Differences between symmetric and asymmetric facilitation matter: exploring the interplay between modes of positive and negative plant interactions

Yue Lin[1,2]*, Uta Berger[1], Volker Grimm[2,3] and Qian-Ru Ji[4]

[1]*Institute of Forest Growth and Computer Science, Dresden University of Technology, PO Box 1117, 01735, Tharandt, Germany;* [2]*Department of Ecological Modelling, UFZ – Helmholtz Centre for Environmental Research, Permoserstr. 15, 04318, Leipzig, Germany;* [3]*Institute for Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, 14469, Potsdam, Germany; and* [4]*Institute of Hydrobiology, Dresden University of Technology, Zellescher Weg 40, 01062, Dresden, Germany*

Summary

1. Facilitation (positive interaction) has received increasing attention in plant ecology over the last decade. Just as for competition, distinguishing different modes of facilitation (mutualistic, commensal or even antagonistic) may be crucial.

2. We therefore introduce the new concept of symmetric versus asymmetric facilitation and present a generic individual-based zone-of-influence model. The model simultaneously implements different modes of both facilitation and competition among individual plants via their overlapping zone of influence. Because we consider facilitation modes as a continuum related to environmental context, we integrated this concept with the stress-gradient hypothesis (SGH) by exploring differences in spatial pattern formation in self-thinning plants along a stress gradient in our model.

3. The interplay among modes of interaction creates distinctly varied spatial patterns along stress gradients. When competition was symmetric, symmetric facilitation (mutualism) consistently led to plant aggregation along stress gradients. However, asymmetric facilitation (commensalism) produces plant aggregation only under more benign conditions but tends to intensify local competition and spatial segregation when conditions are harsh. When competition was completely asymmetric, different modes of facilitation contributed little to spatial aggregation.

4. Symmetric facilitation significantly increased survival at the severe end of the stress gradient, which supports the claim of the SGH that facilitation should have generally positive net effects on plants under high stress levels. Asymmetric facilitation, however, was found to increase survival only under intermediate stress conditions, which contradicts the current predictions of the SGH.

5. *Synthesis*. Our modelling study demonstrates that the interplay between modes of facilitation and competition affects different aspects of plant populations and communities, implying context-dependent outcomes and consequences. The explicit consideration of the modes and mechanisms of interactions (both facilitation and competition) and the nature of stress factors will help to extend the framework of the SGH and foster research on facilitation in plant ecology.

Key-words: asymmetry, competition, metabolic scaling theory, plant population and community dynamics, plant–plant interaction, self-thinning, spatial pattern, stress-gradient hypothesis, symmetry

Introduction

The role of positive interactions in driving population and community dynamics has received significant attention and is now widely recognized in both empirical and theoretical ecology (Bertness & Callaway 1994; Brooker *et al.* 2008;

Bronstein 2009; Maestre *et al.* 2009; Fajardo & McIntire 2011; McIntire & Fajardo 2011). In plant ecology, positive interactions are usually referred to as facilitation, which has been defined as the beneficial effects of neighbours via the amelioration of habitat (Bertness & Callaway 1994; Bronstein 2009); for example, via moderation of stress, enrichment of nutrients or increased access to nutrients. Facilitation has been shown particularly important when considering the

*Correspondence author: E-mail: yue.lin.tud@gmail.com

performance of plants under stressful environmental conditions. 'Stress' is not a precise concept (Maestre *et al.* 2009) and can be biotic and abiotic (Bronstein 2009). The best-understood examples of plant facilitation were mostly carried out under abiotic stress conditions (Bronstein 2009). Moreover, the characteristics of abiotic stress factors are also different and can be resource-independent (e.g. wind, frost and salinity) or resource-dependent (e.g. water, nutrient and light; Maestre *et al.* 2009).

The 'stress-gradient hypothesis' (SGH) proposes that competition and facilitation may act simultaneously, but the relative importance of facilitation and competition will vary inversely along gradients of abiotic stress (Bertness & Callaway 1994). Under high stress conditions, facilitation should be dominant over competition in affecting community structures (Bertness & Callaway 1994; Brooker *et al.* 2008; Maestre *et al.* 2009). The SGH was originally formulated at the interspecific level, but recent studies revealed that SGH is also valid at the intraspecific level (Chu *et al.* 2008, 2009; Eränen & Kozlov 2008; McIntire & Fajardo 2011). The interplay between facilitation and competition can thus drive intraspecific population dynamics (Chu *et al.* 2008, 2009, 2010; Jia *et al.* 2011; McIntire & Fajardo 2011), community structure (Gross 2008; Michalet *et al.* 2011), community diversity (Cavieres & Badano 2009) and ecosystem functions (Callaway *et al.* 2002; Kikvidze *et al.* 2005) and can even have evolutionary consequences (Bronstein 2009; McIntire & Fajardo 2011).

However, there are also studies which do not support SGH predictions, as facilitative effects have not been detected under some extreme stress conditions (Tielbörger & Kadmon 2000; Maestre, Valladares & Reynolds 2005; Maestre *et al.* 2009). This indicates that the conceptual framework underlying the SGH might need further refinement (Maestre *et al.* 2009). Moreover, whereas numerous studies have explored the consequences of different modes of competition, that is, symmetric versus asymmetric competition (Schwinning & Weiner 1998; Weiner *et al.* 2001; Stoll & Bergius 2005; Berger *et al.* 2008), different modes of facilitation have not yet been explored. Inconsistent definitions of facilitation and the lack of differentiation between the impacts of plant–plant interactions on beneficiary and benefactor individuals have recently been identified as important gaps in current research (Brooker *et al.* 2008; Bronstein 2009; Brooker & Callaway 2009; Pakeman *et al.* 2009). Refining and clarifying the concept of facilitation is crucial for understanding how facilitation arises, persists and evolves, and then could help extend the general SGH framework and improve plant ecology research in general (Brooker *et al.* 2008; Bronstein 2009; Maestre *et al.* 2009).

According to different definitions, modes of facilitation can be mutualistic (+/+) or commensal (+/0) amongst plants (Brooker *et al.* 2008; Bronstein 2009). However, a more continuous approach to facilitative interactions might be more accurate and useful, as has been the case for the corresponding continuous approach to exploring competitive interactions (Schwinning & Weiner 1998). We therefore suggest using a new concept of modes of facilitation: any facilitation among plants, no matter whether inter- or intraspecific, can be placed along a continuum ranging from completely symmetric facilitation (interacting plants receive the same amount of benefit from each other, irrespective of their species or sizes) to completely asymmetric facilitation (Vellend 2008; the beneficiary plant receives all benefits but there are no positive effects on the benefactor; Table 1). Thus, mutualistic cases are expected to be at the symmetric end of the facilitation continuum, and commensal cases at the asymmetric end (Fig. S1 in Supporting Information).

