

# Size-specific fecundity and the influence of lifetime size variation upon effective population size in *Abies balsamea*

MIKE E. DODD & JONATHAN SILVERTOWN\*

Ecology and Evolution Research Group, Department of Biological Sciences, Open University,  
Milton Keynes MK7 6AA, UK

The hierarchy of plant size often present in dense populations of plants and the close correlation found between size and fecundity can result in an unequal distribution of fecundity, which reduces the ratio of effective population size/census number ( $N_e/N$ ). Such an effect has been found previously in annuals, but no study has hitherto tested for the effect in the lifetime fecundity variation of a perennial population. We use the demographically stable size distribution to be found in natural, wave-regenerating populations of balsam fir, *Abies balsamea*, in order to estimate  $N_e/N$ . In both wave-regenerating and normal forests our estimated values of  $N_e/N$  were about twice those previously reported for annuals. We suggest that fecundity variance is expected to be smaller in trees and other long-lived perennials than in annuals because density-dependent mortality operates more strongly in the prereproductive phase of long-lived plants.

**Keywords:** *Abies balsamea*, effective population size, fecundity variation, fir waves, drift, population size structure.

## Introduction

Size variation is a feature of virtually all wild populations of plants (Weiner, 1990), and because fecundity is generally correlated with individual plant size, this variation can result in a few large plants of one generation contributing disproportionately to the next, with a consequent reduction in effective population size ( $N_e$ ) (Gottlieb, 1977). In simulation models Levin & Wilson (1978; Wilson & Levin, 1986) found that a leptokurtic distribution of fecundity resulted in a faster response to selection, a more rapid loss of rare alleles and a greater propensity for genetic drift when compared with model populations in which fecundity variation was Poisson distributed. Size variation in plants is a result of the ecological process of competition, especially intraspecific competition for light, and thus its potential influence upon  $N_e$  forms a bridge between ecology and population genetics.

Heywood (1986) derived a formula by which the proportionate reduction in  $N_e$  caused by a skewed distribution of fecundity could be compared with the value expected for a Poisson distribution in an idealized population ( $N$ ). Applying this formula to 34 species of

annuals Heywood (1986) found that fecundity variation reduced  $N_e$  in all cases and that in many it made a greater contribution to drift than the random sampling of gametes. In populations of annual ryegrass, *Lolium multiflorum*, grown for germplasm collection, Johnson (1998) found a less extreme but still significant effect of fecundity variation on the ratio  $N_e/N$ . Hamilton (1997) used Heywood's formula to estimate the influence of fecundity variation in a single year on  $N_e$  in wild populations of the long-lived perennial herb *Limonium carolinianum*. Although effects were similar in magnitude to Heywood's, Hamilton's estimates for *L. carolinianum* were not based upon variation in lifetime fecundity.

To our knowledge, no study has yet estimated the effect of variation in lifetime fecundity upon  $N_e/N$  for any perennial plant. Short-term measurements can be misleading. Scheiner (1987) recorded the fecundity of 50 genets of the grass *Danthonia spicata* at each of five sites over five years; in four recently established populations the inequality in fecundity for one year over-estimated the inequality of cumulative fecundity measured over five years. Although inequality in fecundity fell significantly when cumulated over five years in these young populations, it was significantly higher in a much older population, suggesting that even five years was

\*Correspondence. E-mail: j.silvertown@open.ac.uk

insufficient time to gauge the inequality of lifetime fecundity in this perennial.

