Evolutionary Ecology of Seed-Bank Annuals in Temporally Varying Environments
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# EVOLUTIONARY ECOLOGY OF SEED-BANK ANNUALS IN TEMPORALLY VARYING ENVIRONMENTS

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The simplicity of the "annual" life cycle is complicated by the production of long-lived seeds, which introduces an age structure (Roberts and Feast 1973; Venable and Levin 1985). The age structure introduced by a seed bank has at least three distinctive properties. First, though seeds may live a number of years, reproduction occurs only once; thus, seed-bank annuals are invariably semelparous (monocarpic). Second, seeds do not grow; none of the usual survival or reproductive advantages based on delayed reproduction and increased allocation to growth pertain to delayed germination (see Gadgil and Bossert 1970; Schaffer 1974; Bell 1980). Third, the seed stage is uniquely resistant to most of the normal hazards of the vegetative plant, such as competition or drought, so there is a compensatory advantage for the lack of growth (seeds are of course subject to some unique hazards of their own, such as seed predation). These special aspects of age structure must be considered in models of the ecology and evolution of annual plants because they determine many of the properties of annuals. Two that will be explored here are specialization to the environmental conditions occurring in good years (the bad years are avoided by resistant seeds) and the evolutionary adjustment of seed banks.

In a temporally varying environment, the per capita rate of growth is affected positively by the mean annual fitness and negatively by the variance in annual fitness. Both seed banks and specialization to a subset of environmental conditions provide avenues for adjusting the mean and variance of annual fitness. Seed banks tend to lower the variance by removing some seeds from the mortality risks and reproductive opportunities involved in germinating. They tend to lower the mean as well, since at best a dormant seed can yield one seed in the following year. Specializing to environmental conditions favorable to the plant increases fitness variance if such specialization lowers the plants' performance under unfavorable conditions. Theoretical considerations of the evolution of dormancy usually assume an evolutionarily static reproductive schedule that depends on environmental quality in different year types (Cohen 1966, 1967; Venable and Lawlor 1980; Westoby 1981; Freas and Kemp 1983; Ellner 1984).

In a different vein, Templeton and Levin (1979) explored how a given seed-bank

strategy affects the evolution of post-germination traits that determine the repro-
ductive schedule. In nature both dormancy and post-germination adaptations
evolve simultaneously with natural selection operating on the suite of interacting
traits. This results in life history patterns not necessarily predictable from a
consideration of each trait by itself. In this paper we predict the outcome when
both the dormancy schedule and the reproductive schedule can evolve. We are
especially interested in determining whether an integrated approach generates
new predictions.

Cohen (1966) showed that for an annual plant in a temporally varying environ-
ment, a between-year seed bank is favored by natural selection when the har-
monic mean of the reproductive success of seedlings at germination is less than,
and the arithmetic mean is greater than, the survival probability of a dormant
seed. The exact dormancy fraction that maximizes fitness is determined by the
probability of occurrence of different year types and the reproductive success
realized from germination in each year type.

Templeton and Levin (1979) considered the evolution of a trait controlled by a
single locus with two alleles. Each genotype results in a different set of reproduc-
tive successes associated with different year types. The authors compared the
evolutionary outcome for a seed-bank annual with that for an annual with no
between-year dormancy. When there is a between-year seed bank, selection
favors genotypes that experience the highest seed set during good years. Thus, a
population in which a proportion of seeds remains dormant between years will be
selected to specialize more to the good years than a population without a seed
bank. A between-year seed bank minimizes the impact of bad years and allows
other traits to adapt to good years.

Our model combines the salient features of the models of Cohen and of Temple-
ton and Levin. Our approach differs from Templeton and Levin's in that we do
not explicitly consider the genetic basis for heritable variation. Instead, we as-
sume that a continuous set of heritable variation exists for both between-year
dormancy and the reproductive schedule. We assume that a phenotype increases
in frequency relative to those phenotypes with lower fitness.

We assume that an evolutionary trade-off exists such that a plant sacrifices
fitness in one year type to attain higher fitness in another. In particular, the set of
reproductive successes for germinating seedlings in the different kinds of years is
the result of specific adaptations. For example, in desert annuals, mesophytic
traits give rise to high reproductive success in wet years because of high photo-
synthetic efficiency and low nutrient and energy expense. A xerophytic anatomy
and physiology result in higher reproductive success in intermediate years be-
cause they confer an ability to tolerate suboptimal conditions (Orians and Solbrig
1977). Xerophytic traits that should increase fitness in dry years include a reduced
surface-to-volume ratio of leaves, reduction of intercellular spaces, increased
conducting elements, sclerenchyma, and chlorenchyma, sunken stomata, thick-
ened cuticle, high stomatal resistance, low tissue hydration, and high osmotic
pressure. These traits probably reduce fitness in wet years when they are superflu-
ous. The character involved can be any trait or suite of traits that exhibits a trade-
off between reproductive success in different year types.

## Fitness Formula and Constraints

We assume a temporally varying environment in which between-year variation is classified into $n$ year types assumed to occur at random. Let $p_i$ be the probability of occurrence of year type $i = 1, \ldots, n$ where

$$\sum_{i=1}^{n} p_i = 1.$$ (1)

$\mathbf{S} = (S_1, \ldots, S_n)$ is the vector of reproductive successes (individual demographic fitnesses) of seedlings that germinate in each year type $1, \ldots, n$. By reproductive success we mean the expected number of seeds that a seedling germinating one year will produce in the next year. The vector $\mathbf{S}$ is a function of a large number of traits including post-germination traits, such as plant size, structure, and physiology, and seed traits, such as size, structure, and within-year timing of dormancy (see Venable 1985).

