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BRIEF COMMUNICATION

Small variance in growth rates in annual plants has large effects on genetic drift[1]

Erin K. Espeland[2,4] and Michael R. O'Farrell[2,3]

[2]Graduate Group in Ecology, University of California, Davis, California 95616, USA; and [3]National Oceanic and Atmospheric Administration, Fisheries Ecology Division, Southwest Fisheries Science Center, 110 Shaffer Road, Santa Cruz, California 95060, USA

- *Premise of the Study:* Effective population size (N_e) is a critical index of the evolutionary capacity of populations. Low N_e indicates that standing genetic diversity is susceptible to loss via stochastic processes (and inbreeding) and is, therefore, unavailable for natural selection to act upon. Reported N_e in plant populations is often quite low. What biological and ecological factors might produce such low N_e?
- *Methods:* We conducted a simulation model to test the effect of randomly assigned and autocorrelated growth rates of annual plants on plant-size distributions at the end of the growing season. Because plant size is directly correlated with reproductive output in annual plants, variation in plant size reflects variation in reproduction, and thus our modeled size distributions can be used to estimate N_e.
- *Key Results:* Randomly assigned growth rates had a negligble effect on N_e/N. Autocorrelated growth rates decreased N_e/N as the length of the growing season increased. This was the case even when the variance in growth rates was as low as 0.1% of the mean.
- *Conclusions:* While intrinsic plant biology can affect the degree of growth autocorrelation, ecological factors such as competition, herbivory, and abiotic stress can increase or decrease levels of growth autocorrelation. Ecological factors that increase growth autocorrelation can have significant effects on genetic drift within populations.

Key words: annual plants; conservation genetics; effective population size; growth rate variance; variance N_e.

In annual plants, growth is highly correlated with fitness, with larger plants producing more seeds by the end of the growing season (Heywood, 1986; Rice, 1990; Aarssen and Taylor, 1992; Leger and Espeland, 2010). Plant growth rates have been shown to be intrinsically variable (Evans, 1972; Pigliucci and Schlichting, 1996), but growth rate variance is also greatly affected by environmental factors (Herrea and Jovani, 2010). For example, abiotic stress may depress plant growth rate variance (Grime and Hunt, 1975). Abiotic stress limits the ability of plants to grow to their maximum size and also can prevent plants from growing at high enough densities to compete for light. Competition for light is a mechanism by which large plants can depress the growth rates of smaller plants (via shading) and increase population-wide variance in plant growth rates (Weiner and Thomas, 1986). Thus, plant growth rates are not only genetic traits that selection can act upon but are also nonheritable traits influenced by ecological factors (Brophy et al., 2008).

Variance in growth rates can affect genetic drift within annual plant populations by its effect on variance in seed production, which, in turn, influences effective population size (N_e). Effective population size is a critical index of the evolutionary capacity of populations. Populations with low N_e are susceptible to loss of allelic diversity through genetic drift: alleles become absent from populations as a result of stochastic events and, therefore, are unavailable for natural selection to act upon. Another way in which populations with low N_e lose allelic diversity is through inbreeding and concomitant loss of heterozygosity.

Variance N_e describes the variance in allelic frequencies among generations, with increased variance in offspring number leading to a decrease in N_e. Inbreeding N_e describes the probability of mating among relatives, a process that lowers genetic diversity in populations by reducing heterozygosity. Extinction or eigenvalue N_e is the calculation of an asymptotic N_e and describes the rate of loss of heterozygosity. Estimates of these three types of N_e often, but not always, have the same result (Vitalis and Couvet, 2001). Here, we focus on variance N_e to use well-characterized relationships between plant size and fecundity to model variance in reproductive output within plant populations.

Populations with large N_e respond more efficiently to natural selection than populations with low N_e. This is because small populations have less genetic variation for natural selection to act upon, and there is a higher probability that beneficial alleles will not be maintained by selection and will instead be lost from the population because of random drift effects (Willi and Hoffmann, 2009). N_e is of particular concern in plant conservation, in which the maintenance of evolutionary potential in existing rare populations is key for preventing extinction. Awareness is

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[4] Author for correspondence (e-mail: erin.espeland@ars.usda.gov); current address: USDA ARS Northern Plains Agricultural Laboratory, Pest Management Unit, Sidney, Montana 59270, USA.

