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LETTER

Balance between facilitation and resource competition determines biomass–density relationships in plant populations

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Abstract

Theories based on competition for resources predict a monotonic negative relationship between population density and individual biomass in plant populations. They do not consider the role of facilitative interactions, which are known to be important in high stress environments. Using an individual-based 'zone-of-influence' model, we investigated the hypothesis that the balance between facilitative and competitive interactions determines biomass–density relationships. We tested model predictions with a field experiment on the clonal grass *Elymus nutans* in an alpine meadow. In the model, the relationship between mean individual biomass and density shifted from monotonic to humped as abiotic stress increased. The model results were supported by the field experiment, in which the greatest individual and population biomass were found at intermediate densities in a high-stress alpine habitat. Our results show that facilitation can affect biomass–density relationships.

Keywords

Alpine meadow, density dependence, *Elymus nutans,* individual-based model, plant–plant interactions, positive neighbour effects.

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INTRODUCTION

The relationship between body size and density is central to ecology (Damuth 1981; Lawton 1989; Gaston & Blackburn 2000). One of the most basic relationships between the size and density of individuals is density dependence within a single species (Watkinson 1980; Silvertown & Charlesworth 2001). When plant populations are grown at different densities for a given period, total standing biomass initially increases proportionally with density, levels off and then remains constant at ever-higher densities, the so-called 'Law Of Constant Final Yield' (Farazdaghi & Harris 1968; Drew & Flewelling 1977). Resource competition is usually the mechanism invoked to explain the negative relationship between individual size and density: the amount of resources in a fixed area is finite, so increasing the number of individuals implies a reduction in their mean size (Damuth 1981; Silvertown & Charlesworth 2001).

Recent research suggests that populations and communities living in environments characterized by a high degree of abiotic stress may show different size–density relationships (Deng *et al.* 2006). In such environments, the net effect of neighbours on an individual is often facilitative (see Callaway 2007 and Brooker *et al.* 2008 for reviews). Facilitation occurs when positive effects of neighbours, such as habitat amelioration and nutrient enrichment, are stronger than resource competition (Holzapfel & Mahall 1999; Maestre *et al.* 2003). The balance between facilitation and competition is strongly influenced by the degree of abiotic stress experienced by the interacting individuals (Choler *et al.* 2001; Callaway *et al.* 2002; Maestre & Cortina 2004). The 'stress gradient hypothesis' predicts that: (i) facilitation and competition will vary

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inversely across gradients of abiotic stress, with facilitation being the dominant interaction under highly stressful conditions (Bertness & Callaway 1994), while competition dominates in lower stress environments, and (ii) under conditions of high abiotic stress, facilitation increases with density more than competition does (Callaway & Walker 1997). Many, but not all, field studies have supported these predictions (see Callaway 2007 for a review), and there is a vigorous and ongoing debate about the causes of the discrepancies found among studies (Maestre *et al.* 2005, 2006; Lortie & Callaway 2006; Callaway 2007).

To our knowledge, no previous study has explored how the balance between facilitation and resource competition affects biomass–density relationships in plant populations. We do so by developing an individual-based, spatially explicit 'zone-of-influence' model of plant–plant interactions to evaluate: (i) the potential effects of facilitation on the relationship between the density and biomass in a plant population, and (ii) the net outcome of intraspecific interactions along density and stress gradients. Predictions of the model were tested in a field experiment conducted in an alpine meadow of the Tibetan Plateau, where plant growth is strongly limited by low resource availability and low temperatures (Wang *et al.* 2008). We test two hypotheses: (i) the biomass–density relationship is determined by the balance between facilitation and resource competition, and (ii) increasing neighbour density will increase the strength of facilitation relative to competition under high stress conditions.