We define the evolutionary constraint set as all attainable phenotypes (an $\mathbf{S}$ vector describes the fitness of each one) for which it is not feasible to increase $S_i$ without decreasing some $S_j$ where $i, j = 1, \ldots, n$ and $i \neq j$. The phenotypic variation described by the constraint set is assumed to have a heritable component so that the traits can evolve. The constraints could be developmental (e.g., allometric), physiological (e.g., allocational), or genetic (negative genetic covariance). To some extent these are just different conceptual frameworks for considering constraints on evolution. For example, developmental or physiological constraints on evolution can be represented as genetic correlations (e.g., Cheverud et al. 1983). Formally, the constraint set, if continuous and bounded, can be represented by an evolutionary constraint function:

$$F(\mathbf{S}) = 0.$$ (2)

We assume that the phenotypes represented by the evolutionary constraint set defined above are either already present in the population or recur regularly as mutations or recombinants. Thus, in time, natural selection can operate on all the elements of the constraint set.

Since $F(\mathbf{S})$ represents trade-offs between the $S_i$'s, we require that

$$\partial F(\mathbf{S})/\partial S_i > 0.$$ (3)

In addition, a plant cannot experience a negative reproductive success; thus, for all $i$,

$$S_i \geq 0.$$ (4)

In addition to permitting the evolution of the vector $\mathbf{S}$, we will permit the proportion of the seed bank that germinates ($G$) to be an evolutionary parameter whose evolutionary constraint set is the closed interval $[0,1]$.

We define fitness in the Malthusian sense of survival and fecundity. Since fitness is multiplicative over time, the geometric mean of annual fitness is the appropriate fitness criterion in temporally variable environments. Annual fitness

takes into consideration the probability of germination ($G$) and the expected reproductive success of germinating seedlings ($S_i$), as well as the probability that a seed remaining dormant for an additional year will survive until the next germination season ($R$). We can write the geometric mean of annual fitness, $W$, as follows:

$$W = \prod_{i=1}^{n} [GS_i + R(1 - G)]^{p_i}. \tag{5}$$

Throughout this paper, expressions (1)–(5) define the model, where the fitness formula (5) is the objective function and expressions (1)–(4) and $G \in [0,1]$ are the constraints.

### Relationship to Previous Models

This model reduces to an approximation of the Templeton and Levin model if we fix the germination fraction, $G$, and provide a constraint set consisting of three reproductive schedules (**S** vectors) corresponding to the two homozygote and the heterozygote genotypes generated by a single-locus diallelic genetic system. Templeton and Levin's model determines which fitness vector maximizes expression (5).

Our model reduces to Cohen's (1966) model when the vector of reproductive successes, **S**, is held constant. The necessary and sufficient conditions for the evolution of a seed bank are

$$\partial W/\partial G\big|_{G=0} > 0 \tag{6a}$$

$$\partial W/\partial G\big|_{G=1} < 0. \tag{6b}$$

The derivative of $W$ (from eq. 5) with respect to $G$ is

$$\frac{\partial W}{\partial G} = W \sum_{i=1}^{n} \frac{p_i(S_i - R)}{GS_i + R(1 - G)}. \tag{7}$$

Substituting equation (7) into equations (6) gives the conditions for the evolution of a seed bank (Cohen 1966):

$$\sum_{i=1}^{n} p_i S_i > R \tag{8a}$$

$$1\bigg/\sum_{i=1}^{n} (p_i/S_i) < R. \tag{8b}$$

For $G \in (0,1)$ it is necessary and sufficient that the arithmetic mean of the reproductive successes be greater than the probability of surviving for one year in the seed bank, $R$, and that the harmonic mean of the reproductive successes be less then $R$ (Cohen's result, 1966). Condition (8a) ensures that perpetual dormancy is not optimal, and condition (8b) ensures that 100% germination is not optimal. The harmonic mean is reduced relative to the arithmetic mean when variation among the $S_i$'s is large and variance among the $p_i$'s is small, that is, when

the different year types are more equiprobable and reproductive success in different year types is variable. Note that year types with a reproductive success of zero are not necessary but are sufficient for the evolution of a seed bank.

### Fitness Maximization

What happens if both the S vector and the germination fraction, $G$, are permitted to evolve? We use a Lagrange function to maximize fitness (eq. 5), subject to the constraints (1)–(4). The Lagrange function is

$$L = W - \lambda F(\mathbf{S}) - \mu_1(1 - G) - \mu_2 G - \sum_{i=1}^{n} \delta_i S_i,$$

where $\lambda$ is the Lagrange multiplier for the equality constraint (2), $\mu_1$ and $\mu_2$ are the multipliers for the inequality constraints requiring $G \in [0,1]$, and $\delta_i$'s are the multipliers for the inequality constraint (4) for $i = 1, \ldots, n$.