This new conceptual model (with its terminology) has two main advantages: it is analogous and therefore directly comparable to the widely used and important concept of symmetric and asymmetric competition (Schwinning & Weiner 1998; Weiner *et al.* 2001; Stoll & Bergius 2005; Berger *et al.* 2008); it also offers a quantitative and operational means of evaluating facilitative impacts.

The analogy between different modes of competition and facilitation is evident. In reality, competition and facilitation often interact: clusters of cohorts facilitate each other against cold or wind desiccation (symmetric facilitation), but they may also compete for nutrients and water (symmetric competition; Fajardo & McIntire 2011). Adult nurse plants facilitate the growth and survival of small plants of their own or other

Table 1. Definition and description of facilitation modes

Mode of facilitation	Effect and definition	Index value	Expected prevalent nature of stress factor
Complete symmetry	All plants receive the same amount of benefit from each other, irrespective of their species or sizes	$q = 0$	Symmetry: temperature, moisture, nutrient, salinity, pollution, wind desiccation,
Partial symmetry	Benefit increases with benefactor's size, but less than proportionally	$0 < q < 1$	altitude etc.
Proportional symmetry	Benefit is proportional to benefactor's size (equal gain per unit size)	$q = 1$	
Partial asymmetry	Benefit increases with benefactor's size super-linearly	$q > 1$	Asymmetry: light, UV-radiation, transpiration, tide,
Complete asymmetry	The beneficiary plant receives all benefits, with no advantage to the benefactor plants	$q = \infty$	water, nutrient fixation, pollution, wind, herbivory, etc.

The index q determines the mode of facilitation among plants [see eqn (5) and Appendix S1].

species (asymmetric facilitation), which may lead to asymmetric light competition if the crown of an adult plant is very dense or the small plants are not 'stress-tolerant' (Reinhart, Maestre & Callaway 2006; Maestre *et al.* 2009). In general, modes of interaction depend on both the ecological traits of the interacting plants and the nature of the stress factors themselves (Maestre *et al.* 2009).

Competition usually leads to the spatial segregation of plants, implying that distributions are more regular than aggregated (Stoll & Bergius 2005; Perry, Miller & Enright 2006). However, spatial aggregation is ubiquitous amongst varied plant systems, especially in harsh environments (Bertness & Callaway 1994; Haase 2001; Perry, Miller & Enright 2006). Because SGH predicts that facilitation should dominate in such harsh environments, facilitation is believed to be an important factor explaining plant aggregation in addition to other ecological factors (e.g. topography, resource availability and dispersal) (Bertness & Callaway 1994; Haase 2001; Perry, Miller & Enright 2006). It has indeed been shown that facilitation tends to maintain the aggregation of seedling cohorts and established plants (Bertness & Callaway 1994; Fajardo & McIntire 2011; Jia *et al.* 2011; McIntire & Fajardo 2011), but we do not yet know whether this is generally true for different modes of facilitation and at different stress levels.

Consequently, we do not know how different modes of competition modify the effects of facilitation on plants and structure their populations and communities in different environmental contexts (Brooker *et al.* 2008). To address this issue, we implemented different modes of facilitation and competition in a generic individual-based model based on the zone-of-influence (ZOI) approach of Weiner *et al.* (2001). Plant growth and density-dependent mortality are described according to a growth model as deriving from 'metabolic scaling theory' (MST; Brown *et al.* 2004; Savage *et al.* 2010) to provide mechanistic representation of plant response to stress. To simplify, we restrict ourselves to intraspecific plant interactions. Specifically, we addressed the following questions at both the plant population and individual levels: (i) How does the interplay of different modes of competition and facilitation change spatial pattern formation during self-thinning in conspecific cohorts that initially have a random or aggregated distribution and (ii) How do combinations of modes of competition and facilitation alter the intensity of local plant interactions along a stress gradient?

Materials and methods

THE MODEL

Metabolic scaling theory predicts quantitative relationships amongst metabolic processes using empirical measurements and theoretical assumptions (West, Brown & Enquist 2001; Enquist 2002; Enquist, West & Brown 2009; Savage *et al.* 2010). We adopted these relationships as the basis of our individual growth model for plants (see Appendix S1). The model is derived from an energy conservation equation

(Enquist & Niklas 2001; West, Brown & Enquist 2001; Hou *et al.* 2008) and takes into account respiration and three basic energy-demanding processes: biomass maintenance, ion transport and biosynthesis (Lambers, Chapin & Pons 2008). It provides a mechanistic and quantitative basis for linking the energy used in metabolism of plants under abiotic stress to local interactions and population dynamics. The growth model is:

$$dm/dt = am^{3/4} - bm = am^{3/4}[1 - (m/M_0)^{1/4}] \qquad \text{eqn 1}$$

where m is total plant biomass, a and b are species-specific constants (Appendix S1) determined by systematic variation of the *in vivo* metabolic rate of different taxa (West, Brown & Enquist 2001) and $M_0 = (a/b)^4$ is the asymptotic maximum size of a plant (calculated for $dm/dt = 0$). The term $am^{3/4}$ in eqn (1) dominates during early plant growth and provides a good quantitative description of plant growth (Enquist, West & Brown 2009).

Because stress can be resource-independent or resource-dependent (Maestre *et al.* 2009), we assume abiotic stress factors act in one or both of two ways: by restricting the energy intake rate and burdening biomass maintenance. This assumption provides a mechanistic basis for representing the effects of stress on plant performance (Lambers, Chapin & Pons 2008). Accordingly, the growth model with stress is:

$$dm/dt = (1 - S)am^{3/4}[1 - (m/M_s)^{1/4}] \qquad \text{eqn 2}$$

where S is a dimensionless efficiency factor that indicates the level of stress, ranging from 0 (no stress) to 1 (extreme stress). $M_s = (1–S)^4 M_0$ is the maximum plant biomass achievable under stress.