MATERIALS AND METHODS

Model

In a 'zone-of-influence' model, each individual obtains resources from a circular zone, and neighbouring individuals occupy space and compete for resources in areas they overlap (Weiner *et al.* 2001; Weiner & Damgaard 2006). The area occupied by a plant, A, represents the amount of resources potentially available, and is related to its biomass, B, as $A = cB^{2/3}$, where c is a constant. We set $c = 1.0$ in all the simulations presented here; we simulated the model with different c values, and obtained qualitatively similar patterns (results not shown). An individual's potential growth rate (in absence of neighbours) through time (t), is defined by the equation

$$\frac{\mathrm{d}B}{\mathrm{d}t} = r\left(A - \frac{B^2}{B_{\max}^{4/3}}\right) = r\left(cB^{2/3} - \frac{B^2}{B_{\max}^{4/3}}\right), \quad (1)$$

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 in areas they overlap. The effective area of a plant, A_c, is calculated as the area it covers minus that part of the area lost to neighbours, which is determined by the amount of overlap and the degree of 'size asymmetry' of competition (Weiner *et al.* 2001). A_c determines the realized growth rate of the plant according to the equation:

$$\frac{\mathrm{d}B}{\mathrm{d}t} = r\left(A_c - \frac{B^2}{B_{\max}^{4/3}}\right). \quad (2)$$

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.

Equations 1 and 2 do not consider the effects of the environment and facilitation on plant performance. To do this, we assume that the individual growth rate is negatively and linearly related to the degree of abiotic stress (Travis *et al.* 2006), and that interacting plants benefit from the presence of neighbours under harsh environmental conditions, presumably because of habitat amelioration (Callaway 2007). The effective area of a plant with respect to positive interactions, A_f, is calculated as the sum of the areas shared with neighbours, so the average A_f of plants is positively related to population density. For simplicity, we assume that the effect of facilitation is additive (Molofsky *et al.* 2001; Molofsky & Bever 2002), i.e. its effects increase as the overlapping area does. Therefore, both facilitation and resource competition determine the realized growth rate of the plant during the next time interval as follows:

$$\frac{\mathrm{d}B}{\mathrm{d}t} = r\left(A_c - \frac{B^2}{B_{\max}^{4/3}}\right)\left(1 - \frac{s}{A_f + 1}\right), \quad (3)$$

where s indicates the degree of abiotic stress ($0 \leq s < 1$). When s equals 0, eqns 2 and 3 are the same. The second term on the right of eqn 3 represents the effects of abiotic stress and facilitation on the realized growth rate (see Appendix S1 in Supporting Information for the influence of this term on the model behaviour). For simplicity in analysing and interpreting the results, plants cannot have negative growth rates, but continue to live and maintain the maximum size they achieve (Weiner *et al.* 2001; Weiner & Damgaard 2006).

The size symmetry of competition is reflected in the rules for dividing the overlapping areas among individuals. In our simulations, we set a parameter, p, defined as the degree of size-asymmetric competition due to resource uptake (Schwinning & Weiner 1998; Weiner & Damgaard 2006). We consider three theoretically important p-values reflecting three modes of competition: complete size symmetry (the overlapped areas are divided equally among all overlapping individuals, irrespective of their sizes; $p = 0.0$), perfect size symmetry (the overlapping areas individuals are divided in proportional the sizes of the overlapping individuals; $p = 1.0$) and complete size asymmetry (the larger individual obtains all the contested resources; $p = \infty$).

To facilitate the interpretation of the results, we assigned conventional units to measures of mass and area that were consistent with our field experiment (for A_c and A_f, cm^{-2}). The simulations were stochastic: there was random normal independent variation in initial size ($B_0 = 1$ mg; SD = 0.1), initial growth rate ($r_0 = 1$ mg cm^{-2} t^{-1}; SD = 0.1) and asymptotic size ($B_{\max} = 20000$ mg; SD = 2000).