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also growing that revegetation populations (i.e., populations of common species planted to restore landscapes) may also suffer from low N_e, which may reduce their ability to persist (Kramer and Havens, 2009). While N_e is especially relevant in conservation and restoration, it is also important in the evolutionary dynamics of common plants. In addition to low N_e/N ratios reported for common plants (Heywood, 1986), many plant species are increasingly experiencing habitat fragmentation and other rapid ecological changes that may further reduce N_e to levels that may affect the ability of even common plants to persist (Kramer and Havens, 2009).

Most size distributions of in situ plant populations are positively skewed (for reviews, see Koyama and Kira, 1956; Chambers and Aarssen, 2009), which means that they comprise a few large individuals and many small ones. In their survey of 21 herbaceous angiosperm species, Chambers and Aarssen (2009) found that in most cases more than 90% of the individuals in plant populations fall within the smallest two (out of 10) size classes. When plant size and fecundity are linked, as is the case with monocarpic plants (R^2 always >0.7; Aarssen and Taylor, 1992), a positively skewed size distribution results in large individuals contributing disproportionately to the genotypic frequencies of the next generation.

While competition for light could cause these positively skewed size distributions (Weiner and Thomas, 1986), lognormal distribution of plant sizes could also arise purely from exponential growth and variability in growth rates (Koyama and Kira, 1956; Uchmanski, 1985). Variability in seed production from a cohort results in a divergence between the effective population size (N_e) and the census population size (N). This within-generation calculation of variance N_e is strongly correlated with genetic measures of N_e based on gene genealogies through population fluctuations (Taylor, 2009). Recent work by Siol et al. (2007) suggests that relative reproductive variance must be taken into account to correctly estimate N_e N_e can be quite low even in common plants; for example, N_e/N is estimated at 0.1 in *Blackstonia perfoliata* and 0.2 in *Papaver dubium* (Heywood, 1986). When N_e/N is 0.1, this means that a population of 1,000 individuals will experience genetic drift equivalent to an ideal population of 100 individuals. Thus, even for reasonably large populations, N_e/N equal to 0.1 can indicate that drift is a significant driver of allele frequency change within these populations.

Heywood (1986) developed a relationship that describes the ratio of N_e to N resulting from both the variation in reproductive output and the degree of outcrossing in annual plants. This ratio can be used as an index to determine the strength of the relative contributions of (1) variation in reproduction and (2) gametic sampling on genetic drift within an annual plant population. An N_e/N ratio >0.5 indicates that gametic sampling (i.e., the random parental assignation of alleles to individual pollen grains and ovules) contributes more to genetic drift than random variation in seed output among individual plants. An N_e/N ratio <0.5 indicates that variation in reproductive output contributes to genetic drift more strongly than gametic sampling (Heywood, 1986).

Plant growth is nearly always size-dependent and has been successfully modeled with size at time t dependent on size at time $t - 1$ (Evans, 1972; Pfister and Stevens, 2002; Niklas et al., 2005). Growth autocorrelation has been observed in annual plants, for example *Trifolium incarnatum* and *Lolium multiflorum* (Weiner, 1985), *Sinapsis arvensis* (Brophy et al., 2008), and *Chenopodium album* (Damgaard and Weiner, 2008), and is extremely common in other herbaceous species (121 species; Niklas et al., 2005). In natural populations, large plants have also been demonstrated to have the largest growth rates: the relative increase in plant size from time $t - 1$ to time t is larger for large plants than for small ones (Pfister and Stevens, 2002; Niklas et al., 2005; Damgaard and Weiner, 2008). Few field experiments have measured growth rates directly; instead, most have extrapolated the degree to which growth rates are autocorrelated from an examination of the size hierarchy in populations at the end of the growing season, with the presumption that greater size hierarchy (i.e., increasing coefficient of variation in plant sizes) indicates greater autocorrelation.

In this study, we use the exponential growth equation identified by Koyama and Kira (1956) to model plant size (and, thus, seed production) distributions and then calculate N_e/N using the relationship described by Heywood (1986). We compare the results of size-dependent growth models that assign autocorrelated as well as random daily growth rates. A recent review of autocorrelation in growth rates among both plants and animals (Pfister and Stevens, 2002) has shown the value of disentangling size-dependent growth (nearly always the case for plants) and autocorrelated growth rates (less exhaustively studied in plants). Here, we take the neutral case of size-dependent growth with randomly assigned daily growth rate and compare it with size-dependent autocorrelated growth rate to assess the effect of each type of plant growth on N_e/N. By providing a quantitative connection between a model of plant growth and a model of N_e/N, we can develop specific predictions regarding the effect of growth rate variance on genetic drift.

