OIKOS 101: 499–504, 2003

# Do seedlings in gaps interact? A field test of assumptions in ESS seed size models

**Jonathan Silvertown and James M. Bullock**

Silvertown, J. and Bullock, J. M. 2003. Do seedlings in gaps interact? A field test of assumptions in ESS seed size models. – Oikos 101: 499–504.

ESS models for the evolution of seed size variation assume that seedlings compete with each other for the occupancy of 'safe sites' or vegetation gaps. If mortality rates are high and/or frequency-independent, ESS models reduce to the classical model of Smith and Fretwell which predicts that a single, optimum seed size should occur. We tested whether seedlings compete with one another by following the survival of seedlings colonizing experimental gaps in a grazed grassland community. In small gaps (3 cm diameter) the proximity of established plants slightly, though significantly reduced seedling survival, but density-dependent mortality also occurred among seedlings in these gaps. In larger gaps (6 cm, 9 cm diameter) survival was significantly positively frequency-dependent. These results strongly support the validity of ESS models.

*J. Silvertown, Dept of Biology, The Open Univ., Milton Keynes, MK7 6AA UK (j.silvertown@open.ac.uk). – J. M. Bullock, NERC Centre for Ecology & Hydrology, CEH Dorset, Winfrith Technology Centre, Dorchester, Dorset, DT2 8ZD UK.*

Seed size varies greatly between species (Harper et al. 1970, Leishman et al. 1995) and the ecological correlates and evolutionary causes of interspecific differences are fairly well understood (reviewed by Silvertown and Charlesworth 2001). In contrast, intraspecific seed size variation, much of which orginates within individual plants (Michaels et al. 1988), is more of a puzzle because the classic Smith-Fretwell model predicts that seed size within populations should have an optimum (Silvertown 1989). The Smith and Fretwell (1974) model concerns the allocation of resources between offspring size and number when there is a size-number trade-off. An optimum seed size is predicted by this simple model due to a diminishing improvement in offspring survival as seeds are made larger. Up to a point bigger is better, but much bigger is not much better. The Smith-Fretwell model assumes that offspring survival is a frequency-independent function of offspring size.

Geritz (1995) created an alternative and apparently more realistic model in which the survival function is frequency-dependent and offspring compete with one another for safe sites such as vegetation gaps. In this model successful establishment depends upon both dispersal into sites and competition with any other seedlings that may be present. A size-number trade-off causes dispersal and competitive abilities to be negatively correlated. It is assumed that competition among seedlings is asymmetric, with those from bigger seeds winning contests against seedlings from smaller seeds. Smaller seeds win sites from which larger seeds are absent by virtue of the inferior dispersal ability and lower abundance of large seeds. In these circumstances, the Geritz model predicts that a range of seed sizes will be evolutionarily stable. However, if frequency-independent seedling mortality affecting seedlings of all sizes is high, the Geritz model reduces to the Smith-Fretwell case and a single optimum seed size is the predicted result (Geritz et al. 1999). Rees and Westoby (1997) have shown that an ESS model for competition between species that is analagous to the Geritz model predicts the co-existence of species with different seed sizes.

Accepted 28 November 2002

ISSN 0030-1299

The fundamental assumption that distinguishes ESS models from the Smith-Fretwell model is that seedling survival is determined chiefly by competition among seedlings rather than by competition from the established vegetation surrounding a gap. In a recent review of the evidence supporting ESS models of seed-size variation Leishman (2001) noted that quantitative information on the relative importance of seedling-seedling competition is lacking. In this paper we present a field test of the assumption that such competition is important, based upon measurements of seedling survival in gaps in an experimental grassland system. Three tests of necessary conditions are applied: 1. If the ESS model of intraspecific seed size variation is valid, seedling survival in gaps should be negatively density-dependent, indicating that seedlings compete with one another. 2. If the ESS model of interspecific seed size variation is valid, seedling survival in gaps should be positively frequency-dependent, particularly in small-seeded species which ought to survive better when larger-seeded species are rare or absent from a gap. 3. Finally, for either model to be valid, the influence of the vegetation surrounding a gap on seedling survival should not overwhelm effects 1 and 2. We tested for the effect of surrounding vegetation by comparing the survival of seedlings in 3 cm diameter gaps with survival in the 3cm core of gaps 6cm and 9cm wide where seedlings are more distant from the influence of established plants.

