

## Population dynamic consequences of competitive symmetry in annual plants

Susanne Schwinning and Gordon A. Fox

Schwinning, S. and Fox, G. A. 1995. Population dynamic consequences of competitive symmetry in annual plants. – *Oikos* 72: 422–432.

Asymmetric competition is a form of resource division among plants, in which large plants greatly suppress the growth of smaller neighbors. In annual plants, small size differences between seedlings at the onset of competition are magnified into large differences in seed-set by asymmetric competition. We formulate a novel neighborhood model, which reflects this seedling size effect as modified by the type of competitive symmetry. In the model, competition type is represented by a single, biologically meaningful parameter. We implement the model in a population growth model for two species, one at low density (the invader), and one at high density (the resident). The species are the same, except for their seedling biomass distributions. Under these conditions, we find that asymmetric competition always favors invasion by the species with larger average seedling size, but impairs invasion by the other species. Based on this invasibility criterion, we conclude that asymmetric competition always favors competitive exclusion in our model. However, by modifying some of the model assumptions, we suggest scenarios in which asymmetric competition may promote coexistence.

*S. Schwinning and G. A. Fox, Dept of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, AZ 85821, USA (present address of SS: Inst. for Grasslands and Environmental Research, North Wyke Research Station, Okehampton, Devon, U.K. EX20 2SB; present address of GAF: Dept of Biology 0116, Univ. of California, San Diego, 9500 Gilman Dr., La Jolla, CA 92093–0116, USA).*

There are essentially two ways in which competing plants gain resources. They may acquire resources in proportion to biomass, or larger plants may capture more resource per unit biomass, because they have the ability to preempt resources from smaller neighbors. The first of these types of competition is called symmetric, or two-sided competition, and the second is called asymmetric, or one-sided competition (Harper 1977, Aikman and Watkinson 1980, Turner and Rabinowitz 1983, Weiner and Solbrig 1984, Firbank and Watkinson 1985, Weiner 1990). These competition types can have an important influence on plant population dynamics (Watson 1980, Weiner 1990, Pacala and Weiner 1991, Silvertown 1991, Kohyama 1992).

Under strong asymmetric competition, but not under symmetric competition, larger plants have greater relative

growth rates than smaller plants. One consequence of this is that asymmetric competition can generate large size variability in populations during growth, thus establishing "size hierarchies" (e.g. Harper 1967, Watson 1980, Firbank and Watkinson 1985, Weiner and Thomas 1986). Another consequence is that initially small seedling size differences between annual plants are greatly amplified during growth and result in large fitness differences (Hartgerink and Bazzaz 1984, Wall and Begon 1985, Thomas and Bazzaz 1993). Thus, the type of competitive symmetry should be crucial in determining the importance of the seedling stage to individual fitness (Ross and Harper 1972, Harper 1977, Schwinning 1994). This is supported by experimental studies which show that reproductive success in high density stands is correlated

Accepted 15 September 1994

Copyright © OIKOS 1995

ISSN 0030-1299

Printed in Denmark – all rights reserved

with seedling size and time of emergence (e.g. Ross and Harper 1972, Solbrig 1981, Wall and Begon 1985, Waller 1985, Benjamin and Hardwick 1986, Fowler 1988, Thomas and Bazzaz 1993).

If seedling size is an important factor in determining the outcome of intra-specific competition in annual plant populations, it may be an important factor for inter-specific competition as well. There are seemingly plausible verbal arguments that suggest that asymmetric competition also promotes coexistence in annual plant populations, but equally plausible arguments suggest the opposite. For example, in communities of annual plants with seed banks (Harper 1977), populations may be able to coexist through environmental heterogeneity (Hartgerink and Bazzaz 1984, Warner and Chesson 1985, Chesson and Huntly 1989). During unfavorable years or in unfavorable sites, populations persist as dormant seeds, but during favorable years or in favorable sites, they recover rapidly from low density. Coexistence is promoted by differences in what constitutes "favorable conditions" for the species in the community, even if there are differences in the over-all competitive abilities of species. In this context, an increase in reproductive variability promotes coexistence (Warner and Chesson 1985). Thus, asymmetric competition may accelerate recovery from low density by enabling individuals to suppress their heterospecific neighbors more strongly.

On the other hand, asymmetric competition may promote competitive exclusion, if species have consistently different average sizes at the onset of competition. Populations with late germinating, small, or slow growing seedling populations would be excluded faster, the more asymmetric the competition (Fowler 1988, Samson et al. 1992, Zobel 1992).

We hope to clarify this controversy by generating some simple predictions about the effect of initial biomass and the type of competitive symmetry on low-density population growth rates. Thus, we focus on the aspect of persistence in a heterogeneous environment. Within this framework, any factor that raises the average low-density growth rates of all populations in the community is considered coexistence-promoting (Turelli 1981, Chesson 1985).

Our model involves two species of annual plants with seed dormancy. One species is at low density (the invader), and the other at high density (the resident). The two species interact locally in neighborhoods. To study the effect of the competition type, we formalized and generalized Weiner's symmetry concept (Weiner 1990) by introducing an explicit, one-parameter index for the type of competitive symmetry. This index is not simply an abstraction in a model. As we show below, it can easily be estimated from data.

## The model

Here we explain the central ideas behind the model, which we fully describe in Appendix B. Constants and variables are listed in Appendix A. The two species in this model are morphologically similar, such that they experience the same symmetry condition. Species may differ in the initial seedling biomass distribution and in the efficiency with which they convert resources into seeds. The competitive interaction is restricted to neighborhoods. The total resource available to all plants in a neighborhood during the course of a season,  $r$ , is fixed. This resource is partitioned among individuals in relation to their seedling biomass proportions. The seed-set of individuals that are small in relation to their neighbors can be close to zero, but we assume that seedlings do not die, once they have started to interact.