Our simulated populations were subjected to two different gradients: density (plants m^{-2}, from 4 to 9 on the natural logarithm scale) and abiotic stress ($0 \leq s < 1$). The density gradients in the simulations encompassed the range of densities employed in the field experiment (see below). In addition to the exploration of the relationship between density and mean individual biomass ($\bar{x}$), we evaluated how the effects of neighbours at the population level changed through both density and abiotic stress gradients. To do this, we estimated the relative neighbour effect (RNE) as follows:

$$\mathrm{RNE} = \frac{\bar{x}_1 - \bar{x}_0}{\bar{x}_{\max}}, \tag{4}$$

where $\bar{x}_1$ and $\bar{x}_0$ are the mean individual biomass within the population with and without interactions respectively, and $\bar{x}_{\max}$ is the greatest of the two. RNE ranges from −1 to +1, with negative and positive values indicating competition and facilitation respectively. For estimating $\bar{x}_0$, we calculated the individual growth rate without interactions as follows:

$$\frac{\mathrm{d}B}{\mathrm{d}t} = r\left(A - \frac{B^2}{B_{\max}^{4/3}}\right)(1 - s). \tag{5}$$

We take a 'wraparound' (torus) approach to avoid edge effects (Grimm & Railsback 2005). To test the effects of initial spatial distribution of individuals, selected model runs were repeated three times for both random and uniform patterns. We present here the results for the random spatial distributions; the results for the uniform distribution are shown in the Supporting Information (Figs S1 and S2). All simulations were performed in NetLogo (Wilensky 1999).

Field experiment

To test the 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 average annual temperature and precipitation are 1.2°C and 620 mm respectively. 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). It is classified as alpine meadow soil (Gong 1999).

Elymus nutans was chosen as the target species because its high capacity for clonal growth should produce clear density effects, it is 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). A total of 48 1 m × 1 m plots were randomly selected in a homogeneous portion of the site in 2006, with a 50-cm walkway between plots. Before sowing, we removed all the aboveground vegetation and then turned the soil by hand. Roots within the plots were also removed. *Elymus nutans* is cespitose. Modules (culms) occur individually or in tufts, both of which can be whole genets, or ramets connected by rhizomes. We consider both individually occurring culms and tufts as individual ramets (Gorham 1979; Cheplick 1998; Scrosati 2000). The plots were seeded with a varying number of *E. nutans* seeds to obtain 16 different ramet densities ranging from 900 to 11 000 individuals m^{-2} (see Table S1 in Supporting Information). 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. We also set up three control plots to obtain populations without competition or facilitation. These plots were seeded with 200 seeds each, and all neighbours within a 10-cm diameter circle centred on each target seedling were removed by hand. Target seedlings were chosen randomly in each plot. While the objective was to obtain a density too low for plant–plant interactions, individuals further away than 10 cm might still have had some facilitative effects by ameliorating wind speed, and plants may have competed somewhat for below-ground resources, which may misestimate RNEs slightly.

To avoid edge effects, we set up a 30 cm × 30 cm subplot within each plot for measurements. Periodic inspection and hand weeding of non-target vegetation were performed during the growing season. Plants were harvested from the subplots in early September 2007, after a full growing season but before the arrival of low temperatures, which can result in negative growth. Individuals were counted within each subplot, harvested and dried at 80 °C until constant weight. Mean individual biomass was calculated as total biomass/ramet density. RNE values were calculated according to eqn 4.

RESULTS

The degree of abiotic stress (s) strongly influenced the relationships between individual density and mean individual biomass in the simulated populations, as the shape of the