## Methods

### The field experiment

The study was conducted within a sheep grazing experiment at Little Wittenham, near Oxford, England (15° 37′N, 1° 10′W). The vegetation at this site is typical of fertile, lowland calcareous grasslands in the region and is dominated by perennial grasses, particularly *Lolium perenne* and *Agrostis stolonifera*. Plant population and community dynamics in the Little Wittenham grazing experiment have been intensively studied (Bullock et al. 1994a, b, 1996, 2001, Treweek et al. 1997, Tofts and Silvertown 2000a, b, 2002) and the importance of vegetation gaps is well-documented (Silvertown and Smith 1988, 1989a, b, Silvertown et al. 1992, Bullock et al. 1994c, 1995). Bullock et al. (1994b) found no seedling recruitment by grasses in the closed vegetation, suggesting that gaps are the only ‘safe site’ for seedlings. Variation among gaps in the density and identity of seedlings was correlated with the abundance of each grass species at the gap edge, suggesting that recruitment into gaps was dispersal limited (Bullock et al. 2002).

The present study is based upon a new analysis of seedling survival data from a previously reported experiment on the colonization of experimentally-created gaps (Bullock et al. 1995). Bullock et al. (1995) did not analyse seedling survival. They created experimental vegetation gaps of 3 cm, 6 cm and 9 cm diameter in May 1991 and monitored natural colonization over the following 12 months. (In a separate study at the same site, Bullock et al. 1994c, found that seedlings colonizing gaps were derived mainly from the seed rain rather than the seed bank.) Each seedling which appeared in a gap was identified, recorded and marked with a small spot of colored acrylic paint. A color code was used to identify the census date ( = cohort) on which a seedling was first recorded. Seedlings in 6 cm and 9 cm gaps were separately recorded in the 3 cm core of each gap and in the outer annulus around the core. Eight replicate gaps of each size were made in each of eight paddocks, making a total of 192 gaps. Paddocks were distributed in two blocks, with four grazing treaments in each block.

A total of 7,048 seedlings belonging to 20 species were recorded. Ninety-five percent of seedlings belonged to one of five grass species, so analysis was confined to these abundant species only. Seedlings were censussed 14 times at approximately 15 day intervals between 4 June 1991 and 21 January 1992 and at two additional censuses on 26 March and 29 April 1992. To minimise the number of right-censored survival records for younger seedlings, only those appearing on or before 21 January 1992 were included in the analysis. This precaution produced a sample size of 5,961 for the five grass species. Seed size varied by more than an order of magnitude among the five species. Mean seed masses are, in descending order: *Hordeum secalinum* (4.19 mg), *Bromus hordeaceus* (2.9 mg), *Lolium perenne* (1.79 mg), *Cynosurus cristatus* (0.70 mg), *Poa* spp (mean 0.20 mg) (Grime et al. 1988). Seedlings in the genus *Poa* could not be identified to species and belonged to *P. pratensis* (0.25 mg), *P. trivialis* (0.09 mg) and *P.annua* (0.26 mg). All species except *B. hordeaceus* and *Poa annua* are perennial.

### Data analysis

Survival time was calculated as the number of days between the first census record for a seedling and the last date it was recorded alive. Seedlings still alive on the final census (29 April 1992) were coded as right-censored. The relationships between the hazard rate (i.e. the mortality probability per unit time) and total seedling density in a gap (density), the frequency of a species in a gap (frequency) and gap size (size) were estimated using Cox’s proportional hazard regression as implemented in STATISTICA 6 (StatSoft 2001). The Cox regression was chosen because it is non-parametric and because hazards calculated from life tables showed that species and gap-size effects satisfied the proportionality assumptions of this model (Fox 2001). The form of the model is:

$$h\{(t), (z_1, z_2, \ldots z_m)\} = h_0(t)\exp(\beta_1 z_1 + \beta_2 z_2 + \ldots + \beta_m z_m)$$

in which the dependent variable is the hazard ($h$) for the survival time ($t$) and values of the covariates ($z_1 \ldots z_m$) for each respective individual. The baseline hazard $h_0(t)$ applies to the respective individual when all covariates are set to zero. Independent variables are the $m$ covariates ($z_1 \ldots z_m$) with coefficients ($\beta_1 \ldots \beta_m$). Data were stratified by cohort, which allows a different hazard to apply to seedlings emerging on different dates. In addition to the covariates of direct interest to the study, in preliminary data analysis we included experimental block (values 1 or 2), two seasonal grazing treatments (values 0 or 1 in spring and 0 or 1 in summer) and replicate (values 1–8) as factors. Only block was found to be significant and thus the other covariates were dropped from the subsequent models that are reported here.