MATERIALS AND METHODS

Size distributions of even-aged plants were generated assuming normally distributed seed sizes and plant growth rates for various growing-season lengths. Our model parameters are shown in Table 1 along with the measured ranges of these parameters from the literature. We generated size distributions of populations composed of 100, 500, 1000, 5000, 10 000, 50 000, 100 000, and 500 000 individuals and assumed that no mortality occurs during the growing season. The distribution of seed size was truncated normal, with a mean (± SD) of 50 ± 15, with truncation occurring at ±3 SD. We chose to model the coefficient of variation (CV) conservatively at 30%, near the low end of what has been documented empirically (Table 1). Because the initial distribution of seed size is truncated normal and we were only interested in modeling discrete

TABLE 1. Empirically documented values and model parameters (N/A = not applicable).

Parameter	Empirically documented values	Modeled values
Census size (N)	N/A	100–500 000
Daily growth rate (r)		
Distribution	Normal[a]	Normal
CV	0.1–2.27[a,b,c]	0.1–0.9
Seed size		
Distribution	Normal[d,e]	Normal
CV	0.15–6.0[e,f,g]	0.3
Growing season	25 to >119 d[a,b,h]	28–42 d

[a]Grime and Hunt 1975.
[b]Evans 1972.
[c]Garnier 1992.
[d]But see Michaels et al. 1988.
[e]Turnbull et al. 2006.
[f]Harper et al. 1970.
[g]Marshall et al. 1985.
[h]White and Harper 1970.

plants, rounding the initial seed distribution resulted in true sample sizes of 90, 498, 996, 5000, 10 000, 50 006, 100 000, and 499 996 plants. These sample sizes are used in all calculations below.

Plant growth from seeds was exponential: $w_{(t)} = w_{(0)}e^{rt}$, with $w_{(0)}$ a vector of initial seed weights, r a vector of daily instantaneous growth rates, and t the growing season in days (Koyama and Kira, 1956; Uchmanski, 1985). In all cases, we initially assumed r to be a normally distributed random variable with a mean of 0.1 and variance equal to either 0.0001, 0.0004, or 0.0009 (or 0.1%, 0.3%, and 0.9% of the mean). We again truncated this normal distribution at ±3 SD so that random realizations of the growth rate would not be negative or extraordinarily large. As a result of truncation, the mean of the r vector remained the same (0.01), but the calculated variances decreased to 0.00008, 0.0003, or 0.0007 (or 0.08%, 0.3%, and 0.7% of the mean). Growing-season length was 28, 33, 37, and 42 d.

To model growth rate autocorrelation, we paired the ranked vector of initial seed sizes with a ranked vector of r for each growing day. The result is that each seed experiences the same r (large r for large plants and small r for small plants) for each day of growth. In this scenario, the largest plants have the greatest growth rates because plants normally gain resources in proportion to their size (Evans, 1972). We also considered random growth by assigning plants randomly selected values of r from the normally distributed vector of r values each day of the growing season. In this case, daily plant growth for individual plants was determined by a random draw with replacement from the vector of r values (MatLab program available from the authors upon request).

The mean and variance of the final size distribution resulting from these programs were then used to calculate N_e/N (Heywood, 1986):

$$\frac{N_e}{N} = \frac{1}{[(1+F)(\sigma^2/\mu^2)+1]} \qquad (1)$$

In this equation, $F = 0$ for a completely outcrossing breeding system, $F = 1$ for a completely inbreeding breeding system, and σ^2 and μ are the variance and mean of seed outputs. Thus, as variance becomes larger in relation to the mean, N_e/N becomes smaller, which would be the case when a few large individuals produce many seeds and many small individuals produce few seeds each. The inbreeding index, F, results in N_e/N of inbreeding plants being equal to half that of completely outcrossing plants. When the variance and mean are equal to one another (i.e., Poisson distribution, defined by CV = 1), N_e/N is 1 in outcrossing plants and 0.5 in inbreeding plants. N_e/N equal to 1 indicates that the population census size accurately reflects the effective population size.

