

Modeling the Evolutionary Ecology of Seed Banks

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I. Why Model the Population Dynamic Consequences of Seed Banks?

At the symposium motivating this volume, the term "seed bank science" was used by Jim McGraw with humorous intent. The point was that,

rather than being a coordinated research program with well-defined goals, approaches, and funding, the study of seed banks has been a collection of isolated works using varied approaches, often undertaken as side projects in investigations with other primary foci. This state of affairs justifies the following remarks on the relevance of modeling to the development of our empirical understanding of seed banks. In a more mature science these comments would hopefully be superfluous.

One role of modeling is to provide interpretation. For example, we know that there is a predominance of annual and early successional plant species represented in the seed banks of even late successional communities in temperate deciduous forests (Pickett and McDonnell, Chapter 8, this volume). Does this pattern have something to do with the relative importance of dispersal in space versus time for plants of different life history strategies? Does it have something to do with the relative importance of seed regeneration versus perennation? Mathematical models can formalize the different hypotheses and double check their logical coherence. In the process, additional mechanisms and selective forces often become apparent.

A second role of models is that they can suggest appropriate data to collect. We might, for example, be interested in the relative importance of dispersal and dormancy in the persistence of early successional species in a particular habitat. From a careful consideration of models of these phenomena, it becomes clear that we need to understand patterns of spatial and temporal variation in the expected fecundity of germinating seeds; correlations in temporal, spatial, and temporal-spatial variation; the survival of dormant seeds; and the proportion of a plant's seed output that can be expected to move to microsites of different quality. Attempts to measure some of these parameters can be incorporated in subsequent research designs.

Models can often be tailored to capture the essential elements of a specific experimental system. Then the model can be manipulated to generate predictions that can be tested with the experimental system. For example, I am interested in the evolution of seed proportions in the seed heteromorphic composite, *Heterosperma pinnatum*, in central Mexico (Venable *et al.*, 1987). Each plant produces seed morphs with differences in within-year timing of germination, correlated differences in dispersal, no between-year seed bank, and proportions that vary among populations. Elements of some of the more general models discussed below combine easily to mimic this system and predict how environmental changes favor different seed proportions. Predicted differences in seed proportions can then be checked against those observed in different environments in which this species is found.

A final role of models, often forgotten in our search for testable predictions, is that they permit exploration of questions that cannot be

easily answered experimentally at present. We may have only 4–5 yr of data on germination patterns, the demographic success of germinating seeds, and the survival of dormant seeds. We might want to know what the population dynamic consequences of such variation would be after 100 or 1000 yr, or how certain environmental changes might favor different germination strategies. While we may be able to collect data on the results of environmental differences along some environmental gradient, the actual selective mechanisms and the operation of population dynamic forces cannot be reasonably measured over long periods of time. The value of models for quickly answering, at least in a hypothetical way, many of our "What if . . . ?" questions should not be underestimated, particularly in the developmental stages of a young science.

II. Issues Relevant to Understanding Seed Banks

First, I shall briefly outline three basic issues of seed biology relevant to understanding seed banks: the within-year timing of germination, the production of a between-year seed bank, and predictive or plastic germination. I shall restrict my discussion to density-independent models of annual plants because such models are fairly easy to understand and construct. Modeling annuals avoids the difficulties of perennation, vegetative propagation, and other complications.

A. The Within-Year Timing of Germination

The within-year timing of germination affects the study of seed banks because it determines how many seeds will be in the soil at different times of the year. What factors determine how natural selection shapes the within-year germination schedule; that is, at what season(s) should seeds germinate? The simplest case is if there is no seed bank carry-over between years. In this case the question becomes, given that it is this year or never, when should seeds germinate to yield highest fitness? In general seeds will germinate according to some distribution within one or more germination seasons of a single year (Fig. 1). The question is, what proportion of seeds should germinate in each of the possible windows of opportunity (Fig. 1)? The simplest case is with a choice of two windows of opportunity. For example, some temperate zone annuals germinate in the fall, some germinate in the spring, and some germinate in both periods (e.g., *Papaver dubium*, Arthur *et al.*, 1973; *Bromus tectorum*, Mack and Pyke, 1983). Similarly, desert winter annuals around Tucson, Arizona, often germinate predominantly in October–November, December–January, or in both periods.

