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DELAYED GERMINATION OF SEEDS: A LOOK AT THE EFFECTS OF ADULT LONGEVITY, THE TIMING OF REPRODUCTION, AND POPULATION AGE/STAGE STRUCTURE

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Abstract.—The effects of adult longevity, the timing of reproduction, and population age/stage structure on the evolution of seed dormancy are explored in both constant and variable environment models. In the constant environment models complete germination is the evolutionarily stable strategy (ESS) regardless of adult longevity. Incorporating a cost of reproduction on subsequent survival does not alter this result. In contrast, in a variable environment changes in adult longevity can exert a strong selection pressure against seed dormancy. Incorporating a cost of reproduction for iteroparous species reduces adult longevity, which selects for more seed dormancy. The magnitude of the change in ESS germination probability depends on several factors, including which life-history stage is variable (e.g., fecundity, seedling survival), whether seeds can detect favorable sites for establishment, and the age/stage structure of the population. In general, increases in adult longevity select against seed dormancy, but exceptions to this pattern are discussed. The idea that established plant traits are uncoupled from those of the regenerative phase, as assumed by J. P. Grime's competition-stress-ruderal model, is considered critically.

All environments vary, and organisms exploiting them must develop adaptations for dealing with fluctuations in favorability or become extinct. Life-history theory has demonstrated that seed dormancy, dispersal, and iteroparity may evolve in response to environmental uncertainty (Cohen 1966; Bulmer 1984, 1985; Goodman 1984; Ellner 1985*a*, 1985*b;* Venable and Brown 1988; Cohen and Levin 1991). Consider the simple case in which seeds have no information on the quality of the environment, which varies so that in some years the conditions are suitable for reproduction, whereas in others reproduction fails completely. In such an environment an annual plant genotype with no seed dormancy would maximize its arithmetic average population growth rate but become extinct the first year reproduction failed. A genotype that never germinated would also become extinct as a result of seed mortality. Hence, in a variable environment we would expect an intermediate germination strategy to be optimal (Cohen 1966). Cohen also demonstrated that, if the per capita seed production is large, the optimal germination fraction is approximately equal to the probability of successful reproduction. This result can be understood as a bet-hedging strategy (Stearns 1976; Seger and

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Brockman 1987); seed dormancy spreads the risk of germination over time, which becomes more advantageous the higher the frequency of bad years.

A few theoretical studies have considered the joint evolution of several life-history traits (Bulmer 1984; Levin et al. 1984; Venable and Brown 1988). Venable and Brown (1988) examined the selective interactions among seed size, dormancy, and dispersal and predicted that trade-offs should exist between each of the variables. These arise because an increase in any one of the variables reduces the realized variance in environmental quality, thus selecting for a reduction in the other two.

Several authors have considered, using verbal arguments, the effect of adult longevity on the evolution of seed dormancy. Stebbins (1950) suggested that annuals live in more unstable habitats than perennials and this selects for increased dormancy. This argument has been dismissed by others (Cook 1980) because there is no a priori reason "unstable" early successional habitats are any more unpredictable for seedling establishment than later successional "stable" habitats. For example, after a disturbance a species of annual and a species of perennial grasses would both be able to recruit successfully from seed. However, in those years when there is no disturbance to remove established plants, neither will be able to recruit from seed. Thus, both species experience the same probability of successful recruitment, and if Cohen's results can be applied, each species should have the same probability of germination. It has also been argued that, because seedling establishment rarely occurs in the vicinity of long-lived species, "this, of course, favours further reductions in sexual reproduction, as well as increased dispersal and/or dormancy" (Waller 1988, p. 221). Hence, long-lived species should have more, not less, dormancy than short-lived species. Thompson suggested that, because perennials have larger seeds and these are more easily found by herbivores, the cost of forming a seed bank in perennial species is greater and this selects against seed dormancy (Thompson 1987). Finally, it has also been asserted that adult and juvenile traits are uncoupled, and thus changes in adult longevity should have no effect on seed dormancy (Grime 1979). Thus, it is clear there is no consensus on the effect of adult longevity on the evolution of dormancy.

Here I explore how adult longevity, the timing of reproduction, and population age/stage structure influence the evolution of seed dormancy. I do this by developing a series of models, first in a constant and then in a random environment. In each environment two broad classes of model are presented: in the first the probability of flowering is independent of adult age, whereas in the second the probability of flowering is age-dependent, being concentrated in a single age class, as in some monocarpic species. In the random environment models the effects on the evolutionarily stable strategy (ESS) germination fraction of variability in adult fecundity and seedling survival are considered initially. The models are then extended to allow temporal variation in adult survival and differences in seed germination in occupied and unoccupied microsites. The technique used is to find a germination probability that is an ESS, in the sense that it is uninvadable by rare mutants with different germination behaviors. I use the term "seed dormancy" to indicate that germination is spread across years and that seeds do not

germinate even though it is possible. The models presented address the question, Given that all seeds have the ability to germinate, what is the ESS germination fraction? The assumptions underlying the ESS approach have been discussed by several authors (Maynard Smith 1982; Cressman and Hines 1984; Ellner 1985a, 1985b).

All the models presented follow both the number of established adults, N, and the number of seeds, S. The simplest model assumes there are K microsites, each capable of supporting a single adult. A fraction P_a adults survive from one year to the next. In those microsites where adults have died, recruitment occurs as a result of a fair lottery between seedlings. Models of this general form have been widely used in studies of competition (e.g., Chesson 1982; Comins and Noble 1985). A population model for the ith strategy incorporating these assumptions has the following form:

$$S_{t+1,i} = P_s(1 - g_i)S_{t,i} + F\left[\left(K - P_a\sum_h N_{t,h}\right)\left(g_i S_{t,i}\bigg/\sum_h g_h S_{t,h}\right) + P_a N_{t,i}\right],$$

and $\hspace{11cm}$ (1)

$$N_{t+1,i} = P_a N_{t,i} + \left(K - P_a\sum_h N_{t,h}\right)\left(g_i S_{t,i}\bigg/\sum_h g_h S_{t,h}\right),$$

where $S_{t,i}$ and $N_{t,i}$ are the numbers of seeds and established plants, respectively, at time t of strategy i; P_s is the probability of seed survival; g_i is the germination probability of the ith strategy; and F is the per capita fecundity. It is assumed that the strategies differ only in their germination probability. The seed equation has two terms; the first represents the seed bank, and the second is the current seed production from new recruits and established plants. It is assumed that seeds germinating in a microsite containing an established plant fail to establish. This assumption agrees with numerous empirical studies demonstrating that successful seedling establishment rarely occurs in the presence of established plants (Harper 1977; Fenner 1985; Rees and Brown 1991). The established plant equation also has two components, adult survival and recruitment into unoccupied microsites.