Two sets of regression models were run. In the first set of models data were restricted to 3 cm gaps and 3 cm cores of 6 cm and 9 cm gaps. This equalized the area in which seedlings were monitored and allowed us to estimate the effect of gap size on hazard rate without a confounding effect of differing sample areas. Densities and frequencies were calculated cumulatively over time, but for the 3 cm cores only in this analysis. The second set of models were run separately for 3 cm, 6 cm and 9 cm gaps and included cumulative observations of seedlings in the whole area of each gap, not just those in the 3 cm core. Both kinds of model were run for all species together, with species identity included as a covariate, and for each species separately where sample sizes were sufficient to permit this. All analyses treated the seedlings within a gap as independent observations, though strictly they were not. There is no way around this problem which does not also average-out the individual differences among seedlings within a gap (Fox 2001). Note, however, that gaps were replicated and that when included as a covariate replicate was not significant in any of the analyses. This suggests that pseudo-replication was not a problem.

## Results

Results of regression models for seedlings in 3 cm gaps and the 3 cm core of 6 cm and 9 cm gaps are shown in Table 1a. Note that because the dependent variable in the models is a hazard rate, negative coefficients ($\beta$) indicate that a factor has a positive effect upon survival and vice-versa. All effects, including species identity, were significant (Table 1a). Hazard decreased slightly, though significantly with gap size (Fig. 1a). Survival was significantly, negatively density-dependent (Table 1a), with a 65% reduction in survival to the end of the experiment when cumulative seedling density was at the maximum observed (50/gap), compared to a density of 5/gap (Fig. 1b). Survival was significantly, positively frequency-dependent across the range of observed values (Fig. 1c, Table 1a). Separate models were run for four species with sufficient sample size, but only in *Hordeum* did the model show a significant fit ($\chi^2 = 27.766$, $df = 4$, $p < 0.0001$). This species showed a significant positive effect of gap diameter ($p = 0.002$) and a negative effect of density ($p = 0.01$) upon survival.

In the second set of regressions, in which separate models were fitted to all seedlings in 3 cm, 6 cm and 9 cm gaps, only density was significant in 3 cm gaps,

Table 1. Cox proportional hazard regression of seedling survival on density and frequency, stratified by cohort. Results are shown (a) for seedlings in 3 cm gaps and the inner 3 cm core of 6 cm and 9 cm gaps, with gap size as a factor and (b) separately for seedlings in the whole area of gaps of diameter 3 cm, 6 cm and 9 cm. A block effect was significant in all regressions but is not shown. Significant effects are shown in bold.