Our individual-based model (IBM; Grimm & Railsback 2005) is described in detail in the Supporting Information, following the ODD protocol (Overview, Design concepts, Details) for describing individual-based models (Grimm *et al.* 2006, 2010). In the following, we describe the model's main elements. In our IBM, a plant's circular ZOI (Weiner *et al.* 2001), A, is the physical space in which a plant acquires resources and represents the energy and resources potentially available to the plant. This space is allometrically related to plant biomass, m, as $c_0 A = m^{3/4}$ (Enquist & Niklas 2001), where c_0 is a normalization constant. We represent plant interaction by calculating the overlapping areas among the plants' ZOIs (Weiner *et al.* 2001; Chu *et al.* 2008, 2009, 2010). Competition and facilitation under abiotic stress are incorporated using dimensionless indices, f_p and f_q, respectively. With these assumptions, eqn (2) becomes:

$$dm/dt = f_p f_q cA[1 - (m/M)^{1/4}] \qquad \text{eqn 3}$$

where f_p is the index of competition, f_q refers to the abiotic stress (S) modified by facilitation (see below), $c = ac_0$ is the initial growth rate in units of biomass per area and time and $M = (f_p f_q)^4 M_0$ is the maximum biomass achievable under stress in the presence of competition and facilitation. Modes of competition among plants can be defined along a continuum from completely asymmetric competition (largest plants obtain all contested resources) to completely symmetric

competition (resources in areas of overlap are divided equally among all overlapping individuals, irrespective of their relative sizes; Schwinning & Weiner 1998). To represent the different modes of competition, we define the index of competition, f_p, as

$$f_p = (A_{no} + \sum_{k=1}^{n_o} \frac{v_i m_i^p}{\sum_{j=1}^{n_j} v_j m_j^p} A_{o,k})/A \qquad \text{eqn 4}$$

This index refers to the fraction of resources available in a given area to a plant i after the loss of potential resources from areas overlapping neighbours with biomass m_j (Schwinning & Weiner 1998). A_{no} is the area with no overlap from neighbours, and $A_{o,k}$ denotes the n_o areas overlapping n_j different neighbours. The number of overlapping areas, n_o, can vary due to the position and number of neighbours (see Appendix S1). Parameter p indicates the mode of competition, ranging from complete symmetry ($p = 0$) to complete asymmetry (p approaching infinity). In this article, we restrict ourselves to intraspecific competition and facilitation and assume, therefore, that the species-specific weighting constants of competition v_i and v_j equal 1.

Similarly, we define the index of facilitation modifying abiotic stress, f_q, as

$$f_q = 1 - \frac{S}{A_f + 1} = 1 - \frac{S}{\sum_{k=1}^{n_o} (1 - \frac{w_i m_i^q}{\sum_{j=1}^{n_j} w_j m_j^q}) A_{o,k} + 1} \qquad \text{eqn 5}$$

This term is based on SGH, which reflects the facilitative effect of relieving stress, and is consistent with earlier models (Chu *et al.* 2008, 2009, 2010). Our definition includes earlier indices of facilitation as a special case, all of which only represent symmetric facilitation (Brooker *et al.* 2008; Chu *et al.* 2008, 2009, 2010; Jia *et al.* 2011; see Appendix S1). Here, A_f indicates the benefits gained by a plant from all interactive neighbours under abiotic stress (S), which is calculated as the sum of the areas overlapping ZOIs of neighbour plants. Index q determines the mode of facilitation among plants, ranging from complete symmetry ($q = 0$, algorithmic equivalent to the form used in Chu *et al.* 2008, 2009) to complete asymmetry (q approaching infinity; Table 1). When there is no facilitation ($A_f = 0$), eqn (5) becomes 1–S, which reflects the effect of abiotic stress. As for competition, the species-specific weighting constants of facilitation, w_i and w_j, equal 1 when considering intraspecific interactions, as we do here.

Eqn (3) describes how plants grow under local competition, abiotic stress and facilitation. Eqns (1), (2) and (3) are similar to the von Bertalanffy growth function and other phenomenological growth functions (Weiner *et al.* 2001; Chu *et al.* 2008, 2009, 2010; Jia *et al.* 2011). However, these equations are derived from first principles and their parameters are directly linked to physical and biological processes.

Because individual plant mortality is proportional to mass-specific metabolic rate (Brown *et al.* 2004), we assume that individuals die if their actual growth rate (realistic metabolic rate) falls below a threshold fraction of their basal metabolic rate (scaled by current biomass, i.e. 5% of $m^{3/4}$). Therefore, individual plants may die due to metabolic inactivation caused by environmental stress, local competition, senescence (when m approaches M) or combinations thereof.

Our model was implemented in NETLOGO 4.1.3 (Wilensky 1999). The source code is in Appendix S2.

SCENARIOS AND ANALYSIS

We investigated two modes of facilitation ($q = 0$: completely symmetric and $q = \infty$: completely asymmetric) and two modes of competition ($p = 0$: completely symmetric and $p = \infty$: completely asymmetric), at three stress levels ($S = 0.1, 0.5$ and 0.9). Two initial conditions were used: 300 initial plants distributed over space either with aggregation or randomly (Fig. 1). For both aggregated and random initial location scenarios, all simulations (42 scenarios in total) began with exactly the same plant locations (i.e. using the same random number seed), so that differences in results can be ascribed entirely to the interplay among modes of competition and facilitation at different stress levels. (In simulations not reported here, we used other initial densities, initial locations and interaction combinations to confirm that our general conclusions were not artefacts of initial conditions.)

Ripley's K function is widely used to analyse the spatial point pattern of plants (Ripley 1981; Stoll & Bergius 2005; Perry, Miller & Enright 2006). Here, we employed the variance-stabilizing K function, the so-called Ripley's L function, to evaluate spatial pattern dynamics. The L function, $L(r)$, characterizes the point pattern at certain scales (r), with an expected value of zero under the null hypothesis of complete spatial randomness (CSR). We carried out 499 Monte Carlo simulations for each scenario to determine the 95% confidence envelopes of the L function for CSR. Observed $L(r)$ values out of the envelopes indicate significant aggregation or regularity. Spatial point pattern data were collected at six densities (300, 250, 200, 150, 100 and 50 plants) during the self-thinning process. All statistical analyses were accomplished using R 2.11.1 (R Development Core Team 2010).

To evaluate the net outcome of local interactions (interplay between competition and facilitation) on the performance of individual plants, we used the relative interaction index RII (Armas, Ordiales & Pugnaire 2004):

$$\text{RII} = (m_1 - m_0)/(m_1 + m_0) \qquad \text{eqn 6}$$

where m_1 and m_0 are the performance (mean biomass) of surviving plants at the same resource level with and without local interactions (i.e. isolated plants), respectively. Values of RII from -1 to 1 indicate the net outcome of interactions as negative (from -1 to 0), neutral (equal to 0) and positive (from 0 to 1). To estimate m_0, we used eqn (2) for plant growth in all scenarios.