To determine the ESS germination strategy we consider the dynamics of a resident $(N_{t,1}, S_{t,1})$ and an invading strategy $(N_{t,2}, S_{t,2})$. The dynamics of the resident are given by

$$S_{t+1,1} = P_s(1 - g_1)S_{t,1} + FK \hspace{4cm} (2a)$$

and

$$N_{t+1,1} = K. \hspace{4cm} (2b)$$

The equilibrium seed bank, $\overline{S}_1$, is given as follows:

$$\overline{S}_1 = \frac{FK}{1 - P_s(1 - g_1)}. \tag{3}$$

The invader's dynamics are given by

$$S_{t+1,2} = P_s(1 - g_2)S_{t,2} + F\left[K(1 - P_a)\left(\frac{g_2 S_{t,2}}{g_1 \overline{S}_1}\right) + P_a N_{t,2}\right]$$

and $\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad$ (4)

$$N_{t+1,2} = P_a N_{t,2} + K(1 - P_a)\left(\frac{g_2 S_{t,2}}{g_1 \overline{S}_1}\right).$$

Note that because the invader is rare its density has no effect on population growth. Hence, sib-sib interactions are not included in the model and dormancy cannot evolve as a mechanism by which a parent reduces competition between its offspring (Ellner 1986). The invader's dynamics may be neatly described in matrix form,

$$n_{t+1} = Bn_t, \tag{5}$$

where

$$n_t = \begin{pmatrix} S_{t,2} \\ N_{t,2} \end{pmatrix} \tag{6}$$

and

$$B = \begin{bmatrix} P_s(1 - g_2) + FK(1 - P_a)\left(\dfrac{g_2}{g_1 \overline{S}_1}\right) & FP_a \\[2ex] K(1 - P_a)\left(\dfrac{g_2}{g_1 \overline{S}_1}\right) & P_a \end{bmatrix}. \tag{7}$$

The invader will become extinct if the dominant eigenvalue of B is less than one; otherwise the invasion will be successful and the resident will become extinct. For the invading strategy the characteristic equation, the roots of which are the eigenvalues of B, equals

$$P_a P_s(1 - g_2) - \left[\left(\frac{g_2}{g_1}\right)(1 - P_a)(1 - P_s) + P_a + P_s - g_2 P_a P_s\right]\lambda + \lambda^2 = 0. \tag{8}$$

Hence, it is straightforward to show that if the invader has the lower germin-

ation probability $(g_2 < g_1)$ then its dominant eigenvalue will be less than one providing $P_a \neq 1$ and $P_s \neq 1$. So, in a constant environment, complete germination is the ESS if there is some seed mortality and adults are not infinitely long-lived.

Costs of Reproduction

These results assume that reproduction has no effect on subsequent plant survival. However, for many species reproduction is known to reduce the probability of survival; indeed, in monocarpic plant species reproduction is invariably lethal (Law 1979; Reznick 1985; Watkinson and White 1985; Geber 1990). When discussing biennials Kelly (1985) distinguished two types: strict biennials, which only flower in their second year, and facultative biennials, which often flower in their second year but may take 3 or 4 yr. Here, I consider two types of model. In the first all plants have the same probability of flowering, P_f, and those that flower have a probability, P_{af}, of survival, whereas those that remain vegetative have a survival probability of P_{ar}. Thus, the probability of adult survival can be written as

$$P_a = P_f P_{af} + (1 - P_f) P_{ar}. \tag{9}$$

Redefining F as the average per capita fecundity of all plants in the population and using the above definition of P_a, we may reanalyze equation (1), and as before the ESS germination fraction is one. Thus, incorporating a cost of reproduction on subsequent survival has no effect on the ESS germination fraction.

In the second type of model, the life cycle has a rigid temporal sequence, as in strict biennials and some long-lived monocarpic plants, such as bamboo (Janzen 1976), and a different model structure is required. Assuming reproduction occurs at age M and all individuals that flower die, we obtain

$$S_{t+1,i} = P_s(1 - g_i)S_{t,i} + FP_a N_{t,i,M-1},$$

$$N_{t+1,i,1} = \left(K - P_a \sum_{k} \sum_{h=1}^{M-1} N_{t,k,h}\right)\left(\frac{g_i S_{t,i}}{\sum_{h} g_h S_{t,h}}\right),$$

and

$$N_{t+1,i,j} = P_a N_{t,i,j-1},$$

where $j = 2, 3, 4, \ldots, M$, $N_{t,i,j}$ is the number of individuals of strategy i of age j at time t. The other symbols are as before, except P_a is the probability of survival of the prereproductive stages. Note that in the seed equation this year's seed production is calculated from the adults aged $M - 1$; this is to ensure that the seeds produced by flowering plants this year can colonize the gaps created by postreproductive mortality. For a single strategy, providing $P_a \neq 1$ and $g_i \neq$
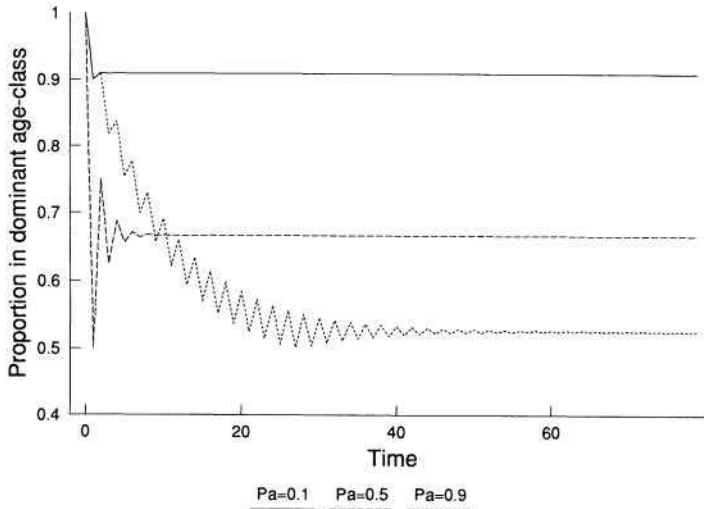
FIG. 1.—Convergence to a stable age structure for the strict biennial model. Note that, as P_a increases, the time to a convergence increases. Three values of P_a are shown; in each case the equilibrium proportion of individuals in the dominant age class equals $1/(1 + P_a)$.

