



## The Evolutionary Ecology of Seed Heteromorphism

D. Lawrence Venable

*The American Naturalist*, Vol. 126, No. 5. (Nov., 1985), pp. 577-595.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0147%28198511%29126%3A5%3C577%3AATEESH%3E2.0.CO%3B2-1>

*The American Naturalist* is currently published by The University of Chicago Press.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ucpress.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

## THE EVOLUTIONARY ECOLOGY OF SEED HETEROMORPHISM

D. LAWRENCE VENABLE

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721

*Submitted December 4, 1984; Accepted April 3, 1985*

Because of their modular structure and loose developmental integration, single plants are capable of simultaneously producing two or more distinct types of structures that perform the same general function. Examples include the production of both male and female organs, both selfed and outcrossed progeny, both clonal and sexual progeny. Lloyd (1984) called such within-plant variations "multiple strategies." This paper deals with an important class of multiple strategies variously called somatic seed polymorphism, diaspore heteromorphism, and amphicarp. I use the more familiar "seed" in preference to the more correct "diaspore," and "heteromorphism" rather than "polymorphism," which is widely used as an abbreviation for genetic polymorphism. Thus, *seed heteromorphism* is the production by single individuals of seeds (or sometimes single-seeded fruits) of different form or behavior.

Many species produce seeds with grossly divergent morphology (e.g., *Gymnarrhena micrantha*, Koller and Roth 1964; *Hypochoeris glabra*, Baker and O'Dowd 1982; *Heterotheca latifolia*, Venable and Levin 1985a). Many more species exhibit forms of cryptic heteromorphism such as continuous variation in size, shape, or germination time (Silvertown 1984). Why do some plants produce heteromorphic seeds and others not? Most authors suggest that seed heteromorphism represents a form of bet-hedging in the face of temporal variation in environmental suitability (Stebbins 1974; Harper 1977; Real 1980; Westoby 1981; Silvertown 1984; but regarding spatial variation, see Schoen and Lloyd 1984). It is often suggested that seed heteromorphism occurs because environmental differences are extreme and because intermediate adaptations have low fitness. For example, Harper (1977, p. 74) summarized the fitness-set arguments of Levins (1968) and suggested that heteromorphism may evolve in response to extreme environmental variation (concave fitness sets) when the environment is coarse-grained. Similarly, Stebbins suggested that seed heteromorphism "greatly increases the flexibility of adaptation to highly variable environments" (1974, p. 91). However, phylogenetic or developmental constraints in addition to selection may determine which species evolve seed heteromorphisms (Silvertown 1984). Frequently, "the floral structure or arrangement of the inflorescence lends itself to a division of labour" (Harper 1977, p. 72).

I present here a model of the ecology and evolution of seed heteromorphism in temporally variable environments. The model considers not only the kinds of environments that select for heteromorphism, but also the role of constraints (which could be constraints of design, physiology, development, or genetics), especially constraints that vary within plants and predispose certain species toward heteromorphism. I compare experimental data on the relative success of seed morphs with the ecological predictions of the model and evaluate the evolutionary predictions in light of the biology and natural history of heteromorphic-seeded species. There has been relatively little theoretical consideration of any multiple strategies, and seed heteromorphism is no exception. Many of the basic ideas developed here should be readily extendable to the consideration of other multiple strategies.

#### THE MODEL

Consider the simple model for the life history of an annual plant developed by Schaffer and Gadgil (1975). The finite rate of increase (or fitness),  $W$ , is given by  $W = cB$ , where  $c$  is the survival probability and  $B$  is the fecundity. For simplicity, redefine  $cB = U$ , the seed yield per seed. To introduce temporal environmental variation, let  $\mathbf{U} = (U_1, \dots, U_i, \dots, U_n)$  be a vector of expected yields per seed in different year types  $i = 1, \dots, n$ , where  $p_i$  is the probability of year type  $i$  and  $\sum_{i=1}^n p_i = 1$ . Since annual population growth is multiplicative, the fitness criterion is given by  $W = \Pi (U_i)^{p_i}$ . Seed heteromorphism can be introduced by letting each individual plant produce the proportion  $q$  of one seed type, whose success in different years is described by the vector  $\mathbf{U}^a$ , and the proportion  $(1 - q)$  of another seed type, whose success is described by the vector  $\mathbf{U}^b$ :

$$W = \Pi [q(U_i^a) + (1 - q)(U_i^b)]^{p_i}.$$

Throughout this paper the superscript on  $\mathbf{U}$ , the vector of expected yields, refers to the seed type, and the subscript refers to the year type.

This is the basic model, but note that either seed morph could have an inter-year seed bank if, for example,  $U_i = GS_i + 1 - G$ , where  $G$  is the germination fraction and  $S_i$  is the expected fecundity in year type  $i$  given germination (see Cohen 1966; Brown and Venable 1986). Likewise, one could take unequal seed size or "cost" into account by letting  $q$  represent the proportion of allocation to one seed type and letting  $\mathbf{U}$  vectors be the yield (e.g., seed biomass) per unit investment for each seed type. For the sake of simplicity and clarity I do not explicitly consider these possibilities in developing the model.

Fitness,  $W$ , is defined in terms of the survival and reproduction of phenotypes. Such phenotypic models bypass the complexities of genetic models but permit a more detailed examination of the ecology of selection. I assume that strategies with higher demographic success are better represented in future generations than those with lower demographic success. The types of genetic systems for which such strategic models are strictly true have been discussed by Lloyd (1977) and Bomze et al. (1983).

CONDITIONS FOR HETEROMORPHISM

Regardless of the specific form of  $W$ , a heteromorphic strategy is favored if each monomorphic strategy can be invaded by mutants that produce a few of the other seed type (and thereby attain higher fitness). A heteromorphism should evolve if

$$\frac{\partial W}{\partial q} \Big|_{q=0} > 0 \tag{1}$$

and

$$\frac{\partial W}{\partial q} \Big|_{q=1} < 0. \tag{2}$$

Since

$$\frac{\partial W}{\partial q} = W \sum_i \frac{p_i(U_i^a - U_i^b)}{q(U_i^a) + (1 - q)(U_i^b)},$$

equation (1) is satisfied when

$$\Sigma [p_i(U_i^a - U_i^b)/U_i^b] > 0$$

or

$$\Sigma (p_i U_i^a / U_i^b) > 1. \tag{3}$$

Similarly, (2) is satisfied when

$$\Sigma (p_i U_i^b / U_i^a) > 1. \tag{4}$$

Thus, the necessary and sufficient conditions for natural selection to favor a seed heteromorphism are that the expected values of  $U_i^a/U_i^b$  and  $U_i^b/U_i^a$  must both be greater than one. These conditions can be expanded as follows:

$$\begin{aligned} E(U_i^a) E(U_i^{b^{-1}}) + \text{cov}(U_i^a U_i^{b^{-1}}) &> 1 \\ E(U_i^b) E(U_i^{a^{-1}}) + \text{cov}(U_i^b U_i^{a^{-1}}) &> 1. \end{aligned}$$