Results

The interplay between competition and facilitation strongly influenced spatial pattern formation in the plant population along the stress gradient. Different modes of competition and facilitation also led to distinct spatial patterns. With
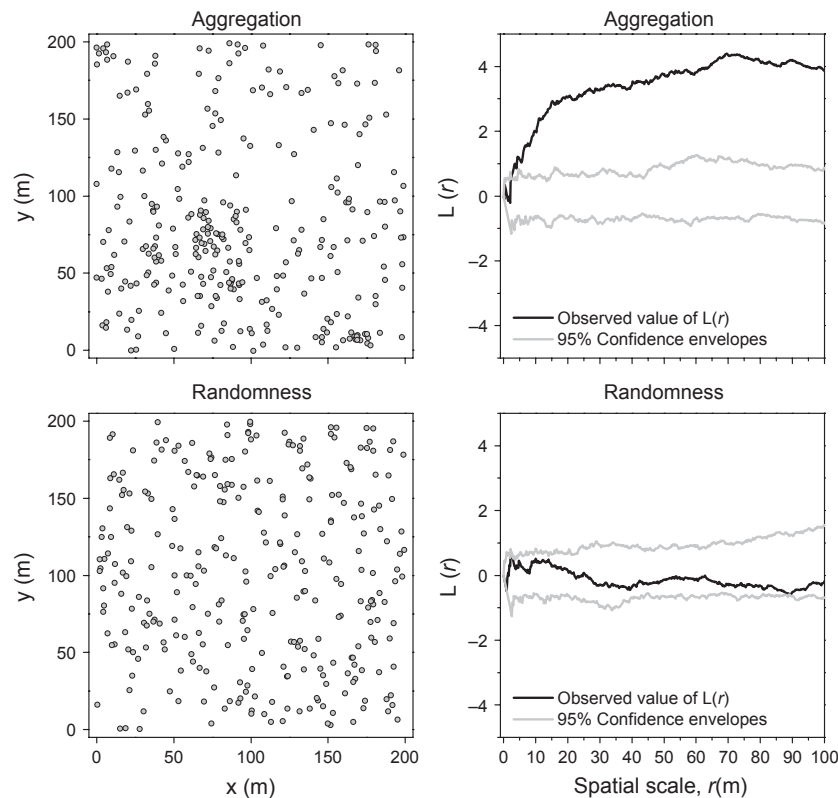
Fig. 1. Initial spatial pattern (left) and corresponding spatial point analysis (Ripley's *L* function, right) of simulated populations. The relative position of observed value of *L(r)* in relation to 95% confidence envelopes indicates the spatial pattern at certain scales (*r*): above the bounds indicates aggregation, between the bounds indicates randomness and below them indicates regularity.

aggregated initial locations (Fig. 1), facilitation was vital for maintaining aggregated patterns if competition was completely symmetric (C_{CS}, $p = 0$) (Fig. 2). Without facilitation (NF), aggregation was maintained only until the number of surviving plants decreased to 200 (Fig. 2a–c). With symmetric facilitation (F_{CS}, $q = 0$), plant aggregation patterns can be maintained (Fig. 2d–f) even at quite low density (100 plants), depending on the level of stress. Aggregated patterns are particularly robust at high stress levels, which is consistent with the predictions of SGH.

In contrast, with asymmetric facilitation (F_{CA}, $q = \infty$), aggregating (Fig. 2g,h) can be maintained only at mild or intermediate stress levels ($S = 0.1$ and 0.5). Under harsh conditions ($S = 0.9$), aggregation disappears early in the self-thinning process (Fig. 2i), a result that deviates from predictions of SGH. However, modes of facilitation had little effect on maintaining aggregation when competition was completely asymmetric (C_{CA}, $p = \infty$; Fig. S2).

The importance of facilitation for creating aggregation became more obvious when the initial pattern was random (Fig. 3). Under completely symmetric competition without facilitation and under benign condition, there was some slight spatial aggregation (values of *L(r)* were very close to the upper boundary of the 95% confidence envelopes defining lack of aggregation) at very small scales (Fig. 3a), but this aggregation instantly disappeared when stress increased (Fig. 3b,c). In contrast, more pronounced aggregation patterns

emerged in the presence of facilitation: symmetric facilitation consistently forced aggregation under harsh conditions (Fig. 3d–f); asymmetric facilitation led to aggregation only when stress was milder (Fig. 3g–i). Nevertheless, asymmetric competition can largely override the effects of facilitation on spatial pattern formation at all stress levels, leading to non-aggregative (even regular) spatial distributions (Fig. S3). This is in agreement with empirical findings (Stoll & Bergius 2005).

The relationship between net outcome of local plant interactions (as evaluated with the RII index) and spatial pattern formation also depended on the modes of interaction and the level of abiotic stress (Fig. 4). In the case of symmetric competition, the net outcome of local interactions was significantly negative (RII close to −1) under mild and intermediate stress conditions independent of the mode of facilitation. RII increased with stress levels and had clearly positive values (RII close to 1) at high stress levels in the presence of symmetric facilitation. In the case of asymmetric competition, the net outcome of local interactions was slightly negative under mild conditions. RII increased monotonically with increasing abiotic stress under symmetric facilitation, but first increased then decreased with increasing abiotic stress under asymmetric facilitation.

