

Positive interactions can increase size inequality in plant populations

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Summary

1. Large variation in the size of individuals is a ubiquitous feature of natural plant populations. While the role of competition in generating this variation has been studied extensively, the potential effects of positive interactions among plants, which are common in high-stress environments, have not been investigated.

2. Using an individual-based 'zone-of-influence' model, we investigate the effects of competition, abiotic stress and facilitation on size inequality in plant monocultures. In the model, stress reduces the growth rate of plants, and facilitation ameliorates the effects of stress. Both facilitation and competition occur in overlapping zones of influence. We tested some of the model's predictions with a field experiment using the clonal grass *Elymus nutans* in an alpine meadow.

3. Facilitation increased the size inequality of model populations when there was no density-dependent mortality. This effect decreased with density as competition overwhelmed facilitation. The lowest size inequality was found at intermediate densities both with the model and in the field.

4. When density-dependent mortality was included in the model, stress delayed its onset and reduced its rate by reducing growth rates, so the number of survivors at any point in time was higher under harsh than under more benign conditions. Facilitation increased size inequality during self-thinning.

5. *Synthesis.* Our results demonstrate that facilitation interacts with abiotic stress and competition to influence the degree of size inequality in plant populations. Facilitation increased size inequality at low to intermediate densities and during self-thinning.

Key-words: alpine meadow, density-dependent mortality, *Elymus nutans*, facilitation, individual-based model, plant–plant interactions, size inequality

Introduction

Large variation in individual size is a ubiquitous feature of natural plant populations, and this variation has major implications for plant ecology and evolution. There have been numerous studies on the effects of competition among individuals on size inequality (e.g. Shumway & Koide 1995; Weiner *et al.* 2001). Competition for resources usually increases size inequality, but it can decrease variation under certain conditions and mechanisms of competition (Wyszomirski, Wyszomirska & Jarzyna 1999; Weiner & Damgaard 2006). Many plant–plant interactions are, however, not competitive. Studies

in recent decades have shown that facilitative interactions are widespread in plant communities, especially in ecosystems characterized by harsh environmental conditions (for recent reviews see Callaway 2007 & Brooker *et al.* 2008). Recent experimental and theoretical studies have shown the potential impact of positive interactions on the structure of populations and communities (Michalet *et al.* 2006; Chu *et al.* 2008; Gross 2008) and on ecosystem functioning (Kikvidze *et al.* 2005), but we know of no studies on the effects of facilitation on size variability within populations.

Simple density dependence has been studied in two ways, and these serve as the starting point to investigate the effects of competition and facilitation on size variability. In the first approach, the production of stands of plants grown at different

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densities is compared over a given growth interval: a density series. This is a logical starting point for the study of facilitation as well as competition and size variation. The other way to study density dependence has been to follow the development of very crowded stands of plants, in which some individuals grow while others die (density-dependent mortality or self-thinning). Self-thinning is usually modelled as $w = k\rho^\beta$, a demographic relationship between mean biomass (w) and plant density (ρ), where k and β are the self-thinning coefficient and exponent respectively. The value of β has been a topic of heated debate (e.g. Weller 1987; Enquist, Brown & West 1998). Our focus here is not β but size variation among individuals. It has been shown that density-dependent mortality is concentrated among the smallest individuals, reducing size variation (Weiner & Thomas 1986). It is not clear how facilitation might affect this variation.

To investigate the effects of abiotic stress, facilitation and competition on size variation in populations without and with density-dependent mortality, we extended a recently developed model (Chu *et al.* 2008) and tested some of the predictions of the model with a field experiment in an alpine meadow on the Tibetan Plateau, where positive interactions have been shown to play a critical role in plant growth and population development (Chu *et al.* 2008; Wang *et al.* 2008).

Materials and methods

MODEL

Our model is similar to that described previously (Chu *et al.* 2008), which itself was an extension of Weiner *et al.*'s (2001) 'zone-of-influence' model. In the model, each individual obtains resources from a circular zone, and neighbouring individuals compete for resources where these zones overlap (Weiner *et al.* 2001). The area occupied by a plant, A , represents the amount of resources potentially available and is related to the plant's biomass, B , as $A = cB^{2/3}$, where c is a constant ($c = 1.0$ in all the simulations presented here). An individual's potential growth rate (i.e. in the absence of neighbours) is defined by the equation:

$$\frac{dB}{dt} = r\left(A - \frac{B^2}{B_{\max}^{4/3}}\right) = r\left(cB^{2/3} - \frac{B^2}{B_{\max}^{4/3}}\right), \quad \text{eqn 1}$$

where B_{\max} is the maximum (asymptotic) plant mass, and r is the initial (maximum) growth rate (in units of mass area⁻¹ time⁻¹).