Note that  $1/E(U_i^{-1})$  equals the harmonic mean,  $H(U_i)$ , which when substituted gives

$$\begin{aligned} E(U_i^a)/H(U_i^b) &> 1 - \text{cov}(U_i^a U_i^{b^{-1}}) \\ E(U_i^b)/H(U_i^a) &> 1 - \text{cov}(U_i^b U_i^{a^{-1}}). \end{aligned} \tag{5}$$

The negative covariance of one event with the inverse of another can be loosely thought of as a positive correlation. Thus, the greater the correlation of success of the two seed types, the greater the right-hand side of inequalities (5) and the harder it becomes to satisfy the inequalities required for heteromorphism. Since arithmetic means are usually larger than harmonic means, conditions promoting seed heteromorphisms should be easily attained if the average fitnesses of seed morphs are approximately equal and if the expected yields of the two seed types

are not too positively correlated. Furthermore, holding the arithmetic mean constant while increasing the variance lowers the harmonic mean. Thus, increasing the variability of the environment should also promote heteromorphism.

Another way to think about the evolution of seed heteromorphism is to realize that the measure of fitness,  $W$ , is a geometric mean; it can be increased by either increasing the arithmetic mean of the annual seed yields or reducing the variance (Gillespie 1977). Only a single seed type is necessary to maximize the arithmetic mean of annual fecundities. Because one or the other seed morph has a higher mean yield, the production of some of the lower-yielding morph would lower the mean yield of the heteromorphic strategy. In contrast, the production of two morphs may increase the geometric mean above that of either morph alone (a second morph would not increase the arithmetic average fitness but might reduce the variance). For example, consider two seed types for 3 yr, during which one seed type yields 2, 5, and 8 seeds and the other yields 8, 5, and 2 seeds. If the seed types represent different strategies, there are 80 descendants of a single individual after 3 yr. If they are morphs produced in a 1:1 ratio by a heteromorphic strategy, however, the average offspring fitness will be 5 seeds in each year or 125 seeds after 3 yr. All three strategies average 5 seeds per year, but the heteromorphic strategy has the highest yield by virtue of lower between-year variance. If the above yields represent three equiprobable types, substituting them into inequalities (3) and (4) or (5) (general analytic solutions for the intuitive logic above) verifies that heteromorphism is favored.

#### FITTING EXPERIMENTAL DATA TO THE MODEL

The input variables for the model are the expected demographic successes of each seed morph in different possible year types and the probability distribution of year types. If an inter-year seed bank exists for one morph, an alternative set of parameters includes the expected demographic success given germination in different year types and the proportion of nongerminating seeds that survive to the following year (see Cohen 1966; Brown and Venable 1986). The model then predicts either mono- or heteromorphism as an optimal solution, and in the case of heteromorphism the proportion of seed types that maximizes fitness can be calculated by iteration.

A small body of literature documents the relative success of different seed morphs. Most available data come from experiments in which environmental variables were manipulated and seed-morph performance evaluated. When model parameters are estimated from such data, the necessary and sufficient conditions for seed heteromorphism can be evaluated and the optimal proportion of morphs can be predicted. A short interactive program written in Microsoft Basic, which makes these calculations, is available from the author.

In the annual composite *Gymnarrhena micrantha*, subterranean achenes are produced from cleistogamous flowers, and smaller aerial achenes are produced from chasmogamous flowers (Koller and Roth 1964). The subterranean achenes weigh 12 times as much as aerial ones. The differential expense of producing the two achene morphs can be taken into account by including a constant in the fitness

formula to reflect the fact that 12 aerial achenes may be sacrificed for an increment of one subterranean achene (more-complicated constraint functions reflecting different allometric realities for the trade-off between achene types could be constructed).

Koller and Roth measured the survival of seedlings exposed to different watering treatments considered representative of natural conditions in the desert. For lack of better information, I assume that the different experimental treatments represented different equiprobable year types and that survival is a suitable measure of fitness. As a partial rationale, note that the necessary and sufficient conditions for heteromorphism and the optimal proportion are determined by the relative rather than absolute success of seed morphs in different year types. Estimates based on survival differences between morphs are accurate only to the extent that relative survival is proportional to relative fitness. Differences resulting from the breeding system need not be explicitly considered if we assume that they are reflected in the demographic success of the offspring. In one experiment, seedlings were exposed to ambient desert conditions for 1–7 days without water. The survival values are found in table 1. Using these data and the assumptions specified above, the model predicts heteromorphism with 62% allocation to aerial achenes. The aerial achenes represent a strategy for high arithmetic-mean survival (per unit investment), whereas the subterranean achenes represent a low-variance strategy.

In a second experiment, different but constant levels of soil water were maintained. If these levels are assumed to represent different equiprobable year types, the model predicts only aerial achenes. Indeed, aerial achenes outperform subterranean achenes under all conditions (when success is considered per unit investment). If the conditions simulated in the two experiments are considered as eight equiprobable year types, the model predicts heteromorphism with 84% allocation to aerial achenes. Koller and Roth reported that plants produce from one to three subterranean inflorescences with one or two achenes each. Aerial inflorescences produce numerous small achenes, and plants produce from zero to several inflorescences, depending on plant size. Thus, on the average, the plants allocate more to aerial achenes as predicted by the model. Once heteromorphism exists, varying the seed-morph proportions in response to reliable information about environmental quality further increases fitness.