Short-term measurements do not suffice for perennials for two reasons, both rooted in the relationship between fecundity and plant size: (i) the shape of size frequency distributions changes greatly in populations through time, particularly when plant density is high (e.g. Westoby, 1984; Hara, 1988); and (ii) perennials must generally reach a size threshold before they reproduce (e.g. Schmid *et al.*, 1994). In trees, diameter distributions in single-species, even-aged stands are initially normally distributed but become first log-normal and later more nearly normal again as small trees are first suppressed and then killed by competition for light with taller neighbours (Silvertown & Lovett Doust, 1993). Because diameter distributions change in this way, the variance in lifetime fecundity for a tree population depends upon both the time-specific and the size-specific distribution of seed production and it cannot usually be assumed that the structure of a population sampled at one point in time and space is representative of size or fecundity variation throughout life. An exception to this occurs where a population is at demographic equilibrium because then it possesses a stable size and age structure (Caswell, 1989). In this paper we exploit the stable structure to be found in wave-regenerating monospecific stands of balsam fir, *Abies balsamea*, to estimate the effect of variation in lifetime fecundity upon  $N_e/N$  in natural, subalpine populations of this tree. When age structure is invariant, the effective size for a population with overlapping generations such as *A. balsamea* is equivalent to the value for a population with discrete generations such as is found in annuals (Caballero, 1994). Hence, it is possible to use Heywood's (1986) formula on our tree data and to compare our results with his for annuals.

## Methods

### *Study system and sampling*

We measured size-specific fecundity and population size structure in fir waves of *A. balsamea* and in samples in a nearby nonwave *A. balsamea* forest for comparison. Fir waves are natural populations of *Abies* spp. found in the subalpine zones of mountains in eastern North America and Japan in which even-aged cohorts representing every stage of the life cycle from seedlings to large, senescent trees occur in an ordered chronosequence. The chronosequence is produced by recruitment following in the wake of a wave of mortality which propagates downwind through subalpine populations that are exposed to severe winter winds (Sato & Iwasa, 1993). The mortality wave kills the tallest trees, which die

standing up, creating a linear gap in the forest canopy beneath which a new seedling cohort is recruited. Mortality waves tend to move at a constant rate so chronosequences are continuous and the overall size and age structure of the forest is in a stable steady-state (Sprugel, 1976; Kohyama & Fujita, 1981). Moloney (1986) found that population structure was similar in wave-regenerating forest and in nonwave (normal) stands in a more sheltered location at our study site, the only difference being the spatial arrangement of cohorts that result from the different modes of regeneration.

Our fieldwork was conducted between June and August 1999 at Whiteface Mountain in New York State (Latitude 44°22'N, Longitude 73°54'W). Sprugel (1976) describes the site in more detail and Mohler *et al.* (1978) report how size frequency distributions in *A. balsamea* change along chronosequences at Whiteface Mt. In the present study, three fir waves were sampled near the summit of Mt. Lookout (a subsidiary peak of Whiteface Mt.) between an altitude of 1128 m and 1227 m, in one of the areas sampled previously by Silvertown & Dodd (1999a,b). Nonwave forest at an elevation of 1150–1200 m was sampled nearby at a site used previously by Silvertown & Dodd (1999a) and Moloney (1986). All sites contained mono-specific stands of *A. balsamea*, with only a very few individuals of *Betula papyrifera* and *Picea rubens* encountered during sampling.

Stem diameter at breast height (d.b.h., measured 1.4 m from the ground) was recorded for all trees of reproductive size (see Results) falling into a 10-m wide belt transect. Smaller trees, which occurred at much higher densities, were sampled in 1 m or 2 m-wide belts and results were converted to numbers per m<sup>2</sup>. Transects were laid in the direction of wave travel or, in nonwave forest, ran approximately along contours. In wave forest transect length was determined by the distance between successive zones of high forest (i.e. one wavelength). In nonwave forest, we attempted to obtain a representative sample of trees by recording along a total length of 200 m of transect that traversed all life history stages.

The individual fecundity of a balsam fir tree may be determined retrospectively. Female cones of *A. balsamea* shed seeds and scales, but the cone rachis remains attached to the tree for up to 40 years (Morris, 1951). New cones are produced only at the tips of branches and in the upper part of the tree. Branches and the main axis of the tree produce one whorl each year, so the fecundity of a tree in a particular year may be determined from the sum of all rachises on all the relevant whorls, and the sum for different years gives total fecundity to date. Rachis and cone counts were made for a subsample of all trees by climbing, or by counting through binoculars from vantage points in neighbouring trees, a mobile

scaffolding tower or nearby rocks. We recorded fecundity in all trees along transects where we could gain a clear view of the canopy, and therefore the composition of this subsample was determined by logistic considerations and was not random.