Since we are primarily interested in factors that influence the likelihood of an invasion, we assume that one species is at high density (the resident) and the other at low density (the invader). Since the invader is rare, we assume that all invader individuals compete only against individuals of the resident population. We use the superscripts  $A$  for the invader and  $B$  for the resident. An invader in the  $i$ th neighborhood converts the captured portion of the seasonally available resource,  $r$ , into a number of seeds,  $s^A$ , with conversion efficiency  $c^A$ :

$$s^A = \frac{c^A r}{1 + \sum_{j=1}^n \left( \frac{b_j^B}{b_i^A} \right)^\theta} \quad (1)$$

$b_i^A$  is the seedling biomass of the  $i$ th invader, and  $b_j^B$  of the  $j$ th resident in the  $i$ th neighborhood. This equation is derived in Appendix B. Eq. 1 says that only seedling biomass ratios determine the seed yields of competitors, not their absolute biomass. This is a consequence of the assumption that the plants in one neighborhood produce a fixed number of seeds, in agreement with the constant-yield law. There is a lower and an upper limit to seed yield. Invader seed yield approaches the lower limit, zero, if the invading seedlings' biomass is much smaller than the resident seedlings' biomass. Invader seed yield approaches maximum yield,  $c^A r$ , if the invader is much larger than its neighbors.

Note the formal equivalence of this model to certain hyperbolic neighborhood models for annual plants (e.g. Shinozaki and Kira 1956, Vandermeer et al. 1984, Pacala and Silander 1985, Silander and Pacala 1985, Pacala 1986). In these models the effect of neighbors on focal plants is expressed in terms of an empirical regression coefficient. In our model, the effect of neighbors on focal plants is expressed in terms of seedling size ratios and the index of symmetry. Thus, our model refines neighborhood models by replacing an empirical regression coefficient with variables that can be measured independently.

Fig. 1 illustrates how  $\theta$  can be measured independent

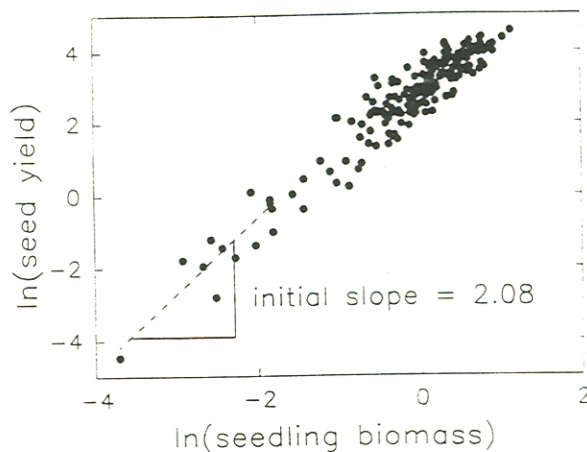


Fig. 1. The regression of log seed yield on log seedling biomass. Data simulated using eq. 1 with normal seedling biomass variation and  $n = 3$  and  $\theta = 2$ . The linear approximation of the slope for low seedling biomass is indicated in the graph.

of the neighborhood model. It shows the correlation between the logs of individual seed yields and seedling sizes at the onset of competition for a hypothetical population. These data were generated by simulating eq. 1 for normally distributed seedling sizes within neighborhoods, but natural populations of non-thinning annual plants have quite similar characteristics (Schwinning 1994). In particular, there is a wide range of seedling sizes for which seedling biomass and seed yield are nearly log-linearly related.  $\theta$  is the initial slope of the regression of log seedling biomass on log seed yield. This is further explained in Appendix C.

The exponent in eq. 1,  $\theta$ , determines the sensitivity of seed yield to differences in seedling biomass. Therefore,  $\theta$  is an index for the type of competitive symmetry.  $\theta = 1$  implies symmetric competition, because the resources used to generate seed are divided in proportion to the biomass of competitors.  $\theta > 1$  implies asymmetric competition, because larger seedlings capture a greater than proportional share of the resource. In general, the larger  $\theta$ , the greater the advantage of large seedlings.  $\theta$  may vary with density and species composition (Schwinning 1994). The significance and the consequences of  $\theta$  for population size structure is summarized in Table 1.

$\bar{s}^A$  is the average seed yield of invading individuals across neighborhoods. It determines the per capita population growth rate  $G^A$  for the invader:

$$G^A = (1 - \mu^A) (1 - \gamma^A + \gamma^A \bar{s}^A), \quad (2)$$

where  $\mu^A$  is the seed and seedling mortality rate and  $\gamma^A$  fraction of the invader, both assumed constant. We assess changes in the likelihood of an invasion as changes in the invader's population growth rate. An invasion is promoted by factors that increase the average invader's growth rate (Turelli 1981, Chesson 1985).

## Simulation methods

First, we examine eq. 1, assuming that invader and resident have fixed seedling biomass ratios. Second, we examine the average population growth rate of the invader if seedling biomass ratios vary within or across years. In these simulations, we give seedlings normal or log-normal biomass distributions and estimate the invader's population growth rate. The seedling biomass of neighbors is either randomized within years, or fixed within years and randomized across years. In the case of within-year seedling biomass variation, we average the seed production of the invaders across 100 neighborhoods to estimate the population growth rate. In the case of between-year variation, we estimate the geometric average of the invader growth rate based on 500 yr. Population growth rates for the invader are calculated according to eq. (2), setting  $\mu^A = 0.9$  and  $\gamma^A = 0.8$ . All parameter settings are summarized in Appendix A.

## Simulation results

### Fixed seedling biomass ratios

We begin by assuming that species have fixed seedling biomass ratios at the onset of competition. There may be considerable variation in actual seedling biomass between sites or years, as long as such variation between neighbors is fully correlated. Fig. 2 shows the population growth rate of the invader,  $G^A$ , as a function of the log-transformed seedling biomass ratio. Several curves are shown for different values of  $\theta$ . These curves in-

Table 1. Meaning and significance of the index for competitive symmetry.

$\theta$	Resource division	Seed yield	Size structure	Competition (Weiner 1990)
0	same for all plants	$\frac{c^A r}{n+1}$	constant	absolute symmetric
< 1	relatively more for small plants	$\frac{c^A r}{1 + \sum_{j=1}^n \left(\frac{b_j^{\theta}}{b_i^{\theta}}\right)}$	- skewed	relative symmetric
1	proportional to biomass	$\frac{c^A r}{1 + \sum_{j=1}^n \left(\frac{b_j^{\theta}}{b_i^{\theta}}\right)}$	0 skewed	relative symmetric
> 1	relatively more for large plants	$\frac{c^A r}{1 + \sum_{j=1}^n \left(\frac{b_j^{\theta}}{b_i^{\theta}}\right)}$	+ skewed, bimodal	relative asymmetric
$\infty$	all to the largest plant	0 or $c^A r$	bimodal	absolute asymmetric