Facilitation sometimes resulted in spatial aggregation (Figs 2 and 3) even though the net outcome (RII) of local interaction was negative. This spatial patterning also
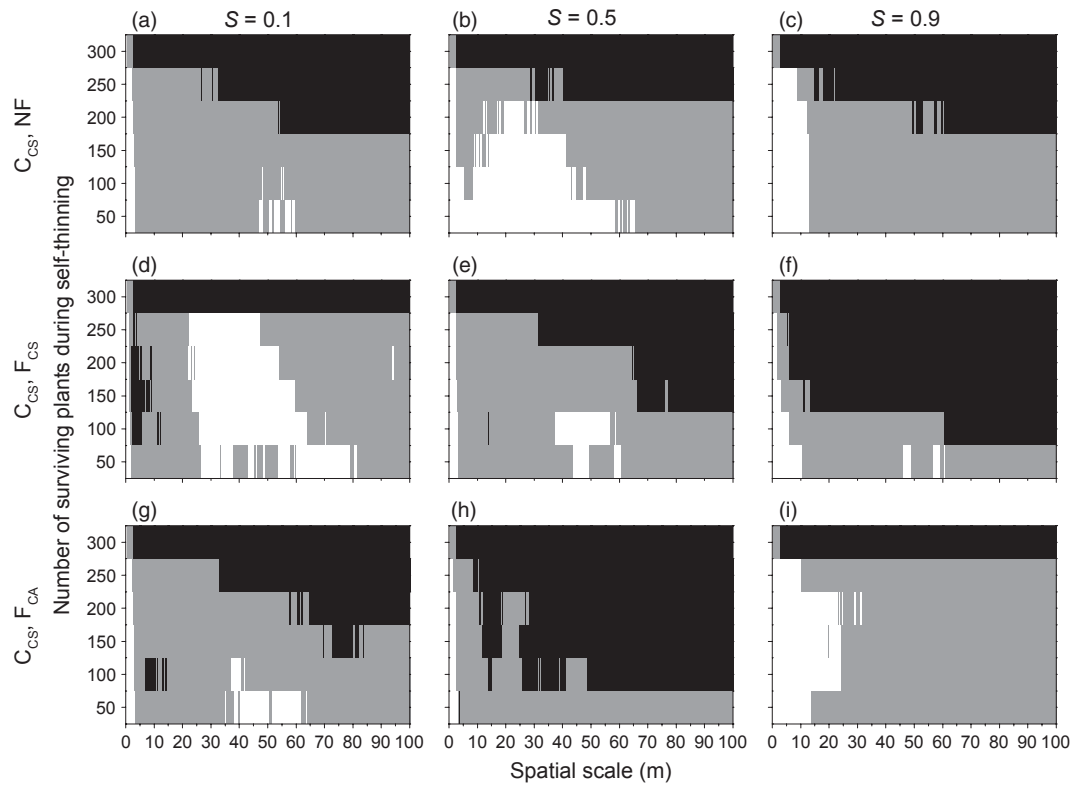
Fig. 2. Spatial dynamics (black, aggregation; grey, randomness; white, regularity) during self-thinning, with aggregated initial locations and completely symmetric competition (C_{CS}, $p = 0$) in the absence (NF) or presence of facilitation (F_{CS}, completely symmetric facilitation, $q = 0$; F_{CA}, completely asymmetric facilitation, $q = \infty$) at different levels of abiotic stress (S).
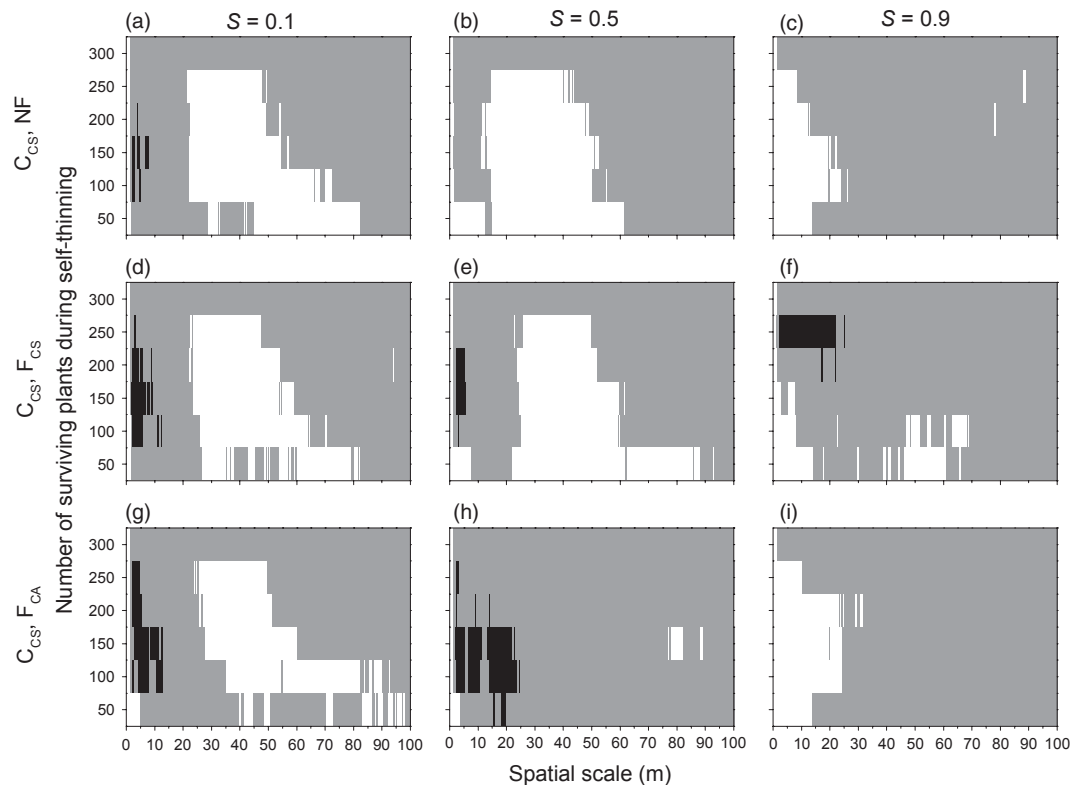