#### Data analysis and estimation of $N_e/N$

Heywood (1986) showed that when there is a good correlation between fecundity and some surrogate variable such as size, size variation may be used to estimate the effect of fecundity variation upon  $N_e$  using the formula:

$$\frac{N_e}{N} = \frac{1}{(1 + F_{is})\left(\frac{\sigma^2}{\mu^2}\right) + 1}$$

where  $N_e$  is the genetic effective population size,  $N$  is the census number,  $F_{is}$  is the fixation index, and  $\sigma^2$  and  $\mu$  are the size variance and mean size of adults, respectively. If the term  $N_e/N < 0.5$ , then the contribution of fecundity variation among adults to drift is greater than that of sampling from the gamete pool (Heywood, 1986).

In the Fisher–Wright idealized population, that is the basis for the definition of  $N_e$ , the census number is the number of individuals born and there is no mortality between birth and adulthood (Caballero, 1994). However, in real populations pre-reproductive mortality can be very high and the number of reproductive adults may be a small fraction of the number born. This presents practical difficulties in calculating  $N_e/N$  for real populations because its value will depend upon how  $N$  is determined (Frankham, 1995). All published estimates of  $N_e/N$  for wild plants (the majority being Heywood's) reviewed by Frankham (1995) define  $N$  as the number of adults or the number of breeding adults. In order to permit comparison with these values we defined  $N$  as all trees that had reached the threshold size for reproduction (see below).

Logistical problems prevented us from obtaining a random subsample with which to estimate  $\sigma^2$  and  $\mu$  for fecundity directly. We therefore used our data to establish a correlation between fecundity and size, and used size variation as a surrogate for fecundity variation. Linear regression was used to determine the threshold size for reproduction from the intercept on the d.b.h. axis of the linear regression of fecundity on d.b.h. These calculations were done separately for wave and normal populations.

Neale & Adams (1985) estimated  $F_{is} = 0.05$  in populations of *A. balsamea* at a similar altitude to our own on Mt. Moosilauke in New Hampshire. Neale and Adams' estimated value was so low that we assumed  $F_{is} = 0$  for the purposes of the present study.

