. 4a, b).

3.2. Experiment 2

The slope of the line relating plant weight and stem length on a log-log scale varied significantly among the treatments of experiment 2 ($F = 5.6$, $P < 0.001$; Fig. 5, Table 4). The slope of that relationship increased significantly with population density ($P < 0.05$) both for supported and for unsupported plants. Tukey' HSD tests determined that the presence of physical support did not affect significantly the slope of the weight/length allometric relationship for each density, although the mean slope was consistently higher for supported than for unsupported plants (Table 4).

4. Discussion

4.1. Competition and hierarchies in crowded *Galium aparine* populations

In most plant populations studied, the loss of biomass caused by density-dependent mortality is over-compensated by the growth of the surviving plants, so that the biomass of the whole population increases over time (see WELLER 1987, ZEIDE 1987). In *G. aparine* populations biomass may not increase as mortality takes place, as found in the present study for experimental populations and in a previous study for roadside populations of this species (PUNTIERI & HALL 1996). In view of our current knowledge on plant interactions, population biomass accumulation during density-dependent mortality may be restricted by the absence of competitive hierarchy development among neighbour plants, perhaps as a consequence of strong below-ground competition (WEINER et al. 1997). However, there were clear signs of competitive hierarchy development by the time of the first harvest of the over-crowded populations studied here: after 58 days of growth, when each plant consisted of an erect, unbranched stem, two groups of individuals with different mean biomass and different size allometry could be distinguished. Large, tall plants had a higher biomass accumulation in proportion to their stem length than their smaller neighbours.

The initial differentiation between small and large

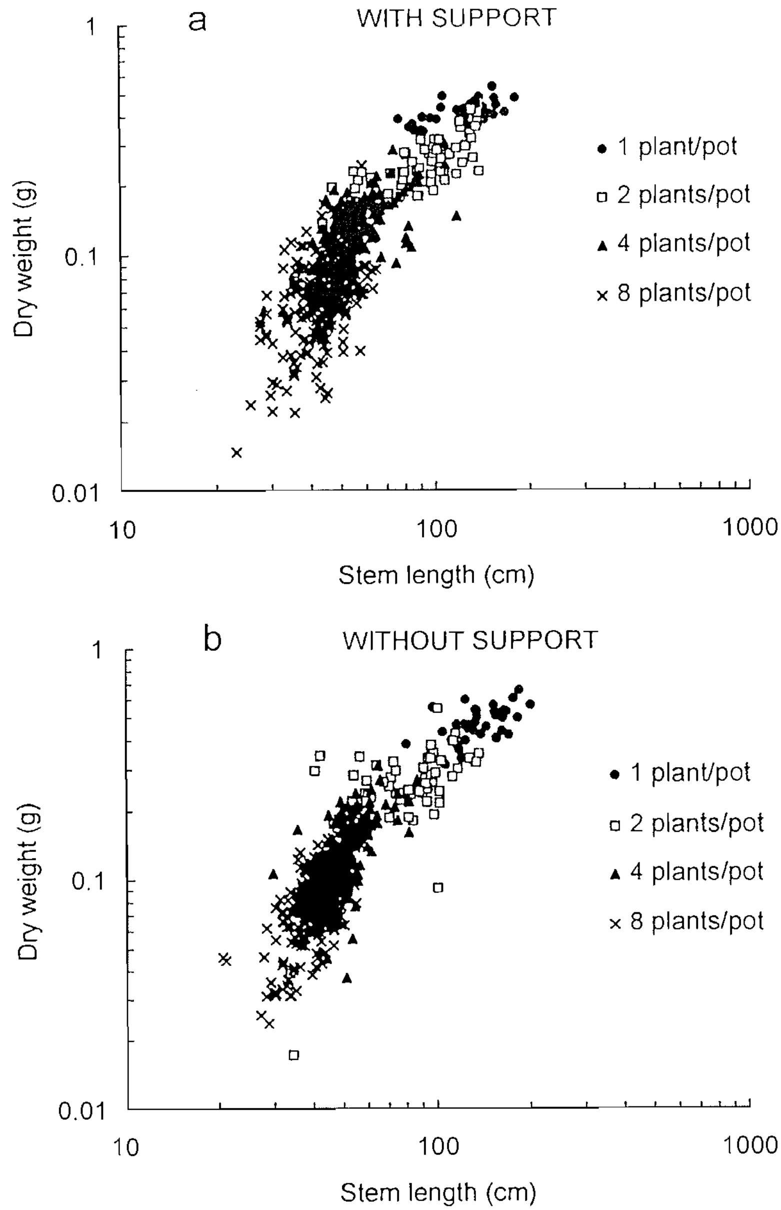

Fig. 5. Relationship between plant dry weight and stem length (log-log scale) for plants grown with support (a) or without support (b) at four population densities (1, 2, 4 and 8 plants per pot) for 54 days.