| Gaps | Obs. (censored) | $\chi^2$ (df) | p | Effect | Beta | SE | t | Exponent beta | Wald Statist. | p |
|---|---|---|---|---|---|---|---|---|---|---|
| (a) | | | | | | | | | | |
| 3 cm & cores of 6 cm & 9 cm | 1689 (484) | 60.89 (5) | <0.0001 | **Spp.** | 0.104 | 0.024 | 4.316 | 1.110 | 18.625 | <0.0001 |
| | | | | **Size** | −0.025 | 0.012 | −2.103 | 0.976 | 4.423 | 0.036 |
| | | | | **Dens.** | 0.011 | 0.003 | 3.702 | 1.011 | 13.706 | 0.0002 |
| | | | | **Freq.** | −0.390 | 0.116 | −3.373 | 0.677 | 11.378 | 0.0007 |
| (b) | | | | | | | | | | |
| 3 cm | 587 (141) | 22.17 (4) | 0.0002 | Spp. | 0.078 | 0.041 | 1.919 | 1.081 | 3.681 | 0.055 |
| | | | | **Dens.** | 0.011 | 0.004 | 2.867 | 1.012 | 8.220 | 0.004 |
| | | | | Freq. | −0.239 | 0.197 | −1.214 | 0.788 | 1.475 | 0.225 |
| 6 cm | 1876 (539) | 60.09 (4) | <0.0001 | **Spp.** | 0.122 | 0.026 | 4.776 | 1.130 | 22.806 | <0.0001 |
| | | | | Dens. | 0.002 | 0.001 | 1.393 | 1.002 | 1.940 | 0.164 |
| | | | | **Freq.** | −0.536 | 0.128 | −4.181 | 0.585 | 17.477 | <0.0001 |
| 9 cm | 2745 (990) | 237.137 (4) | <0.0001 | **Spp.** | 0.195 | 0.023 | 8.607 | 1.216 | 74.081 | <0.0001 |
| | | | | Dens. | −0.001 | 0.001 | −0.531 | 1.000 | 0.282 | 0.596 |
| | | | | **Freq.** | −0.796 | 0.110 | −7.266 | 0.451 | 52.799 | <0.0001 |

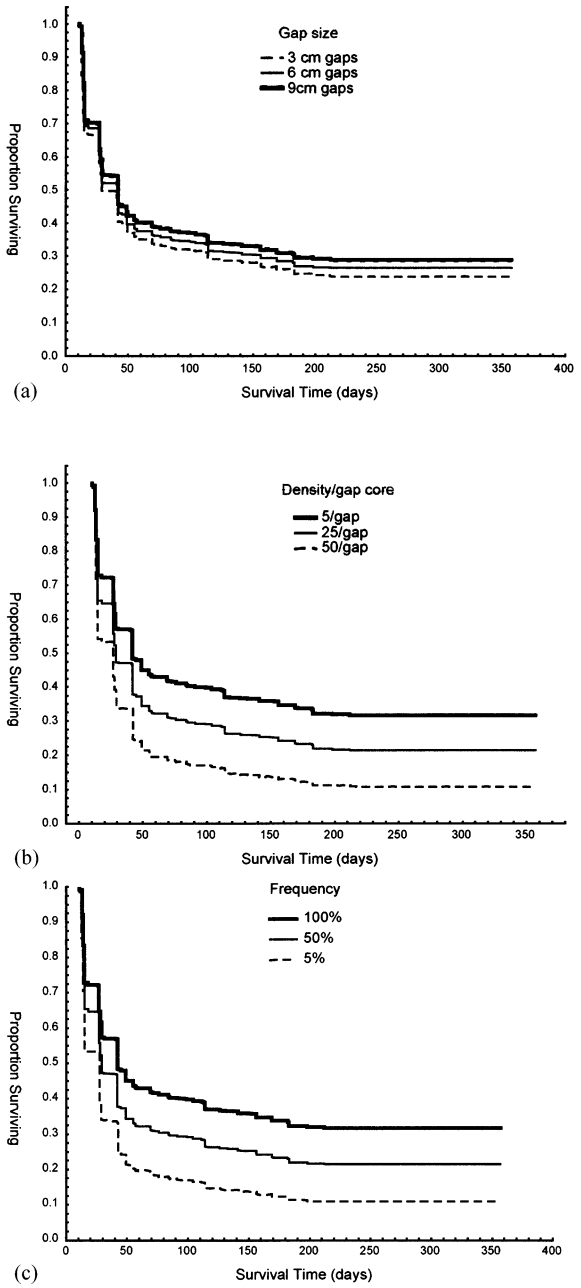

Fig. 1. Effect on seedling survivorship in 3 cm gaps and the 3 cm core of 6 cm and 9 cm gaps of (a) gap size (diameter), (b) seedling density in the core over the observed range of natural variation, (c) species' frequency in the core over the observed range of natural variation.

while species identity and frequency were highly significant in both larger sizes of gap (Table 1b). When models restricted to individual species were run, only those for *Hordeum* fit consistently for 3 cm, 6 cm and 9 cm gaps. Only in 3 cm gaps did this species show significant, negative density-dependent survival ($p = 0.031$) and in no instance did frequency significantly affect survival.