We performed general linear model analyses in JMP, version 6.0 (SAS, Cary, North Carolina, USA), to assess the relationship among the model parameters. The model included census size (N), growth type (randomly assigned or autocorrelated), variance of r (Var_r), and growing-season length as well as two-way interactions between N and the other parameters. Estimated N_e/N was the dependent variable, and we used $F = 0$ for this calculation. Because the estimate we used (Eq. 1) is not appropriate for extremely small N (Heywood 1986), we excluded $N = 100$ from the analysis. We used a significance level of $P < 0.05$.

RESULTS

Randomly assigned daily growth rates resulted in symmetrical to slightly skewed final distributions of plant sizes (Fig. 1A, B). Autocorrelated plant growth rates resulted in heavily skewed, lognormal distributions of final plant sizes (Fig. 1A, B).

Results of the statistical analysis are shown in Table 2. Census size (N) was not a significant determinant of N_e/N, either as a main effect or as an interaction ($P > 0.4$; Table 2), but growth type, variance of r, and growing-season length all significantly affected N_e/N (all $P < 0.0001$; Table 2). When plant growth rates were autocorrelated, estimated N_e/N decreased dramatically with increasing growing-season length (Fig. 2A, B). The decrease in N_e/N with each day of the growing season was 7× greater when the variance of growth rates was 0.9% (Fig. 2B) than when it was 0.1% (Fig. 2A). As expected, randomly assigned growth rates had small effects on N_e/N as growing-season length increased (Fig. 2A, B). When growth rate variance was 0.1%, the regression for the autocorrelated scenario was $N_e/N = 0.95 - 0.0007$*days ($R = 0.99$), and the regression for the random scenario was $N_e/N = 0.92 - 0.0001$*days ($R = 0.48$), where R is the correlation coefficient. When growth rate variance was 0.9%, the autocorrelated scenario resulted in $N_e/N = 0.74 - 0.013$*days ($R = 0.98$), and the random scenario resulted in $N_e/N = 0.92 - 0.0007$*days ($R = 0.89$).

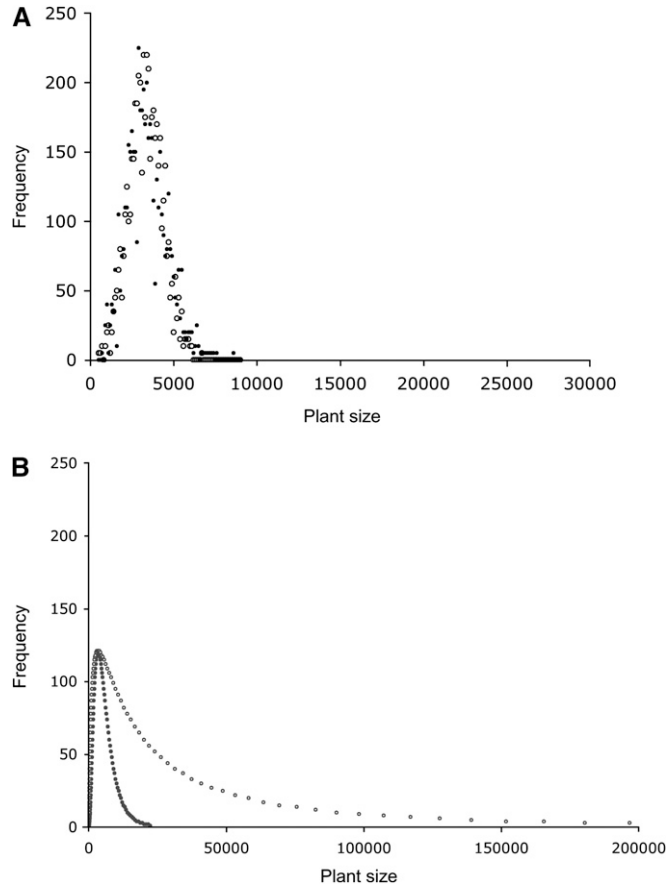

Fig. 1. Distributions of final plant sizes for (A) random and (B) autocorrelated growth rates (N = 5000, days = 42). Filled circles indicate model where Var_r (variance in growth rate) is 0.1% of the mean growth rate. Unfilled circles indicate model results where Var_r is 0.9% of the mean.