Neighbouring plants compete for the resources where their areas (A) overlap. The realized growth rate of the plant is described by the equation:

$$\frac{dB}{dt} = r\left(A_c - \frac{B^2}{B_{\max}^{4/3}}\right), \quad \text{eqn 2}$$

where A_c , the effective area of a plant, is calculated as the area it covers minus that part of the area lost to neighbours. After Weiner *et al.* (2001), we used a discrete approximation of continuous two-dimensional space, divided into a fine grid, to obtain the overlapped area.

Abiotic stress is included in the model with a parameter s , which ranges from 0 (no stress) to 1 (maximum stress), and which decreased the growth rate of all plants in a simple linear fashion (Molofsky & Bever 2002). Based on current understanding of facilitation, we

assume facilitation only occurs when there is stress ($s > 0$), and it acts to ameliorate the negative effects of stress on plant performance (Callaway 2007). We assume that facilitation is a function of the total of all areas of overlap with neighbouring plants, A_f . Thus, the average A_f of plants within a population is positively related to population density and to mean plant size. The realized growth rate of the plant is modelled as

$$\frac{dB}{dt} = r\left(A_c - \frac{B^2}{B_{\max}^{4/3}}\right)\left(1 - \frac{s}{A_f + 1}\right) \quad \text{eqn 3}$$

In our simulations, we consider the effects of competition, environmental stress and facilitation on populations with and without mortality. To explore the size inequality in populations without mortality, we assume that plants cannot have negative growth rates, but continue to live and maintain the maximum size they achieve (Weiner *et al.* 2001). We looked at a wide range of population densities (4.5–9.5, on a natural logarithmic scale), and we use the coefficient of variation (CV) of mass as the measure of size variation within the population (Weiner *et al.* 2001). To study self-thinning, we simulated a high initial population density (\ln density = 9.1, equivalent to a density of 9000 individuals m⁻²). We also simulated other initial densities and the results were similar to those presented below. Dead individuals do not compete with or facilitate other plants and are excluded from the statistical analyses (Weiner *et al.* 2001).

Due to the association of harsh conditions and positive interactions, it is difficult to separate their effects on performance in field experiments, but easy to do so in simulations. To investigate the effects of stress without facilitation, we set $A_f = 0$ in eqn 3, and the realized growth rate becomes

$$\frac{dB}{dt} = r\left(A_c - \frac{B^2}{B_{\max}^{4/3}}\right)(1 - s) \quad \text{eqn 4}$$

To explore the effect of the size symmetry of competition on the model, we consider three degrees of competitive size symmetry, expressed through the parameter p . They reflect three different ways of dividing areas of overlap among competing individuals (parameter b in eqn 4 and table 1 in Weiner & Damgaard 2006) to determine a plant's effective area (A_c): $P = 0.0$ for complete symmetry (areas of overlap are divided equally among all overlapping individuals, irrespective of their sizes), $P = 1.0$ for size symmetry (areas of overlap divided according to the relative sizes of the overlapping individuals) and $P = 5.0$ for size asymmetry (larger individuals get a disproportionate share of areas of overlap). To have mortality occur under symmetric as well as asymmetric competition, we assume that individuals die if their actual growth rate falls below 2% (Stoll *et al.* 2002).

The simulations were stochastic, there was random normal independent variation in initial size ($B_0 = 1$ mg; SD = 0.1), the initial growth rate was set up as $r_0 = 1$ mg cm⁻² t⁻¹ (SD = 0.1), and the maximum individual mass was asymptotic ($B_{\max} = 20$ 000 mg; SD = 2000). We take a 'wraparound' (torus) approach to avoid edge effects (Grimm & Railsback 2005). Individuals were distributed randomly in space. For populations without mortality, we collected data from simulations every five time steps after the first 10 steps, and we present here the results at 50 time steps. For self-thinning, the data collected was dependent on the mode of competitive (160, 120 and 90 steps for complete-symmetric, size-symmetric and size-asymmetric competition respectively), because it has been shown that growth and competition occur more slowly under symmetric than asymmetric competition (Stoll *et al.* 2002). All simulations were conducted on landscapes with the size of 120 × 120 grids and were performed in NetLogo (Wilensky 1999).