## Discussion

The fates of nearly 6,000 seedlings censused over a 10 month period quite clearly indicated that they interacted in the manner assumed by ESS models of seed size variation. Negative density-dependence is assumed by the Geritz (1995) model of intraspecific seed size variation and we found that seedling survival was indeed negatively density-dependent (Fig. 1b). This effect appeared in the combined analysis of the cores of all three gap sizes (Table 1a), but only in 3 cm gaps when gaps of different size were analysed separately (Table 1b). The coeffecients for the effect of density in 3 cm gaps were nearly identical to those for the density effect seen in the combined analysis (Table 1), indicating that negative density-dependence was largely confined to 3 cm gaps.

Seedling survival was positively frequency-dependent in 6 cm and 9 cm gaps (Fig. 1c, 2). This result supports ESS models of coexistence between species that differ in seed size (Rees and Westoby 1997) because it indicates that a species survived better in gaps where competing species were at low frequency. Positive frequency dependence permits small-seeded species to win some gaps by default when larger-seeded species are rare or absent. Insufficient sample sizes (too few species) prevented us from testing whether positive frequency-dependence was strongest in species with small seeds, as one might expect. However, *Hordeum*, which has the largest seeds of the five species observed, was separately modelled and, as would be predicted, did not show positive frequency-dependence. A comparative field study specifically aimed at this question would be a useful next step.

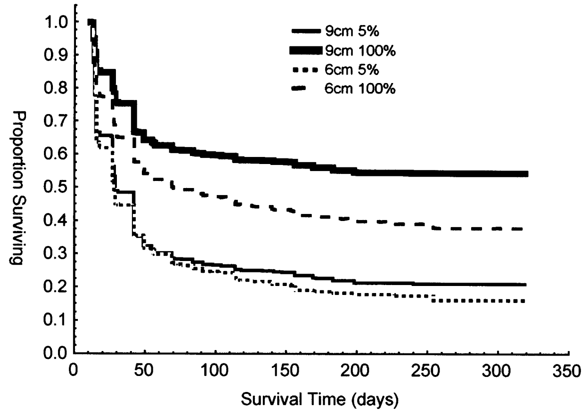

Fig. 2. Effect of species' frequency over the observed range of natural variation in the whole gap area upon seedling survival in 6 cm and 9 cm diameter gaps.

Density- and frequency-dependence were detectable even though seedlings were subject to significant mortality caused by the vegetation around the gap margin. Seedlings growing in the center of a gap had a significantly higher chance of death if the gap was small than if it was large (Table 1a), though this effect was small (Fig. 1a). The likeliest cause of this effect is the proximity to established vegetation, and thus competition. Differential effects of vertebrate herbivory can be ruled out (the possibility of grazing treatment effects was eliminated in preliminary analyses), and although insect and slug herbivory cannot, Hanley et al. (1996) found no effect of gap size on mollusc herbivory in a similar grassland.

The clear picture emerges that in smaller (3 cm) gaps, competition from established vegetation and from other seedlings are significant mortality hazards while in larger gaps positive frequency-dependence occurs. These differences were due to the greater proximity of established vegetation to seedlings in the smaller gaps and because maximum seedling densities were greater in 3 cm gaps (7.1 cm$^{-2}$) than in 6 cm (3.9 cm$^{-2}$) or 9 cm (1.9 cm$^{-2}$) gaps. Density differences were caused by poor dispersal of seeds into the centre of the larger gaps (Bullock et al. 1995). Thus, frequency dependence is mainly detected when competition from conspecifics or established plants is not too severe. However, by comparing Fig. 1a, b and c, it can be seen that the effect of size of gap (3, 6 or 9 cm diameter) on mortality was less than the effect of a species' frequency across the observed ranges of the variables. Overall, then, our results strongly support the assumptions of ESS models regarding seedling-seedling interactions. Note, however, that although these assumptions are fundamental and necessary for the validity of ESS seed-size models, they are not sufficient on their own to show the models actually operate in nature. It is also necessary that larger seeds beat smaller ones and that there is a seed size-number trade-off.