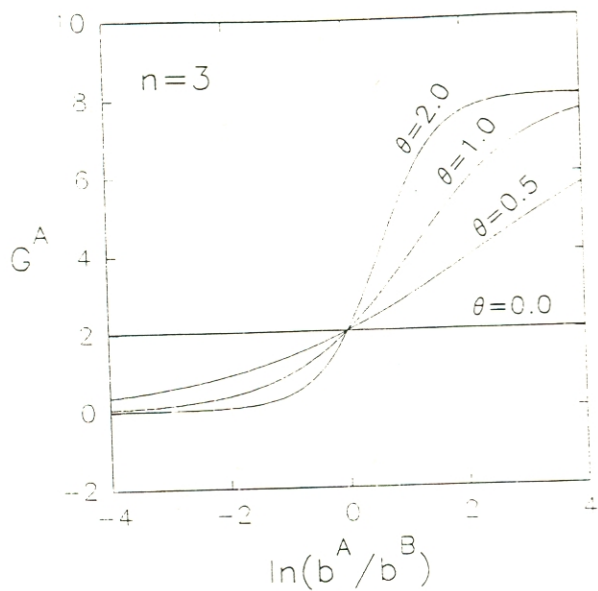


Fig. 2. The effect of seedling biomass ratios ( $\ln(b^A/b^B)$ ) and symmetry ( $\theta$ ) on invader growth rate ( $G^A$ ) (eq. 1). The seedling biomass of both species,  $b^A$  and  $b^B$  is fixed. All neighborhoods contain three residents and one invader ( $n = 3$ ). The four curves correspond to four symmetry conditions, indicated by the  $\theta$  values.

intersect at 0, where invader seedling biomass equals resident seedling biomass. At this point, the type of competitive symmetry makes no difference, because the invader and the resident have equal starting conditions for the competitive interaction.

Under any symmetry condition, with the exception of  $\theta = 0$ , an increase in the seedling biomass ratio results in an increase in the invader's population growth rate. Thus, larger seedlings almost always invade more successfully than smaller seedlings. Therefore, if the invader has a seedling size advantage over the resident, an invasion is favored by asymmetric competition. The more asymmetric the competition, the larger the value of  $\theta$ , the greater the effect of a small seedling size advantage on population growth. On the other hand, if seedling size differences are large, the type of competitive symmetry is less important. The population growth rate of invaders with extremely small seedlings compared to the resident are close to  $(1-\mu^A)(1-\gamma^A)$  since  $s^A \approx 0$  (eq. 2). The growth rate of invaders with extremely large seedlings is close to  $(1-\mu^A)(1+\gamma^A(c^A/r))$  since  $s^A \approx c^A/r$ .

If invader seedlings are smaller than resident seedlings, invasion is more difficult the more asymmetric the competitive interaction. This means that if two species have fixed seedling biomass differences, asymmetric competition cannot give both species an advantage at low density. Asymmetric competition reduces the low-density growth rate of the population with smaller seedlings, and increases the low-density growth rate of the population

with larger seedlings. Therefore, asymmetric competition facilitates the competitive exclusion of the species with the smaller seedling biomass.

When there are more neighbors to compete with, the effects of seedling biomass ratios and symmetry type are qualitatively the same (Fig. 3). If the degree of asymmetry stays constant, all populations grow slower at higher density, since more plants have to share a fixed amount of resource. Density also reduces the sensitivity of the population growth rate to differences in seedling biomass, because it is more difficult to suppress more neighbors.

The degree of asymmetry may often increase with density, however (Schwinning 1994). An increase in  $\theta$  that is mediated through an increase in density does not always increase the low-density growth rate for the population with larger seedlings (Fig. 4). If the invader seedling is only slightly larger than the resident seedling, a density increase combined with an increase in the degree of asymmetry can actually lower its population growth rate. An increase in population density favors the invasion of a population with seedlings that are larger than resident seedlings only if the invader exceeds a minimal size advantage. On the other hand, if the invader has smaller seedlings than the resident, invasion is always more difficult at higher density. Thus, the conclusion is the same as before. Since the low-density growth rate of the population with smaller seedlings is suppressed more than the low-density growth rate of the population with larger seedlings, asymmetric competition favors the exclusion of the first.

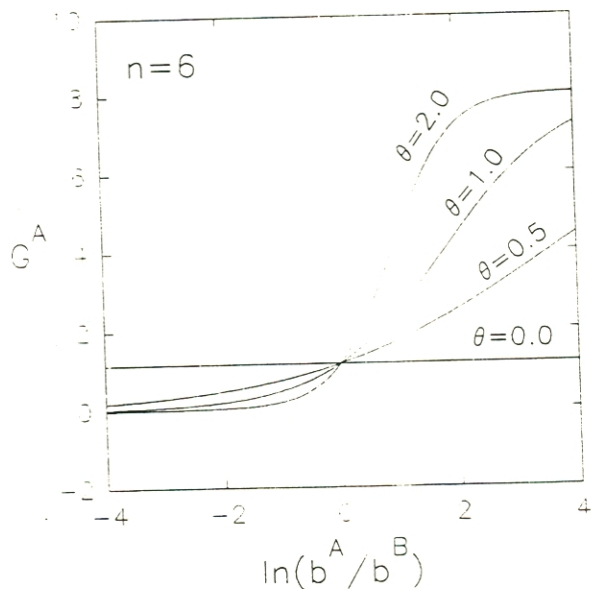


Fig. 3. The effect of seedling biomass ratios ( $\ln(b^A/b^B)$ ) and symmetry ( $\theta$ ) on invader growth rate ( $G^A$ ) (eq. 1). The seedling biomass of both species,  $b^A$  and  $b^B$  is fixed. All neighborhoods contain three residents and one invader ( $n = 6$ ). The four curves correspond to four symmetry conditions, indicated by the  $\theta$  values.