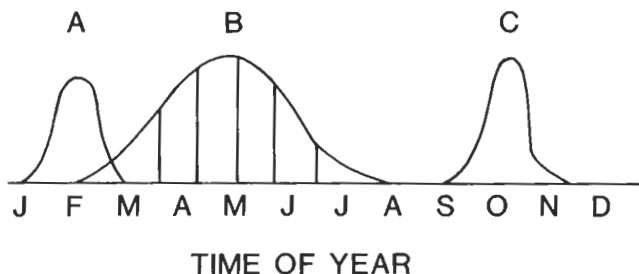


Figure 1. Possible within-year germination schedules. What proportion of seeds should germinate during each census interval to yield highest fitness? Some annuals germinate predominantly in the fall (C), some in the winter (A), and some during both (A and C). Some species have fairly synchronous germination (e.g., A or C), while others spread germination over a longer season (e.g., B).

Consider a population described by the following simple growth equation:

$$\lambda = S^E q + (1 - q) S^L$$

where λ is the finite rate of increase, q is the proportion of seeds germinating early, and S^E is sum of $l_x b_x$ for early germinating seeds (i.e., the average seed yield per early germinating seed). In a constant environment, either S^E would be higher, in which case all seeds should germinate early, or S^L (where L stands for late) would be higher, in which case all seeds should germinate late (if $S^E = S^L$, it does not matter when seeds germinate). However, year-to-year variation in the success of early and late cohorts can favor the simultaneous production of both. In some years early germination might yield higher fitness, while in others, late germination might be better. We can incorporate this into the model by allowing S^E and S^L to vary from year to year (define S_i^E to equal $\sum l_x b_x$ in year type i). Now, rather than consider a single λ , we are interested in the geometric average of λ after a series of years (we use the geometric mean because population growth is multiplicative through time; see Leon, 1985):

$$\text{GEO}(\lambda) = \Pi(qS_i^E + (1 - q)S_i^L)^{p_i} \quad (1)$$

where p_i is the probability of year-type i occurring.

We can now ask what germination strategy, q , yields the highest geometric mean fitness (Fig. 2). If the highest geometric mean fitness is at $q = 0$, selection favors all seeds germinating late; if the maximum is at $q = 1$, all seeds should germinate early; if the maximum is between 0 and 1, multiple germination cohorts are favored. Algebraic manipulation of

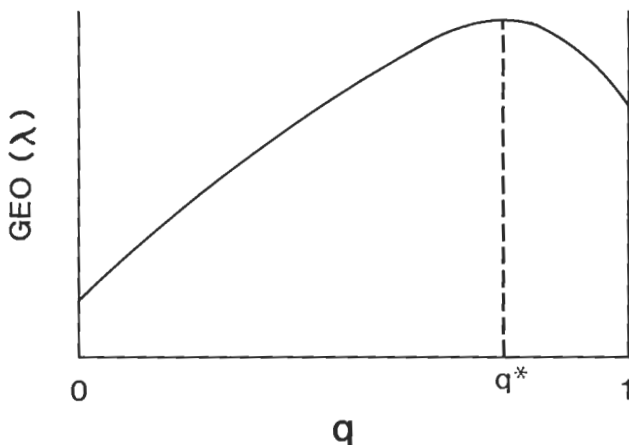


Figure 2. To determine what proportion of seeds should germinate in each of two windows of opportunity, we determine what proportion, q , of early germination and what proportion, $1 - q$, of late germination yield highest geometric mean fitness, $GEO(\lambda)$, where geometric mean fitness is described by Eq. (1) in the text. If q^* , the proportion of early germination that yields highest fitness, is 0, selection favors only late germination. If q^* is 1, selection favors only early germination. Multiple cohorts are favored when $0 < q^* < 1$.