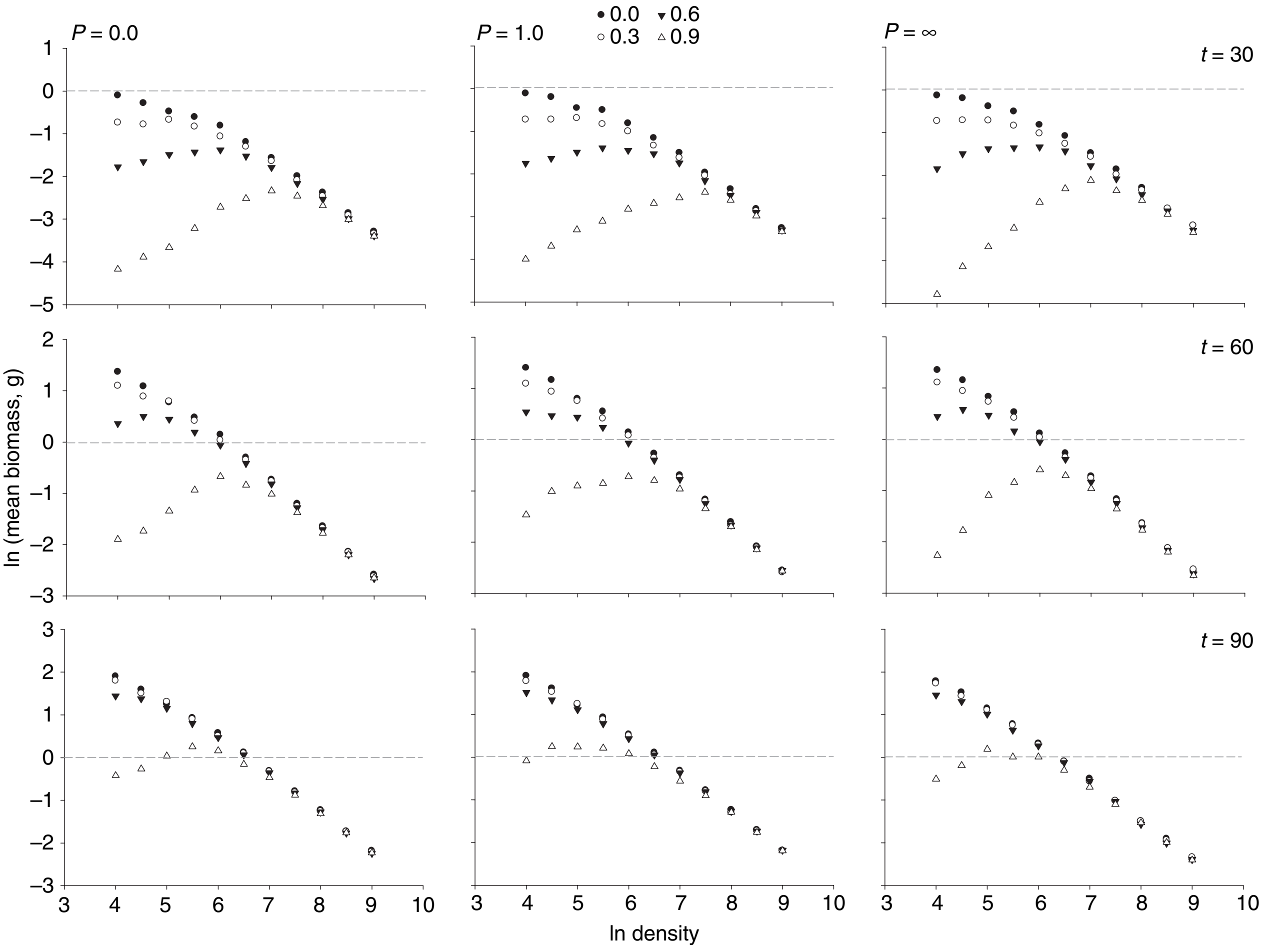

Figure 1 Relationships between mean individual biomass and density in the simulated populations under different stress levels (0.0, 0.3, 0.6 and 0.9 respectively) and simulation runs (defined by the parameter *t*; 30, 60 and 90 time intervals respectively). Left, middle and right panels show results for complete symmetry ($p = 0.0$), perfect size symmetry ($p = 1.0$) and complete asymmetry ($p = \infty$) respectively. Abiotic stress increases concomitantly with *s*.

curves gradually shifted from linear to hump-shaped with the increase of *s* (Fig. 1). Total biomass was also highest at intermediate densities (results not shown). In the field experiment, the largest mean individual (Fig. 2a) and total (Fig. 2b) biomass were observed at intermediate densities.