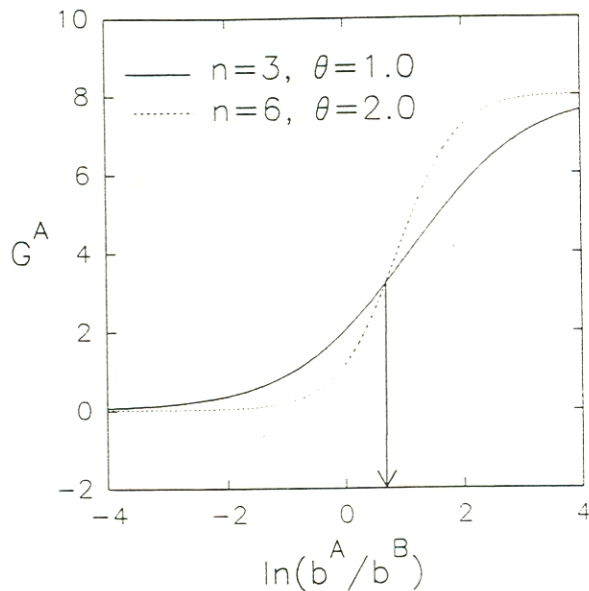


Fig. 4. The effect of seedling biomass ratios ( $\ln(b^A/b^B)$ ) and symmetry ( $\theta$ ) on invader growth rate ( $G^A$ ) if asymmetry ( $\theta$ ) increases with the number of resident individuals per neighborhood ( $n$ ). The seedling biomass of both species,  $b^A$  and  $b^B$  is fixed. The arrow indicates the minimal biomass ratio above which an increase in  $\theta$  and  $n$  is advantageous for the invader.

#### Variable seedling biomass ratios

In the preceding section we showed, for populations with fixed seedling biomass ratios, that asymmetric competition favors populations with larger than average seedlings. However, if biomass ratios vary between neighborhoods or years, there will be competitive reversals in some neighborhoods or years. Does asymmetric competition favor coexistence under variable seedling biomass ratios?

We estimated the distribution of local biomass ratios by assuming that seedlings of populations  $A$  and  $B$  are either normally or log-normally distributed and that the seedling sizes of neighbors are fully uncorrelated. Fig. 5 shows how population differences in average seedling biomass affects the invader growth rate when seedling biomass is normally distributed. As in the case of fixed biomass ratios, asymmetric competition increases the low-density growth rates of the population with greater seedling biomass, and decreases the low-density growth rate of the population with smaller average seedling biomass. If average seedling sizes are equal, the type of competitive symmetry has no effect. Thus, asymmetry favors populations with greater seedling biomass, even if seedling biomass is only greater on average. This result is qualitatively unchanged if seedling biomass is log-normally distributed (results not shown).

However, given that competition is asymmetric, and there are differences in the seedling biomass of compet-

ing populations, seedling biomass variation can increase the average low-density growth rate of populations with small seedlings (Fig. 6). In this case, seedling biomass variation is log-normal and varies within years, but not between years. This positive effect of seedling variation is explained by the fact that large seedlings more than compensate for the loss of seed yield brought on by small seedlings. On the other hand, seedling size variation in populations with large average seedlings decreases the low-density population growth rate, because small seedlings depress the growth rate more than large seedlings can enhance it. We find similar results for normal seedling biomass variation within years.

Interestingly, log-normal variation in seedling biomass between years also has similar effects. However, if seedling biomass varies normally, the growth rate of populations with large average seedlings is little affected by seedling size variation, while populations with small average seedlings still have a growth rate advantage through seedling variation (Fig. 7).

Thus, under this model, asymmetric competition is not coexistence-promoting (Figs 2-5). However, if competition is asymmetric, seedling size variation can increase the low-density growth rates of populations with small average seedling size (Figs 6 and 7).

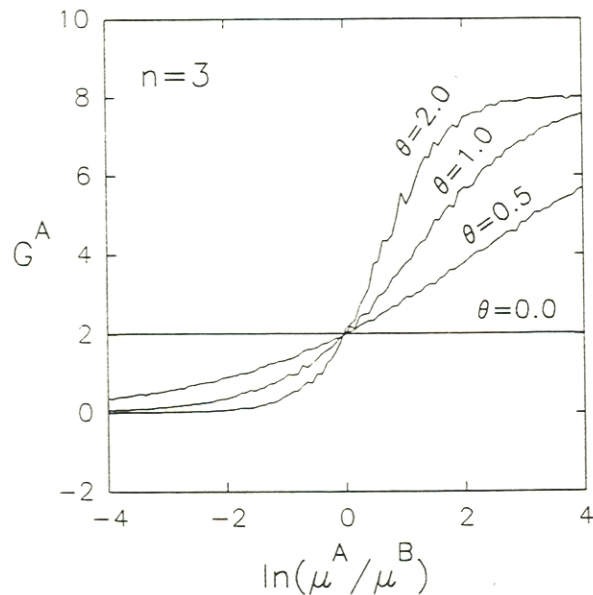


Fig. 5: The effect of average seedling biomass ratios ( $\ln(\mu^A/\mu^B)$ ) and symmetry ( $\theta$ ) on the invader growth rate ( $G^A$ ). The seedling biomass of both species varies normally. The mean of the resident seedling size distribution is fixed at  $\mu^B = 1.0$  with standard deviation  $\gamma^B = 0.3$ . The mean of the invader seedling distribution,  $\mu^A$ , is varied, but the coefficient of variation is held constant and is set equal to the coefficient of variation for the resident seedling size distribution ( $\gamma^A/\mu^A = 0.3$ ). All neighborhoods (100) contain three residents and one invader ( $n = 3$ ). The four curves correspond to four symmetry conditions, indicated by the  $\theta$  values.

G<sup>A</sup>  
Fig.  
grow  
Seed  
locat  
fixe  
is va  
inva  
resid

App  
The  
sults  
the  
ling  
norm  
over  
app  
lytic  
In  
its  
 $\sum_{j=1}^n$   
The  
the  
we  
stit  
 $\bar{x}^A$   
Co  
OIK

crease  
s with  
mass  
it not  
iation  
: than  
small  
on in  
s the  
cause  
large  
s for  
  
mass  
seed-  
pop-  
ed by  
ll av-  
ough  
  
s not  
peti-  
rease  
small

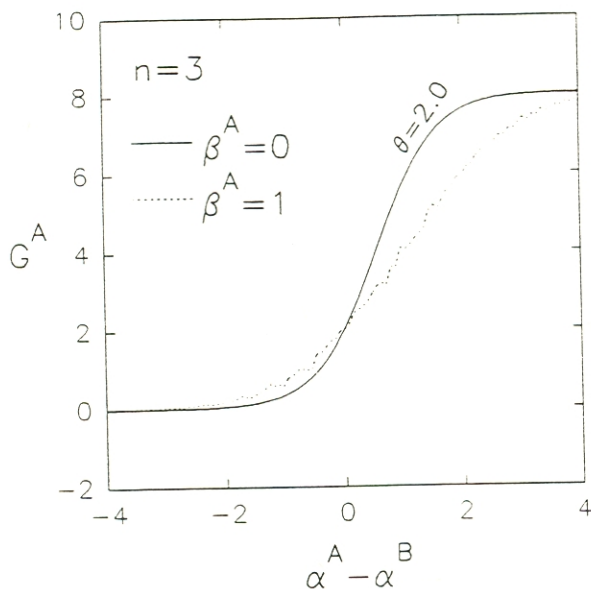


Fig. 6. The effect of seedling size variation on the invader growth rate ( $G^A$ ) when competition is asymmetric ( $\theta = 2.0$ ). Seedlings of both species vary log-normally within years. The location parameter for the resident seedling size distribution is fixed at  $\alpha^B = 0$ , while the location parameter for the invader,  $\alpha^A$ , is varied. Variability for the resident is  $\beta^B = 1.0$ , and for the invader is  $\beta^A = 0$  or 1. All neighborhoods (100) contain three residents and one invader ( $n = 3$ ).