TABLE 2. Statistical table of the effects of model parameters on estimated N_e/N.

	df	Sum of squares	F	$P > F$
Census size (N)	1	0.006	0.710	0.40
Growth type	1	7.10	964.7	<0.0001
Var_r	1	1.52	183.0	<0.0001
Growing-season length (days)	1	0.157	18.93	<0.0001
N*Var_r	1	0.001	0.087	0.77
N*growth type	1	0.003	0.367	0.55
N*days	1	0.0004	0.005	0.94

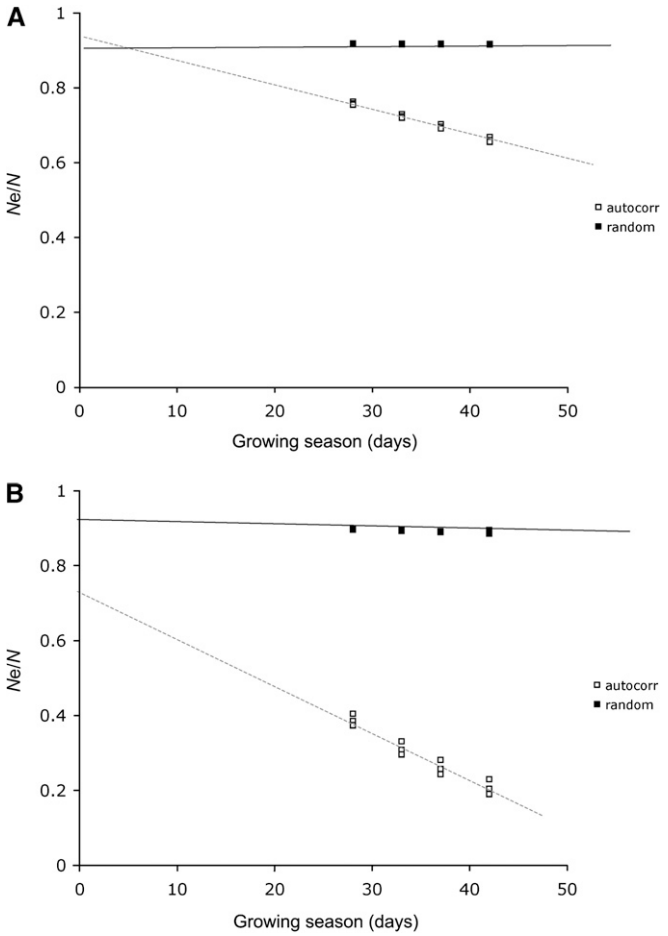

Fig. 2. Relationship of estimated N_e/N to growing-season length for randomly assigned daily growth rates (solid line, unfilled squares) and autocorrelated daily growth rates (dashed line, filled squares). N = 500–500 000. (A) Var_r (variance in growth rate) is 0.1% of the mean growth rate, and (B) Var_r is 0.9% of the mean.

DISCUSSION

Autocorrelation in growth rates can result in significant reductions in N_e/N even when the variance in growth rates is quite small and increasing variation in growth rates results in greater reductions in N_e/N. In the randomly assigned growth-rate model, variance in growth rates had a negligible effect on N_e/N. High variance in plant growth rates is commonly found in plants even when they are grown individually in containers. Grime and Hunt (1975) reported variance ranging from 1% to 227% of the mean in a collection of 130 annual and perennial plants, and Garnier (1992) reported growth rate variance values greater than 140% of the mean in seven annual grasses. This indicates that intrinsic variance in plant growth rates often generates reproductive hierarchies that contribute significantly to genetic drift.

Although intrinsic variation in plant growth rates affects N_e, ecologically driven variation in growth rates affects N_e in turn. For example, Rice (1990) showed that increased variation in growth rates in *Erodium* that resulted from increased competition among plants actually reduced N_e, even though census size (N) is larger when plants are more dense. Many empirical studies have shown that competition for light can increase the degree to which plant growth rates are autocorrelated, with larger plants shading smaller ones and, thus, interfering with smaller plants' ability to capture light (Harper, 1977; Schmitt et al., 1986; Weiner and Thomas, 1986; Rice, 1990). However, in many cases, plant–plant interactions have been shown to decrease variation in plant growth rates (for examples, see Weiner et al., 1997; van Kleunen et al., 2001, 2005), with increasing plant densities leading to smaller variation in plant sizes at the end of the growing season. Thus, ecological factors can affect both the variation in growth rates in natural populations and the degree to which plant growth is autocorrelated.