FIELD EXPERIMENT

To test some predictions of the model, we conducted an experiment in an alpine meadow located in the eastern part of the Qing-Hai Tibetan Plateau, China (33°58' N, 101°53' E; 3500 m a.s.l.; 5° slope). The experiment was similar in design to an earlier experiment, which focused on mean plant size (Chu *et al.* 2008). The average annual temperature is 1.2 °C and precipitation is 620 mm year⁻¹ at the study site. The vegetation is dominated by sedges, most notably *Scirpus pumilus* Vahl and *Kobresia macrantha* Boeck, and by grasses such as *Elymus nutans* Griseb (Wang *et al.* 2008). Soils are classified as alpine meadow soils (Gong 1999). We chose *E. nutans* as our experimental species because its high capacity for clonal growth produces clear density effects. It is also a dominant species at the study site, and previous studies conducted there have found that it is strongly facilitated by neighbours (Wang *et al.* 2008). Modules (culms) of this species occur individually or in tufts, both of which can be whole genets or connected by rhizomes. We consider both individually occurring culms and tufts as individual ramets (Scrosati 2000).

A total of 18 1 × 1 m plots were randomly selected in a relatively homogeneous area within the site in 2006, with a 50-cm walkway between plots. The site was an *Avena sativa* field in previous years and was tilled before the experiment. The plots were seeded on 28 June with a varying number of *E. nutans* seeds (collected locally in September 2005), to obtain six different ramet densities, from 700 to 2800 individuals m⁻². Before sowing, a thin layer of soil was sieved over the plots to provide a surface as smooth as possible with minimal spatial heterogeneity. For the random initial distribution, seeds were mixed with sand and sown with a sieve. Each density level was replicated three times. One plot was destroyed by voles (*Microtus oeconomus*). To avoid edge effects, we collected data only from a 25 × 25 cm subplot within each plot for measurements. Above-ground biomass was harvested from the subplots in early September 2008, after a full growing season but before the arrival of low temperatures. Below-ground biomass cannot be measured with any degree of confidence in *E. nutans*. Individuals were counted within each subplot, individually harvested and dried at 80 °C until constant weight. We analysed the relationships among size variability, measured as the CV of mass, population density and mean individual mass, although low sample sizes did not permit statistical testing of density effects.

Results

POPULATIONS WITHOUT MORTALITY

Abiotic stress (*s*) and facilitation strongly influenced the size inequality of the simulated populations without mortality after 50 time steps (Fig. 1). In general, both size-asymmetric competition and facilitation increased size inequality, while stress without facilitation decreased inequality. In the absence of facilitation, size inequality was higher under benign conditions, although the effect was smaller when competition was completely symmetric (Fig. 1). Under abiotic stress with facilitation, size inequality decreased monotonically with density when competition was completely symmetric, but decreased and then increased with density when competition was size-symmetric or asymmetric, with the lowest size inequality at intermediate density levels. This pattern was also observed in the field experiment (Fig. 2a).