### Approximations

These simulation results are supported by analytical results, based on the simple approximation of substituting the median seedling biomass for the distribution of seedling biomass. This approximation is quite accurate for normal and log-normal seedling biomass distributions over a wide parameter range. Here, we merely present the approximation, while in Appendix D we derive the analytical results.

In eq. 1, we first replace the resident distribution with its median:

$$\sum_{j=1}^n (b_j^B)^\theta \approx n (\tilde{b}^B)^\theta. \quad (3)$$

The tilde indicates the median of a distribution, and  $n$  is the number of residents in the neighborhood. Secondly, we approximate the mean invader seed yield by substituting the median seedling size into eq. 1.

$$\bar{s}^A = \frac{c^A r}{1 + \sum_{j=1}^n \left( \frac{b_j^B}{\tilde{b}^A} \right)^\theta}. \quad (4)$$

Combining these two approximations yields:

$$\bar{s}^A = \frac{c^A r}{1 + n \left( \frac{\tilde{b}^B}{\tilde{b}^A} \right)^\theta}. \quad (5)$$

Thus, as in standard single or multi-species plant competition models, the average seed yield of individuals is a hyperbolic function of density (e.g. Shinozaki and Kira 1956, Vandermeer et al. 1984, Pacala and Silander 1985, Silander and Pacala 1985, Pacala 1986). However, in this case, the effect of density is modified by the seedling size relationship of the competing species and the index of competitive symmetry,  $\theta$ .

### Discussion

We have introduced a novel neighborhood-based plant competition model in which the type of competitive symmetry is represented by a single continuous parameter. The model thus provides a simple, theoretically explicit definition of seasonally integrated competition type for annual plants. Moreover, the symmetry index  $\theta$  can be directly estimated from experimental data (Fig. 1).

Thomas and Weiner (1989) introduced an index for the type of competitive symmetry into an empirical neigh-

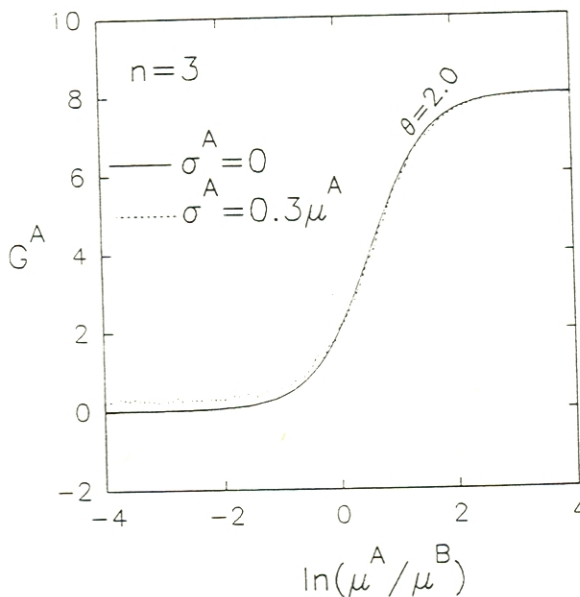


Fig. 7. The effect of seedling size variation on the invader growth rate ( $G^A$ ) when competition is asymmetric ( $\theta = 2.0$ ). Seedlings of both species vary normally between years, and do not vary within years. The mean of the resident seedling size distribution is fixed at  $\mu^B = 1$  with standard deviation  $\sigma^B = 0.3$ . The mean of the invader seedling size distribution,  $\mu^A$ , is varied, but the coefficient of variation is held constant and is set equal to the coefficient of variation for the resident seedling size distribution. Neighborhoods in all years (500) contain three residents and one invader ( $n = 3$ ).

$\mu^A/\mu^B$ )  
lling  
the  
with  
lling  
held  
the  
bor-  
The  
ated

neighborhood model. In their model, the competitive effects of neighbors on focal plants are expressed by a term that includes the sizes and distances of neighbors and a regression coefficient. The type of competitive symmetry is expressed by a factor "a", between zero and one, which discounts the effect of neighbors that are smaller than the focal plant. The smaller "a", the more asymmetric is the competitive interaction. Thus, the authors used a step function to express the modulation of plant size effects by competition type. We used a continuous function, instead. The measure of asymmetry in Thomas' and Weiner's approach (1989) is found by determining the value of "a" that maximizes the  $r^2$  of the neighborhood regression. In our model, an estimate for  $\theta$  can be generated independent of the neighborhood model (see Appendix C). However, unlike Thomas and Weiner (1989), we have not tested our approach against field data.

In our model, the outcome of competition depends on the initial seedling sizes of competitors in a neighborhood. Theoretical and experimental studies (e.g. Ross and Harper 1972, Grubb 1977, 1986, Solbrig 1981, Gross 1984, Hartgerink and Bazzaz 1984, Symonides et al. 1986, Biere 1987, Pacala and Weiner 1991, Wilson and Tilman 1991, Thomas and Bazzaz 1993) suggest that the reproductive success of some annual plant populations indeed depends strongly on the germination phase. Here, we generalize this idea by showing how the importance of the seedling stage is modified by the type of competitive symmetry.

The type of competitive symmetry is usually not known a priori for populations. This suggests that there is a need to include seedling biomass – or empirical estimates of  $\theta$  – in the design of competition experiments, so that the importance of seedling size variation can be determined. Traditional experimental designs seek to eliminate variance due to seedling variation by holding seedling biomass constant, or simply by ignoring seedling size as a factor in analysis of variance and covariance. The implicit assumption here is that competition is absolute symmetric (sensu Weiner 1990: Table 1), but this may often not be true. Moreover, correlations between seedling size and other biologically important factors (such as spatial patterns, seed age, predictive germination) could greatly modify the effect of seedling size. Therefore, assuming that initial seedling biomass variation is just noise may miss important aspects of population ecology.