The necessary conditions for maximizing $W$ are

$$\partial L/\partial S_i = \partial W/\partial S_i - \lambda (\partial F/\partial S_i) - \delta_i = 0$$

$$\partial L/\partial G = \partial W/\partial G + \mu_1 - \mu_2 = 0$$

$$\partial L/\partial \lambda = -F(\mathbf{S}) = 0$$

$$(1 - G) \geq 0 \quad \text{and} \quad G \geq 0 \tag{9}$$

$$S_i \geq 0$$

$$\mu_1 \geq 0 \quad \text{and} \quad \mu_2 \geq 0$$

$$\delta_i \geq 0,$$

where $i = 1, \ldots, n$.

When the solution is interior (i.e., $G \in (0,1)$ and $S_i > 0$ for all $i$), then all the Lagrange multipliers for the inequality constraints equal zero and the necessary conditions for maximizing $W$ reduce from conditions (9) to

$$\partial W/\partial S_i = \lambda \partial F(\mathbf{S})/\partial S_i \tag{10a}$$

$$\partial W/\partial G = 0 \tag{10b}$$

$$F(\mathbf{S}) = 0, \tag{10c}$$

for all $i = 1, \ldots, n$.

### Graphical Representation

The fitness-maximizing solution can be represented graphically using the fitness-set approach of Levins (1968). Rearranging equation (10a) gives

$$(\partial W/\partial S_i) / (\partial F/\partial S_i) = \lambda \tag{11}$$

for $i = 1, \ldots, n$.

Since equation (11) holds for all year types, we can compare any two year types by combining expression (11) for arbitrary year types $i$ and $j$. This modifies the
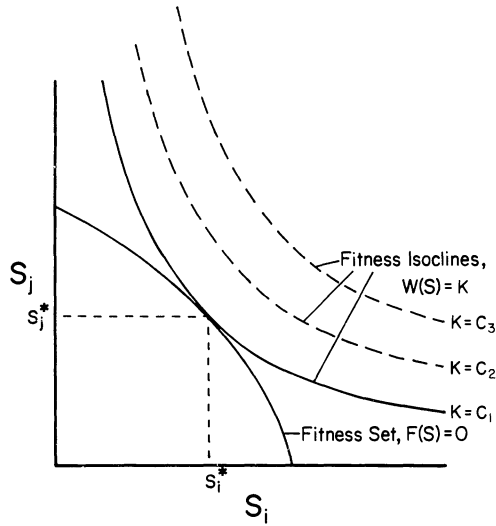
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FIG. 1.—A graphical presentation of the evolutionary constraint on reproductive successes given germination in two different kinds of years, $i$ and $j$. The negative slope of the constraint function implies a trade-off, such that adaptations increasing reproductive success in one year type lower reproductive success in the other. Several fitness isopleths are plotted as dashed lines. The solid fitness isopleth is tangent to the constraint function, and $S_i^*$ and $S_j^*$ are the pair of evolutionarily feasible reproductive successes that yields highest fitness.

necessary condition for maximizing $W$ to

$$-(\partial W/\partial S_i) \,/\, (\partial W/\partial S_j) \;=\; -(\partial F/\partial S_i) \,/\, (\partial F/\partial S_j) \tag{12}$$

for all $i, j = 1, \ldots , n$.

A graphical representation of the optimal values for $S_i$ and $S_j$ can be constructed from expression (12). In accordance with the implicit-function rule, the right-hand term is equal to the slope of the constraint function, $F(\mathbf{S})$, when $S_j$ is plotted against $S_i$ (fig. 1), and the left-hand term is the slope of the fitness isopleths (lines of equal fitness) in this same space. Fitness is maximized at the point of tangency between the constraint function and a fitness isopleth.

Since we are assuming that there exist trade-offs among fitnesses in different year types, the constraint function will always have a negative slope (condition 3). There are no restrictions on whether the constraint function is convex or concave to the origin. Because we are considering temporal variation and because the geometric mean of fitnesses is the objective function, the fitness isopleths will always be concave to the origin (see Levins 1968).

When the constraint function is convex to the origin, the optimal value of $\mathbf{S}$ will be interior and conditions (10) are the necessary conditions. When the constraint function is concave to the origin, there may be either an interior solution or a corner solution, depending on the relative concavity of the constraint function and fitness isopleths. A corner solution obtains with $S_j = 0$ for some $j$ when the constraint function is more concave than the fitness isopleths.

Taking the derivatives of fitness, equation (5), with respect to $S_i$ and $S_j$ and substituting them into the left side of necessary condition (12) gives an explicit expression for the slope of the fitness isopleth, which we call $g$ $(\mathbf{p}, R, \mathbf{S}, G)$ or $g(\cdot)$,

$$g\ (\mathbf{p},R,\mathbf{S},G) = \frac{-p_i[GS_j + R(1 - G)]}{p_j[GS_i + R(1 - G)]} \ . \tag{13}$$

According to expression (12), fitness is maximized at the point where the slope of the fitness isopleth equals the slope of the constraint function. Maximum fitness occurs at the point where the fitness isopleth is tangent to the constraint function (fig. 1).

We have developed the model and determined the necessary conditions for maximizing $W$. In the following section we examine the evolutionary relationship of the reproductive schedule, $\mathbf{S}$, and the germination fraction, $G$, to changes in the frequency of year types, $\mathbf{p}$, and changes in the probability of surviving in the seed bank, $R$.