1, the system rapidly converges to a stable age/stage structure (see fig. 1). The equilibrium age/stage structure of the system is expressed as

$$\overline{S} = \frac{FP_a^{M-1}(1 - P_a)K}{(1 - P_s(1 - g))(1 - P_a^M)}$$

and   (11)

$$\overline{N}_j = \frac{P_a^{j-1}(1 - P_a)K}{(1 - P_a^M)},$$

where $j = 1, 2, 3, \ldots, M$. The characteristic equation, the roots of which determine the success of an initially rare invader with germination probability, g_2, into a resident equilibrium population with germination probability, g_1, is

$$(-1)^{M+1}\left\{\left[\left(\frac{g_2}{g_1}\right)(1 - P_s) + g_2 P_s\right]\lambda + P_s(1 - g_2)\lambda^M - \lambda^{M+1}\right\} = 0 . \quad (12)$$

Clearly, $\lambda = 0$ is one root, and if $g_2 < g_1$ then there are no roots greater than one. Hence, invasion by a strategy with lower germination probability will fail. However, if the invader has a higher germination fraction it will be able to displace the resident and as a result the ESS germination fraction is one.

When either $g_1 = 1$ or $P_a = 1$ the system of equations (10) need not converge to the equilibrium described by equations (11). This occurs when (i) $P_a = 1$ so the initial age structure is preserved over time because no spaces for recruitment are created in the prereproductive age classes and (ii) the initial population does not contain individuals from all age classes, $P_a < 1$ and $g_1 = 1$, so there are no
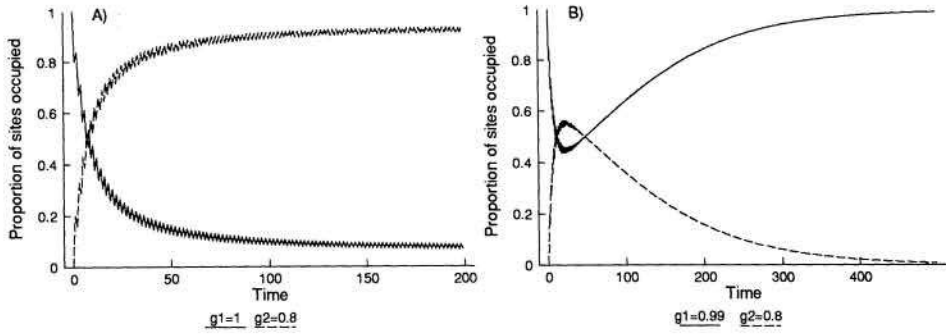
Fig. 2.—Coexistence of strategies with different germination fractions. A, The g_1 population initially contains only individuals from age-class 1 and there is complete germination; as a result, gaps formed by adult mortality cannot be colonized and coexistence is possible. B, The g_1 population only contains individuals from age-class 1 but $g_1 < 1$; consequently, gaps formed by adult mortality can be colonized and the strategy with the lower germination probability is excluded.

seeds to colonize gaps created by prereproductive mortality, and as a result the age structure varies in a cyclic manner. Under these conditions coexistence of different germination strategies is possible (see fig. 2).

RANDOM ENVIRONMENT MODELS

In the previous models the population parameters are assumed to be constant from one year to the next and the dominant eigenvalue of the invasion matrix (e.g., eq. [7]) determines the success of a rare invader with a different germination strategy. In a random environment, the success of a rare invader is determined by the dominant Lyapunov exponent, s, which is defined as

$$s = \lim_{t \to \infty} t^{-1} E[\ln(|n_t|)], \qquad (13)$$

where E is the expected value or average and $|n_t|$ is total population size (Tuljapurkar 1990; Metz et al. 1992). In calculating s we are assuming that the invader is rare and so its density has no effect on its population growth rate. This number, s, is simply a long-run growth rate, and if it is negative the strategy will become extinct. For evolutionary stability we require that

$$ds/dg_2|_{g_2=g_1} = 0 \qquad (14a)$$

and

$$d^2s/dg_2^2|_{g_2=g_1} < 0. \qquad (14b)$$

These conditions imply that the relation between the Lyapunov exponent and the invader's germination fraction has a maximum when the invader has the same germination probability as the resident. The resident is at stochastic equilibrium, and so its Lyapunov exponent is zero. Hence, if the best an invader can do is to

have a long-term growth rate of zero, when it has the same germination probabil-
ity as the resident, then all other invading strategies will have negative growth
rates and become extinct. Unfortunately, analytic determination of the dominant
Lyapunov exponent is not possible and so simulation was used to determine the
germination strategy that would exclude all others by systematically searching
the unit interval. The procedure used to determine the ESS germination probabil-
ity for a particular model was to iterate two strategy versions of the model,
starting with an equal frequency of both strategies, until one of them had an
overall frequency (seeds plus adults) of less than 0.1%. An upper bound of
10,000,000 iterations was used because in some cases, normally with very long-
lived adults and seeds, the rate of exclusion was very slow. In these cases the
most abundant (seeds plus adults) was declared the winner. Other simulation
procedures, for example, competing sets of 10 or more germination strategies
drawn from successively smaller intervals, invariably gave the same results.

Having found a germination probability that would exclude all others, I checked
the evolutionary stability by numerical calculation of the dominant Lyapunov
exponent. Heyde and Cohen (1985) have shown that the maximum likelihood
estimator of s is

$$\hat{s} = \frac{\ln|n_t| - \ln|n_1|}{t - 1}, \tag{15}$$

where, as before, $|n_t|$ is the total population size at time t. This estimator is
equivalent to calculating a series of one-step estimates and averaging them (Cohen
et al. 1983), giving

$$\hat{s}_i = \ln|n_{i+1}| - \ln|n_i| \tag{16a}$$

and

$$\hat{s} = \frac{1}{t - 1} \sum_i \hat{s}_i. \tag{16b}$$

The procedure used was to iterate the resident's and invader's dynamics for 2,000
time intervals to remove any transients. In each time step the invader's total
population size was normalized to 1×10^{-6}. The system was then iterated for a
further 1,000,000 time steps and the Lyapunov exponent for the invader estimated
from the time series. By setting the resident's germination probability to the
putative ESS, obtained by competing strategies against each other, and calculat-
ing the Lyapunov exponents for a wide range of invader's germination probabili-
ties, it was possible to determine whether the putative ESS was indeed uninvad-
able by rare mutants. In all cases I considered, a single strategy excluded all
others and was found to be uninvadable by alternative strategies.