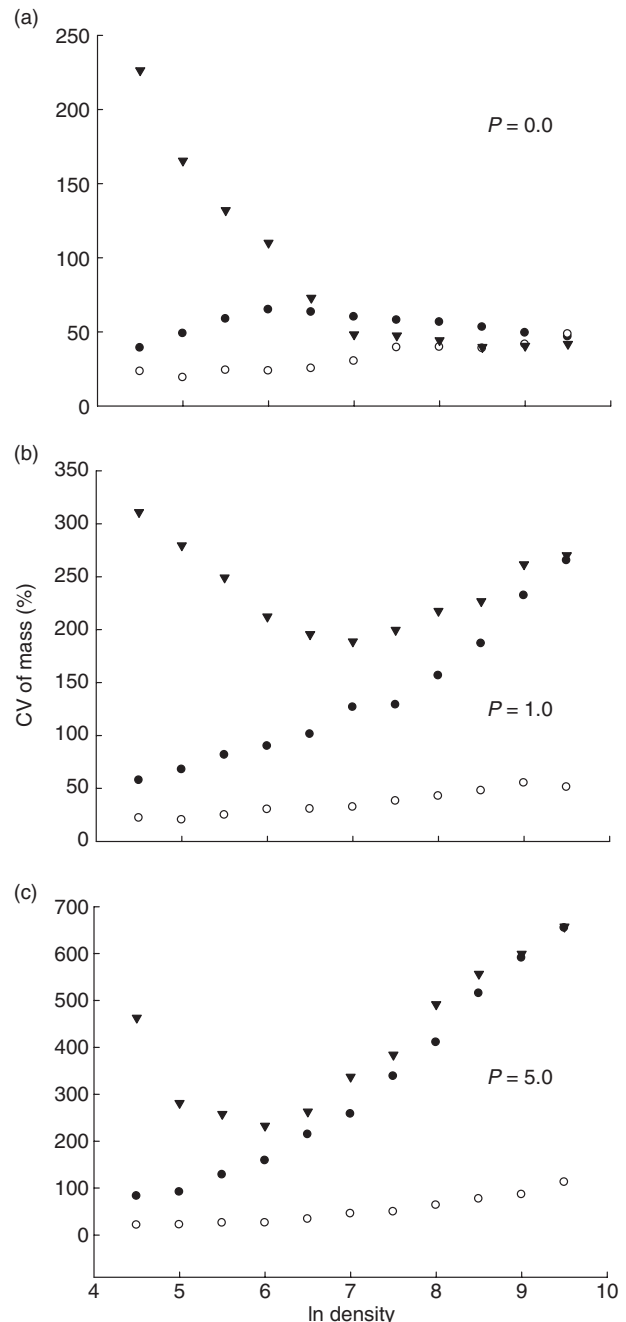


Fig. 1. Coefficient of variation of individual plant size in simulated populations without mortality events at different densities after 50 time steps, under benign environmental conditions (●), harsh conditions without facilitation (○) and harsh conditions with facilitation (▼). Upper, middle and lower panels show results for (a) completely symmetric ($P = 0.0$), (b) size-symmetric ($P = 1.0$) and (c) asymmetric ($P = 5.0$) competition respectively.

In the simulated populations, size inequality increased monotonically with an increase in density under benign environmental conditions, but only when competition was size-symmetric or asymmetric. In the case of complete symmetry, size inequality initially increased, but then slightly decreased as density increased (Fig. 1, see Appendix S1 in Supporting Information). Populations had lower size inequality under abiotic

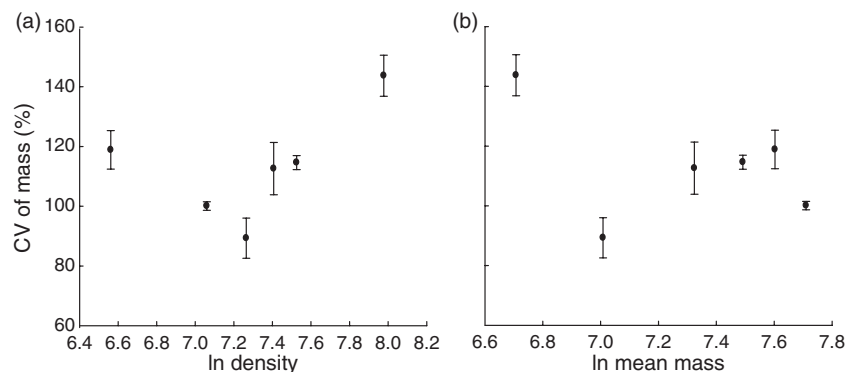


Fig. 2. Relationships between the coefficient of variation of the size of *Elymus nutans* individuals and both population density (a) and mean individual mass (b) in a field experiment conducted in an alpine meadow. Each data point represents the average of three plots (except for the second density level of 7.06, which had only two replicates).

stress without facilitation than under benign environmental conditions. Under abiotic stress with facilitation, size variation decreased with increasing mean plant mass as plants grew when competition was size-asymmetric, but the pattern was more complicated when competition was more symmetric (Fig. 3).

In the field experiment, the lowest size inequality was observed at intermediate densities, where mean biomass was relatively low (Fig. 2b). The greatest size inequality was found at the highest density and lowest mean size (Fig. 2b). The relationship between mean individual mass and the CV of size inequality found in the field study was somewhat more complicated than that produced by our simulation model (Figs 2b and 3 and Appendix S1).