How representative are these results? Vegetation gaps are important for seedling recruitment in many perennial plant communities, including temperate grassland, sub-alpine grassland, alpine tundra, savannah, arid grassland, desert, temperate forest and tropical forest (reviewed by Bullock 2000). This phenomenon is so striking that research has concentrated on the need of seedlings for gaps and how gap size affects recruitment. In contrast, there are few studies of seedling interactions within gaps. Frequency-dependence of survival is particularly poorly studied, but work on density-dependence provides some agreement with our findings. McConnaughay and Bazzaz (1990) found that presence of other seedlings in grassland gaps decreased survival of a range of species. However, two studies of gap recruitment in tallgrass prairies (Platt and Weiss 1985, Rabinowitz and Rapp 1985) found only weak effects of seedling density on mortality. Recruitment in tropical forest gaps has been better studied and density-dependent seedling survival has been shown several times (Augspurger and Kelly 1984; Brokaw 1985, Augspurger and Kitajima 1992). Two recent studies in tropical forests have shown density-dependent seedling-seedling interactions to be both pervasive across many species (Harms et al. 2000; 53 species of liana, shrub and tree) and, in some cases, to be stronger than seedling-adult interactions (Webb and Peart 1999). These studies suggest that seedling-seedling interactions do have some importance in recruitment into vegetation gaps, but empirical evidence to support the ESS assumptions is sparse. Our study has shown that gap size may determine which processes affect seedling survival and this may account for some of the variation among studies. In particular, the present results call for greater attention to be paid to the importance of seed size and positive frequency-dependence in determining the outcome of interspecific competition in gaps.

*Acknowledgements* – We thank the Northmoor Trust for the use of the grazing experiment and for providing facilities and the staff of Little Wittenham Nature Reserve for logistical support. The data were collected under the Joint Agriculture and Environment Programme with support from AFRC (now BBSRC). We are grateful to Bronwen Clear Hill, Martin Sutton, Cathy Lines and Frank Straub for field assisstance and to Gordon Fox for advice on the analysis and for comments on a draft manuscript.

## References

Augspurger, C. K. and Kelly, C. K. 1984. Pathogen mortality of tree seedlings: experimental studies of the effects of dispersal distance, seedling density and light conditions. – Oecologia 61: 211–217.

Augspurger, C. K. and Kitajima, K. 1992. Experimental studies of seedling recruitment from contrasting seed distributions. – Ecology 73: 1270–1284.

Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. – Ecology 66: 682–687.

Bullock, J. M. 2000. Gaps and seedling colonization. – In: Fenner, M. (ed.), Seeds: the ecology of regeneration in plant communities. CAB International, pp. 375–395.

Bullock, J. M., Clear Hill, B. and Silvertown, J. 1994a. Demography of *Cirsium vulgare* in a grazing experiment. – J. Ecol. 82: 101–111.

Bullock, J. M., Clear Hill, B. and Silvertown, J. 1994b. Tiller dynamics of two grasses – responses to grazing, density and weather. – J. Ecol. 82: 331–340.

Bullock, J. M., Clear Hill, B., Dale, M. P. and Silvertown, J. 1994c. An experimental study of the effects of sheep grazing on vegetation change in a species-poor grassland and the role of seedlings recruitment into gaps. – J. Appl. Ecol. 31: 493–507.

Bullock, J. M., Clear Hill, B., Silvertown, J. and Sutton, M. 1995. Gap colonization as a source of grassland community change – effects of gap size and grazing on the rate and mode of colonization by different species. – Oikos 72: 273–282.

Bullock, J. M., Silvertown, J. and Clear Hill, B. 1996. Plant demographic responses to environmental variation: distinguishing between effects on age structure and effects on age-specific vital rates. – J. Ecol. 84: 733–743.

Bullock, J. M., Franklin, J., Stevenson, M. J. et al. 2001. A plant trait analysis of responses to grazing in a long-term experiment. – J. Appl. Ecol. 38: 253–267.

Bullock, J. M., Moy, I. L., Pywell, R. F. et al. 2002. Plant dispersal and colonisation processes at local and landscape scales. – In: Bullock, J. M., Kenward, R. E. and Hails, R. S. (eds), Dispersal ecology. Blackwell Science.

Fox, G. A. 2001. Failure-time analysis: studying times-to-events and rates at which events occur. – In: Scheiner, S. M. and Gurevitch, J. (eds), Design and analysis of ecological experiments. Chapman & Hall, pp. 253–289.