Data also exist for *Heterotheca latifolia*, an annual composite of the eastern United States that is abundant in open and disturbed sites. Rather than producing achene morphs on different heads as does *G. micrantha*, the ray and disk florets of each head give rise to different morphs (Venable and Levin 1985a). The circumference-area relationship of ray and disk florets ensures a fairly constant achene proportion. Since the mean mass of ray and disk achenes did not differ in the population studied, fitness of achene types need not be weighted by allocation. In a greenhouse experiment (Venable 1985), ray and disk achenes were sown together and subjected to droughts of short or long duration, beginning early (3 days after initiation of the experiment) or late (after 2 wk). Performance was measured as biomass (dry weight) after 111 days. A 25% seed-bank carryover between years has been documented in the field for ray achenes (Venable and Levin 1985b). All

TABLE 1  
RELATIVE SUCCESS OF PROPAGULE TYPES

<i>Gymnarrhena micrantha</i> . No. seedlings surviving (of 24)				
SEED TYPE	DAYS OF DROUGHT			
	1	3	5	7
Aerial	17	7	3	0
Subterranean	24	24	24	15
Adjusted subterranean	2.01	2.01	2.01	1.26
EXPERIMENT 2				
SEED TYPE	WATER CONTENT OF SOIL			
	20%	25%	45%	60%
Aerial	11	14	23	21
Subterranean	21	22	24	24
Adjusted subterranean	1.76	1.85	2.01	2.01

Predictions from the model:

Data from experiment 1: heteromorphism, 62% allocation to aerial achenes

Data from experiment 2: monomorphism, aerial

Combined data: heteromorphism, 84% allocation to aerial achenes

*Heterotheca latifolia*. Total biomass (g)

SEED TYPE	WATERING REGIME			
	Regular watering	Short early drought	Short late drought	Long late drought
Disk	71.1	19.8	64.4	0
Ray	7.2	23.3	4.1	0.92
Adjusted ray	9.6	31.1	5.5	1.23

Prediction from the model: heteromorphism, 38% ray achenes

NOTE.—Data for *Gymnarrhena micrantha* are from Koller and Roth 1964; those for *Heterotheca latifolia* are from Venable 1985. Success of *G. micrantha* was originally measured in terms of the number of seedlings surviving. An equivalence factor, calculated from the ratio of weights of the two achene types (weight of aerial achenes divided by weight of subterranean achenes, 0.084), is used here to adjust the success of subterranean achenes to the same level of investment as that of aerial achenes. Success of *H. latifolia* was measured in terms of biomass per 250 achenes sown (achenes have equal weight). Since ray achenes have a 25% between-year seed bank, their performance was adjusted to reflect the 75% "nondormant" achenes (by dividing by 0.75).

except these dormant ray achenes are considered to "germinate." In this way achenes that germinated and died are not differentiated from those that never emerged but would not in any case have remained viable until the following germination season. In keeping with these assumptions, disk-achene success is measured as biomass per achene sown, and ray-achene success is measured per 75% of achenes sown. Again for lack of long-term demographic data, the experimental treatments were assumed to be equiprobable year types. With these data the model predicts heteromorphism with 38% ray achenes. Plants over 35 cm in height produce approximately 33% ray achenes, with small plants producing smaller heads and relatively more ray achenes, providing a close match to the

predicted value (Venable and Levin 1985a). An examination of the data reveals that the heteromorphism in *H. latifolia* involves the marriage of a high-mean-performance, high-risk strategy with a low-variance, low-mean strategy.

For both heteromorphic species the model predicted that heteromorphism should yield higher fitness than either morph alone in environments like the experimental ones. The models also predicted morph proportions similar to those observed in these species. The application of the model to empirical data sets also pointed toward modifications that increase realism. More data are needed to test the predictive ability of the model. Better estimates of model parameters could be obtained by measuring the actual temporal distribution of demographic success for heteromorphic seeds. Perhaps several years of field data could be obtained and extrapolations to other years could be based on long-term weather records and controlled-environment studies.

#### THE EVOLUTION OF SEED BEHAVIOR

How should seed morphs evolve as part of a heteromorphic strategy? The evolution of morph behavior can be explored if the possible seed behaviors are described by an evolutionary-constraint function (which represents the developmental, genetic, or physiological constraints on the evolution of seed yield in different year types) rather than by a fixed vector of seed yields. Yield in year type  $i$  will now be allowed to increase evolutionarily, but the constraint function  $F(\mathbf{U}) = 0$  will dictate the consequences of this change for the yield of other year types. For example, the evolution of a stricter water requirement for germination might increase the expected yield in dry years by ensuring that seeds germinate only when conditions are adequate for survival. The higher water requirement, however, might result in lesser or later germination in wet years in which seeds would have done better before the evolutionary change in dormancy. Thus, the constraint function might specify that, if  $U_j$  increases evolutionarily,  $U_i$  decreases (fig. 1). Under these circumstances, seed morphs may specialize on different year types, evolve different means and variances, and interact evolutionarily with the alternative morph in a heteromorphic strategy, but such evolution is subject to constraints imposed by design possibilities, genetic correlations, development, etc. When considering heteromorphic strategies I assume that the necessary and sufficient conditions for maintaining heteromorphism that were developed previously are satisfied. If they are not, then monomorphism is favored.

Let two seed morphs evolve subject to some evolutionary constraint defined by the function  $F^a(\mathbf{U}^a) = 0$  for one seed morph and  $F^b(\mathbf{U}^b) = 0$  for the other morph, where  $U_i^a \geq 0$  and  $U_i^b \geq 0$  for all  $i$ . Let the morph proportions take any value on the closed interval  $[0,1]$ . If either morph can form a seed bank (i.e., if  $U_i = GS_i + (1 - G)$ , where  $S_i$  is the expected yield given germination), let the germination fraction,  $G$ , be constrained on  $[0,1]$ . The fitness function remains

$$W = \Pi [q(U^a) + (1 - q)(U^b)]^{p_i}.$$

To maximize  $W$  subject to the stated constraints, I will use the method of



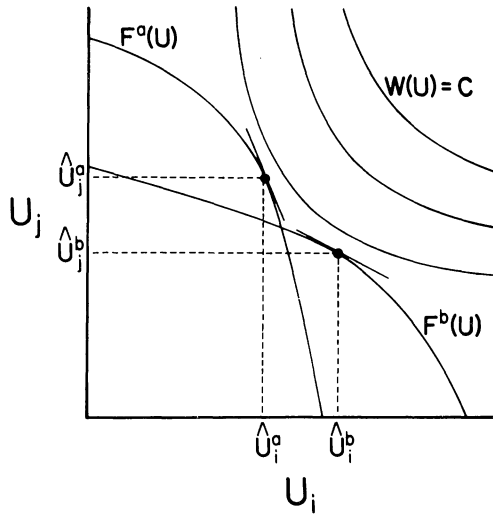


FIG. 1.—Fitness-set representation of the evolutionary constraint on  $U$ , the expected fecundities in two different kinds of years,  $i$  and  $j$ , for two different species or populations,  $F^a(U)$  and  $F^b(U)$ . The negative slope implies that adaptations increasing fecundity in one year type reduce fecundity in the other. The fitness isopleths  $W(U)$  are determined by the probability distribution of  $U$  but not by the shape of the constraint function. Thus, the same set of fitness isopleths applies to  $F^a$  and  $F^b$ , and the tangent where  $F^a(U)$  touches  $W(U)$  has a steeper slope than the tangent where  $F^b(U)$  touches  $W(U)$  for the curves as drawn.