Having obtained a putative ESS and checked its stability, I determined whether
a population currently with a non-ESS germination probability could be invaded
by strategies closer to the ESS. The resident's germination probability was set
at a non-ESS value and the Lyapunov exponents for strategies lying between the
resident's strategy and the ESS calculated. For all cases examined, the Lyapunov

exponents were positive, indicating that the population would evolve toward the ESS. Thus, it appears the ESSs obtained from the simulations are, in fact, continuously stable (sensu Eshel 1983). However, it should be noted that these are numerical results and I have no analytic proof that there is a single, continuously stable ESS.

The simple models described in the first section allow the environment to vary spatially but assume there is no temporal variability in demographic parameters. Two types of stochastic variation will initially be considered: variation in seedling establishment success and variation in adult fecundity. First we consider equation (1); incorporating these two forms of variability leads to the following model:

$$S_{t+1,i} = P_s(1 - g_i)S_{t,i}$$

$$+ FX\left[Y\left(K - P_a \sum_h N_{t,h}\right)\left(g_i S_{t,i} \Big/ \sum_h g_h S_{t,h}\right) + P_a N_{t,i} \right],$$

and (17)

$$N_{t+1,i} = P_a N_{t,i} + Y\left(K - P_a \sum_h N_{t,h}\right)\left(g_i S_{t,i} \Big/ \sum_h g_h S_{t,h}\right),$$

where X and Y are binary random variables taking the values zero and one. The probability of successful reproduction ($X = 1$) is P and the probability of successful seedling establishment ($Y = 1$) is P_{ss}. The probabilities P and P_{ss} are assumed to be independent. Thus, we are assuming that we have an iteroparous population, there is no cost of reproduction, and the environment varies such that in some years reproduction and/or seedling recruitment may fail completely. Where the type of variability incorporated into the model qualitatively affects the results obtained, the effects of other types of variability will be discussed. Three cases are considered.

1. *Variation in adult fecundity.*—The simulation results demonstrate that increasing adult longevity selects against seed dormancy (see table 1). However, the effects were relatively slight, and, in extensive simulation studies in which average adult longevity varied from 1 to 100 yr, the increase in ESS germination fraction was never greater than 0.05. It is easy to see why even when adults are extremely long-lived complete germination is not an ESS, as might be expected. Consider two strategies, one with complete germination and the other forming a seed bank. After a year when reproduction has been successful, the strategy with no seed dormancy will capture more than half the available sites because all its seeds germinate and as a result do not suffer any mortality in the seed bank. However, after a year when reproduction fails the strategy with a seed bank will capture all the available microsites, giving it the advantage and so enabling it to exclude the other strategy.

2. *Variation in seedling establishment success.*—Seedlings are highly susceptible to a wide range of biotic and abiotic hazards. One would therefore expect the likelihood of successful seedling establishment to vary greatly between years (Harper 1977; Fenner 1985; Rees and Long 1992). The simulation studies demon-

TABLE 1

EFFECT OF ADULT LONGEVITY ON THE ESS GERMINATION
PROBABILITY IN THE ITEROPAROUS PERENNIAL MODEL (EQ. [17])
WHERE ONLY ADULT FECUNDITY IS VARIABLE

P	P_s	AVERAGE ADULT LONGEVITY (yr)				
		1	2	5	10	100
.1	.1	.1	.1	.1	.1	.1
	.9	.07	.07	.08	.08	.09
.5	.1	.49	.49	.49	.49	.49
	.9	.27	.29	.30	.31	.32
.9	.1	.89	.89	.89	.89	.89
	.9	.61	.63	.65	.65	.66

NOTE.—P, Probability of successful reproduction; P_s, probability of seed survival. In all simulations, $P_{ss} = 1$.

TABLE 2

EFFECT OF ADULT LONGEVITY ON THE ESS GERMINATION
PROBABILITY IN THE ITEROPAROUS PERENNIAL MODEL (EQ. [17])
WHERE ONLY SEEDLING ESTABLISHMENT SUCCESS IS VARIABLE

P_{ss}	P_s	AVERAGE ADULT LONGEVITY (yr)				
		1	2	5	10	100
.1	.1	.10	1.0	1.0	1.0	1.0
	.9	.07	.08	.14	1.0	1.0
.5	.1	.49	1.0	1.0	1.0	1.0
	.9	.27	.37	.91	1.0	1.0
.9	.1	.89	1.0	1.0	1.0	1.0
	.9	.61	1.0	1.0	1.0	1.0

NOTE.—P_{ss}, Probability of successful seedling establishment; P_s, probability of seed survival. In all simulations, $P = 1$.

strate that, if variation in demographic parameters arises primarily from seedling establishment success, increases in adult longevity can strongly select against dormancy (see table 2). This occurs because established plants can always produce enough seeds to colonize the vacant microsites. Therefore, because adults are long-lived, current seed production will be buffered from variability acting on seedling establishment success. Hence, a strategy will maximize the number of microsites it captures by having all its seeds germinate immediately, providing the adults are sufficiently long-lived.

3. *Variation in both adult fecundity and seedling establishment success.*— When both seedling establishment success and adult fecundity are variable the likelihood of successful reproduction from new recruits is reduced relative to the two cases considered above. As expected, this selects for more dormancy in annuals. However, as adult longevity increases, the ESS germination fraction

TABLE 3

Effect of Adult Longevity on the ESS Germination
Probability in the Iteroparous Perennial Model (eq. [17])
Where Both Adult Fecundity and Seedling Establishment
Success Vary from Year to Year

$P_{ss} = P$	P_s	Average Adult Longevity (yr)				
		1	2	5	10	100
.1	.1	.01	.10	.10	.10	.10
	.9	.01	.04	.06	.08	.085
.5	.1	.25	.49	.49	.49	.49
	.9	.15	.23	.29	.31	.32
.9	.1	.80	.89	.89	.89	.89
	.9	.48	.595	.64	.65	.66

Note.—P, Probability of successful reproduction; P_{ss}, probability of successful seedling establishment; P_s, probability of seed survival.

reverts to that observed when only adult fecundity varies (see table 3). This effect occurs because when adults are long-lived only a small number die in any single year, and so the total number of established plants is largely unaffected by variation in seedling establishment success. This neutralizes the effect of variability acting on seedling establishment, and so the results converge on those obtained when only adult fecundity varies (cf. tables 1 and 3).

As the probability of seed survival becomes small, then in all cases considered, the ESS germination fraction tends to the probability of successful reproduction/establishment, not to one, as might be expected; this is a direct result of bet hedging (Bulmer 1984). Computed Lyapunov exponents for several of the ESSs are shown in figure 3, and in all cases the shape of the graph appears to satisfy equations (14a) and (14b). This demonstrates that the ESSs obtained from the simulation studies are indeed uninvadable by strategies with differing germination probabilities.