the model shows that multiple cohorts within years (or more generally the spread of germination within years) are favored by a high year-to-year variation in the seed yield per germinating seed, and by a low or negative correlation between the seed yield per seed of early and late cohorts (i.e., if years that the early cohort does well tend to be years that the late cohort does poorly and vice versa). For multiple cohorts to be favored, the expected seed yield per seed must be greater for each cohort in some year types (obviously if early germination always resulted in lower seed set, it would not be favored). Finally, more germination in one or another cohort is favored by a greater probability of favorable conditions for that cohort. Equation (1) was analyzed in Venable (1985) where the two sources of reproduction referred to two seed morphs; the same algebra and conclusions apply for early and late germination. A simple elaboration of this model would be to consider multiple windows of opportunity and the proportion of seeds that should germinate in each to maximize plant fitness. Leon (1985) has outlined a mathematically more sophisticated approach to the within-year timing of germination, considering the optimal continuous germination schedule.

B. The Production of a Between-Year Seed Bank

The second issue relevant to understanding seed banks is the production of a between-year seed bank. This issue can be addressed in a similar manner. Consider the following equation:

$$\lambda = GS + R(1 - G)$$

where G is the proportion of seeds germinating, $(1 - G)$ is the proportion remaining dormant between years, and R is the survival of dormant seeds. In what follows I will often use the term "dormancy" in the ecological sense of not germinating for whatever reason. This usage should not be confused with the more physiological usage meaning unable to germinate for some physiological or morphological reason (see Baskin and Baskin, Chapter 4, this volume). If we let the seed yield per seed vary, the geometric mean growth rate becomes

$$\text{GEO}(\lambda) = \Pi(GS_i + R(1 - G)^{p_i}) \quad (2)$$

If the germination fraction resulting in highest geometric mean fitness is 1, selection favors no between-year seed bank; if it is less than 1, the production of a seed bank is favored (Fig. 3). Analysis of this model

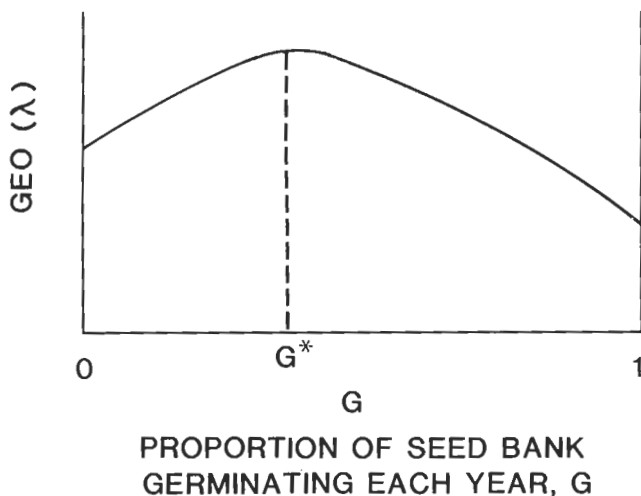


Figure 3. To determine what proportion of seeds should enter a between-year seed bank we determine what proportion, G , of the seed bank should germinate each year to yield highest geometric mean fitness, $\text{GEO}(\lambda)$, where geometric mean fitness is described by Eq. (2) in the text. If G^* , the germination fraction that maximizes fitness, is 1, selection favors complete germination (i.e., no seed bank). If G^* is less than 1, the production of a seed bank is favored.

shows that a between-year seed bank is favored by (1) a low probability of high seed yield, (2) high year-to-year variance in seed yield, and (3) a high survival rate of seeds in the soil. This model was first analyzed by Cohen (1966) and has been recently summarized in Leon (1985) and Brown and Venable (1986). For a particular application more complicated possibilities can be imagined. For example, one could simultaneously explore within- and among-year timing of germination by putting together Eqs. (1) and (2) and finding the optimal combination of G and q .