The relationship between abiotic stress and the outcome of intraspecific interactions, as measured with the RNE index, was dependent on population density in the simulated populations (Fig. 3a). RNE index first increased and then decreased with increasing stress at low densities (at 4.0 on the ln scale). At high densities (such as at 8.0 on the ln scale), intraspecific interactions changed from competition to facilitation with increasing abiotic stress.

The relationship between density and the RNE index in the simulations was dependent on the degree of abiotic stress (Fig. 3b). Under relatively benign conditions, the net outcome of intraspecific interactions was negative, irrespective of the density considered. Under high abiotic stress conditions, the relationship between density and the RNE index was humped, indicating that competition was prevalent at both extremes of the density gradient (this hump-shaped pattern was more pronounced when individuals were distributed in a uniform spatial pattern; see Fig. S2 in Supporting Information). These results were consistent with those from the field experiment (Fig. 4), where RNE values shifted from negative to positive, and then to negative again as ramet density increased. Facilitation was dominant at intermediate densities.

The degree of size-asymmetric competition (*p*) did not significantly influence the simulation results, as the curves observed under different *p*-values were qualitatively similar (Figs 1 and 3). When *s* was 0 or 0.3, size distributions were similar to those produced in other 'zone-of-influence' model studies and empirical studies on plant competition.

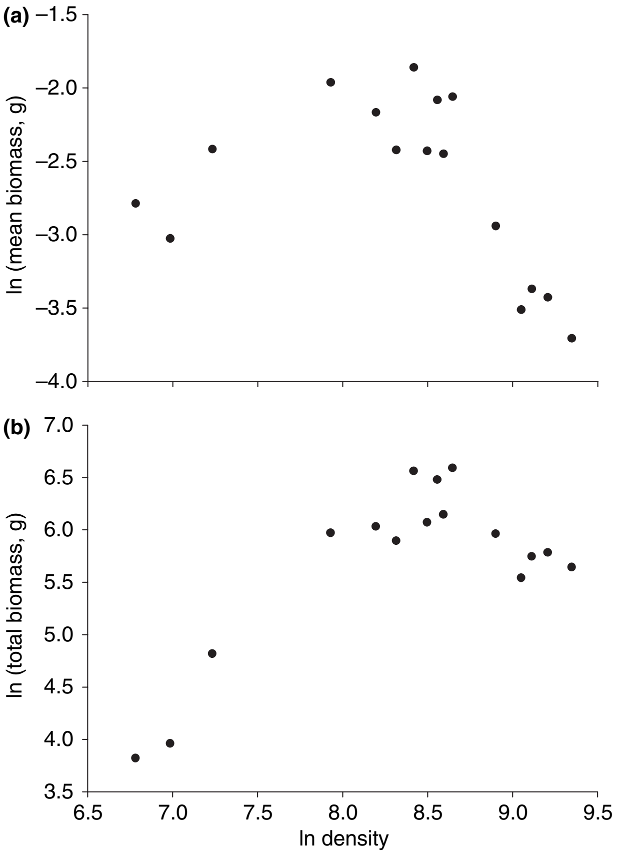

Figure 2 Relationship between density and mean individual (a) and total (b) biomass in the field experiment. Each data point represents the average of three plots.

DISCUSSION

Consistent with our first hypothesis, the biomass–density relationship was strongly affected by facilitation in both the simulations and the field experiment. Under the most benign conditions, ln mean individual biomass was linearly and negatively associated with ln population density, as in numerous previous studies (Damuth 1981; Silvertown & Charlesworth 2001; White *et al.* 2007). As abiotic stress and therefore facilitation increased, the relationship shifted from linear to humped, suggesting that the benefits from habitat amelioration because of aggregation of conspecifics offset the negative effects of resource competition at low-to-intermediate densities. These modelling results were supported by the field experiment, where the greatest biomass was found at intermediate densities.