Incorporating Temporal Variation in Adult Survival and Seed Germination Behavior

The models presented above assume that seedling establishment and adult fecundity are temporally variable. These two aspects of plant performance were chosen because a priori it was expected that they would be highly variable. However, in some ecosystems adult survival rates may also vary strongly from year to year as a result of fire or flooding (Naveh 1975; Harper 1977; Mooney and Conrad 1977). The models also make the assumption that the probability of seed germination is the same in microsites occupied by established plants and those that are empty. Experimental studies have demonstrated that is generally not the case (Fenner 1985; Rees and Brown 1991; Rees and Long 1992). The effects of allowing adult survival rates to vary from year to year and the ability of seeds to detect the presence of established plants were explored by assuming
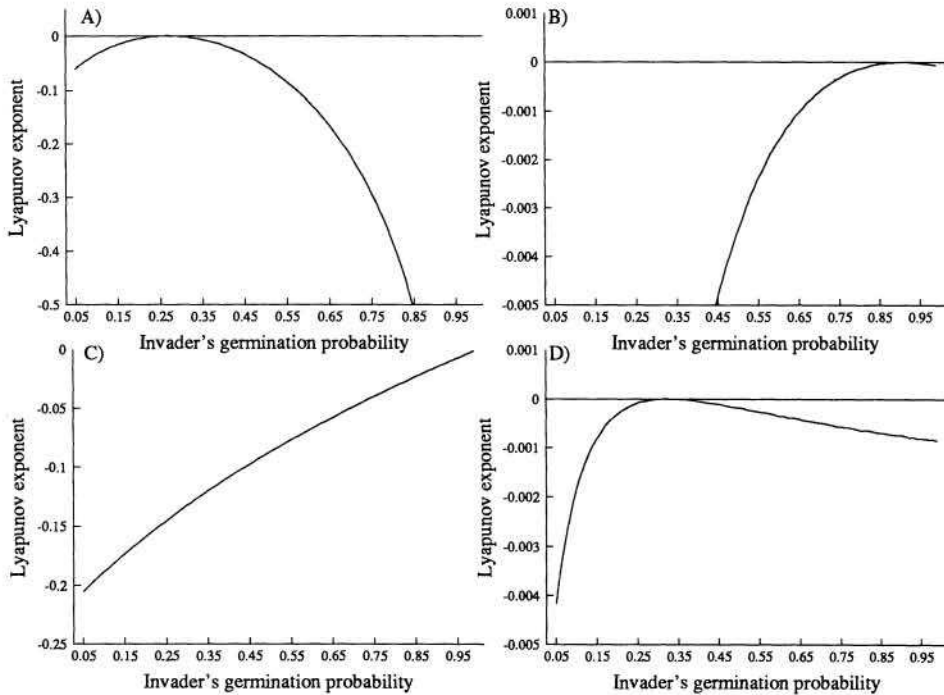
Fig. 3.—Computed Lyapunov exponents at four of the ESSs from the iteroparous peren-
nial model (eq. [17]); see text for details. A, ESS germination fraction equals 0.27, adult
fecundity is constant, there is variable seedling establishment success (P_{ss} = .5), P_s = .9, aver-
age adult longevity is 1 yr; B, as in A, but ESS germination fraction equals 0.91 and average
adult longevity is 5 yr; C, as in A, but ESS germination fraction equals 1.0,
P_s = .1, average adult longevity is 5 yr; D, ESS germination fraction equals 0.32, there is
variable adult fecundity (P = .5), seedling establishment success is constant, P_s = .9, and
average adult longevity is 100 yr.

that (i) the probability of seed germination in a microsite occupied by an estab-
lished plant was fixed at .01 and (ii) adult survival rate was reduced from P_a to
.01 with a probability of .05. As a result, on the average, in 1 yr of 20, 99% of
the adults die. When adult survival rate was not reduced to .01 then a fraction
P_a survived from one year to the next. The ESS germination fraction in those
microsites not containing an established plant was then determined. Thus we are
assuming we have an iteroparous population, there is no cost of reproduction,
and the environment varies such that in some years reproduction and/or seed-
ling recruitment may fail completely. As before three cases are considered.

  1. *Variation in adult fecundity.*—Allowing adult survival rates to fall occasion-
ally to low values will obviously result in a decrease in average adult longevity.
As expected, this selects for more seed dormancy and the ESS germination frac-
tions are reduced slightly, relative to those presented in table 1. In contrast,
setting the probability of germination to .01 in microsites containing established
plants resulted in a dramatic increase in the ESS germination fraction in unoccu-
pied microsites. If we assume that adults live on the average 100 yr (adult survival
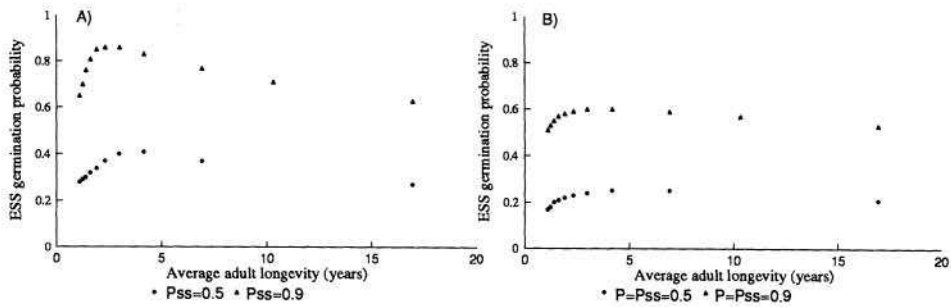
FIG. 4.—Effect of increased adult longevity on the ESS germination probability. *A*, Seedling establishment success and adult survival probability are variable; see text for details; *B*, as in *A* but with adult fecundity also variable. It is assumed that seeds cannot detect the presence of established plants. Qualitatively similar results were obtained when seeds could discriminate between occupied and unoccupied microsites. In both cases, $P_s = .9$.

rate is constant), the probability of seed survival (P_s) is .1, and the probability of successful reproduction (P) is .1, then the ESS germination probability is .1, assuming seeds cannot differentiate between occupied and unoccupied microsites (see table 1). However, if the probability of germination in a microsite containing an established plant is .01, the ESS germination fraction in an unoccupied microsite is one.

2. *Variation in seedling establishment success.*—When seedling establishment success varied, allowing seeds to detect established plants increased the ESS germination fraction in unoccupied microsites. However, allowing adult survival rate to vary produced a completely unexpected result. The ESS germination probability initially increased, reached a maximum, and then declined as adult longevity increased (see fig. 4*A*).