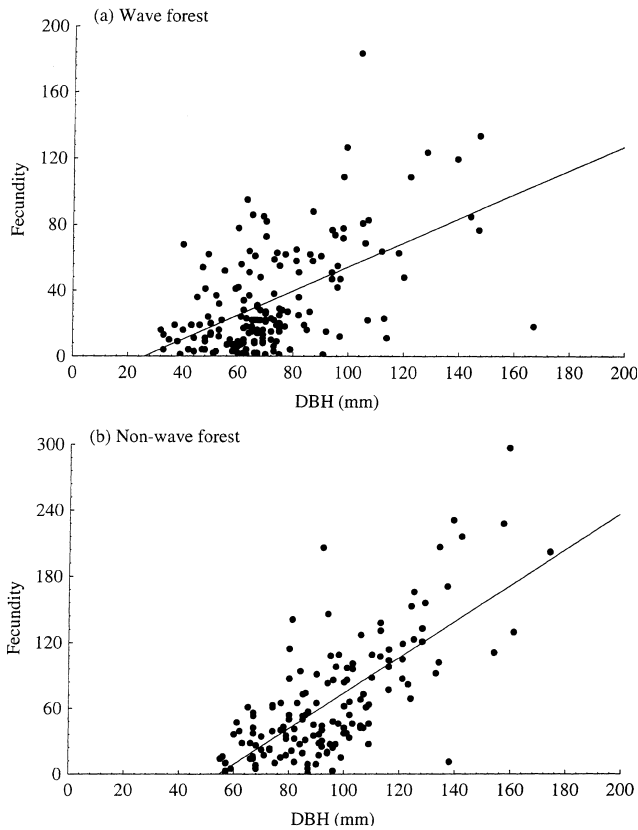
## Results

We found that it was possible to record rachis numbers accurately for up to eight whorls (= years) back along branches, but that the repeatability of counts was poor further back than this. Tree fecundity estimates were therefore based upon the most recent eight years. Most cones during the eight year period were produced during two mast years. Preliminary analysis of the data by multiple linear regression of fecundity on tree age and d.b.h. showed that age was a nonsignificant variable in all cases. Seki (1994) found that cone production in *Abies mariesii* in Japan depended upon the square of stem or branch diameter, but using a quadratic term for d.b.h. in our regressions did not improve  $r^2$  significantly over the linear model and we used this. Regressions did not differ significantly among the three waves, so samples were combined. Separate regressions for wave and nonwave forest are shown in Fig. 1. Intercepts of regression lines with the d.b.h. axis were used to determine the size-threshold for reproduction in each type of forest and these values were used to exclude trees that were too small to reproduce from analyses of size structure. Threshold sizes were 26.1 mm in wave forest and 54.6 mm in nonwave forest. The threshold value for wave forest is smaller than we reported for waves in a previous study in the same area (Silvertown & Dodd, 1999b) because sample size was larger and we were able to search canopies more thoroughly for small numbers of inconspicuous rachises in the present study.

Size structure statistics and  $N_e/N$  estimates for wave and nonwave populations are given in Table 1. The size structure of one representative wave population and of the normal population are shown in Fig. 2.

## Discussion

Effective population size ( $N_e$ ) is a key parameter in population genetics with consequences for drift, selection, genetic substructuring and the maintenance of heterozygosity. Newman & Pilson (1997) also found that an experimental reduction in  $N_e$  increased the extinction rate in small populations of the annual *Clarkia pulchella*. Conifers possess many of the life history characteristics associated with high values of  $N_e$ : wind pollination; high levels of outcrossing and gene flow; significant inbreeding depression; low values of  $F_{st}$  measured at allozyme loci and long generation times (Govindaraju, 1988, 1989; Hamrick & Godt, 1996). In this study we found that size hierarchies created by intraspecific competition, which are another characteristic of conifer populations, lead to variance in lifetime fecundity in *A. balsamea* sufficient to reduce  $N_e$  to about 80% of the census number. This value was estimated in



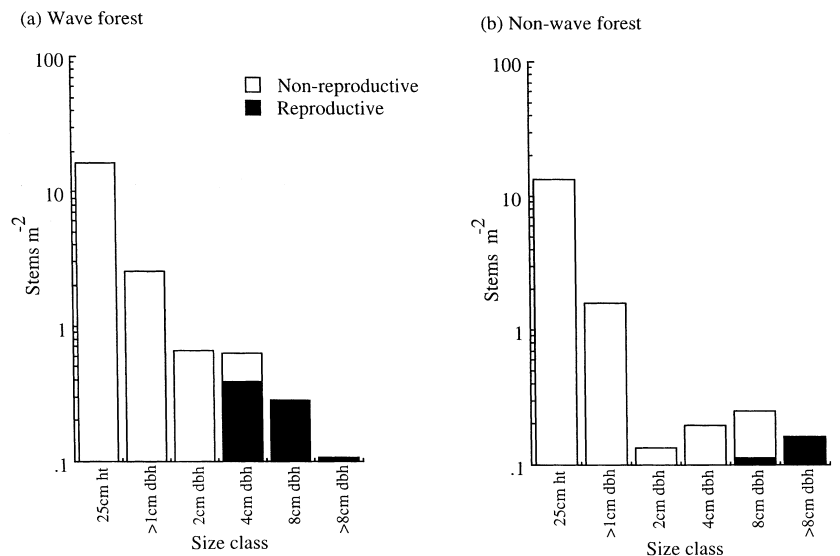
**Fig. 1** Linear regressions of rachis and cone number in *Abies balsamea* over eight years on d.b.h. in (a) fir wave and (b) nonwave forest. Regression equations and statistics are: Fir wave:  $Fecundity = -19.23 + 0.738 * d.b.h.$ ;  $F_{1,65} = 68.18$ ,  $P < 0.000001$ ,  $R^2 = 0.292$ , SE of intercept = 6.76, SE of coefficient = 0.089. Non-wave:  $Fecundity = -89.1 + 1.633 * d.b.h.$ ;  $F_{1,142} = 148.1$ ,  $P < 0.000001$ ,  $R^2 = 0.511$ , SE of intercept = 13.15, SE of coefficient = 0.134.