Previous studies conducted in the same study area have found that *E. nutans* is strongly facilitated by neighbours, which increase soil water availability and temperature, and provide protection from low air temperatures and strong winds (Wang *et al.* 2008; C.-J. Chu, unpublished data). It has been suggested that in harsh environments, such as those studied here, facilitation should occur only when positive effects of neighbours, in terms of improved resources and microclimate, are greater than negative effects because of competition for resources (Gómez-Aparicio *et al.* 2004; Liancourt *et al.* 2005; Maestre *et al.* 2005). Our simulated and experimental results provide support for this prediction, and are consistent with observations from other communities in which facilitation is important: seedling density and growth were positively and negatively correlated at low and high densities respectively in forest edges (Dickie *et al.* 2005), and the frequency of breeding barnacles in experimental and natural populations was greatest at intermediate densities (Leslie 2005).

Current controversies concerning size–density relationships have focused on the slope of the log biomass–log density relationship, but not its shape, which is assumed to be negative and linear in all current models and theories (Farrell-Gray & Gotelli 2005; White *et al.* 2007). Our results from both the simulation and the field experiment challenge this assumption, as they fit this general pattern only at high densities. At low-to-moderate densities under conditions of high abiotic stress, however, positive intraspecific interactions modulated the shape of the biomass–density relationship. Nor are our results consistent with the 'Law of Constant Final Yield' (Farazdaghi & Harris 1968) because total population biomass was highest at intermediate densities (Fig. 2b).

The relationship between RNE and abiotic stress in the simulated populations was dependent on their density (Fig. 3a). At relatively low densities, competition dominated in both benign and harsh conditions, while facilitation was significant only at intermediate abiotic stress levels. The curve first increased and then decreased, presumably reflecting the relative importance of facilitation and competition along the stress gradient evaluated. While we assume that facilitation increases with increasing abiotic stress (eqn 3), the net effect of positive and negative interactions was also affected by density. At relatively low densities, there were fewer neighbours around target individuals, minimizing potential facilitative effects. Facilitation increased with an increase in abiotic stress, and the net effect shifted from negative to positive, but high levels of competition for limited resources under harsh conditions offset and eventually overwhelmed facilitative effects (Fig. 3a). This pattern is consistent with results obtained with acorn barnacle populations (Bertness 1989). At low tidal heights, no barnacle recruits survived to reproduce at any density because of intraspecific crowding, algal overgrowth and predation. Lower recruitment density decreased intraspecific crowding, increased survivorship at intermediate tidal heights and decreased survivorship at high tidal heights.