POPULATIONS WITH MORTALITY

When mortality was included in the simulations, abiotic stress delayed its onset, except when competition was completely symmetric (Fig. 4, left side). Size inequality among survivors at a given mean mass was usually highest under harsh conditions with facilitation (Fig. 4, right side). As self-thinning progressed, populations experiencing stress and facilitation had many more survivors than populations growing under more benign conditions at the same point in time. In the early stages of self-thinning, the size inequality of populations under benign conditions was similar to that under harsh conditions, and facilitation did not have a large effect on individual size variation. Size inequality increased and then decreased, with the greatest variation at the intermediate mean mass, except under harsh conditions without facilitation (Fig. 4, right panel).

The size symmetry of competition had major effects on the mortality rate and size variation among survivors. Self-thinning occurred much faster when competition was size-asymmetric (Fig. 4, left panels). Size inequality in the simulated populations was higher under more asymmetric competition before self-thinning started, but size-asymmetric competition also increased the mortality rate, resulting in lower size variation among survivors in some cases (Fig. 4, right panels).

Discussion

Our simulation results partially supported the hypothesis that positive interactions could enhance the size inequality of populations growing at different densities. However, this was not the case when competition was completely symmetric (Fig. 1). The effect of facilitation was particularly evident under low to medium population densities, but was not observed at high densities: the lowest size inequality occurred at intermediate densities, not at the lowest densities, as observed in most studies on competition (such as Weiner & Thomas 1986; Weiner *et al.* 2001; Xiao *et al.* 2006). This pattern is consistent with our previous results (Chu *et al.* 2008), which suggest that positive interactions dominate population behaviour at low to medium densities, while competition dominates in high-density populations (see also Dickie *et al.* 2005; Leslie 2005).

In our model, individuals grow in a random spatial pattern, which inevitably results in variation in local crowding (Bonan 1991), contributing to size variation (Weiner *et al.* 2001). The fact that, at low densities, some individuals are facilitated by neighbours while others are not, and larger individuals tend to benefit more than smaller ones because the former have more overlapping area, thus increases the overall size inequality of the population. Our experimental results were consistent with this prediction (Fig. 2). Studies conducted in other physically stressful ecosystems, such as a subalpine meadow and a semi-arid forest, exhibit similar patterns: size variation decreases with increases in density at relatively low densities (Du & Wang 1992; Sumanta 2007). We conclude that abiotic stress *per se* does not increase size variation in plant populations (Xin, Wang & Zhao 1998; Pan *et al.* 2003). Stress without facilitation simply decreases the growth rate of all individuals, slowing growth, size divergence and death. Rather, facilitation induced by stress is likely the mechanism underlying the patterns observed in the field. Under benign conditions, size inequality increases strongly with population density except when competition is completely symmetric (Weiner *et al.* 2001).