**Table 1** Size structure statistics and  $N_e/N$  estimates for wave and nonwave *Abies balsamea* forests.  $N_e/N$  was calculated using Eqn (1) and a value of  $F_{is} = 0$ . The weighted mean and standard error for the wave populations were calculated from log-transformed values and then back-transformed

Population	Sample size	$\mu^2$	$\sigma^2$	$N_e/N$
Wave 1	374	3849	851	0.82
Wave 2	511	2486	821	0.75
Wave 3	525	2259	606	0.79
Weighted mean (SE) of waves 1–3	—	—	—	0.78 (0.0274)
Nonwave	578	9454	2156	0.81

wave populations with a stable population structure, but was very similar in nearby normal forest.

Our results for *A. balsamea* stand in contrast to those of Heywood (1986) who found much stronger effects of fecundity variation upon  $N_e$  in annuals (mean  $N_e/N = 0.42$ , range 0.15–0.68 for 27 species, assuming  $F_{is} = 0$ ). The difference may in part be a result of overestimation of  $N_e/N$  in our study and we consider this point below. However, there are ecological differences between the mode of action of density dependence and the development of size hierarchies in short-lived plants and long-lived ones that might lead one to expect this result. Density dependence occurs in wild plant populations of all types and creates a large class of small, suppressed individuals. In short-lived species such as annuals small individuals often survive to reproduce (Watkinson & Davy, 1985), but in trees they invariably



**Fig. 2** Size frequency distributions of *Abies balsamea* stems sampled in (a) a typical wave population (Wave 2) and (b) in nonwave forest. Note the log scale on the frequency axis. The upper bounds of size classes are shown. The class in which the size threshold for reproduction fell is shown divided between reproductive and nonreproductive individuals in proportion to their numbers.

die before they can flower (White, 1985). The result of this difference is that small plants in annual populations reproduce with low fecundity and thus contribute to the adult population variance, while the death of small trees before reproduction reduces the size and fecundity variance in the adult population compared to the population as a whole. This effect can be seen in our study populations by comparing the size distribution of the whole population with that of the reproductive plants alone (Fig. 2).

The measurement of variance effective population size and the ratio  $N_e/N$  clearly depends upon how census size ( $N$ ) is defined and estimated. As described under Methods, we have used the definition of census size most often employed in the literature, which does not count juveniles that will die before reaching sexual maturity. By adopting this definition we were able to compare our results with  $N_e/N$  estimates made by Heywood (1986) for annuals. Adopting a broader definition that includes juveniles reduces  $N_e/N$  drastically. For example, if we recalculate  $N_e/N$  for all individuals except seedlings under a year of age we obtain a ratio of 0.13 with a sample size of 3579 for the nonwave forest. By including young seedlings  $N_e/N$  is reduced to 0.06 with a sample size of 15 319. The latter estimate was made in a year when many seedlings were present in the population, but this varies greatly from year-to-year. Eguiarte *et al.* (1993) estimated  $N_e/N$  for a natural population of the palm *Astrocaryum mexicanum* using 13 years of data on fecundity and included juveniles in the census number. They report a ratio of between 0.18 and 0.43, depending upon the plot and the method used to estimate  $N_e$ . The lower end of this range is similar to the value of 0.13 we obtain when juveniles but not seedlings are included in our census number.

There are possible sources of experimental error in our study which suggest that we may have underestimated fecundity variance and hence overestimated  $N_e/N$ . First, we used size variation as a surrogate for fecundity variation and the correlation between the two was not as high as desirable. Correlations in field data are rarely high, and the unexplained variance in the regressions of fecundity on d.b.h. (Fig. 1) suggests that our procedure actually underestimated fecundity variance. Secondly, in calibrating the size/fecundity relationship we counted cone numbers but did not allow for seed set per cone, which may vary with tree size. If larger trees have higher seed set per cone, ignoring this variation would have underestimated the degree to which the seed production of a few large trees dominated the population. Thirdly, as in previous studies, we also ignored reproductive success through male function, and because this can be expected to be even more skewed than female fecundity

(Meagher, 1991), this too implies that our results are conservative.