Geritz, S. A. H. 1995. Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density. – Am. Nat. 146: 685–707.

Geritz, S. A. H., van der Meijden, E. and Metz, J. A. J. 1999. Evolutionary dynamics of seed size and seedling competitive ability. – Theor. Popul. Biol. 55: 324–343.

Grime, J. P., Hodgson, J. G. and Hunt, R. 1988. Comparative plant ecology. – Allen & Unwin, London.

Hanley, M. E., Fenner, M. and Edwards, P. J. 1996. The effect of mollusc: grazing on seedling recruitment in artificially created grassland gaps. – Oecologia 106: 240–246.

Harms, K. E., Wright, S. J., Calderon, O. et al. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. – Nature 404: 493–495.

Harper, J. L., Lovell, P. H. and Moore, K. G. 1970. The shapes and size of seeds. – Annu. Rev. Ecol. Syst. 1: 327–356.

Leishman, M. R. 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. – Oikos 93: 294–302.

Leishman, M. R., Westoby, M. and Jurado, E. 1995. Correlates of seed size variation: a comparison among five temperate floras. – J. Ecol. 83: 517–529.

McConnaughay, K. D. M. and Bazzaz, F. A. 1990. Interactions among colonizing annuals – is there an effect of gap size. – Ecology 71: 1941–1951.

Michaels, H. J., Benner, B., Hartgerink, A. P. et al. 1988. Seed size variation: magnitude, distribution, and ecological correlates. – Evol. Ecol. 2: 157–166.

Platt, W. J. and Weiss, I. M. 1985. An experimental study of competition among fugitive prairie plants. – Ecology 66: 708–720.

Rabinowitz, D. R. and Rapp, J. K. 1985. Colonization and establishment of Missouri prairie plants on artificial soil disturbances. II. Detecting small-scale plant-to-plant interactions and separating disturbance from resource provision. – Am. J. Bot. 72: 1629–1634.

Rees, M. and Westoby, M. 1997. Game-theoretical evolution of seed mass in multi-species ecological models. – Oikos 78: 116–126.

Silvertown, J. 1989. The paradox of seed size and adaptation. – Trends Ecol. Evol. 4: 24–26.

Silvertown, J. and Charlesworth, D. 2001. Introduction to plant population biology, 4th ed. – Blackwell Science.

Silvertown, J. and Smith, B. 1988. Gaps in the canopy: the missing dimension in vegetation dynamics. – Vegetatio 77: 56–60.

Silvertown, J. and Smith, B. 1989a. Germination and population structure of spear thistle *Cirsium vulgare* in relation to sheep grazing management of pasture. – Oecologia 81: 369–373.

Silvertown, J. and Smith, B. 1989b. Mapping the microenvironment for seed germination in the field. – Ann. Bot. Lond. 63: 163–167.

Silvertown, J., Watt, T. A., Smith, B. and Treweek, J. R. 1992. Complex effects of grazing treatment on the establishment, growth, survival & reproduction of an annual in a species-poor grassland community. – J. Veg. Sci. 3: 35–40.

Smith, C. C. and Fretwell, S. D. 1974. The optimal balance between the size and the number of offspring. – Am. Nat. 108: 499–506.

StatSoft, I. 2001. STATISTICA for Windows [Computer program manual]. – StatSoft, Inc., Tulsa, OK, USA.

Tofts, R. and Silvertown, J. 2000a. A phylogenetic approach to community assembly from a local species pool. – Proc. R. Soc. Lond. B 267: 363–370.

Tofts, R. and Silvertown, J. 2000b. Niche differences and their relation to species' traits in *Cirsium vulgare* and *Cirsium eriophorum*. – Folia Geobot. 35: 231–240.

Tofts, R. and Silvertown, J. 2002. Community assembly from the local species pool: an experimental study using congeneric species pairs. – J. Ecol. 90: 385–393.

Treweek, J. R., Watt, T. A. and Hambler, C. 1997. Integration of sheep production and nature conservation: experimental management. – J. Env. Manage. 50: 193–210.

Webb, C. O. and Peart, D. R. 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. – Ecology 80: 2006–2017.