Lagrange multipliers, which can be graphically interpreted with fitness-set representation. The Lagrange function is

$$L = W + \lambda_1 F^a(U^a) + \lambda_2 F^b(U^b) + \mu_1(1 - q) + \mu_2(q) + \mu_3(1 - G) + \mu_4(G),$$

where  $\lambda_1$  and  $\lambda_2$  are the Lagrange multipliers for the constraints on the first and second seed morphs, respectively;  $\mu_1$  and  $\mu_2$  are the multipliers for the inequality constraints requiring that  $q \in [0,1]$ , and  $\mu_3$  and  $\mu_4$  are the multipliers for the constraints on  $G$  (these drop out in the present case, in which I do not explicitly consider a seed bank).

The necessary conditions for maximizing  $W$  are

$$\begin{aligned} \frac{\partial L}{\partial q} &= \frac{\partial W}{\partial q} - \mu_1 + \mu_2 = 0 \\ \frac{\partial L}{\partial U_i^a} &= \frac{\partial W}{\partial U_i^a} + \lambda_1 \frac{\partial F^a}{\partial U_i^a} = 0 \quad \text{for each year type } i \\ \frac{\partial L}{\partial U_i^b} &= \frac{\partial W}{\partial U_i^b} + \lambda_2 \frac{\partial F^b}{\partial U_i^b} = 0 \quad \text{for each year type } i \end{aligned} \quad (6)$$

and that the initial constraints are satisfied.

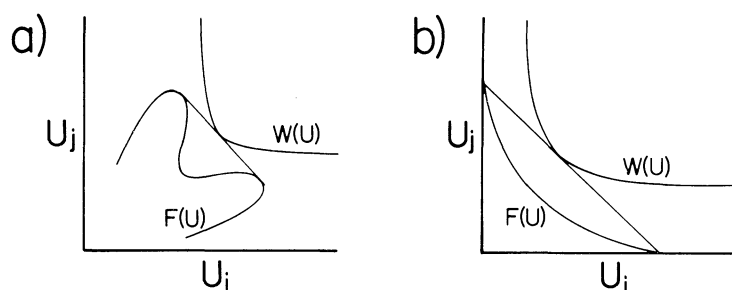


FIG. 2.—A single concave fitness set can give rise to seed heteromorphism. *a*, A standard (Levins 1968) concave fitness set (concave in the middle and convex at the margins), having more than one point with a given slope. *b*, A fitness set that is concave for all possible values of  $U$  and for which no two points have the same slope (fitness maximization yields heteromorphic corner solutions).

The problem of maximizing fitness subject to the constraints on seed behavior can be visualized in terms of fitness sets in the following way. At maximum fitness,

$$\frac{\partial W}{\partial U_i^a} \bigg/ \frac{\partial W}{\partial U_j^a} = \frac{\partial F^a}{\partial U_i^a} \bigg/ \frac{\partial F^a}{\partial U_j^a}. \quad (7)$$

This is ensured by the above set of simultaneous equations, which must be satisfied to maximize fitness (solve eq. 6 for  $\lambda_1$  for two different values of  $i$ , and set the two resulting expressions equal to one another). By the implicit function rule,

$$-\frac{\partial W}{\partial U_i^a} \bigg/ \frac{\partial W}{\partial U_j^a} = \frac{dU_j^a}{dU_i^a},$$

which is the slope of the fitness function (objective function) when the axes represent success in the year types,  $U_i$  and  $U_j$  (fig. 1). Similarly,  $-(\partial F^a/\partial U_i^a)/(\partial F^a/\partial U_j^a)$  equals the slope of the constraint function (fitness set) plotted on the same axes. Thus, equation (7) states that, at maximum fitness, the slope of the objective function equals the slope of the fitness set; the Lagrange problem becomes a fitness-set problem.

There are two main pathways to the evolution of seed heteromorphism. If all the seeds on a plant are limited by the same evolutionary constraints, then seed heteromorphism can evolve only if the constraint curve is concave (fig. 2*a*). This is the concave fitness-set result of Levins (1968) cited by Harper (1977, p. 74) in connection with the evolution of seed heteromorphism. The fundamental aspect of concave fitness-set heteromorphisms is that intermediate adaptations experience low fitness, either because they are not ecologically feasible or because of some structural or physiological constraint.

Seed heteromorphism may also arise if different seeds on the same plant are constrained by different convex fitness sets. In this alternative scenario intermediate adaptations are feasible and may have high fitness. Yet different evolu-

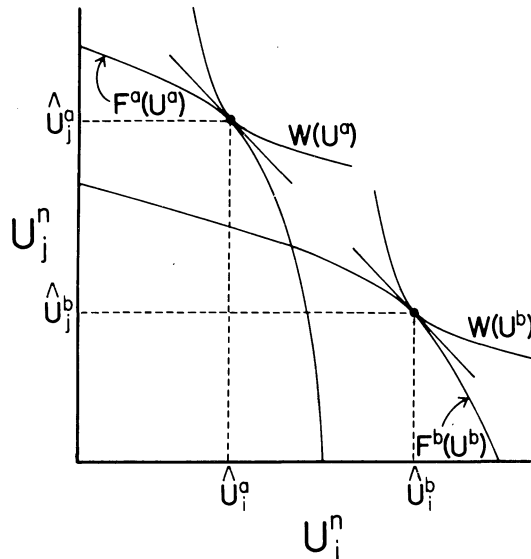


FIG. 3.—Fitness-set representation of the evolutionary constraint on expected fecundities in two different kinds of years,  $i$  and  $j$ , for two seed morphs of a heteromorphic species. One of the conditions for maximizing fitness when each individual produces two seed morphs is that the slope where the constraint function  $F^a(U^a)$  is tangent to the fitness isopleth  $W(U^a)$  must equal the slope where  $F^b(U^b)$  is tangent to the fitness isopleth  $W(U^b)$  (see text). This implies that if the evolutionary constraints for the two morphs did not differ (i.e., either  $F^a$  or  $F^b$  applied for both morphs), seed heteromorphism would not evolve because no two points on one constraint function have the same slope. Comparing the equilibrium seed strategies when each individual produces two seed morphs (this figure) to the equilibrium seed strategies for two monomorphic species having the same two evolutionary constraint curves (fig. 1) shows that the seed strategies diverge more in the heteromorphic case. For the curves drawn, this divergence results in higher mean and higher between-year variance in fecundity for each seed morph and a lower covariance of fecundity between morphs (cf. fig. 4).

tionary constraints (perhaps physiological) must apply to different seeds on a single individual. For example, it might be true that seeds near the bottom of a plant are closer to the bulk of the plant's photosynthetic machinery and therefore are more effective nutrient sinks. If large seed size aids establishment in dry years, the physiological constraint based on position might make it easier for seeds on the bottom of the plant to be specialized for conditions occurring in dry years. Perhaps in wet years, suitable habitats expand and it is easier for seeds on top of the plant to disperse to new sites.