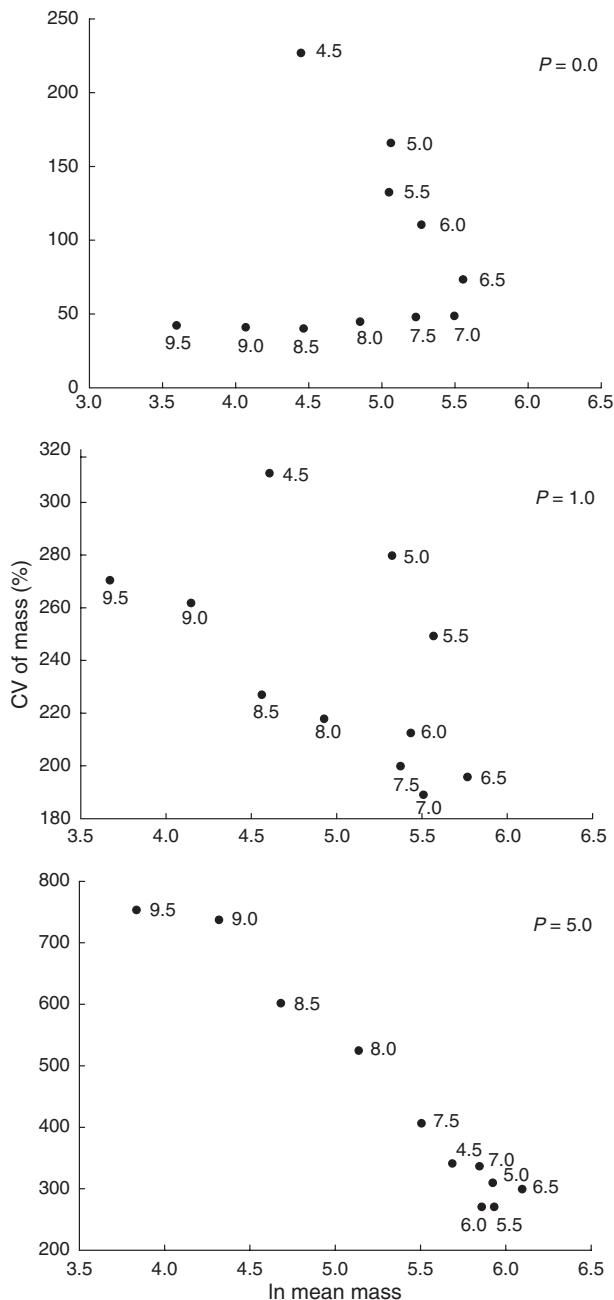


Fig. 3. Relationship between the coefficient of variation in size and mean individual mass in simulated populations at different densities in harsh conditions with facilitation and without density-dependent mortality after 50 time steps. Upper, middle and lower panels show results for complete symmetric ($P = 0.0$), size-symmetric ($P = 1.0$) and asymmetric ($P = 5.0$) competition respectively. The number next to each point indicates the density. The other two cases (benign conditions and harsh conditions without facilitation) are shown in Appendix S1.

Competition and facilitation interact with density and time to determine mean size and size inequality, such that populations with similar mean individual size can be very different in their size inequality (Fig. 3). This result is consistent with our previous work showing that the populations with similar mean biomass can be obtained under different densities when there is facilitation (Chu *et al.* 2008). Similarly, populations growing at

different densities can produce similar degrees of size variation (Fig. 1).

Size inequality among survivors changed greatly over time in populations undergoing density-dependent mortality. In the early phases of stand development, populations growing in harsh conditions were similar in size inequality to populations growing under benign conditions (Fig. 4, right panel). Previous studies in this system found that facilitation had a negligible impact on population biomass at densities over 9000 individuals m^{-2} (Chu *et al.* 2008). Harsh environmental conditions and intense competition made all individuals grow slowly, and this substantially limited size divergence within the population (Fig. 4, right panel). In the early stages of stand development, facilitation seems to have only minor effects. The role of facilitation increases as self-thinning becomes extensive and population density decreases. During this phase of stand development, populations growing in harsh conditions had greater size variation than those under benign conditions when compared at the same mean plant mass (Fig. 4). The balance between positive interactions (increasing variation) and mortality driven by competition (decreasing variation) determined the size structure of the simulated populations.

Harsh conditions postponed the onset of self-thinning in simulated populations (Fig. 4, left panel), consistent with previous results from a wide variety of studies showing that the rate of mortality during self-thinning is correlated with the rate of growth (Harper 1977). For example, high-density populations of *Triticum aestivum* (spring wheat) growing under water-stressed conditions had more survivors than populations growing under well-watered conditions (Liu *et al.* 2006).

Most previous studies considered competition to be the only plant–plant interaction when interpreting the effects of environmental stress (Xin, Wang & Zhao 1998; Pan *et al.* 2003; Liu *et al.* 2006; Sumanta 2007). However, in ecosystems characterized by harsh environmental conditions, positive interactions can play an important role in population development (Tirado & Pugnaire 2003; Deng *et al.* 2006; Callaway 2007). Under such conditions, abiotic stress cannot explain the increased size inequality in harsh conditions relative to that found under benign conditions (Figs 1, 4), but facilitation can.

Our modelling and experimental results demonstrate that facilitation can play an important role in determining the size structure of plant populations in stressful environments. Positive interactions affected the onset of self-thinning and size inequality in most cases. Our results provide new impetus for the further development of allometric theory, which has been mainly built on competition. Future research should explicitly evaluate how the incorporation of positive interactions into current conceptual and mathematical models can modify the self-thinning trajectory. Our paper also presents another example of how the explicit consideration of facilitation is necessary if we aim to fully understand population behaviour in stressful environments.