Our results showed that, for a wide range of parameters, the median seedling biomass can be substituted for the distribution of seedling biomass with little loss of accuracy. The approximation works for both normally and log-normally distributed seedling biomass. Since most data sets show that seedling size distributions are somewhere between these two cases (Benjamin and Hardwick 1986), we suspect that this approximation may be generally useful, and suggest that this warrants further study.

Our analysis reveals that, all else being equal, asym-

metric competition promotes the competitive suppression of populations with smaller than average seedlings. However, all else may not be equal. Below, we discuss some conditions for which asymmetry might have a coexistence-promoting effect:

1) In our model, the individuals of the invading population are scattered across neighborhoods consisting mostly of the resident species. However, if seed dispersal is fairly local, seeds of a population may accumulate in sites where seedlings have a size advantage. If they do, populations form monospecific patches, which are difficult to invade. In this case, asymmetric competition should foster coexistence by inhibiting local invasions. Weiner and Conte (1981) showed that either exclusion or coexistence can occur in plant populations, depending on the amount of long-distance dispersal and therefore on the ability of each species to form monospecific patches.

2) We assumed that seedling biomass variation is independent of characteristics of the seed populations. However, the age of seeds may influence seedling germination. For example, older seeds might germinate sooner than younger seeds, if they have fewer dormancy-inducing factors. Thus, declining populations with older seeds in the seed bank may produce larger seedlings at the onset of competition than increasing populations. If this is true, asymmetric competition should promote coexistence by enhancing the plant size advantage of declining populations.

3) Resource conversion efficiency into seed,  $c^A$ , is constant in our model. However, if seedlings are larger in the sites or years in which they will produce more seeds, the positive effect of large seedlings on population growth would be enhanced, while negative effect of small seedlings would be diminished. This may be interpreted as a form of "predictive germination" (Cohen 1967, Venable and Lawlor 1980). It depends on the existence of environmental cues of future success during the time of germination. If germination is predictive in this sense, asymmetric competition could foster coexistence by enhancing the positive effect of productive sites or years for all species.

To our knowledge, these hypotheses are new and have not been tested in the field. Therefore, we do not know if these mechanisms exist. It seems necessary to consider these possibilities to fully understand the role of competition type at the population level. Competition type is likely to have profound effects on population dynamics and coexistence in communities of annual plants. However, it may not have the same effect in all communities. We showed evidence that asymmetry can promote competitive exclusion, but we also argued that under specific circumstances, asymmetry may have the opposite effect. The role of asymmetric competition in any particular community may depend on fairly subtle characteristics of the resident populations and their environment.

*Acknowledgements* – We thank B. Kendall for discussion during the development of these ideas and J. Weiner for the critical review of the manuscript.

## References

- Aikman, D. P. and Watkinson, A. R. 1980. A model for growth and self-thinning in even-aged monocultures of plants. – *Ann. Bot.* 45: 419–427.
- Benjamin, L. R. and Hardwick, R. C. 1986. Sources of variation and measures of variability in even-aged stands of plants. – *Ann. Bot.* 58: 757–778.
- Biere, A. 1987. Ecological significance of size variation within populations. – In: Vanandel, J., Bakker, J. P. and Snaydon, R. W. (eds), *Disturbance in grasslands*. Junk, Netherlands, pp. 253–263.
- Chesson, P. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. – *Theor. Popul. Biol.* 28: 263–287.
- and Huntly, N. 1989. Short-term instabilities and long-term community dynamics. – *Trends Ecol. Evol.* 4: 293–298.
- Cohen, D. 1967. Optimizing reproduction in a randomly variable environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. – *J. Theor. Biol.* 16: 1–14.
- Firbank, L. G. and Watkinson, A. R. 1985. A model of interference within plant monocultures. – *J. Theor. Biol.* 116: 291–311.
- Fowler, N. L. 1988. What is a safe site?: neighbor, litter, germination date and patch effects. – *Ecology* 69: 947–961.
- Gross, K. L. 1984. Effects of seed size and growth form on seedling establishment of size monocarpic perennial plants. – *J. Ecol.* 72: 369–387.
- Grubb, P. J. 1977. The maintenance of species richness in plant communities: the regeneration niche. – *Biol. Rev.* 52: 107–145.
- 1986. Problems posed by sparse and patchily distributed species in species-rich plant communities. – In: Diamond, J. and T. Case (eds), *Community ecology*. Harper and Row, New York, pp. 207–225.
- Harper, J. L. 1967. A darwinian approach to plant ecology. – *J. Ecol.* 55: 247–270.
- 1977. *Population biology of plants*. – Academic Press, London.
- Hartgerink, A. P. and Bazzaz, F. A. 1984. Seedling-scale environmental heterogeneity influences individual fitness and population structure. – *Ecology* 65: 198–206.
- Kohyama, T. 1992. Size-structured multi-species of rain forest trees. – *Funct. Ecol.* 6: 206–212.
- Pacala, S. W. 1986. Neighborhood models of plant population dynamics. 2. Multi-species models of annuals. – *Theor. Popul. Biol.* 29: 262–292.
- and Silander, J. A. Jr. 1985. Neighborhood models of plant population dynamics. 1. Single species models of annuals. – *Am. Nat.* 125: 385–411.
- and Weiner, J. 1991. Effects of competitive asymmetry on a local density model of plant interference. – *J. Theor. Biol.* 149: 165–179.
- Ross, M. A. and Harper, J. L. 1972. Occupation of biological space during seedling establishment. – *J. Ecol.* 64: 77–88.
- Samson, D. A., Philippi, T. E. and Davidson, D. W. 1992. Granivory and competition as determinants of annual plant diversity in the Chihuahuan desert. – *Oikos* 65: 61–80.
- Schwinning, S. 1994. Effects of competitive symmetry on populations of annual plants. – Ph. D. Thesis, Univ. of Arizona, Tucson, AZ.
- Shinozaki, K. and Kira, T. 1956. Intra-specific competition among higher plants. VII. Logistic theory and the C-D effect. – *J. Inst. Polytech. Osaka City Univ. Ser. D* 7: 35–72.
- Silander, J. A. Jr. and Pacala, S. W. 1985. Neighborhood predictors of plant performance. – *Oecologia* 66: 256–263.
- Silvertown, J. 1991. Modularity, reproductive thresholds and plant population dynamics. – *Funct. Ecol.* 5: 577–580.
- Solbrig, O. T. 1981. Studies on the population biology of the genus *Viola*. II. The effect of plant size on fitness in *Viola sororia*. – *Evolution* 35: 1080–1093.
- Symonides, E., Silvertown, J. and Andreasen, V. 1986. Population cycles caused by overcompensating density-dependence in an annual plant. – *Oecologia* 71: 557–580.
- Thomas, S. C. and Weiner, J. 1989. Including competitive asymmetry in measures of local interference in plant populations. – *Oecologia* 80: 349–355.
- and Bazzaz, F. A. 1993. The genetic component in plant size hierarchies: norms of reaction to density in *Polygonum* species. – *Ecol. Monogr.* 63: 231–249.
- Turelli, M. 1981. Niche overlap and invasion of competitors in random environments I. Models without demographic stochasticity. – *Theor. Popul. Biol.* 20: 1–56.
- Turner, D. M. and Rabinowitz, D. 1983. Factors affecting frequency distribution of plant mass: the absence of dominance and suppression in competing monocultures of *Festuca paradoxa*. – *Ecology* 64: 469–475.
- Vandermeer, J., Ambrose, R., Hansen, M., McGuinness, H., Perfecto, I., Phillips, C., Rosset, P. and Schultz, B. 1984. An ecologically-based approach to the design of intercrop agroecosystems: an intercropping system of soybeans and tomatoes in Southern Michigan. – *Ecol. Model.* 25: 121–150.
- Venable, D. L. and Lawlor, L. 1980. Delayed germination and dispersal in desert annuals: escape in space and time. – *Oecologia* 46: 272–282.
- Wall, R. and Begon, M. 1985. Competition and fitness. – *Oikos* 44: 356–360.
- Waller, D. M. 1985. The genesis of size hierarchies in seedling populations of *Impatiens capensis* Meerb. – *New Phytol.* 100: 243–260.
- Warner, R. R. and Chesson, P. L. 1985. Coexistence by recruitment fluctuations: a field guide to the storage effect. – *Am. Nat.* 125: 769–787.
- Watson, A. R. 1980. Density-dependence in single species populations of plants. – *J. Theor. Biol.* 83: 345–357.
- Weiner, J. 1990. Asymmetric competition in plant populations. – *Trends Ecol. Evol.* 5: 360–364.
- and Conte, P. T. 1981. Dispersal and neighborhood effects in an annual plant competition model. – *Ecol. Model.* 13: 131–147.
- and Solbrig, O. T. 1984. The meaning and measurement of size hierarchies in plant populations. – *Oecologia* 61: 334–336.
- and Thomas, S. C. 1986. Size variability and competition in plant monocultures. – *Oikos* 47: 211–222.
- Wilson, S. D. and Tilman, D. 1991. Components of plant competition along an experimental gradient of nitrogen availability. – *Ecology* 72: 1050–1065.
- Zobel, M. 1992. Plant species coexistence – the role of historical, evolutionary and ecological factors. – *Oikos* 65: 314–320.