Consider figure 3, in which the two evolutionary-constraint functions apply to different seeds on the same plant. Selection will favor the evolution of seed behavior until the slope on the two constraint functions is equal. This can be shown as follows:

$$\frac{\partial W}{\partial U_i^a} = \frac{p_i q W}{q U_i^a + (1 - q) U_i^b}$$

so that

$$\frac{\partial W}{\partial U_i^a} / \frac{\partial W}{\partial U_j^a} = \frac{p_i[qU_j^a + (1 - q)U_j^b]}{p_j[qU_i^a + (1 - q)U_i^b]} \quad (8)$$

Likewise,

$$\frac{\partial W}{\partial U_i^b} = \frac{p_i(1 - q)}{qU_i^a + (1 - q)U_i^b}$$

and

$$\frac{\partial W}{\partial U_i^b} / \frac{\partial W}{\partial U_j^b} = \frac{\partial W}{\partial U_i^a} / \frac{\partial W}{\partial U_j^a} \quad (9)$$

By the implicit-function rule, these two terms represent the slopes of the fitness isopleths (defined as lines connecting points of equal fitness) tangent to the constraints on  $U^b$  and  $U^a$ , respectively. Since for one convex constraint curve no two points have the same slope, fitness maximization will always result in a monomorphic strategy. Of course, the standard concave fitness set (fig. 2*a*) has more than one point with the same slope (because it is concave in the middle but convex on the margins) and can thus give rise to seed heteromorphism. A constraint function that is convex throughout its domain (e.g., fig. 2*b*) does not have two points with the same slope, but maximum fitness involves corner solutions and is thus not subject to conditions (6).

The outer halves of the two constraint functions in figure 3 actually form a concave fitness set, and this is why there is more than one point with the same slope when there are two convex fitness sets. There are, however, important differences between having two convex fitness sets and one concave set. With a concave function, seed heteromorphism may evolve even though all seeds on a plant have the same evolutionary constraints. Yet intermediate morphs must have low fitness for this to occur. The environments in different years must be different enough that the structural or behavioral adjustments necessary to do well in both are difficult to construct. In contrast, no such restrictions on compromise adaptations are required when more than one constraint function applies. Thus, a broader range of environments meets the assumptions of the model, but it is necessary that differences in evolutionary constraints (constraints of development, genetics, or design) exist for different seeds on single individuals. For concave fitness sets all seeds are under the same constraints but the environments are divergent. With two convex fitness sets, the developmental, genetic, or design possibilities are divergent. Thus, convex-fitness-set heteromorphisms should be found only among taxa in which preexisting differences in evolutionary constraints predispose the seeds toward divergence.

How should seed behavior evolve when more than one morph is produced? In the case of a single concave fitness set, the plants will, of course, produce the kinds of seed morphs that function well (have high fitness), and seed behavior is rather strictly determined by the shape of the fitness set. In the case of two convex constraints, the population dynamics and interaction of morph strategies are more important, and heteromorphism favors divergence in seed behavior. Consider the

two constraint functions in figure 1. The optimal seed behaviors are more divergent when the two constraint functions correspond to the different morphs of a heteromorphic strategy than when they correspond to two separate monomorphic strategies (e.g., different species). I demonstrate this analytically in the Appendix but it can be seen intuitively by examining figures 1 and 3. Because the fitness criterion is a geometric mean, the shape of the fitness isopleths (the objective function) plotted in the  $U_i, U_j$  plane will be concave upward (Levins 1968) and will, of course, not depend on the shape of the constraint function (fig. 1; see Brown and Venable 1986). If the constraints are convex and the objective function concave, the slope of the fitness isopleth tangent to the constraint  $F^a$  will always be steeper (more negative) than the isopleth tangent to  $F^b$  for the curves as drawn in figure 1. From equation (9) we know that, in the heteromorphic case, fitness is maximized when the slopes on  $F^a$  and  $F^b$  are the same; a comparison of figures 1 and 3 shows that seed behaviors will be more divergent when this occurs. Divergence of morph behaviors decreases the correlation of seed behavior among morphs. Such a decreased correlation increases the stability of the heteromorphism by making the necessary and sufficient conditions for heteromorphism (5) more readily attainable.

The increased divergence of performance of seed morphs can lead to two different kinds of seed heteromorphisms depending on the similarity of the evolutionary constraints of the two seed types. When the evolutionary constraints differ substantially, as in figures 1 and 3, divergence results in each morph's specializing on the year type in which it has an inherently higher potential for success (year type  $i$  for the second seed type and year type  $j$  for the first in figs. 1 and 3). For example, imagine that the constraints are such that on one part of the plant seeds would be higher yielding if they were selected for performance in wet rather than dry years (i.e., let year type  $j$  represent wet years and year type  $i$  dry years in fig. 3). Suppose that seeds on another part of the plant are subject to heavy predation, which is worse in wet years. Because of this predation they will not do as well if selected for performance in wet rather than dry years (see the constraint  $F^b$  in fig. 3). When the seed morphs have such disparate evolutionary constraints, divergence of morph behavior results in each seed morph being specialized for the year type in which it can potentially do best, such that each seed type experiences a higher mean and a higher variance of yield. In what follows, such heteromorphisms will be called *high-risk-high-risk (HRHR) heteromorphisms*.