<center>EVOLUTIONARY RELATIONSHIPS</center>

The germination fraction and the reproductive schedule that maximize fitness, $G^*$ and $\mathbf{S}^*$, are functions of each other, of the probability of the occurrence of different year types, and of the probability of survival in the seed bank. We first examine the direct (or independent) effect of changing $\mathbf{S}$, $\mathbf{p}$, or $R$ on $G^*$ and the direct effect of changing $G$, $\mathbf{p}$, or $R$ on $\mathbf{S}^*$. We then examine the total effect on $G^*$ and $\mathbf{S}^*$ of changing $\mathbf{p}$ and $R$. A comparative static analysis is used to determine qualitative effects. It is assumed that $G^* \in (0,1)$ and that $S_i^* > 0$ for all $i$; that is, we assume an interior solution.

We use "specialization" in the special sense of increasing the variance in $\mathbf{S}$ by the evolution of higher reproductive success in years that already have high $S_i$'s at the expense of reproductive success in years that already have low $S_i$'s. Less specialization means an increase in low $S_i$'s and a decrease in high $S_i$'s. Also, changes in the probabilities of year types ($p_i$) are called "changes in the environment."

### The Effect on Between-Year Dormancy of Changing the Environment and Changing Seed-Bank Mortality

For a given set of probabilities of year types, reproductive schedule, and probability of surviving in the seed bank, the optimal germination fraction, $G^*$, is found by setting equation (7) equal to zero. Thus, $G^*$ satisfies

$$\sum_{i=1}^{n} \frac{p_i(S_i - R)}{GS_i + R(1 - G)} = 0 \ . \tag{14}$$

To determine the effect on the optimal germination fraction of increasing the probability of year type $i$ at the expense of year type $j$, take the derivative of expression (14) with respect to $p_i$ where $dp_j/dp_i = -1$:

$$\frac{S_i - S_j}{[GS_i + R(1 - G)] [GS_j + R(1 - G)]} \ . \tag{15}$$

When $S_i > S_j$, expression (15) is positive, which implies that $\partial W/\partial G > 0$ at the old $G^*$. Thus, the germination fraction must increase to maximize $W$. This result repeats that of Cohen (1966), showing that an increase in the probability of a good year at the expense of a poor one selects for an increase in the germination fraction. Likewise, a decrease in the probability of a good year selects for a decrease in the germination fraction.

The effect of seed-bank survival, $R$, on $G^*$ can be found in a similar fashion. By taking the derivative of equation (14) with respect to $R$, one recovers another result of Cohen (1966): an increase in the probability of survival in the seed bank selects for a decrease in the optimal germination fraction.

### The Effect of Specialization on Between-Year Dormancy

To determine the effect of an evolutionary change that increases reproductive success in year type $i$ at the expense of reproductive success in year type $j$, take the derivative of expression (14) with respect to $S_i$:

$$
\frac{p_i[GS_i + R(1 - G)] - p_iG(S_i - R)}{[GS_i + R(1 - G)]^2} \tag{16}
$$
$$
+ \frac{p_j(\partial S_j/\partial S_i) [GS_i + R(1 - G)] - p_jG(\partial S_j/\partial S_i) (S_j - R)}{[GS_j + R(1 - G)]^2} .
$$

If we assume that the reproductive schedule $\mathbf{S}$ is very near $\mathbf{S}^*$, then $\partial S_j/\partial S_i$ is approximately equal to $g(\cdot)$. Substituting $g(\cdot)$ from expression (13) into (16) gives

$$
\frac{p_iG(S_j - S_i)}{[GS_i + R(1 - G)]^2 [GS_j + R(1 - G)]} .
$$

If $S_i > S_j$, then $\partial W/\partial G < 0$. Thus, when $S_i > S_j$, increasing $S_i$ and decreasing $S_j$ (increased specialization on good years) selects for a decrease in the germination fraction. When $S_i < S_j$, increasing $S_i$ selects for an increase in the germination fraction.

### The Effect of Dormancy on Specialization

Consider the effect on $\mathbf{S}^*$ of changing the germination fraction, $G$. If $\mathbf{p}$, $G$, and $R$ are fixed, the optimal reproductive schedule, $\mathbf{S}^*$, satisfies expression (12) for all $i$ and $j$. Recall that the left-hand side of (12) is $g(\cdot)$ in equation (13), and notice that the right-hand side of (12) is only a function of $\mathbf{S}$ and is independent of $G$, $\mathbf{p}$, and $R$. The derivative of $g(\cdot)$ with respect to $G$ is

$$
\frac{\partial g(\cdot)}{\partial G} = \frac{p_i(S_i - S_j)}{p_j [GS_i + R(1 - G)]^2} . \tag{17}
$$