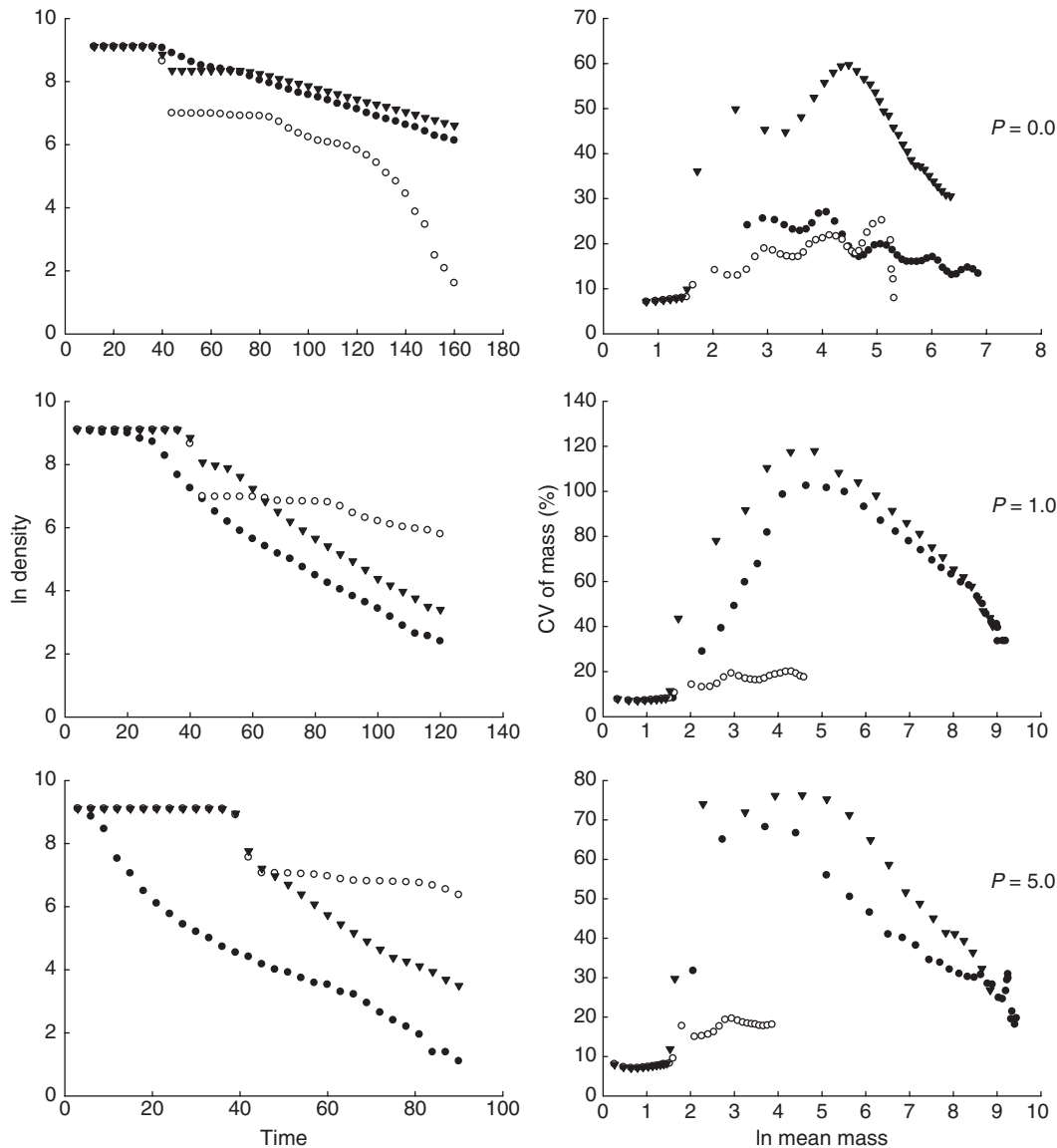


Fig. 4. Relationships between the number of survivors and time (left panel), and between the coefficient of variation of individual plant size and mean individual mass (right panel) in model populations with density-dependent mortality under benign environmental conditions (●), harsh conditions without facilitation (○) and harsh conditions with facilitation (▼). All dead individuals were excluded from the analysis. Upper, middle and lower panels show results for complete symmetric ($P = 0.0$), perfect size-symmetric ($P = 1.0$) and partially asymmetric ($P = 5.0$) competition respectively. Please note the different y-labels for left and right panels.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Relationships of size inequality with mean individual mass in simulated population without mortality after 50 time steps.

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