A second type of seed heteromorphism involves the marriage of a high-mean, high-variance seed morph and a low-mean, low-variance seed morph. This kind of heteromorphism, *high-risk-low-risk (HRLR) heteromorphism*, will be favored when both seed morphs have the same inherent "preference" for year types, but differ somewhat in their constraints. Imagine a plant, all of whose seeds are constrained such that they could be modified by selection to yield more in wet years than they could ever (in the evolutionary sense) yield in dry years. Assume that seeds on the bottom of the plant are more effective nutrient sinks than those on the top. If larger seed size improves performance in dry years, the physiological constraint based on position makes it easier to select for superior performance

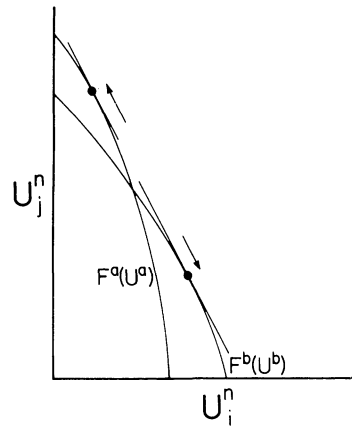


FIG. 4.—Fitness-set representation of the evolutionary constraint on expected fecundities in two kinds of years,  $i$  and  $j$ , for two seed morphs of a heteromorphic species. The constraints are similar, and high fecundity is attained more easily in year type  $j$  than in year type  $i$  for both morphs (cf. figs. 1 and 3, where one morph has the potential to evolve greater fecundity in year type  $i$ , the other in year type  $j$ ). The divergence of behavior of seed morphs inherent in seed heteromorphism results in higher mean fecundity and higher between-year variance for the seed type constrained by  $F^a$  but a lower mean and lower variance for the seed type constrained by  $F^b$ .

of seed on the bottom of the plant in dry years. Suppose also that, in wet years, suitable habitat for establishment expands and it is easier for seeds on top of the plant to disperse to new sites. Both seed morphs would have a higher average yield if they specialized to excel under wet-year conditions, but it is easier to modify the seeds on top of the plant in this direction. This describes the situation illustrated in figure 4 (year type  $j$  represents wet years). As selection causes seed behaviors to diverge, the seed types constrained by  $F^a$  (those on top of the plant) will have a higher mean ( $U_j^n$  increases more than  $U_i^n$  decreases) and a higher variance (performance increases in what are already high-performance years and decreases in what are low-performance years). In contrast, seeds constrained by  $F^b$  (those on the bottom of the plant) will evolve a lower mean but also a lower variance.

One way such HRLR heteromorphisms could occur is if one of the seed morphs forms a between-year seed bank. This automatically lowers the mean performance of that seed morph because some seeds remain dormant in years in which they could have produced more seeds had they germinated. Variance is also lowered because, although maximum yield is reduced, the minimum yield is increased since the seed bank represents a minimum expected contribution.

The predictions arising from this exploration of the evolution of morph behavior can be summarized as follows.

1. If all seeds on a plant are subject to the same evolutionary constraints, seed heteromorphism will occur only if the constraint curve is concave.
2. If seeds on the same plant have different evolutionary constraints, selection

will favor divergent seed behavior with a more negative covariance of yield among the seed types than would occur if the same constraints applied to two separate monomorphic strategies.

3. Under some conditions the evolutionary divergence in seed behavior results in one morph with a high mean and variance of yield and another morph with a low mean and variance. This type of heteromorphism arises when the evolutionary constraints on seed evolution differ slightly for different seeds on a plant such that the same year types are inherently better. They are better in the sense that each seed type would have highest yield if it were specialized for the same year type. Since this would imply convergence, divergence results in one seed type evolving away from its inherently "best" year type (fig. 4).

4. If the constraint curves differ substantially such that different year types represent "best evolutionary bets" for the seed morphs, then divergence will result in each morph being specialized for its inherently best year types. This will create high mean and high variance for each seed morph (figs. 1, 3).

5. A fitness-set heteromorphism in the traditional, concave form should be more or less randomly distributed among taxa but should only occur where selective pressures in different year types conflict sufficiently that intermediate adaptations have low fitness.

6. A convex-fitness-set heteromorphism should only occur in groups in which different seeds on the same plant have different evolutionary possibilities.

7. Under some conditions HRLR polymorphisms are predicted from dual convex constraint functions but not from a single concave constraint function.

#### EVALUATION OF THE EVOLUTIONARY PREDICTIONS

Several of the predictions of the evolution of seed behavior can be evaluated by considering the kinds of plants in which heteromorphisms are found and the nature of the seed behaviors reported. The taxonomic distribution of seed heteromorphisms is distinctly nonrandom. Somatic seed heteromorphism is often reported in groups with some preexisting floral heteromorphism. In the Compositae it is usually associated with the formation of ray and disk florets. The preexisting difference in floral type ensures different evolutionary possibilities for ray and disk achenes. The centripetal development of the composite head gives ray achenes longer to grow, thus predisposing them to larger size (McEvoy 1984). Ray and disk florets also often differ in sex expression, may differ in susceptibility to predation, and thus may pose different constraints on specialization. Among the grasses and several other families, somatic heteromorphism is associated with the production of cleistogamous and chasmogamous flowers (Campbell et al. 1983). In *Impatiens biflora* (Balsaminaceae) the dimorphic seeds correspond to cleistogamous and chasmogamous flowers (Schemske 1978), as also occurs in heteromorphic *Emex spinosa* (Polygonaceae; Weiss 1980). For all of these cases the two floral types have different levels of inbreeding and different floral function and structure, and they may have differences in position or phenology. Thus, seeds from cleistogamous flowers should have different evolutionary constraints from seeds produced by chasmogamous flowers. Chenopodiaceae and

Amaranthaceae produce small single-seeded fruits among which heteromorphism is often associated with position in an inflorescence. Although the differences in evolutionary possibilities are less clear in these families than in Compositae and in species that produce cleistogamous flowers, position effects may result in different timing constraints or different access to nutrients and energy. Seed heteromorphisms are reported for a number of legumes and crucifers. Silvertown (1984) discussed how somatic heterochrony may create within-plant differences in developmental constraints in species of legumes. Similar constraints probably apply for the fruits of Cruciferae.

One might argue that different evolutionary possibilities for seeds on different parts of a plant should be an almost universal phenomenon. For seed heteromorphism to be an optimal strategy, however, the evolutionary constraint curves must cross. If they do not, one seed type will always be superior (though the plant may be forced to make some inferior seeds, as appears to be the case for a number of species discussed in Silvertown 1984). According to Harper (1977, p. 72) and Silvertown (1984), cryptic seed heteromorphism (variable seed behavior not accompanied by dramatic morphological variation) may be a widespread phenomenon affecting many plant species. The nature and taxonomic distribution of such cryptic heteromorphisms are not well documented, and the nature of the evolutionary constraints is, of course, less well known. The models presented here provide a framework of theoretical expectations for the exploration of such cryptic heteromorphisms. Available data do indicate that gross morphological heteromorphisms, often with discrete seed types, have evolved in plants with obvious dimorphic sets of evolutionary possibilities. This association of well-developed seed heteromorphisms with taxonomic groups having preexisting differences in evolutionary possibilities was not predicted by the concave-fitness-set model but was predicted by the dual-constraint-function model.