Fig. 3. Spatial dynamics during self-thinning with random initial locations. Symbols and abbreviations are the same as in Fig. 2.
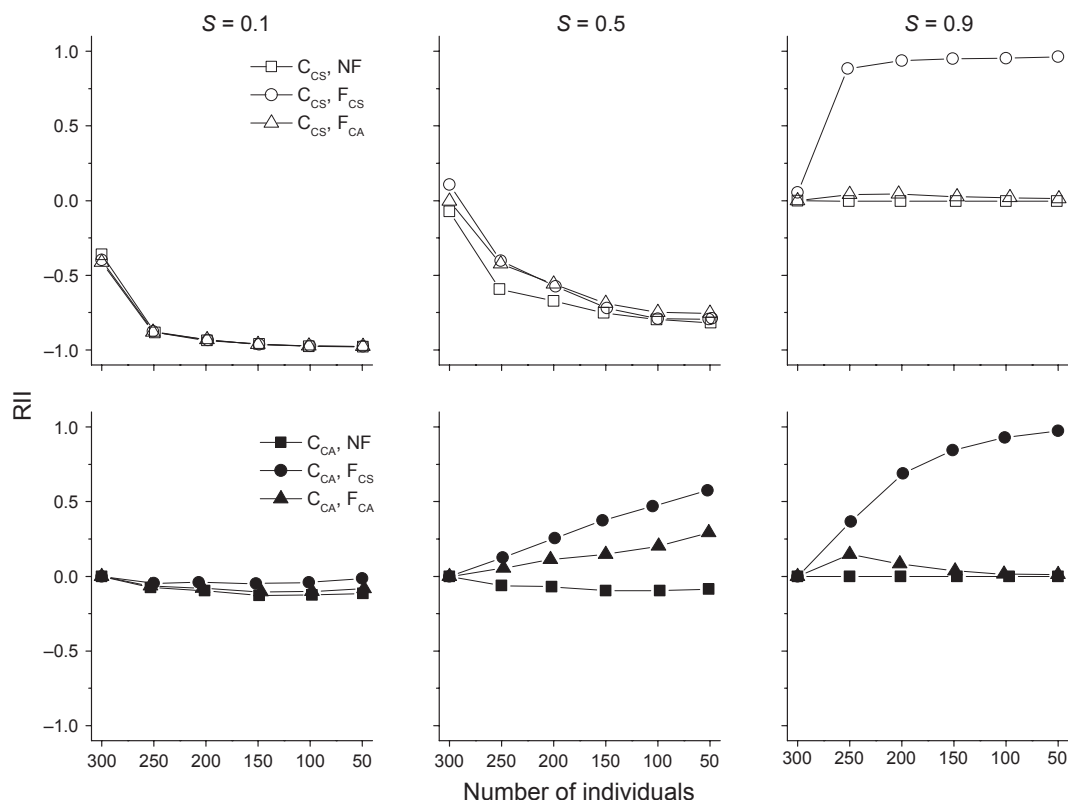
Fig. 4. Relative interaction intensity (RII) during self-thinning under different modes of competition (C_{CS}, completely symmetric competition, $p = 0$; C_{CA}, completely asymmetric competition, $p = \infty$) in the absence (NF) or presence of facilitation (F_{CS}, completely symmetric facilitation, $q = 0$; F_{CA}, completely asymmetric facilitation, $q = \infty$) at different levels of abiotic stress (S) and with aggregated initial locations.

depended on the mode of competition. Such results indicate that even though facilitation was responsible for resulting plant aggregation, the net outcome of local interaction was not always positive under harsh conditions. In other words, modes of interaction can have different effects on different population characteristics, that is, here individual growth (RII) and spatial pattern.

Symmetric facilitation not only mitigated abiotic stress but also delayed the onset of mortality in the case of symmetric competition, at all stress levels (Duncan's test, $P < 0.05$). Symmetric facilitation delayed the self-thinning process, as indicated by the increased survival over time (Fig. S4). Asymmetric facilitation had the same effect only at intermediate stress levels, not at harsh conditions (Duncan's test, $P > 0.05$). However, in the case of asymmetric competition, the effects of facilitation were relatively weak.

Discussion

We have introduced the new concept of modes of facilitation, that is symmetric versus asymmetric facilitation, and have used an individual-based model to explore how these facilitation modes affect plant populations differently. Specifically, we explored how the interplay between different modes of competition and facilitation changes spatial pattern formation during self-thinning in populations that start with either random or aggregated distributions and how combinations of

competition and facilitation modes alter the intensity of local plant interactions along a stress gradient.

Our main finding was that the spatial aggregation of plants can be attributed to different modes of facilitation if competition is symmetric rather than asymmetric, whereas non-aggregative (regular) patterns indicate strong asymmetric competition driving density-dependent mortality (Stoll & Bergius 2005). Facilitation by itself can play an important role in promoting plant aggregation independent of other ecological factors ignored in our scenarios (e.g. seed dispersal, recruitment and environmental heterogeneity); moreover, different modes of facilitation led to different spatial and temporal patterns.

In our simulations of harsh conditions, plants had highest biomass accumulation and survival under the combination of symmetric competition and facilitation. This result emerged from growing in association with neighbours due to facilitation and the increased importance of facilitation at higher stress levels as predicted by SGH. McIntire & Fajardo (2011) found that spatial aggregation and symmetric interactions in *Nothofagus pumilio* are essential for the species' success under harsh conditions. Seedlings growing in clustered cohorts facilitate each other and have higher survival rates than isolated individuals under stress of wind desiccation. With seedlings growing in clusters, natural grafts (physiological and physical merging of stem, branch or root) occur in later growth stages, and multi-stemmed trees survive better than single-stemmed trees. The mode of facilitation and com-

petition among grafted plants is considered to be symmetric because the transport of resources and assimilates is bidirectional (Silvertown & Charlesworth 2001; Lambers, Chapin & Pons 2008). The combination of symmetric facilitation and competition in these tree clusters decreases the impact of stress and the onset of competition among them (Fajardo & McIntire 2010; Tarroux & DesRochers 2011). Therefore, mortality is lower within clusters and leads to aggregation, an outcome we also found in our model.

Because we based our model of facilitation on SGH, a monotonic increase in the importance of facilitation with increasing stress should be expected due to the assumptions underlying eqn (5). Surprisingly, this effect was outweighed by asymmetric facilitation. Our study indicated that with symmetric competition, asymmetric facilitation first promotes plant aggregation under mild and intermediate stress conditions, but then brings about spatial disaggregation at the more stressful end of the gradient (Fig. 2g–i). Moreover, asymmetric facilitation was found to delay the self-thinning process (indicated by increased survival over time) only under intermediate stress conditions (Fig. S4). This is because under very stressful conditions, plants are very sensitive to physical stress and local competition. Competition will thus aggravate the mortality of those individuals that were disadvantaged by asymmetric facilitation. Asymmetric facilitation can thus promote plant survival and aggregation only if the environment is less harsh, as we observed in our model.

Our results regarding asymmetric facilitation are consistent with recent empirical findings that the SGH is not fully supported by observations (Maestre *et al.* 2009). Reduced positive effects on plant survival have been observed in arid areas at high stress levels (Tielbörger & Kadmon 2000; Maestre, Valladares & Reynolds 2005; Maestre *et al.* 2009). A switch from negative to positive and back to negative effects on plant survival was found in a semi-arid steppe along a gradient of decreasing rainfall (Maestre & Cortina 2004). Similarly, Tielbörger & Kadmon (2000) found that the effect of desert shrubs on abundance and reproductive success of understorey annuals shifted from positive to neutral and to negative with decreasing annual rainfall.