## Appendix A

List of symbols

Indices	Definition	
A	Index of the invading species.	
B	Index of the resident species.	

Parameters	Definition	Value
$\mu$	Annual seed mortality.	0.9
$\gamma$	Annual germination fraction.	0.8
$r$	Annually available resource in one neighborhood.	100
$c^A$	Resource-to-seed conversion efficiency for species A.	1
$n$	Number of resident seedlings in a neighborhood.	3 or 6
$\theta$	Symmetry index (see Table 1)	{0, 0.5, 1.0, 2.0}

Initial conditions	Definition	Value
$b_i^A$	Biomass of the <i>i</i> th seedling of species A.	random variable
$b_j^B$	Biomass of the <i>j</i> th seedling of species B in a neighborhood.	random variable
$\bar{b}^A$	Median of A's seedling size distribution.	variable
$\bar{b}^B$	Median of B's seedling size distribution.	1 or 1.02

Final conditions	Definition	Value
$s^A$	Number of seeds produced by an A seedling.	variable
$\bar{s}^A$	Average number of seeds produced by A seedlings within a year.	variable
$G^A$	Per capita population growth rate of species A.	variable
$g^A$	$\ln(G^A)$ , the log-transformed per capita growth rate of species A.	variable

## Appendix B

### Derivation of the model

The central assumption of the model is that an annually available resource,  $r$ , is divided entirely between the members of a neighborhood. The fraction of the total resource each individual captures depends on seedling biomass, but is not necessarily a linear function of biomass. Thus,

$$s_i = rc \frac{b_i^\theta}{\sum_{j=1}^n b_j^\theta}, \quad (\text{B1})$$

where  $s_i$  is the seed yield of the *i*th plant in a neighborhood,  $b_i$  is its seedling biomass, measured at some time after the germination of all seedlings in that year and

before plants start to compete.  $c$  is the efficiency of resource-to-seed conversion, and  $n$  is the total number of seedlings in the neighborhood.  $\theta$  may be a function of density.

Eq. (B1) can be generalized to a two-species case, if it is assumed that species morphologies are similar and that the biomass of one species can be rescaled into biomass equivalents of another species with equal efficiency to capture a limiting resource. Below, we express the seedling biomass of an individual of species A in equivalents of the seedling biomass of species B. Assuming that  $h$  units of A's biomass are equivalent to one unit of B's biomass, eq. (B1) can be rewritten:

$$s_i^A = c^A r \frac{(hb_i^A)^\theta}{\sum_{j=1}^n (hb_j^A)^\theta + \sum_{k=1}^m (b_k^B)^\theta}, \quad (\text{B2})$$

where  $c^A$  is the resource-to-seed yield conversion efficiency of species A,  $b^A$  and  $b^B$  are the seedling biomass of species A and B, respectively, and  $n$  and  $m$  the number of individuals of species A and B in the neighborhood. Thus, we are assuming that both species experience the same symmetry of competition  $\theta$ .

If species A is rare (the invader) and species B is frequent (the resident), most individuals of species A will be found in neighborhoods with no other individuals of species A. With the approximation that all individuals of species are found in such neighborhoods, eq. B2 can be simplified and rearranged:

$$s_i^A = \frac{c^A r}{1 + \sum_{k=1}^m \left( \frac{b_k^B}{hb_i^A} \right)^\theta}. \quad (\text{B3})$$

For simplicity, we set  $h=1$  to produce eq. 1.