The dual-fitness-set scenario predicted either HRHR or HRLR heteromorphisms depending on the nature of the evolutionary constraints. In table 2 a number of species are classified into these two categories. When the available literature reports that one morph has more restricted and the other has less restricted (but overlapping) conditions for germination, I inferred an HRLR heteromorphism. For example, the disk achenes of *Grindelia squarrosa* germinate more rapidly and over a broader temperature range than the ray achenes (McDonough 1975). They are also less inhibited by darkness. When the germination of one seed type is more strictly controlled by one environmental factor and the germination of the other is controlled by a different factor, I inferred an HRHR heteromorphism. An example of a species classified as an HRHR heteromorphism is *Hypochoeris glabra*. Beaked achenes are more light sensitive, whereas unbeaked achenes are more temperature sensitive (Baker and O'Dowd 1982). Although the data regarding the relative importance of the two types of heteromorphisms is limited, it appears that HRLR heteromorphisms are more common. Since the concave-fitness-set model does not predict this latter kind of heteromorphism, the evidence further supports the scenario of a dual convex fitness set for the evolution of seed heteromorphism.

Lloyd (1984) has noted that multiple strategies are more common in plants than animals. There is no clear a priori difference between plants and animals regarding



TABLE 2  
CLASSIFICATION OF SEED HETEROMORPHISMS

Species	Family	Source
<b>High-Risk–Low-Risk Heteromorphisms</b>		
<i>Atriplex dimorphostegia</i>	Chenopodiaceae	Koller 1957
<i>Chenopodium album</i>	Chenopodiaceae	Williams and Harper 1965
<i>Halogeton glomeratus</i>	Chenopodiaceae	Williams 1960
<i>Salicornia europaea</i>	Chenopodiaceae	Ungar 1979
<i>Grindelia squarrosa</i>	Compositae	McDonough 1975
<i>Gymnarrhena micrantha</i>	Compositae	Koller and Roth 1964
<i>Heterotheca latifolia</i>	Compositae	Venable 1985
<i>H. grandiflora</i>	Compositae	Flint and Palmblad 1978
<i>Heterosperma pinnatum</i>	Compositae	Venable et al., MS
<i>Senecio jacobaea</i>	Compositae	McEvoy 1984
<i>Xanthium canadense</i>	Compositae	Thornton 1935
<i>Alysicarpus monilifer</i>	Leguminosae	Maurya and Ambasht 1973
<b>High-Risk–High-Risk Heteromorphisms</b>		
<i>Hypochoeris glabra</i>	Compositae	Baker and O'Dowd 1982
<i>Emex spinosa</i>	Polygonaceae	Evenari et al. 1977

NOTE.—A high-risk–low-risk heteromorphism is inferred here when the conditions for germination are similar for two seed morphs but more restricted for one of them. A high-risk–high-risk heteromorphism is inferred when the germination of one seed morph is controlled by one environmental factor, while germination of the other seed type is controlled by a different factor. Relative germination and yield need to be measured in a variety of experimental or natural conditions to verify the inferred relationship between germination behavior and yielding strategy.

the likelihood of concave-fitness-set heteromorphisms. In a loosely integrated modular organism, however, different constraints probably apply to the different repeated units of structure (seeds, fruits, leaves, flowers) produced on different parts of a plant.

#### SUMMARY

I develop a model of the ecology and evolution of seed heteromorphism. Heteromorphism is promoted over monomorphism by low correlation of the demographic success of the different morphs and high temporal variation in seed success. Available experimental data from two heteromorphic-seeded species satisfy the model conditions for heteromorphism and produce morph proportions similar to those predicted. Seed heteromorphism can arise when the evolution of morph behavior is constrained by a single concave fitness set or when different seeds on the same individual plant are constrained by different convex fitness sets. The fitness sets represent constraints on demographic success in different year types (trade-offs resulting from constraints in design, development, physiology, or genetics). Two kinds of heteromorphism may arise when the constraints differ for different seeds on the same plant. Whether a high-risk–low-risk heteromorphism or high-risk–high-risk heteromorphism evolves depends on the similarity of the evolutionary constraints. I evaluate the different evolutionary scenarios developed here in light of what is known about the natural history of seed heteromorphism.

## ACKNOWLEDGMENTS

I would like to thank J. S. Brown, C. Martínez del Rio, and J. Soberón for valuable discussions of the evolution of seed heteromorphisms. Comments by D. Queller and three anonymous reviewers were helpful in revising this paper.

## APPENDIX

To demonstrate that morph optima diverge more when part of a seed heteromorphism than when they represent two separate monomorphic strategies, consider what happens to the slope of the constraint function  $F^b$  in figure 3 at the point of maximal fitness when we go from making no seeds of a second morph to making some. The slope is defined as

$$\frac{dU_j^b}{dU_i^b} = - \frac{\partial W}{\partial U_i^b} \bigg/ \frac{\partial W}{\partial U_j^b}.$$

At maximum fitness, we know from (6) and (7) that this slope, which we will call  $g$ , equals

$$- \frac{\partial W}{\partial U_i^b} \bigg/ \frac{\partial W}{\partial U_j^b} = \frac{p_i[qU_j^a + (1 - q)U_j^b]}{p_j[qU_i^a + (1 - q)U_i^b]}.$$

To see how the slope changes with the proportion of seed morphs,  $q$ , define the numerator of the above expression as  $a(q)$  and the denominator as  $b(q)$  so that

$$\frac{\partial g}{\partial q} = - \left[ \frac{\frac{\partial a(q)}{\partial q} b(q) - \frac{\partial b(q)}{\partial q} a(q)}{b(q)^2} \right]$$

where  $\partial a(q)/\partial q = p_i U_j^a - p_i U_j^b$  and  $\partial b(q)/\partial q = p_i U_i^a - p_j U_i^b$ . Evaluated at  $q = 0$ , this becomes

$$\frac{\partial g}{\partial q} \bigg|_{q=0} = - \left[ \frac{p_i(U_j^a U_i^b - U_j^b U_i^a)}{U_i^b p_i} \right].$$

How does the slope at maximum fitness of the constraint on  $U^b$  change when we go from making none of the second morph to dimorphism? The slope will become steeper (more negative) when  $U_j^a U_i^b > U_j^b U_i^a$  or

$$\frac{U_j^a}{U_i^a} > \frac{U_j^b}{U_i^b}. \quad (\text{A1})$$

At  $q = 0$  we are only making the morph constrained by  $F^b$ . Becoming heteromorphous will make the tangent at maximum fitness more negative (the original seed type becomes more specialized for conditions occurring in year type  $i$  in fig. 3) if the initial optima were situated such that the new seed type (constrained by  $F^a$ ) did better in year type  $j$  than in  $i$ , relative to the performance of the original seed type constrained by  $F^b$ . An equivalent argument holds for beginning with only the seed type constrained by  $F^a$  and becoming heteromorphous (i.e., define  $r = [1 - q]$  as the proportion of the other seed type). Thus for the constraint curves as drawn in figures 1, 3, and 4, heteromorphism results in achene types diverging and specializing more for conditions occurring in the year type in which each does best (best relative to the other seed type in the special sense of inequality A1).