plants in experiment 1 could, in our view, be attributed to more than one, not necessarily excluding, factors. Unlike what we expected, emergence time, usually a major contributor to plant success in a competitive environment (ROSS & HARPER 1972, FOWLER 1984, STANTON 1985, MILLER 1987, BENJAMIN, 1990), played only a secondary role in the position of plants within the ranking of sizes. Although both the number and the total biomass of late-emerging plants in experiment 1 after 124 days of growth were proportionally lower than those of earlier-emerging plants, late emergers were present in most size classes throughout the experiment, rather than only in the small-size classes. A number of studies have shown that *G. aparine* may consist of a variety of ecotypes which differ from each other in some morphological and allometric features and which seem to be adapted to open environments such as arable lands or to closed environments such as woodlands and hedgerows (FROUD-WILLIAMS 1985, BAIN & ATTRIDGE 1988, BERKEFELD 1988, MALIK & VANDEN BORN 1988, NIEMANN 1988, AUGE & MAHN 1988, 1991). Since such ecotypes may be found in geographically close sites, it is possible that more than one of them were represented in the sample of seeds used in the present study. Thus, genetically-determined features may well have been involved in the early size and shape differences among competing *G. aparine*. Once early size differences were established, the plastic allocation of photosynthates of *G. aparine* plants in response to variations in light availability (AUGE & MAHN 1988, DEN DUBBELDEN 1994) would have enhanced the initial differences among neighbours. The importance of light availability in the allometric differentiation between small and large *G. aparine* plants found for experiment 1 after 58 days of growth is supported by the fact that the less crowded populations of experiment 2 did not exhibit a similar allometric differentiation in approximately the same period.

Even though the early differentiation in size and allometry between large and small plants found in experiment 1 proved to be related to plant success at later stages of growth, some small individuals were able to survive up to the end of the experiment whereas some of the largest individuals died during this experiment. Size differentiation in crowded populations of plants is usually interpreted as a dominance-suppression relationship in which large, dominant individuals tend to monopolize photosynthetic radiation (WEINER & THOMAS 1986, WEINER 1988). In the case of crowded *G. aparine* populations, plant size may not be directly related to the position of a plant in the hierarchy of resource exploitation of the population. This could be, at least partly, due to the dynamics of the canopy derived from biomechanical and morphological features of this species.

At early growth stages, large individuals in a crowded *G. aparine* population have (as shown in experiment 1) a higher biomass per stem length unit (or plant height) than their smaller neighbours and would, therefore, provide most of the biomechanical support of the population. As *G. aparine* plants grow, their self-supporting capacity decreases as stem length increases disproportionately more than stem biomass. Neighbour *G. aparine* plants are fastened to one another by their hooked hairs. At early growth stages, plant-to-plant fastening enables all individuals, even the weakest ones, to grow upright, but at later growth stages it causes massive lodging as the largest individuals collapse. Whether an individual is positively or negatively affected by lodging would depend on its position relative to the direction in which the canopy falls, rather than solely by the position of that individual in the size ranking of the population before lodging. This "re-setting" of the competitive hierarchy of the population would explain the death of some of the largest, previously dominant, individuals, which, in turn, may account for the absence of over-compensatory growth during density-dependent mortality.

The variation over time in the allometry of plants after the early differentiation could have been the result of several factors. A number of studies have stressed the importance on plant growth allometries of exogenous factors such as competition (KING 1990, WEINER & THOMAS 1992, WEINER & FISHMAN 1994), presence of mechanical support (HOLDBROOK & PUTZ 1989, DEN DUBBELDEN 1994), soil resource availabiltiy (FREER 1992) and mechanical loading (PATTERSON 1992, JEFFE & FORBES 1993, OLSER et al. 1996). In view of the results of experiment 2, the presence of mechanical support is not one of the most important factors affecting *G. aparine* allometries. It is possible that the time variation of *G. aparine* allometries has an important ontogenetic component. Each individual would tend to increase elongation relative to biomass accumulation as it develops, thus shifting from a self-supporting to a climbing habit. In view of a recently published study, this shift would be paralleled by a decrease in leaf area growth over biomass accumulation (KAZINCZI et al. 1998). The more crowded a *G. aparine* population, the more it would take for each plant to reach the stage of low biomass accumulation per stem length unit (Fig. 5). In crowded populations larger plants would move faster along the ontogenetic trend than smaller plants, so that the former would reach the stage of less steep biomass/stem length allometry line before the latter (Fig. 4).

4.2. Conclusions

Climbing plants are, by definition, more adapted to profitting from the presence of other plants than self-supporting species (see KLIMEŠ & KLIMEŠOVÁ 1994). Nevertheless, the presence of other plants also means a restriction in photosynthetic capacity due to shading. These opposing effects of crowding on the growth of climbing plants may result in a less pronounced dominance-suppression relationship than that found for self-supporting species (see WEINER & THOMAS 1986). Positive plant-plant interactions other than mutual support (see BERTNESS & CALLAWAY 1994, HACKER & BERTNESS 1995) may also reduce the dominance-suppression effect of competition for light and make plant success in crowded populations less size-dependent. This could explain the absence of dominance and suppression found for some populations of self-supporting species (e.g. TURNER & RABINOWITZ 1983, OLIVER & LARSON 1990). Models of the biomass/density relationship which consider competition as the only type of interaction among neighbour plants (such as the self-thinning rule; YODA et al. 1963, WHITE & HARPER 1979) fail to describe that relationship for some plant populations, including those of *G. aparine*. Such models assume size differences among plants to drive to progressively more asymmetric competitive effects and, therefore, to strongly size-related survival probabilities, which may not hold when other types of interactions are taken into consideration.

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