3. *Variation in both adult fecundity and seedling establishment success.*— When a seed can discriminate between empty and occupied microsites, then, as before, the ESS germination probability in the empty microsites was increased compared with the case in which seeds cannot discriminate. It was also found that the ESS germination probability initially increased and then declined with increasing adult longevity, as in case 2 above (see fig. 4*B*).

Costs of Reproduction

In the simple stochastic models considered above reproduction has no effect on subsequent survival. If, as in Constant Environment Models (above), we assume that all plants have a probability of flowering, P_f, and that those that flower have a probability of survival, P_{af}, whereas those that do not have a probability of survival, P_{ar}, then average adult longevity is

$$E[\text{adult longevity}] = \frac{1}{1 - P_f P_{af} - (1 - P_f) P_{ar}}; \qquad (18)$$

hence, it is clear that incorporating a cost of reproduction on subsequent survival (i.e., $P_{ar} > P_{af}$) will reduce average adult longevity and so should select for more seed dormancy. This is indeed the case, and it was found that the effects scale
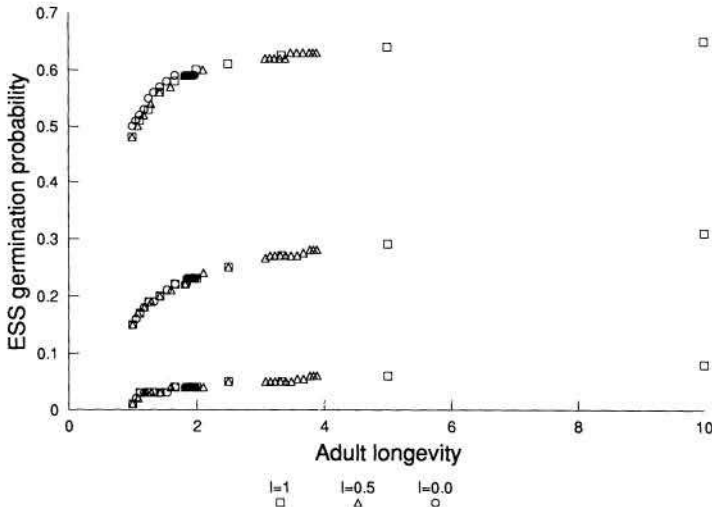
FIG. 5.—Effect of a reduction in adult survival as a result of reproduction on the ESS germination probabilities. The probability of adult survival after flowering, P_{af}, was set at a fraction, l, times the probability of survival of nonreproducing adults (i.e., $P_{af} = lP_{ar}$). The *curves* come from simulation studies in which the probability of seedling establishment and reproduction are both variable. Three values are shown: $P = P_{ss} = 0.1$ (*lower curve*); $P = P_{ss} = 0.5$ (*middle curve*); and $P = P_{ss} = 0.9$ (*upper curve*). Other parameters are $P_f = .5$ and $P_s = .9$.

precisely with average adult longevity (see fig. 5). Therefore, in a given environment, it is possible to predict the ESS germination fraction from adult longevity.

In semelparous species in which the timing of reproduction is age-dependent, the life cycle follows a rigid sequence (Kelly 1985) and models of the form described by equation (10) are required. Such life cycles can affect the evolution of seed dormancy in several possible ways, particularly when the population becomes dominated by a single cohort. When this occurs the dominant cohort prevents recruitment from seed, and this increases the cost of dormancy as a result of seed mortality (seeds have to survive until the adults die) selecting against dormancy. It also increases the average time between successful reproductive events, which favors increased dormancy. The interaction of these countervailing selection pressures is illustrated below. The model used was a stochastic version of equation (10):

$$S_{t+1,i} = P_s(1 - g_i)S_{t,i} + FXP_aN_{t,i,M-1},$$

$$N_{t+1,i,1} = Y\left(K - P_a\sum_{k}\sum_{h=1}^{M-1} N_{t,k,h}\right)\left(\frac{g_iS_{t,i}}{\sum_h g_hS_{t,h}}\right), \tag{19}$$

and

$$N_{t+1,i,j} = P_aN_{t,i,j-1},$$

TABLE 4

EFFECT OF ADULT LONGEVITY ON THE ESS GERMINATION
PROBABILITY IN THE STRICT MONOCARPIC MODEL (EQ. [19]) WHERE
ONLY ADULT FECUNDITY IS VARIABLE

P	P_s	ADULT LONGEVITY (yr)		
		2	5	10
.1	.1	.10 (.08)	.10 (<.01)	.10 (<.01)
	.9	.07 (.04)	.08 (.02)	.08 (.01)
.5	.1	.49 (.34)	.49 (.17)	.49 (.10)
	.9	.29 (.21)	.32 (.125)	.32 (.085)
.9	.1	.89 (.82)	.89 (.64)	.89 (.48)
	.9	.65 (.76)	.655 (.635)	.66 (.48)

NOTE.—P_s, Probability of seed survival. Table entries are ESS germination fractions, assuming an even initial age distribution. Figures in parentheses are ESSs calculated when the adults all belong to a single age class. In all simulations, $P_{ss} = 1$, $P_a = 1$.

where $j = 2, 3, 4, \ldots, M$ and X and Y are binary random variables taking the values zero and one. The probability of successful reproduction ($X = 1$) is P and the probability of successful seedling establishment ($Y = 1$) is P_{ss}. The probabilities P and P_{ss} are assumed to be independent. This set of equations describes a population of strict monocarpic plants. The seeds are assumed to have no information on the quality of the environment, and prereproductive mortality (P_a) is constant from year to year. As before three cases were considered.

1. *Variation in adult fecundity.*—In all simulations $P_a = 1$, which preserves the initial age structure for all time. Two extreme age structures are contrasted; in the first equal numbers of all ages are present in the population, and in the second all individuals occur in a single age class. When the population has an even age structure the ESS germination fractions are nearly identical to those obtained for the iteroparous perennial model (cf. tables 1 and 4); there is slight selection against dormancy as adult longevity increases. However, when the population is dominated by a single age class, the frequency with which successful reproduction occurs is reduced as adults become longer-lived and this selects for more dormancy. The ESSs calculated for the aggregated age structure are generally lower than those for the even age structure. However, when adults are relatively short-lived and the probabilities of seed survival and successful reproduction are high, this pattern is reversed. This occurs because the fitness of seeds that germinate is increased relative to those that remain dormant, thus selecting for less dormancy (see table 4).