## Appendix C

### Symmetry and the index $\theta$

Weiner (1990) classified resource competition into four types based on the way resources are divided between competitors. He called a competitive interaction "absolute symmetric" if plants of all sizes receive the same absolute amount of resource, and "relative symmetric" if plants of all sizes intercept resources in proportion to their sizes. He called an interaction "relative asymmetric" if large plants intercept a greater than proportional share of the resources, and "absolute asymmetric" if the resource interception of the larger plant is not affected by smaller neighbors at all.

These definitions can be used to interpret the parameter  $\theta$  as an index of competitive symmetry. Table 1 shows how the value of  $\theta$  corresponds to Weiner's definitions, and determines the seed yield distribution of the population.

### Estimating $\theta$

$\theta$  can be estimated by regression analysis (Fig. 1). Log-transforming eq. (B3) yields:

$$\ln(s_i) = \theta \ln(b_i) + \ln \left( \frac{cr}{b_i^\theta + \sum_{j \neq i} b_j^\theta} \right) \quad (C1)$$

For small  $b_i$  or at high density, the regression of  $\ln(s)$  on  $\ln(b)$  is approximately linear with slope  $\theta$ . Thus,  $\theta$  can be determined by linear regression. Empirical studies confirm that  $\ln(s)$  and  $\ln(b)$  are often linearly correlated and that  $\theta$  depends on plant density, the type of growth limitations encountered during a year, and certain morphological and physiological properties of the competitors (Schwinning 1994). Increasing density tends to increase the value of  $\theta$  (in effect, making it more important to be initially large). The magnitude of this density response depends on the symmetry of competition in the spaces where zones of resource uptake overlap (Schwinning 1994). In other words, a great deal of plant biology and ecology is summarized in the value of  $\theta$ .

### Appendix D

#### Analyses of the "median approximation" model

Here we show that the simulation results can be supported analytically on the basis of the two approximations described in the main text (eqs 3–5). For simplicity, we limit ourselves to deriving the effects of seedling size, symmetry, density, and invader seedling variation on the average seed yield  $\bar{s}^A$ . The same qualitative results hold for the population growth rate  $G^A$ , as it is a linear function of  $\bar{s}^A$  (eq. 2).

*Effect of seedling size.* The effect of changing the average invader seedling size on seed yield is:

$$\frac{\partial \bar{s}}{\partial \bar{b}^A} = \frac{\theta c^A r n (\bar{b}^B)^\theta (\bar{b}^A)^{\theta-1}}{[(\bar{b}^A)^\theta + n (\bar{b}^B)^\theta]^2} \quad (D1)$$

This partial derivative has no negative terms. Therefore, the effect of increasing seedling size is always to increase the average yield, unless  $\theta = 0$ , in which case it has no effect. The effect of invader seedling size is proportional to the potential number of seeds ( $c^A r$ ) a plant can produce and increases with  $\theta$ . However, the effect of seedling size approaches zero for very large and for very small seedlings. If  $\theta \geq 1$ , the effect of seedling size is maximal at

$$\frac{\bar{b}^A}{\bar{b}^B} \left( \frac{n(\theta-1)}{\theta+1} \right)^{\frac{1}{\theta}} \quad (D2)$$

If  $\theta < 1$ , the effect of seedling size continuously declines with seedling size.

*Effect of symmetry.* The effect of  $\theta$  on the invader's average seed yield is:

$$\frac{\partial \bar{s}}{\partial \theta} = \frac{c^A r n \ln \left( \frac{\bar{b}^A}{\bar{b}^B} \right) \times \left( \frac{\bar{b}^B}{\bar{b}^A} \right)^\theta}{\left[ 1 + n \left( \frac{\bar{b}^B}{\bar{b}^A} \right)^\theta \right]^2} \quad (D3)$$

The sign of this partial derivative is determined by the sign of  $\ln(\bar{b}^A/\bar{b}^B)$ , since all other terms are positive. Therefore, the seed yield increases with  $\theta$  if  $\bar{b}^A > \bar{b}^B$ ; it decreases with  $\theta$ , if  $\bar{b}^A < \bar{b}^B$ ; and if  $\bar{b}^A = \bar{b}^B$ ,  $\theta$  has no effect. In the latter case, the seed yield of the invader is  $c^A r / (n+1)$  for seedlings of all sizes.

*Effect of density.* The effect of density on the invader's average seed yield is:

$$\frac{\partial \bar{s}^A}{\partial n} = - \frac{c^A r (\bar{b}^A)^\theta (\bar{b}^B)^\theta}{[(\bar{b}^A)^\theta + n (\bar{b}^B)^\theta]^2} \quad (D4)$$

insofar as  $\theta$  is independent of density  $n$ . If this is true, the partial derivative in eq. (D4) is always negative, and therefore density always reduces the average seed yield. If  $\theta$  depends on density, this conclusion does not hold, and increasing density could actually increase seed yield (see Fig. 4).

*Effect of small-scale within-year seedling variation.* We assess the effect of seedling variation by using the approximation in eq. 3, but not that in eq. 4. We assume that biomass variation is symmetric on a log scale. This means that it is equally likely for a seedling to be  $k$  times larger than its geometric mean as it is to be  $1/k$  times its geometric mean. Second, we approximate the effect of large seedling variation, for which we make no particular distribution assumptions.

For small-scale within-year variation, we substitute  $\ln(b^A) = x$  into equation (B3):

$$s^A(x) = \frac{c^A r}{1 + n (\bar{b}^B)^\theta e^{-\theta x}} \quad (D5)$$

The average seed yield of a seedling population with mean  $\bar{x}$  is

$$\bar{s}(\bar{x}) = \sum_{i=1}^m p_i s(\bar{x} + \Delta_i), \quad (D6)$$

where  $p_i$  denotes the frequency of deviations of size  $\Delta_i$ .

Eq. (D6) can be approximated by a Taylor expansion:

$$\bar{s}(\bar{x}) \approx \sum_{i=1}^m p_i \left[ s(\bar{x}) + \frac{\partial s}{\partial x} \Delta_i + \frac{1}{2} \frac{\partial^2 s}{\partial x^2} \Delta_i^2 + \frac{1}{6} \frac{\partial^3 s}{\partial x^3} \Delta_i^3 + \dots \right] \quad (D7)$$

The assumption that deviations around  $x$  are distributed