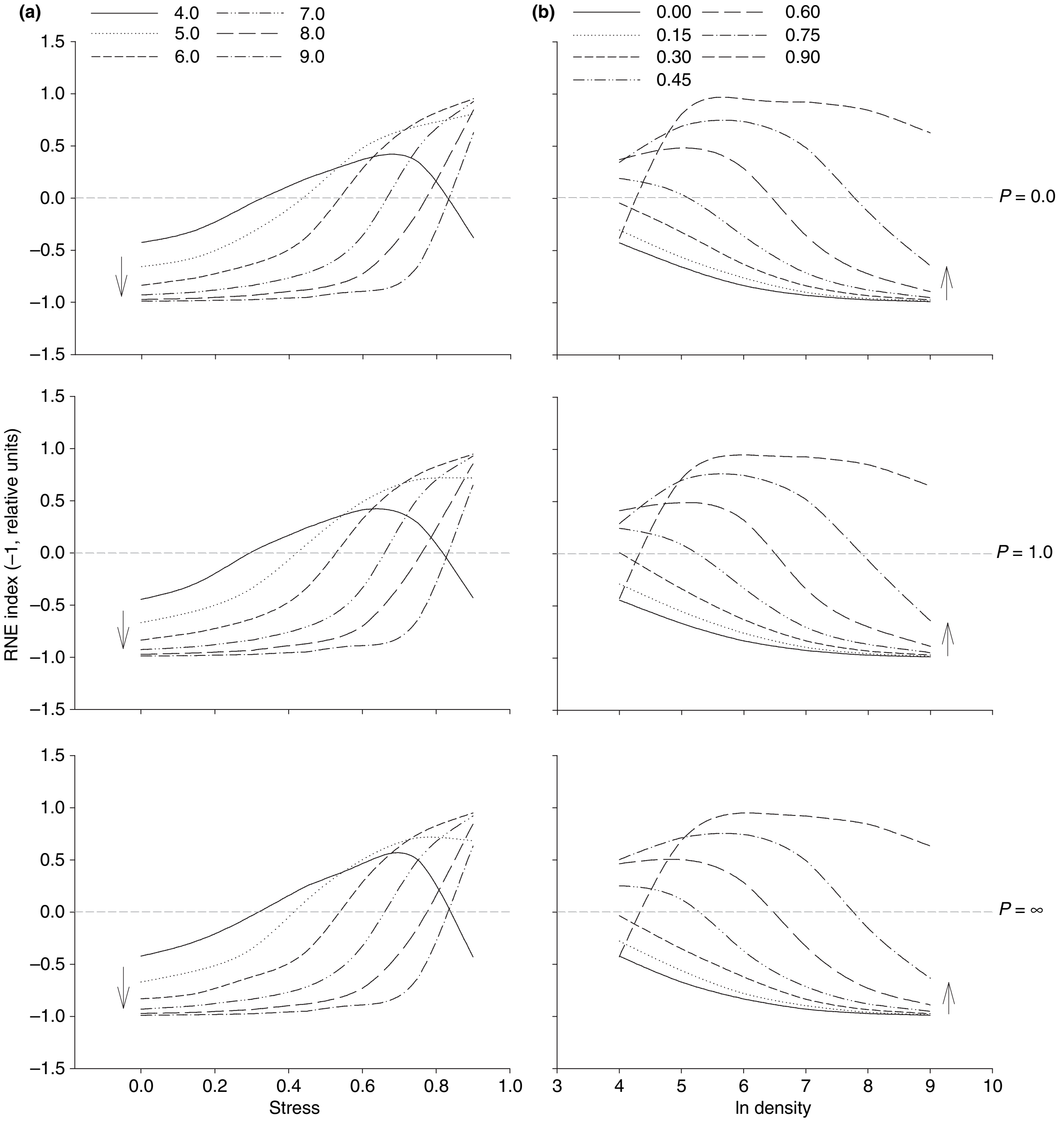

Figure 3 Relationships between the relative neighbour effect (RNE) index and abiotic stress under different density levels (left panels, a), and between this index and density under different stress levels (right panels, b) in the simulated populations. Upper, middle and lower panels show results for complete symmetry ($p = 0.0$), perfect size symmetry ($p = 1.0$) and complete asymmetry ($p = \infty$), respectively. Density and stress increase in the direction pointed by the arrow. 60 time intervals were used in the simulations.

Our second hypothesis, increasing neighbour density will increase the strength of facilitation relative to competition under high stress conditions, was not supported by our simulated results. The net balance between costs and benefits to living in low and high population densities is driven at least partially by the degree of abiotic stress (s in eqn 3; Bruno *et al.* 2003; Callaway & Walker 1997). Under relatively benign conditions, negative interactions were dominant throughout the density gradient, as found in previous studies (Stephens & Sutherland 1999; Hixon *et al.*