Local genetic differentiation and adaptation are frequent in plants and despite the low levels of differentiation observed for allozyme markers in conifers (Hamrick & Godt, 1996), there are several reports of local adaptation in this group (Linhart & Grant, 1996). Specifically in *A. balsamea*, Fryer & Ledig (1972) found a negative correlation between the temperature optimum for photosynthesis in seedlings grown in a common environment and the elevation of the seed source along a transect between 730 m and 1460 m on Mt. Moosilauke, NH. Because we may have overestimated the value of  $N_e/N$ , we believe that it cannot yet be ruled out that a reduction in  $N_e$  caused by inequality of fecundity among adults may play a small though significant role in facilitating local adaptation in dense populations of conifers. The possibility deserves further study.

## Acknowledgements

We acknowledge the financial support of the Natural Environment Research Council. We thank Jennifer Davidson, Sarah Leckie, Mark Waddell, William Whitmore and Molly Hammond, for field assistance. We are grateful to D. Wolfe and S. Kent of the State University of New York (Albany) Atmospheric Sciences Research Center Field Station, Wilmington, New York for logistical support and to J. Rand of the Olympic Region Development Authority and T. H. Wahl of the New York State Department of Environmental Conservation for permission to work on Whiteface Mountain. We thank John Pannell for a discussion of  $N_e/N$  and two anonymous referees for comments on the manuscript.

## References

- CABALLERO, A. 1994. Developments in the prediction of effective population size. *Heredity*, **73**, 657–679.
- CASWELL, H. 1989. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer, Sunderland, MA.
- EGUIARTE, L. E., BURQUEZ, A., RODRIGUEZ, J., MARTINEZ RAMOS, M., SARUKHAN, J. AND PINERO, D. 1993. Direct and indirect estimates of neighborhood and effective population size in a tropical palm, *Astrocaryum mexicanum*. *Evolution*, **47**, 75–87.
- FRANKHAM, R. 1995. Effective population-size adult-population size ratios in wildlife – a review. *Genet. Res.*, **66**, 95–107.
- FRYER, J. H. AND LEDIG, F. T. 1972. Microevolution of the photosynthetic temperature optimum in relation to the elevational complex gradient. *Can. J. Bot.*, **50**, 1231–1235.
- GOTTLIEB, L. D. 1977. Genotypic similarity of large and small individuals in a natural population of the annual plant *Stephanomeria exigua* ssp. *coronaria* (Compositae). *J. Ecol.*, **65**, 127–134.