Curiously, if the constraint curves were drawn as concave outward (fig. 2b), instead of convex, the same argument seems to suggest convergence of seed morphs. It can be shown, however, that the solution is actually a minimum in this situation and that maximum fitness in the heteromorphous case would involve boundary conditions (i.e., seed

morphs would be completely specialized for the conditions of year types in which they can do best, in the sense of inequality A1).

## LITERATURE CITED

- Baker, G. A., and D. J. O'Dowd. 1982. Effects of parent plant density on the production of achene types in the annual *Hypochoeris glabra*. *J. Ecol.* 70:201–215.
- Bomze, I. M., P. Schuster, and K. Sigmund. 1983. The role of Mendelian genetics in strategic models of animal behavior. *J. Theor. Biol.* 101:19–38.
- Brown, J. S., and D. L. Venable. 1986. Evolutionary ecology of seed-bank annuals in temporally varying environments. *Am. Nat.* 127 (in press).
- Campbell, C. S., J. A. Quinn, G. P. Cheplick, and T. J. Bell. 1983. Cleistogamy in grasses. *Annu. Rev. Ecol. Syst.* 14:411–441.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.* 12: 119–129.
- Evenari, M., A. Kadouri, and Y. Gutterman. 1977. Eco-physiological investigations on the amphicarp of *Emex spinosa* (L.) Campd. *Flora (Jena)* 166:223–238.
- Flint, S. D., and I. G. Palmblad. 1978. Germination dimorphism and developmental flexibility in the ruderal weed *Heterotheca grandiflora*. *Oecologia (Berl.)* 36:33–43.
- Gillespie, J. H. 1977. Natural selection for variance in offspring numbers: a new evolutionary principle. *Am. Nat.* 111:1010–1014.
- Harper, J. L. 1977. *The population biology of plants*. Academic Press, New York.
- Koller, D. 1957. Germination-regulating mechanisms in some desert seeds, IV. *Atriplex dimorphostegia* Kar. et Kir. *Ecology* 38:1–13.
- Koller, D., and N. Roth. 1964. Studies on the ecological and physiological significance of amphicarp in *Gymnarrhena micrantha* (Compositae). *Am. J. Bot.* 51:26–35.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, N.J.
- Lloyd, D. G. 1977. Genetic and phenotypic models of natural selection. *J. Theor. Biol.* 69:543–560.
- . 1984. Variation strategies in heterogeneous environments. *Biol. J. Linn. Soc.* 21:357–385.
- Maurya, A. N., and R. S. Ambasht. 1973. Significance of seed dimorphism in *Alysicarpus monilifer* DC. *J. Ecol.* 61:213–217.
- McDonough, W. T. 1975. Germination polymorphism in *Grindelia squarrosa* (Pursh) Dunal. *North-west Sci.* 49:190–200.
- McEvoy, P. B. 1984. Dormancy and dispersal in dimorphic achenes of tansy ragwort, *Senecio jacobaea* L. (Compositae). *Oecologia (Berl.)* 61:160–168.
- Real, L. A. 1980. On uncertainty and the law of diminishing returns in evolution and behavior. Pages 37–64 in J. E. R. Staddon, ed. *Limits to action*. Academic Press, New York.
- Schaffer, W. M., and M. D. Gadgil. 1975. Selection for optimal life histories in plants. Pages 142–157 in M. L. Cody and J. M. Diamond, eds. *Ecology and evolution of communities*. Belknap, Cambridge, Mass.
- Schemske, D. W. 1978. Evolution of reproductive characteristics in *Impatiens pallida* (Balsaminaceae): the significance of cleistogamy and chasmogamy. *Ecology* 59:596–613.
- Schoen, D. J., and D. G. Lloyd. 1984. The selection of cleistogamy and heteromorphic diaspores. *Biol. J. Linn. Soc.* 23:303–322.
- Silvertown, J. W. 1984. Phenotypic variety in seed germination behavior: the ontogeny and evolution of somatic polymorphism in seeds. *Am. Nat.* 124:1–16.
- Stebbins, G. L. 1974. *Flowering plants: evolution above the species level*. Belknap, Cambridge, Mass.
- Thornton, N. C. 1935. Factors influencing germination and development of dormancy in cocklebur seeds. *Contrib. Boyce Thompson Inst.* 7:477–496.
- Ungar, I. A. 1979. Seed dimorphism in *Salicornia europaea* L. *Bot. Gaz.* 140:102–108.
- Venable, D. L. 1985. Ecology of achene dimorphism in *Heterotheca latifolia*: III. Consequences of varied water availability. *J. Ecol.* 73(3) (in press).
- Venable, D. L., and D. A. Levin. 1985a. Ecology of achene dimorphism in *Heterotheca latifolia*: I. Achene structure, germination, and dispersal. *J. Ecol.* 73:133–145.

- . 1985b. Ecology of achene dimorphism in *Heterotheca latifolia*: II. Demographic variation within populations. *J. Ecol.* 73(3) (in press).
- Weiss, P. W. 1980. Germination, reproduction and interference in the amphicarpic annual *Emex spinosa* (L.) Campd. *Oecologia* (Berl.) 45:244–251.
- Westoby, M. 1981. How diversified seed germination behavior is selected. *Am. Nat.* 118:882–885.
- Williams, J. T., and J. L. Harper. 1965. Seed polymorphism and germination. I. The influence of nitrates and low temperatures on the germination of *Chenopodium album*. *Weed Res.* 5: 141–150.
- Williams, M. C. 1960. Biochemical analyses, germination and production of black and brown seed of *Halogeton glomeratus*. *Weeds* 8:452–461.