When $S_i > S_j$, then (17) is positive and the effect of increasing $G$ is to make $g(\cdot)$ less negative. At the old optimum $\mathbf{S}^*$ the fitness isopleth is less negatively sloped, and in effect all fitness isopleths rotate counterclockwise. The new optimum is achieved higher up on the constraint function, and $S_i^*$ decreases relative to $S_j^*$ (fig. 2). When $S_i < S_j$, an increase in $G$ results in a clockwise shift of isopleths and an increase in $S_i^*$ relative to $S_j^*$.
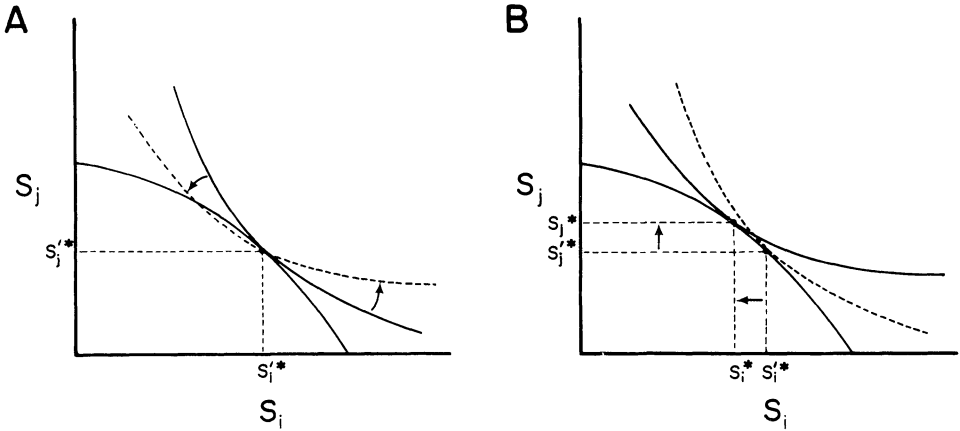
Fig. 2.—The effect of decreasing the between-year seed bank (i.e., increasing $G$) on specialization to year types $i$ and $j$. The original fitness isopleth (the solid curve in A and the dashed curve in B) shows that $S_i'^*$ and $S_j'^*$ are the optimal reproductive successes. When $S_i'^* > S_j'^*$, the increase in $G$ causes the fitness isopleths to rotate counterclockwise (the dashed curve in A). The new isopleth, which is tangent to the constraint function (solid curve in B), results in a new equilibrium, $S_i^*, S_j^*$, which is more specialized to the worse year type, $j$.

Templeton and Levin showed that allowing the germination fraction to shift from a value of one to some lesser value results in the evolution of increased reproductive success during good years and lowered reproductive success during bad years. We generalize their result by showing that a decrease in the germination fraction selects for greater specialization to good years.

### The Effect on Specialization of Changing the Environment

To determine the effect of changing the probability of year type $i$ at the expense of year type $j$, take the derivative of $g(\cdot)$ with respect to $p_i$ where $dp_j/dp_i = -1$:

$$\frac{\partial g(\cdot)}{\partial p_i} = \frac{-(p_i + p_j)\,[GS_j + R(1 - G)]}{p_j^2[GS_i + R(1 - G)]}. \tag{18}$$

Expression (18) is always negative, which means that $g(\cdot)$ becomes more negative. The result is to rotate the fitness isopleths in a clockwise direction. Increasing the probability of year type $i$ increases $S_i^*$ relative to $S_j^*$. Thus, as any year type becomes more frequent, plants tend to specialize more on it, whether it is a good or bad year type.

### The Effect on Specialization of Seed-Bank Mortality

To determine the effect on $S^*$ of changing the probability of survival in the seed bank, take the derivative of $g(\cdot)$ with respect to $R$:

$$\frac{\partial g(\cdot)}{\partial R} = \frac{p_i G(1 - G)\,(S_j - S_i)}{p_j[GS_i + R(1 - G)]^2}. \tag{19}$$

If $S_i > S_j$, expression (19) is negative, and as $R$ increases, $g(\cdot)$ becomes more negative. An increase in $R$ results in a clockwise rotation of fitness isopleths and in
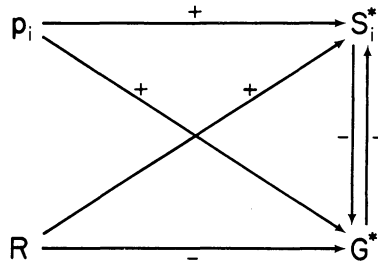
Fig. 3.—Summary of the ecological and evolutionary relationships predicted by the model. An arrow indicates the effect of one parameter on another. + indicates that an increase in the value of one parameter selects for an increase in the value of another parameter; − indicates the opposite effect, decreasing the parameter. $p_i$ is the probability of year type $i$ (year type $i$ increases at the expense of year type $j$, $dp_j/dp_i = -1$, and $i$ is the better year type, $S_i^* > S_j^*$); $G^*$, the optimal germination fraction; $S_i^*$, the optimal reproductive success given germination in year type $i$ ($S_i$ increases at the expense of $S_j$); $R$, the probability that a seed remaining dormant will survive until the next growing season.

an increase of $S_i^*$ relative to $S_j^*$. In other words, greater survival of the between-year seed bank favors specialization to good years.

### Summary of Direct Effects

The results of the comparative statics analysis can be summarized as follows (fig. 3). The objective function maximized by natural selection is the geometric mean of annual fitness. The geometric mean is sensitive to both the expected annual fitness (arithmetic mean) and the variance in annual fitness (Gillespie 1977). Both increasing the expected annual fitness and decreasing the variance in annual fitness increase $W$. Increasing the germination fraction increases the variance in annual fitness, which will select for less specialization to good years (decreasing the variance). Similarly, increasing specialization to good years increases the variance in reproductive success and selects for a decrease in the germination fraction.

Changing the environment selects for greater reproductive success in those year types that increase in frequency, regardless of whether the years are good or bad. As the proportion of good years increases, the plant misses better opportunities by remaining dormant, and so the germination fraction increases. The probability of survival in the seed bank determines the value of staying dormant relative to germinating. A greater survival of seeds in the seed bank enhances the fitness contribution of dormant seeds, which selects for a decrease in the germination fraction. A greater survival of seeds in the seed bank also increases the overlap of generations. This magnifies the impact of good years on $W$ and selects for specialization to good years.