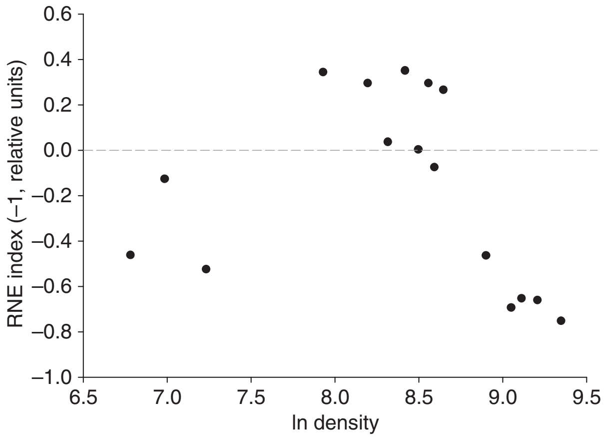

Figure 4 Relationship between ramet density and the relative neighbour effect (RNE) index in the field experiment. Each data point represents the average of three plots.

2002; López & González 2003). As abiotic stress increased, competition dominated at both extremes of the density gradients, with facilitation being prevalent at intermediate densities (Fig. 3b). This pattern was consistent with our experimental results (Fig. 4) and with results on intertidal barnacles, in which breeding was maximized at intermediate densities (Leslie 2005). The balance between facilitation and resource competition is the most likely explanation for these results. The probability of successful reproduction by the barnacles increased with increasing barnacle density, but at very high densities the effects of competition for space were stronger than positive effects of conspecific aggregation.

Positive density dependence has also been observed at high population densities under stressful conditions in other studies (Bruno *et al.* 2003). In a high rocky intertidal environment in southern New England, the reproduction, survivorship and growth of sessile invertebrates and macroalgae were greater at higher than at intermediate densities (Bertness 1989; Bertness & Leonard 1997; Bertness *et al.* 1999). It could be argued that the densities in these marine environments were not high enough to observe negative effects of competition. ‘High’ and ‘low’ densities are relative terms that cannot often be directly compared in different studies. High density in a particular experimental study may not be very high in comparison with what occurs in other areas or ecosystems.

The degree of size-asymmetric competition (*p*) did not significantly influence our simulation results (Figs 1 and 3). Size-asymmetric competition usually has major effects on size variation among individuals in a population, but its effects on mean size are sometimes quite minor unless it results in extensive density-dependent mortality (Weiner *et al.* 2001; Stoll *et al.* 2002). We could not compare size distributions of our simulated and field studies, as we did not determine individual biomass for each plant in the field, and this is a focus of our ongoing research.

Our modelling and experimental results demonstrated that facilitation can affect biomass–density relationships, and that the net outcome of plant–plant interactions at the population level is determined by both density and abiotic stress. They also suggest that current theories aiming to explain biomass–density relationships, such as simple models of resource competition, may not hold in high stress environments, where facilitation plays an important role in intra- and interspecific interactions.

Despite the large and growing body of empirical evidence showing the importance of facilitation for ecosystem structure, functioning and dynamics in a wide variety of environments (Callaway 2007), researchers are only beginning to incorporate it into mainstream ecological theory (Bruno *et al.* 2003; Callaway 2007; Brooker *et al.* 2008; Gross 2008). Although our results need to be corroborated by studies conducted in other strongly resource- or condition-limited communities, they indicate that the consideration of facilitation can substantially modify predictions from resource-based theories, and provide an example of how the explicit consideration of facilitation can help us build more general theories of biomass–density relationships.

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SUPPORTING INFORMATION

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

Appendix S1 The influence of the second term of eqn 3 on the model behaviour.

Table S1 Raw ramet density and total biomass data from the field experiment.

Figure S1 Relationships between mean individual biomass and density in the simulated populations using a uniform spatial distribution of individuals.

Figure S2 Relationships between the relative neighbour effect index and abiotic stress under different density levels, and between this index and density under different stress levels, in the simulated populations using a uniform spatial distribution of individuals.

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