2. *Variation in seedling establishment success.*—When seedling establishment success varies from year to year such that in some years recruitment fails completely, the population eventually becomes dominated by a single cohort no matter what the initial age structure. In the corresponding iteroparous model (table 2), it was found that, as adult longevity increased, complete germination became the ESS because seed production is buffered from variation in seedling establish-

TABLE 5

Effect of Adult Longevity on the ESS
Germination Probability in the Strict
Monocarpic Model (eq. [19]) Where Only
Seedling Establishment Success Is Variable

		Adult Longevity (yr)		
P_{ss}	P_s	2	5	10
.1	.1	.08	.09	.08
	.9	.075	.08	.09
.5	.1	.50	.50	.50
	.9	.34	.48	.50
.9	.1	.90	.90	.90
	.9	.885	.90	.90

Note.—P_s, Probability of seed survival. In all simulations, $P = 1$, $P_a = 1$.

ment. However, when there is a rigid life cycle this is no longer the case and ESSs are always less than the corresponding iteroparous model (cf. tables 2 and 5). Also, as adult longevity increases the ESSs become independent of the probability of seed survival. This occurs because when adults are long-lived few seeds survive between periods of successful recruitment and thus, as in the earlier iteroparous models (tables 1–3), the ESS is equal to the probability of successful establishment/reproduction (see table 5).

3. *Variation in both adult fecundity and seedling establishment success.*—Obviously, the results presented above (in cases 1 and 2 and tables 4–5) depend to a certain extent on the assumption that reproduction and/or recruitment fail completely in some years. Here it is assumed that both seedling establishment success and reproduction are variable, and a favorable environment (neither establishment nor reproduction ever fail completely) is contrasted with a harsh environment (either establishment or reproduction could fail completely). To facilitate comparison with the results presented above and between the two environments, the population is assumed to be composed of a single age-class of established plants. The simulation results are presented in table 6. In the harsh environment increasing adult longevity selects for more dormancy because the average time between successful reproduction events is increased. However, in the favorable environment the opposite occurs and increased adult longevity selects for less dormancy. This is because adult longevity increases the cost of dormancy, as a result of seed mortality between recruitment events, thus selecting against delayed germination.

Long-lived monocarpic species are unlikely to occur in habitats in which adult survival rate varies dramatically, as most individuals would die before having a chance to reproduce (Watkinson and White 1985; Watkinson 1992). Also, the cost of forming a seed bank would be large, even if yearly seed survival were high, because the seeds have to survive for long periods. It is therefore not surprising that in species like bamboo there is little dormancy (Janzen 1976).

TABLE 6

EFFECT OF ADULT LONGEVITY ON THE ESS GERMINATION
PROBABILITY IN THE STRICT MONOCARPIC MODEL (EQ. [19]) WHERE
BOTH ADULT FECUNDITY AND SEEDLING ESTABLISHMENT SUCCESS
VARY FROM YEAR TO YEAR

$P_{ss} = P$	ENVIRONMENT	ADULT LONGEVITY (yr)		
		2	5	10
.1	Favorable	.09	.09	.10
	Harsh	.01	.01	.01
.5	Favorable	.20	.20	.22
	Harsh	.13	.10	.07
.9	Favorable	.68	.74	1.00
	Harsh	.63	.58	.44

NOTE.—In both environments when conditions are suitable for reproduction, $F = 10,000$, and when conditions are suitable for seedling establishment, $Y = 1$. In "harsh" environments individuals produce no seed and no seedlings establish when conditions are unsuitable, whereas in the "favorable" environments individuals produce 10 seeds and 10% ($Y = 0.1$) of the seedlings survive. In all simulations, $P_s = .9$, $P_a = 1$.

Computed Lyapunov exponents for several of the ESSs discussed above are shown in figure 6. In all cases the computed relationships are consistent with equations (14a) and (14b). In figure 6B the countervailing selection pressures created by the dominant age class are clearly illustrated.

DISCUSSION

In the models examined, when the environment is constant, no benefit accrues from seed dormancy regardless of adult longevity or the timing of reproduction. This is a direct consequence of the cost of dormancy due to increased seed mortality. This is analogous with the standard life-history result that early reproduction is favored (Stearns 1976). However, in constant environment models that assume strong sib competition, dormancy may evolve as a method of reducing competition between sibs (Ellner 1986).

In contrast, in a variable environment adult longevity and the timing of reproduction can have a profound impact on the evolution of seed dormancy. In iteroparous and semelparous species, where reproduction in an even-aged cohort occurs in several years, the risks of reproduction are spread over time and thus a negative relation between adult longevity and seed dormancy is expected: both these life-history attributes may be viewed as alternative ways of dealing with environmental uncertainty (Venable and Brown 1988). When variability only acts on adult fecundity the change in the ESS germination fraction was surprisingly small, demonstrating that adult longevity and dormancy are only partially substitutable. This is a direct result of strategies with little seed dormancy obtaining a disproportionately small number of microsites after a period unsuitable for
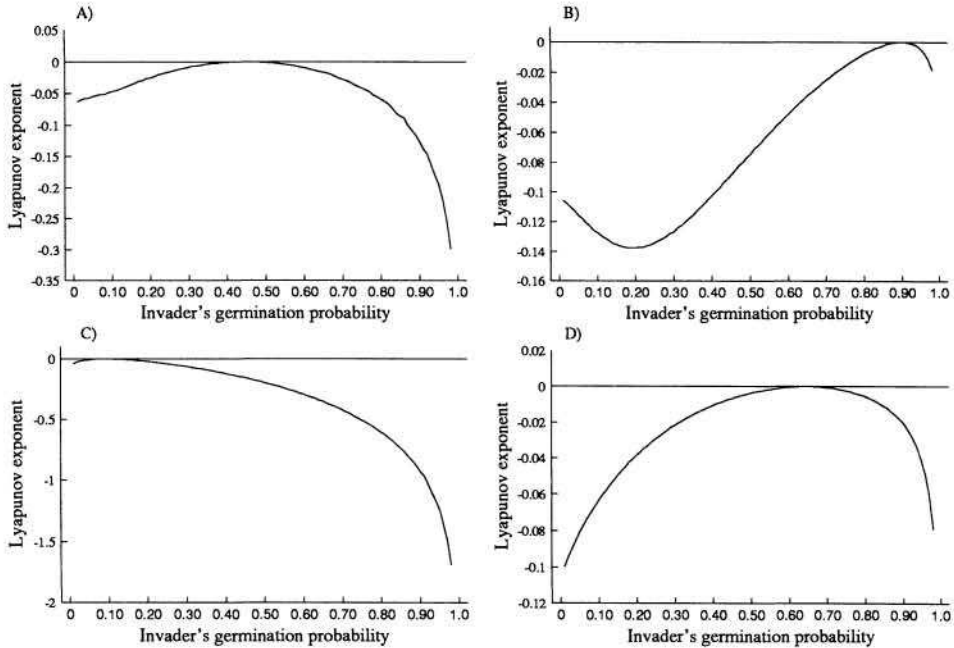
FIG. 6.—Computed Lyapunov exponents at four of the ESSs from the strict monocarpic model (eq. [19]); see text for details. *A*, ESS germination fraction equals 0.44, adult fecundity and seedling establishment success are variable ($P = P_{ss} = .9$), $P_s = .9$, adult longevity is 10 yr, there are favorable environmental conditions (see table 6); *B*, ESS germination fraction equals 0.9, adult fecundity is constant, there is variable seedling establishment success ($P_{ss} = .9$), adult longevity is 5 yr, $P_s = .9$; *C*, as in *B*, but ESS germination fraction equals 0.09, $P_{ss} = .1$, adult longevity is 10 yr; *D*, ESS germination fraction equals 0.65, adult fecundity is variable ($P = .9$), seedling establishment success is constant, $P_s = .9$, adult longevity is 2 yr, and there is even age distribution.