### Direct and Indirect Effects of Changing the Environment and Changing Seed-Bank Survival

The total effect of changing the probability of year types, **p**, or the probability of survival in the seed bank, $R$, on the germination fraction, $G$, and the reproductive

schedule, **S**, includes both direct and indirect effects. The direct and indirect effects of changing $R$ on the optimal values of $G$ and **S** are reinforcing (fig. 3). The direct effect of an increase in $R$ is a decrease in $G$ and increased specialization on good years. As an indirect effect, the decrease in $G$ further encourages increased specialization to good years, and the increased specialization to good years reinforces the evolution of a lower $G$.

The direct and indirect effects on $G$ and **S** of changing **p** have opposite signs. The direct effect of increasing the probability of a good year is to increase $G$ and to increase the specialization to good years. The increase in $G$, however, selects for less specialization to the good years, and the specialization to good years selects for a decrease in $G$. Likewise, increasing the probability of a bad year has opposite direct and indirect effects. What is the net result of these opposing selective pressures?

To examine the direct and indirect effects of changing $p_i$ on the reproductive schedule, **S**, take the total derivative of $g(\cdot)$, where $G$ is a function of **p** and $dp_j/dp_i = -1$:

$$\frac{dg(\cdot)}{dp_i} = \frac{-(p_i + p_j)\,[GS_j + R(1 - G)]}{p_j^2[GS_i + R(1 - G)]} - \frac{p_i(\partial G/\partial p_i)\,(S_j - S_i)}{p_j[GS_i + R(1 - G)]^2} . \quad (20)$$

The first term on the right side of the equation is the direct effect on **S** of changing $p_i$, and it is equal to expression (18). The second term is the indirect effect, and it is given by $[\partial g/\partial G]\,[\partial G/\partial p_i]$ where $\partial g/\partial G$ is given by expression (17). The direct effect is always negative. The indirect effect is always positive, since $\partial g/\partial G$ and $\partial G/\partial p_i$ always have the same sign. When $S_i > S_j$, recall that $\partial g/\partial G$ is positive and $\partial G/\partial p_i$ is positive. When $S_i < S_j$, then both $\partial g/\partial G$ and $\partial G/\partial p_i$ are negative.

We now examine the effect of changing the probabilities of year types for a simplified case in which there are only two year types, whose probabilities of occurrence are $p$ and $(1 - p)$. The fitness criterion is given by

$$W = (GS_1 + 1 - G)^p \, (GS_2 + 1 - G)^{(1-p)} ,$$

where $S_1$ and $S_2$ are the reproductive successes in the two year types, and for convenience the seed survival, $R$, equals 1.

The optimal value for $G$ is

$$G^* = \frac{-(1 - p)\,(S_2 - 1) - p(S_1 - 1)}{(S_1 - 1)\,(S_2 - 1)} , \quad (21)$$

and

$$\frac{dG^*}{dp} = \frac{S_2 - S_1}{(S_1 - 1)\,(S_2 - 1)} . \quad (22)$$

From expression (20) the derivative of $g(\cdot)$ with respect to $p$ is

$$\frac{dg(\cdot)}{dp} = \frac{-[GS_1 + 1 - G]\,[GS_2 + 1 - G] - p(1 - p)\,(dG/dp)\,(S_2 - S_1)}{(1 - p)^2\,[GS_1 + 1 - G]^2} .$$

$$(23)$$

If we substitute expression (21) for $G$ and (22) for $dG/dp$ and reduce, expression (23) equals zero, $dg/dp = 0$. Thus, if there are only two year types, changes in the vector of reproductive successes are not favored by changes in the probabilities of year types. The effect of changing $p$ is completely absorbed by a change in the germination fraction. If the germination fraction is fixed, then changing $p$ selects for a change in the degree of specialization; but if $G$ is allowed to vary on the open interval $(0,1)$, then the reproductive success during different year types remains fixed over a range of environmental qualities.

When there are many types of years, it is generally not the case that the change in the germination fraction is sufficient to cancel any changes in the reproductive schedule. The change in the $S$ vector is more complex when there are many year types. As one moves along an environmental gradient, there is a tendency to decrease the probabilities of bad years, to increase the probabilities of good years, and to rearrange the probabilities of intermediate years. Such a shift in year types selects for an increase in the germination fraction with either little or no change in the degree of specialization. (For a more involved discussion of possible climatic variations in arid regions, see Westoby 1980.)

Under what circumstance does a change in the proportion of year types select for a shift in specialization but virtually no shift in the germination fraction? Cohen (1966) has shown that the optimal germination fraction is most affected by the probabilities of year types in which $S_j$ is close to zero. The optimal germination fraction is approximately equal to the sum of the probabilities of those year types where $S_j \ll 1$. If, in moving along an environmental gradient, the proportion of catastrophic years where $S_j \ll 1$ remains essentially unchanged, then the evolutionary response to changing $p_i$ is to adjust the reproductive schedule with very little change in the germination fraction.