Autocorrelation among growth rates is a reasonable assumption for plants: germination, mortality, and flowering time are often size-linked, with larger seeds more likely to germinate (Baskin and Baskin, 1998), larger seeds producing larger seedlings (Harper et al., 1970), and larger seedlings more likely to survive (Volis et al., 2004). Pfister and Stevens (2002) found support for autocorrelated growth rates in plants, and they also concluded that intraspecific density and competitive effects can influence the degree to which growth is autocorrelated in many organisms. Given that our model shows that autocorrelation in growth rates is an important driver of genetic drift, environmental factors that lead to stronger or weaker growth-rate autocorrelation are also important influences on genetic drift. As a corollary, factors that alter the distribution of seed sizes or the correlation between plant size and fecundity would also affect genetic drift.

We can see the lines in Figure 2 as boundary conditions, with the top line in each panel indicating plant growth rates that vary daily and the bottom line indicating 100% autocorrelation of plant growth. Genetic and ecological factors and their interaction would move plant populations within these conditions by changing the length of the growing season or the degree to which plant growth rates are autocorrelated. In addition, the degree of outcrossing would also influence populations within this space. Figure 2 depicts N_e/N for completely outcrossing populations, but varying degrees of selfing would move predicted N_e/N to half of what is shown.

Competition is just one ecological process that might affect variation in growth rates. A stressor such as drought or nutrient limitation could minimize variation in growth rates by preventing individuals from reaching their maximum size (Grime and Hunt, 1975). Patchy granivory and herbivory increase growth rate variation by increasing intrapopulation heterogeneity (Harmon and Stamp, 1992). Disturbance may increase the variance in growth rates among individuals when it opens up prime habitat; alternatively, it may decrease growth rate variance when it acts as an environmental stressor. These ecological factors are viewed as important selective forces within populations, yet they may also affect allele frequency change that results from drift. When variance in growth rate is largely determined by ecological factors, as opposed to intrinsic, heritable variation, these ecological factors should then play a key role in determining genetic drift within populations.

LITERATURE CITED

AARSSEN, L. W., AND D. R. TAYLOR. 1992. Fecundity allocation in herbaceous plants. *Oikos* 65: 225–232.

BASKIN, C. C., AND J. M. BASKIN. 1998. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, California, USA.

BROPHY, C., D. J. GIBSON, P. M. WAYNE, AND J. CONNOLLY. 2008. How reproductive allocation and flowering probability of individuals in

plant populations are affected by position in stand size hierarchy, plant size and CO2 regime. *Journal of Plant Ecology (UK)* 1: 207–215.

CHAMBERS, J., AND L. W. AARSSEN. 2009. Offspring for the next generation: most are produced by small plants within herbaceous populations. *Evolutionary Ecology* 23: 737–751.

DAMGAARD, C., AND J. WEINER. 2008. Modeling the growth of individuals in crowded plant populations. *Journal of Plant Ecology (UK)* 1: 111–116.

EVANS, G. C. 1972. The quantitative analysis of plant growth. University of California Press, Berkeley, California, USA.

GARNIER, E. 1992. Growth analysis of congeneric annual and perennial grass species. *Journal of Ecology* 80: 665–675.

GRIME, J. P., AND R. HUNT. 1975. Relative growth-rate: its range and adaptive significance in a local flora. *Journal of Ecology* 63: 393–422.

HARMON, G. D., AND N. E. STAMP. 1992. Effects of postdispersal seed predation on spatial inequality and size variability in an annual plant, *Erodium cicutarium* (Geraniaceae). *American Journal of Botany* 79: 300–305.

HARPER, J. L. 1977. Population biology of plants. Academic Press, New York, New York, USA.

HARPER, J. L., P. H. LOVELL, AND K. G. MOORE. 1970. The shapes and sizes of seeds. *Annual Review of Ecology and Systematics* 1: 327–356.

HERRERA, C. M., AND R. JOVANI. 2010. Lognormal distribution of individual lifetime fecundity: insights from a 23-year study. *Ecology* 91: 422–430.

HEYWOOD, J. S. 1986. The effect of plant size variation on genetic drift in populations of annuals. *American Naturalist* 127: 851–861.