reproduction. In contrast, when adult fecundity is constant and variability acts mainly on seedling survival, increasing adult longevity can strongly select against dormancy, because there are always enough seeds produced to colonize the available microsites. Thus, it is important to appreciate that we must specify not only whether the environment is variable but also on which life-history stages the variability acts. Incorporating a rigid age structure into the models adds an extra dimension, demonstrating the importance of age structure and the severity of environmental fluctuations in determining the direction of selection.

The effects of variable adult survival on the ESS germination fraction are counterintuitive, with germination being maximal for intermediate adult longevities (fig. 4). This highlights one of the problems of using stage-structured models to study evolution in variable environments. Because the means and variances of several life-history attributes are altered simultaneously, for example, when changing adult longevity, it is difficult to give precise interpretations of the results obtained. However, the approach does hold considerable promise in allowing the direction of selection to be determined, the effects of complex life cycles on

dormancy and other life-history traits to be explored, and patterns of life-history variation over successional and other gradients to be predicted.

When considering the evolution of dormancy the models presented predict that under a wide range of conditions seed dormancy will be selected against as adult longevity increases. The models indicate that exceptions to this general pattern occur when (i) adult survival and the probability of successful seedling establishment are both variable, resulting in the ESS germination probability's being maximal at intermediate adult longevities, and (ii) reproduction is concentrated in a single, dominant age class and reproduction and/or seedling establishment may fail completely in some years.

Thus, in comparative analyses of species from ecosystems not dominated by long-lived monocarpic species and in which adult survival rate is not highly variable, we would expect a negative correlation between adult longevity and seed dormancy. With modern comparative methods, such a correlation has been found in the British flora (Rees 1993). I (Rees 1993) used data collected from 5-yr field experiments to assess the level of seed dormancy in 171 plant species and related it to several life-history traits. Species used included annual weeds and perennial herbs and grasses. Adult longevity, seed weight, and the efficiency of spatial seed dispersal were all found to be correlated with the degree of dormancy observed. As predicted by the models presented in the main body of this article, an increase in adult longevity was found to be negatively correlated with seed dormancy, even after correcting for seed size and spatial dispersal ability.

However, previous published analyses of species from the British flora (Grime et al. 1987; Grime 1988), Canadian emergent zone macrophyte communities (Shipley et al. 1989), and Australian semiarid woodlands (Leishman and Westoby 1992) found poor associations between established phase traits and those of the regenerative phase. Each of these studies included measures of adult longevity and seed dormancy. The discrepancy between the studies could be a result of (i) the methods used—earlier authors used multivariate methods, whereas I used independent comparison methods that account for the phylogenetic relationships between species (Harvey and Pagel 1991)—or (ii) the relatively crude measures of dormancy used in previous studies. Interestingly, in American herbaceous plants 51% of annuals show full dormancy, compared with 32% and 19% for polycarpic and monocarpic perennials, respectively (data from Baskin and Baskin 1988). A similar pattern holds for the Sheffield flora, where 77% of annual species have a persistent seed bank, compared with 47% of perennials (data from Grime et al. 1988). Although more careful analysis of these data is required, correcting for phylogeny, seed size, and other confounding variables, the trend is certainly in the direction predicted by the models. It has also been suggested that similar patterns occur in deserts (Kemp 1989) and wetlands (Leck 1989), although rigorous comparative analyses of these cases have yet to be undertaken.

The competition-stress-ruderal model (Grime 1979, 1988) assumes that established plant traits are uncoupled from those of the regenerative phase, and multivariate analyses have been presented supporting this assumption (Grime et al. 1987). The theoretical analysis presented here contradicts this and demonstrates how established plant traits can affect the evolution of dormancy. Further theoret-

ical studies looking at other seed properties, such as weight and spatial dispersal, are clearly needed. Cohen and Levin (1991) predicted, on the basis of the temporal correlation between yields in successive years, that short-lived early successional species should have a high dispersal strategy, whereas species that occupied a prolonged successional stage should have lower optimal dispersal fractions (Cohen and Levin 1991). However, comparative analyses among the Compositae demonstrate the opposite, with annuals having a lower proportion of species with plumed seeds than perennials (Venable and Levin 1983). This apparent contradiction is easily understood, since species with efficient spatial dispersal often show reduced seed dormancy (Rees 1993). Thus, the annuals in Venable and Levin's study may well have had more efficient dispersal as a result of seed dormancy. This also illustrates the importance of considering several traits simultaneously in comparative studies.

The models do not include alternative persistent life-history stages such as seedling or sapling banks (Parker et al. 1989). In species with these traits we would expect reduced seed dormancy because these life-history stages represent alternative ways of dealing with environmental uncertainty (Venable and Brown 1988).

The work highlights several ways in which adult life-history traits influence the evolution of seed dormancy. However, no attempt has been made to determine how seed traits influence the evolution of adult traits. For example, species with long-lived seeds that are relatively invulnerable to herbivore attack may be less likely to develop masting as a reproductive strategy than species with short-lived, poorly defended seeds. Similarly, in a variable environment, the presence of a seed bank is likely to alter the relative advantages of iteroparous and semelparous life cycles, because the benefits that accrue to perennials from spreading reproduction over several years may be offset by the presence of a seed bank that allows annuals to spread their reproduction through time. It is clear therefore that a more integrated analysis of life-history evolution is needed and that it is probably unwise to consider properties of the regenerative and adult phases of the life cycle as being uncoupled.

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