In our model, changes in the reproductive schedule and germination fraction occur simultaneously, but this may not necessarily be the case in nature. Since in this model natural selection is the mechanism of evolution, the rate of evolution is influenced by the availability of heritable variation and the rate at which genetically feasible phenotypes occur in the population. If the germination fraction can evolve rapidly in response to changes in the probabilities of different year types, then we do not expect to see changes in specialization in the range $G \in (0,1)$. If dormancy changes relatively slowly, we expect specialization to frequent year types, at least initially. Notice that since the frequency of different year types is the driving force behind the evolution of a seed bank, we always expect conditions that favor a change in specialization to favor a change in dormancy if the optimal germination fraction is on the open interval $(0,1)$.

DISCUSSION

Our model permits simultaneous consideration of selection for between-year dormancy and specialization to conditions pertaining in different years for annual plants in temporally variable environments. In such environments, fitness is a function of both the mean and the temporal variance in annual fitness. If heritable variation exists for both the seed-bank behavior and the traits affecting year-type

specialization, then greater flexibility exists for adjusting the mean and variance of annual fitness.

We use this approach to predict the selective effects on the between-year dormancy and specialization of changes in environmental quality (changes that affect the survival and reproductive success of germinated seeds, and changes that affect the seed-bank survival). When the environment changes and a particular kind of year becomes more frequent, the resulting changes in the seed bank and specialization have a damping effect on each other. The net result is that neither between-year dormancy nor the degree of specialization changes as much as predicted by models considering the evolution of only one or the other of these. Relatively more change occurs in seed-bank dynamics than in the non-seed-bank trait if the environmental changes affect the proportion of year types in which reproductive success is low. Post-germination traits may change more if only the relative frequencies of high-yielding years change.

When the survival of seeds in the soil changes, the resulting changes in dormancy and specialization to different year types have amplifying effects on each other. Thus, environmentally induced changes in seed-bank survival should result in more-dramatic evolutionary shifts in dormancy and specialization than environmental changes affecting the survival and fecundity of plants once germinated.

In this model we have treated the S vector abstractly. Recall that S is the expected reproductive success of germinating seeds in different year types. This general framework permits the exploration of a number of particular traits that have been treated in other models. To explore the evolution of a particular trait or set of traits, one must specify how variation in the trait changes the S vector. When several traits are treated simultaneously, one might also wish to specify the possible kinds of covariation among traits. For illustration, we have compared mesophytic and xerophytic leaf anatomy.

Other traits that could readily be modeled in our framework include root-to-shoot ratios, the temporal schedule of reproductive allocation, and some pre-germination traits like seed size versus number or the within-year timing of germination. High root-to-shoot ratios are likely to be favored in dry years (giving rise to low mean and variance of S) and low root-to-shoot ratios should be favored in wet years (high mean and variance of S). So-called "bang-bang" reproduction might be favored in years with a reliably long wet season, whereas simultaneous allocation to reproduction and vegetative growth might be favored in years with a short wet season (Cohen 1971). A few large seeds might result in a lower mean and variance of S, since few are produced but they are able to sink deep roots before exposing seed leaves to the desiccating effects of transpiration (Baker 1972). Producing many small seeds might result in high yields in wet years but low yields in dry years. Early germination, before the onset of the favorable growth season, may be associated with higher mortality risks but also higher potential fecundities in favorable years because plants have a head start on competitors and have longer to grow (Venable 1984). Later germination may guarantee some reproductive success in all or most year types, while sacrificing the opportunity for high reproductive success in good years.

It is not our intent to make precise predictions about how each of these traits is

likely to evolve, but rather to suggest that the evolution of any of them could be addressed within the framework of this model. What is required in any specific case is some theoretical or empirical model that tells us how variation in the trait maps onto variation in $S$ (e.g., where do various root-to-shoot ratios map onto $F(S)$ in figs. 1 and 2?). Then, our model predicts how the trait should evolve in a seed-bank annual in a temporally varying environment.

The model is more realistic for some kinds of annual plants than for others. The assumptions of the model are most reasonably approximated in annuals of permanently open habitats where environmental quality varies more or less randomly in time. The habitat of early-successional annuals originates by way of a disturbance that may be variable and unpredictable in time. Subsequently, as succession proceeds, a predictable and temporally autocorrelated decline in habitat quality occurs. Post-fire annuals and annuals of old-field succession fit this scheme, and our model is probably not well suited to these. If, however, the disturbances occur frequently and succession does not proceed without interruption for more than a few years, conditions approach those considered in the model. The model should apply reasonably well to desert annuals; annuals of gaps in trampled, grazed pastures; annuals of the more frequently flooded portions of floodplains, lakesides, and mud flats (e.g., Menges and Waller 1983); and arable weeds receiving frequent but variable weeding, herbicide application, or plowing. The model should also be applicable to sand-dune annuals of the seashore, but some evidence suggests that their niches and the corresponding model parameters may not reach the threshold at which the evolution of a seed bank is favored (Watkinson 1981; Westoby 1981).

What are real $S$ vectors like and how can they be measured? How is a year specialist distinguished from a year generalist? The mean reproductive success of germinated seedlings for a representative set of year types could be used to measure the $S$ vector. In the absence of long-term data, we suggest three approaches. First, spatial variation in reproductive success could be measured for sites that in one or a few years experience environmental variation representative of the temporal variation at a single site. Second, based on the reproductive success of a few years and on long-term weather data, an estimate of the distribution of $S$ could be reconstructed. Third, a range of variation mimicking normal temporal variation could be experimentally reconstructed and the demographic consequences measured. The latter approach would be particularly useful in determining year-type specialists versus generalists, perhaps by growing plants along an experimental environmental gradient (e.g., Pickett and Bazzaz 1976).