KOYAMA, H., AND T. KIRA. 1956. Intraspecific competition among higher plants. VIII. Frequency distributions of plant weight as affected by the interaction between plants. *Journal of the Institute of Polytechnics, Osaka City University, Series D* 7: 73–94.

KRAMER, A. T., AND K. HAVENS. 2009. Plant conservation genetics in a changing world. *Trends in Plant Science* 14: 599–607.

LEGER, E. A., AND E. K. ESPELAND. 2010. The shifting balance of facilitation and competition over the life history of California grassland annuals. *Plant Ecology* 208: 333–345.

MARSHALL, D. L., N. L. FOWLER, AND D. A. LEVIN. 1985. Plasticity in yield components in natural populations of three species of Sesbania. *Ecology* 66: 753–761.

MICHAELS, H. J., B. BENNER, A. P. HARTGERINK, T. D. LEE, S. RICE, M. F. WILSON, AND R. I. BERTIN. 1988. Seed size variation: magnitude, distribution and ecological correlates. *Evolutionary Ecology* 2: 157–166.

NIKLAS, K. J., T. OWENS, P. B. REICH, AND E. D. COBB. 2005. Nitrogen/phosphorus leaf stoichiometry and the scaling of plant growth. *Ecology Letters* 8: 636–642.

PFISTER, C. A., AND F. R. STEVENS. 2002. The genesis of growth rate variability in plants and animals. *Ecology* 83: 59–72.

PIGLIUCCI, M., AND C. D. SCHLICHTING. 1996. Reaction norms of *Arabidopsis* 4. Relationships between plasticity and fitness. *Heredity* 76: 427–436.

RICE, K. J. 1990. Reproductive hierarchies in *Erodium*—effects of variation in plant-density and rainfall distribution. *Ecology* 71: 1316–1322.

SCHMITT, J., D. W. EHRHARDT, AND M. CHEO. 1986. Light-dependent dominance and suppression in experimental radish populations. *Ecology* 67: 1502–1507.

SIOL, M., I. BONNIN, I. OLIVERI, J. M. PROSPERI, AND J. RONFORT. 2007. Effective population size associated with self-fertilization: lessons from temporal changes in allele frequencies in the selfing annual *Medicago truncatula. Journal of Evolutionary Biology* 20: 2349–2360.

TAYLOR, J. E. 2009. The genealogical consequences of fecundity variance polymorphism. *Genetics* 182: 813–837.

TURNBULL, L. A., L. SANTAMARIA, T. MARTORELL, J. RALLO, AND A. HECTOR. 2006. Seed size variability: from carob to carats. *Biology Letters* 2: 397–400.

UCHMANSKI, J. 1985. Differentiation and frequency distributions of body weights in plants and animals. *Philosophical Transactions of the Royal Society of London, Series B* 310: 1–75.

VAN KLEUNEN, M., M. FISCHER, AND B. SCHMID. 2001. Effects of intraspecific competition on size variation and reproductive allocation in a clonal plant. *Oikos* 94: 515–524.

VAN KLEUNEN, M., M. FISCHER, AND B. SCHMID. 2005. Three generations under low versus high neighborhood density affect the life history of a clonal plant through differential selection and genetic drift. *Oikos* 108: 573–581.

VITALIS, R., AND D. COUVET. 2001. Estimation of effective population size and migration rate from one- and two-locus identity measures. *Genetics* 157: 911–925.

VOLIS, S., K. J. F. VERHOEVEN, S. MENDLINGER, AND D. WARD. 2004. Phenotypic selection and regulation of reproduction in different environments in wild barley. *Journal of Evolutionary Biology* 17: 1121–1131.

WEINER, J. 1985. Size hierarchies in experimental populations of annual plants. *Ecology* 66: 743–752.

WEINER, J., AND S. C. THOMAS. 1986. Size variability and competition in plant monocultures. *Oikos* 47: 211–222.

WEINER, J., D. B. WRIGHT, AND S. CASTRO. 1997. Symmetry of belowground competition between *Kochia scoparia* individuals. *Oikos* 79: 85–91.

WHITE, J., AND J. L. HARPER. 1970. Correlated changes in plant size and number in plant populations. *Journal of Ecology* 58: 467–485.

WILLI, Y., AND A. A. HOFFMANN. 2009. Demographic factors and genetic variation influence population persistence under environmental change. *Journal of Evolutionary Biology* 22: 124–133.