Our findings suggest a mechanism explaining such exceptions to the SGH's prediction of monotonic increasing net positive effect with stress: the nature of abiotic stress factors is also important (Maestre *et al.* 2009). Abiotic stress factors not only alter the mode of competition (Schwinning & Weiner 1998; Berger *et al.* 2008), but also the mode of facilitation (Maestre *et al.* 2009). It is therefore important to ask how symmetric and asymmetric facilitation are interrelated with different kinds of stress factors. In the light of the new concept presented here, it should be expected that if the effect of stress is symmetrically mitigated by other individuals, symmetric facilitation should usually be prevalent (detected via plant aggregation or positive RII in our simulation). Using an individual-based model, Chu *et al.* (2009) found that symmetric facilitation (mutualism) among plants can increase plant biomass and size inequality in conspecific populations. Their results are consistent with empirical findings for an

annual species (*Elymus nutans*) in alpine meadows (although they worked with clonal ramets, which probably confounded physiological integration with positive interactions among individuals; Fajardo & McIntire 2011). The mode of facilitation in their experiment was probably symmetric because frost is the most important stress factor in their research area (Chu *et al.* 2009): all individuals endure the same degree of low temperature stress, which is not asymmetrically mitigated by other individuals.

In contrast, when the stress factor is 'pre-mitigable' and/or directional (e.g. higher ultraviolet radiation due to ozonosphere depletion or direct damage caused by wind), facilitation should be more asymmetric (Fig. S1). For example, in a conspecific plant population under strong ultraviolet radiation, taller plants (benefactor) will suffer most from radiation stress, but their crowns can reduce stress in the understorey microenvironment. As a result, smaller plants (beneficiary) can receive disproportionately more benefit from their neighbouring taller plants for maintenance and growth and therefore survive longer. Asymmetric facilitation should thus reduce size inequality in plant populations, which is in contrast to symmetric facilitation that can increase size inequality (Chu *et al.* 2009). This effect of asymmetric facilitation is observed in our model and consistent with empirical studies (Lin *et al., unpublished data*). To the best of our knowledge, effects of different modes of facilitation have not been addressed systematically in empirical experiments yet, so we suggest this topic for future research.

To answer our second research question about the effect of different combinations of competition and facilitation on local interactions, we employed the index RII to measure the direction and magnitude of local interactions along a stress gradient. We found a monotonically increasing strength of facilitation relative to competition for symmetric facilitation but not for asymmetric facilitation. Negative interaction was dominant under mild and less harsh conditions.

Our results indicate that even though facilitation can lead to plant aggregation at the population level, the net outcome and intensity of local interactions at the individual plant level is not necessarily positive. In particular, we found that for some scenarios (e.g. C_{CS}, F_{CA}, $S = 0.5$), competition is the dominant process when assessing plant growth (the net outcome is negative as indicated by RII; Fig. 4), whereas the corresponding spatial aggregation and greater survival probability indicate a dominance of facilitation (Figs 2, 3 and S4). In other words, the intensity of interaction (as the net outcome between competition and facilitation) is insufficient to express the relative importance of competition and facilitation on structuring plant systems (Brooker *et al.* 2005). Furthermore, our findings imply that facilitation may be more common than generally believed, but its important role in structuring populations and communities can be hidden simply because it is hard to detect. Thus, establishing whether competition or facilitation is the dominant process in plant populations or communities can be difficult, because competition and facilitation act simultaneously (Callaway 2007) but can affect different aspects of plant populations or communities.

Nevertheless, the importance of facilitation has been clearly detected in arid, alpine and arctic habitats, which are assumed highly sensitive to global change (Callaway *et al.* 2002; Brooker *et al.* 2008). It is therefore crucial to better understand both the mode of facilitation and nature of stress factors, because the facilitative effect from key species is essential for system diversity and stability in such conditions (Brooker *et al.* 2008; Vellend 2008). Although we focused here on intraspecific interactions, our approach can easily be used to analyse communities. Our conclusions may thus also be relevant for plant communities.

To conclude, our study is the first to quantitatively define different modes of facilitation, and it is also the first attempt to integrate different modes of facilitation with different modes of competition into the SGH. We showed that facilitation can have an important influence on population structure. Moreover, different modes of facilitation and competition can affect different aspects of plant populations and communities, implying context-dependent outcomes and consequences. Explicit consideration of modes and mechanisms of interaction (both facilitation and competition) and the nature of stress factors may help us extend the SGH framework and foster research on facilitation in ecology (Brooker *et al.* 2008; Maestre *et al.* 2009).

Acknowledgements

References

Armas, C., Ordiales, R. & Pugnaire, F.I. (2004) Measuring plant interactions: a new comparative index. *Ecology*, **85**, 2682–2686.

Berger, U., Piou, C., Schiffers, K. & Grimm, V. (2008) Competition among plants: concepts, individual-based modelling approaches, and a proposal for a future research strategy. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 121–135.

Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.

Bronstein, J.L. (2009) The evolution of facilitation and mutualism. *Journal of Ecology*, **97**, 1160–1170.

Brooker, R.W. & Callaway, R.M. (2009) Facilitation in the conceptual melting pot. *Journal of Ecology*, **97**, 1117–1120.

Brooker, R., Kikvidze, Z., Pugnaire, F.I., Callaway, R.M., Choler, P., Lortie, C.J. & Michalet, R. (2005) The importance of importance. *Oikos*, **109**, 63–70.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G. *et al.* (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, **96**, 18–34.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Callaway, R.M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.

Cavieres, L.A. & Badano, E.I. (2009) Do facilitative interactions increase species richness at the entire community level? *Journal of Ecology*, **97**, 1181–1191.

Chu, C.J., Maestre, F.T., Xiao, S., Weiner, J., Wang, Y.S., Duan, Z.H. *et al.* (2008) Balance between facilitation and resource competition determines biomass–density relationships in plant populations. *Ecology Letters*, **11**, 1189–1197.

Chu, C.J., Weiner, J., Maestre, F.T., Xiao, S., Wang, Y.S., Li, Q. *et al.* (2009) Positive interactions can increase size inequality in plant populations. *Journal of Ecology*, **97**, 1401–1407.

Chu, C.J., Weiner, J., Maestre, F.T., Wang, Y.S., Morris, C., Xiao, S. *et al.* (2010) Effects of positive interactions, size symmetry of competition and abiotic stress on self-thinning in simulated plant populations. *Annals of Botany*, **106**, 647–652.