$S$ vectors can be characterized by their mean and variance. Along an environmental gradient of habitat quality, the probability of the occurrence of different year types changes, and some year types drop out while others are added. Environmental deterioration is reflected in either a lower mean or a higher variance in $S$. The model suggests that, as the environment deteriorates, annual plants adapt through changes in non-seed-bank traits until conditions become sufficiently bad (harmonic mean of reproductive successes in different years becomes less than the survival of dormant seeds). At this point a seed-bank strategy is favored. Once this "seed-bank threshold" is crossed, further adaptation should occur

primarily through changes in seed-bank dynamics. The seed bank permits evolutionary specialization on a better-than-average subset of the year types encountered.

The transient dynamics for a given species depend on the relative ease of evolutionarily adjusting dormancy and non-seed-bank traits and on the proximate mechanisms involved. For example, post-germination xerophytic adaptations—such as increased hairiness, thickened cuticles, reduced leaf surface-to-volume ratio, and higher root-to-shoot ratio—might respond rapidly to selection, whereas succulence and $C_4$ metabolism or other special physiological traits may require adaptive innovations less readily achieved. Similarly, changes in dormancy might be readily achieved by changes in seed-coat thickness or by changes in the level or leachability of germination inhibitors. Concomitant changes in the levels of defensive compounds might also be required to ensure seed survival. If some sort of dormancy mechanism (perhaps for the within-year timing of germination) is already in operation, between-year dormancy might be readily achieved by merely intensifying the mechanism. If no innate dormancy exists, however, an initial adaptive innovation may be required to achieve a seed bank. The model does not explicitly address the relative rates of adaptation among traits or the origin of adaptive breakthroughs that yield new constraint functions. The latter could be investigated by comparing equilibrium life histories for the old and new constraints. For example, if a large-seeded species cannot adequately defend seeds from predators and pathogens, a seed bank may not be a viable option (low $R$). In this case, a population continues to respond to a deteriorating environment by year-type specialization. If some adaptive innovation in defensive chemistry subsequently permitted the evolution of a seed bank, rapid reequilibration would be expected, with a shift in specialization toward the better year types and an optimal adjustment of the seed bank.

If plants can vary between-year dormancy depending on the year type, an additional level of flexibility for adjusting mean annual fitness and variance is attained. This model has not directly addressed the issue of predictive dormancy; yet many annuals are known to produce seeds with predictive-dormancy strategies (Mayer and Poljakoff-Mayber 1975; Venable and Lawlor 1980). To the extent that predictive dormancy is successful, the germination fraction should be higher in years with a high intrinsic rate of growth and lower in years with a lower growth rate. Predictive dormancy favors less innate dormancy (Venable and Lawlor 1980), which by itself should decrease the level of specialization to good years. Successful predictions of year type, however, should increase the experience of good years relative to bad, which favors specialization to good years. The actual outcome of predictive dormancy for specialization depends on the net result of the direct effect, through changing the experience of good and bad years, and the indirect effect, through an evolutionary reduction of innate dormancy.

We can make several conclusions and predictions.

1. This model combines the approach of Cohen (1966) with that of Templeton and Levin (1979) in a way that allows suites of interacting traits to respond to natural selection.

2. A variety of problems addressed elsewhere can be incorporated into the

model's framework. In addition to seed-bank evolution, these include temporal schedules of reproductive allocation, root-to-shoot ratios, mesophytic versus xerophytic leaf structure, and seed size versus number.

3. The predictions of Cohen and of Templeton and Levin are magnified in some cases and reduced in others when direct and indirect evolutionary effects are considered simultaneously.

4. As the environment becomes less "favorable," in the sense of expected survival and reproduction, plants should initially adapt by means of changes in non-seed-bank traits until a "seed-bank threshold" is crossed, at which point the environment is tracked by the dormancy strategy.

5. Little ecotypic differentiation of root-to-shoot ratios, xerophytic leaf anatomy, etc., is expected along aridity gradients for seed-bank annuals, though it would be expected for non-seed-bank annuals.

6. Seed-bank annuals should have more "mesic" traits than non-seed-bank annuals in the same habitat.

7. Small differences in the survival of the between-year seed bank should select for large differences in between-year dormancy and specialization of non-seed-bank traits.

SUMMARY

The production of long-lived seeds by annual plants introduces a unique form of age structure. In a temporally varying environment the dormant seed may experience many years with different weather, whereas the germinating individual experiences only the weather conditions of a single growing season. Natural selection operates on both the between-year dormancy and on non-seed-bank traits that affect the degree of specialization to conditions pertaining in different year types. We have used an integrated model that permits these two aspects of the life history to evolve simultaneously. This leads to predictions that are not attainable by considering the evolution of each in isolation. Changes in the survival probability of the between-year seed bank select for reinforcing changes in between-year dormancy and specialization. Changes in the probability of occurrence of different year types select for damping changes in between-year dormancy and specialization. Across a gradient in environmental quality, we predict that most change will occur in between-year dormancy, with little change in specialization. If between-year dormancy is fixed, however, a greater change in specialization should occur. The predictions of the model are discussed in terms of environmental gradients, seed-bank versus non-seed-bank annuals, and a variety of plant traits modeled elsewhere that may be involved in specialization to different types of years.

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