- GOVINDARAJU, D. R. 1988. Life histories, neighbourhood sizes, and variance structure in some North American Conifers. *Biol. J. Linnean Soc.*, **35**, 69–78.
- GOVINDARAJU, D. R. 1989. Estimates of gene flow in forest trees. *Biol. J. Linn. Soc.*, **37**, 345–357.
- HAMILTON, M. B. 1997. Genetic fingerprint-inferred population subdivision and spatial genetic tests for isolation by distance and adaptation in the coastal plant *Limonium carolinianum*. *Evolution*, **51**, 1457–1468.
- HAMRICK, J. L. AND GODT, M. J. W. 1996. Effects of life history traits on genetic diversity in plant species. *Phil. Trans. R. Soc. B*, **351**, 1291–1298.
- HARA, T. 1988. Dynamics of size structure in plant populations. *Trends Ecol. Evol.*, **3**, 129–133.
- HEYWOOD, J. S. 1986. The effect of plant size variation on genetic drift in populations of annuals. *Am. Nat.*, **127**, 851–861.
- JOHNSON, R. C. 1998. Genetic structure of regeneration populations of annual ryegrass. *Crop Sci.*, **38**, 851–857.
- KOHYAMA, T. AND FUJITA, N. 1981. Studies on the *Abies* population of Mt Shimagare. I. Survivorship curve. *Bot. Mag., Tokyo*, **94**, 55–68.
- LEVIN, D. A. AND WILSON, J. B. 1978. The genetic implications of ecological adaptations in plants. In: Freyden, A. H. J. and Woldendorp, J. W. (eds) *Structure and Functioning of Plant Communities*, pp. 75–100. PUDOC, Wageningen.
- LINHART, Y. B. AND GRANT, M. C. 1996. Evolutionary significance of local genetic differentiation in plants. *Annual. Rev. Ecol. Syst.*, **27**, 237–277.
- MEAGHER, T. R. 1991. Analysis of paternity within a natural population of *Chamaelirium luteum* II. Patterns of male reproductive success. *Am. Nat.*, **137**, 738–752.
- MOHLER, C. L., MARKS, P. L. AND SPRUGEL, D. G. 1978. Stand structure and allometry of trees during self-thinning of pure stands. *J. Ecol.*, **66**, 599–614.
- MOLONEY, K. A. 1986. Wave and nonwave regeneration processes in a subalpine *Abies balsamea* forest. *Can. J. Bot.*, **64**, 341–349.
- MORRIS, R. F. 1951. The effects of flowering on the foliage production and growth of balsam fir. *Forry Chron.*, **24**, 106–110.
- NEALE, D. B. AND ADAMS, W. T. 1985. Allozyme and mating-system variation in balsam fir (*Abies balsamea*) across a continuous elevational transect. *Can. J. Bot.*, **63**, 2448–2453.
- NEWMAN, D. AND PILSON, D. 1997. Increased probability of extinction due to decreased genetic effective population size: experimental populations of *Clarkia pulchella*. *Evolution*, **51**, 354–362.
- SATO, K. AND IWASA, Y. 1993. Modelling of wave regeneration in sub-alpine *Abies* forests – population dynamics with spatial structure. *Ecology*, **74**, 1538–1550.
- SCHNEIDER, S. M. 1987. Size and fecundity hierarchies in an herbaceous perennial. *Oecologia*, **74**, 128–132.
- SCHMID, B., POLASEK, W., WEINER, J., KRAUSE, A. AND STOLL, P. 1994. Modeling of discontinuous relationships in biology with censored regression. *Am. Nat.*, **143**, 494–507.
- SEKI, T. 1994. Dependency of cone production on tree dimensions in *Abies mariesii*. *Can. J. Bot.*, **72**, 1713–1719.
- SILVERTOWN, J. AND DODD, M. E. 1999a. Evolution of life history in balsam fir (*Abies balsamea*) in sub-alpine forests. *Proc. R. Soc. B*, **266**, 729–733.
- SILVERTOWN, J. AND DODD, M. E. 1999b. The demographic cost of reproduction and its consequences in balsam fir (*Abies balsamea*). *Am. Nat.*, **154**, 321–332.
- SILVERTOWN, J. AND LOVETT DOUST, J. 1993. *Introduction to Plant Population Biology*. Blackwell Scientific Publications, Oxford.
- SPRUGEL, D. G. 1976. Dynamic structure of wave-regenerated *Abies balsamea* forests in the Northeastern United States. *J. Ecol.*, **64**, 889–911.
- WATKINSON, A. R. AND DAVY, A. J. 1985. Population biology of salt marsh and sand dune annuals. *Vegetation*, **62**, 487–497.
- WEINER, J. 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol.*, **5**, 360–364.
- WESTOBY, M. 1984. The self-thinning rule. *Adv. Ecol. Res.*, **14**, 167–225.
- WHITE, J. 1985. The thinning rule and its application to mixtures of plant populations. In: White, J. E. (ed.) *Studies on Plant Demography*, pp. 291–309. Academic Press, London.
- WILSON, J. B. AND LEVIN, D. A. 1986. Some genetic consequences of skewed fecundity distributions in plants. *Theor. Appl. Genet.*, **73**, 113–121.