Enquist, B.J. (2002) Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. *Tree Physiology*, **22**, 1045–1064.

Enquist, B.J. & Niklas, K.J. (2001) Invariant scaling relations across tree-dominated communities. *Nature*, **410**, 655–660.

Enquist, B.J., West, G.B. & Brown, J.H. (2009) Extensions and evaluations of a general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Sciences*, **106**, 7046.

Eränen, J.K. & Kozlov, M.V. (2008) Increasing intraspecific facilitation in exposed environments: consistent results from mountain birch populations in two subarctic stress gradients. *Oikos*, **117**, 1569–1577.

Fajardo, A. & McIntire, E.J. (2010) Merged trees in second-growth, fire-origin forests in Patagonia, Chile: positive spatial association patterns andtheir ecological implications. *American journal of botany*, **97**, 1424–1430.

Fajardo, A. & McIntire, E.J. (2011) Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. *Journal of Ecology*, **99**, 642–650.

Grimm, V. & Railsback, S.F. (2005) *Individual-Based Modeling and Ecology*. Princeton University Press, Princeton and Oxford.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J. *et al.* (2006) A standard protocol for describing individual-based and agent-based models. *Ecological modelling*, **198**, 115–126.

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J. & Railsback, S.F. (2010) The ODD protocol: a review and first update. *Ecological modelling*, **221**, 2760–2768.

Gross, K. (2008) Positive interactions among competitors can produce species-rich communities. *Ecology Letters*, **11**, 929–936.

Haase, P. (2001) Can isotropy vs. anisotropy in the spatial association of plant species reveal physical vs. biotic facilitation? *Journal of Vegetation Science*, **12**, 127–136.

Hou, C., Zuo, W., Moses, M.E., Woodruff, W.H., Brown, J.H. & West, G.B. (2008) Energy uptake and allocation during ontogeny. *Science*, **322**, 736.

Jia, X., Dai, X.F., Shen, Z.X., Zhang, J.Y. & Wang, G.X. (2011) Facilitation can maintain clustered spatial pattern of plant populations during density-dependent mortality: insights from a zone-of-influence model. *Oikos*, **120**, 472–480.

Kikvidze, Z., Pugnaire, F.I., Brooker, R.W., Choler, P., Lortie, C.J., Michalet, R. *et al.* (2005) Linking patterns and processes in alpine plant communities: a global study. *Ecology*, **86**, 1395–1400.

Lambers, H., Chapin, F.S. & Pons, T.L. (2008) *Plant Physiological Ecology*. 2nd edition. Springer Verlag, New York, NY.

Maestre, F.T. & Cortina, J. (2004) Do positive interactions increase with abiotic stress? A test from a semi-arid steppe *Proceedings of the Royal Society of London, Series B*, **271**, S331–S333.

Maestre, F.T., Valladares, F. & Reynolds, J.F. (2005) Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments *Journal of Ecology*, **93**, 748–757.

Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, **97**, 199–205.

McIntire, E.J. & Fajardo, A. (2011) Facilitation within species: a possible origin of group-selected superorganisms. *The American Naturalist*, **178**, 88–97.

Michalet, R., Xiao, S., Touzard, B., Smith, D.S., Cavieres, L.A., Callaway, R.M. & Whitham, T.G. (2011) Phenotypic variation in nurse traits and community feedbacks define an alpine community. *Ecology Letters*, **14**, 433–443.

Pakeman, R.J., Pugnaire, F.I., Michalet, R., Lortie, C.J., Schiffers, K., Maestre, F.T. *et al.* (2009) Is the cask of facilitation ready for bottling? A symposium on the connectivity and future directions of positive plant interactions *Biology Letters*, **5**, 577–579.

Perry, G.L., Miller, B.P. & Enright, N.J. (2006) A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. *Plant Ecology*, **187**, 59–82.

R Development Core Team (2010) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Available at: http://www.R-project.org. (accessed 17 February 2012).

Reinhart, K.O., Maestre, F.T. & Callaway, R.M. (2006) Facilitation and inhibition of seedlings of an invasive tree (*Acer platanoides*) by different tree species in a mountain ecosystem. *Biological Invasions*, **8**, 231–240.

Ripley, B.D. (1981) *Spatial Statistics*. John Wiley and Sons, New York, NY.

Savage, V.M., Bentley, L.P., Enquist, B.J., Sperry, J.S., Smith, D.D., Reich, P. B. *et al.* (2010) Hydraulic trade-offs and space filling enable better predictions of vascular structure and function in plants. *Proceedings of the National Academy of Sciences*, **107**, 22722.

Schwinning, S. & Weiner, J. (1998) Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, **113**, 447–455.

Silvertown, J.W. & Charlesworth, D. (2001) *Introduction to Plant Population Biology*. Blackwell Publishing Limited, Oxford, UK.

Stoll, P. & Bergius, E. (2005) Pattern and process: competition causes regular spacing of individuals within plant populations. *Journal of Ecology*, **93**, 395–403.

Tarroux, E. & DesRochers, A. (2011) Effect of natural root grafting on growth response of jack pine (*Pinus banksiana*; Pinaceae). *American Journal of botany*, **98**, 967–974.

Tielbörger, K. & Kadmon, R. (2000) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology*, **81**, 1544–1553.

Vellend, M. (2008) Effects of diversity on diversity: consequences of competition and facilitation. *Oikos*, **117**, 1075–1085.

Weiner, J., Stoll, P., Muller-Landau, H. & Jasentuliyana, A. (2001) The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. *The American Naturalist*, **158**, 438–450.

West, G.B., Brown, J.H. & Enquist, B.J. (2001) A general model for ontogenetic growth. *Nature*, **413**, 628–631.

Wilensky, U. (1999). *NetLogo*. Center for Connected Learning and Computer-Based Modeling, Northwestern University. Available at: http://ccl.northwestern.edu/netlogo/ (accessed 17 February 2012).

Supporting Information

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

Appendix S1. ODD of pi model.

Appendix S2. NetLogo file of pi model.

Figure S1. Conceptual model of the occurrence of asymmetric- versus symmetric facilitation.

Figure S2. Spatial dynamics during self-thinning under completely asymmetric competition with aggregated initial locations.

Figure S3. Spatial dynamics during self-thinning under completely asymmetric competition with random initial locations.

Figure S4. Temporal dynamics of density-dependent mortality.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.