C. Predictive Germination

Missing from the above discussions is dormancy plasticity, or the modification of the timing or fraction of seeds germinating in response to environmental cues. This may be an important source of variability in seed bank dynamics and it must be dealt with in any complete discussion of the ecology of dormancy. The approach in Sections II,A and II,B was to determine the one "correct" germination strategy and see how different conditions select for a different fixed germination strategy. Plants of many habitats produce seeds whose germination behavior varies considerably, depending on environmental cues. For example, the germination fraction of desert annuals depends critically on temperature

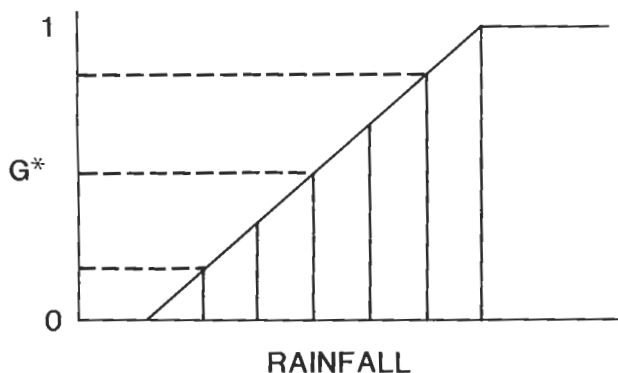


Figure 4. Predictive dormancy. How should the germination fraction that maximizes fitness, G^* , vary with different cues that provide information as to the probability of favorable conditions? For example, for desert annuals, the amount of rainfall (and temperature) at the time of germination is a predictor of the expected fecundity of germinating seeds. The fitness-maximizing germination fraction is determined, where fitness is described by Eq. (2), but the probabilities of different year types (environmental conditions) are replaced by the conditional probabilities of different year types given the cue. Thus there may be a different G^* for each value of the cue.

and the amount of rainfall (Capon and van Asdall, 1966; Freas and Kemp, 1983). This was first modeled by Cohen (1967), who showed that the problem is neatly solved by performing the same analyses as described above, but making the probabilities (the p_i values) conditional on the cues (summarized in Leon, 1985). The question changes from knowing the probability of a high seed-yield year to knowing the probability of a high seed-yield year *given* that, at the time of germination, there are specific environmental cues, such as a temperature of 24°C and 20 mm of precipitation. Thus rather than one optimal germination fraction, there are many, one for each cue (Fig. 4). One prediction of this kind of model is that for an ordered set of cues (that predict increasingly favorable conditions, as in Fig. 4), reliable cues favor an abrupt shift in germination strategy while unreliable cues favor a more gradual shift in germination strategy. In the extreme, the best germination strategy is insensitivity to cues that give no information about the probability of favorable and unfavorable conditions. This is because the conditional probability is the same as the probability in the absence of the cue. Thus, in the example above, different amounts of rainfall would result in the same germination if rainfall were an uninformative cue, because the conditional probabilities would all be the same.

D. Research Questions and Field Tests

The models presented above are simple and straightforward, yet they generate numerous questions in need of empirical examination. What are the expected seed yields of plants from early and late cohorts in different years? How constant is the partition into early and late germination? What cues regulate this partition and how do they correlate with the probability of favorable and unfavorable conditions (i.e., how reliable are the cues)?

To illustrate how such models can guide the collection of field data and aid in its interpretation, I present 4 yr of demographic data on two common desert winter annuals, *Plantago patagonica* and *Schismus barbatus*, growing near Tucson, Arizona (Table 1). This project was motivated by a desire to understand patterns of demographic variability thought to shape the evolution of seed dormancy. Plants emerging following each rainfall event during these years were mapped and their survivals and fecundities were recorded to determine the average seed yield per germinating seed, a critical variable in the models above. In most years there were major germination cohorts in October or November and in December or January; seed was set in March or April. Seed bank samples were collected in February at the end of the germination season to estimate the density of ungerminated viable seeds with the potential for surviving to future seasons. Fitness topographies were gen-

Table 1

Demographic data for two species of desert winter annuals at the Desert Laboratory, Tucson, Arizona, 1982-1986

Species	Year	Cohort	Initial germination	Survival to reproduction (%)	Mean b_x^a	$l_x b_x$
<i>Schismus barbatus</i>	82/83	E	71	70.4	196.20	138.20
		L	25	76	221.10	168.00
	83/84	E	1045	35.7	10.49	3.74
		L	83	42.2	10.37	4.37
	84/85	E	6	0	—	0
		L	61	47.5	70.90	33.70
	85/86	E	135	32.6	95.10	30.99
		L	27	18.5	21.00	3.89
<i>Plantago patagonica</i>	82/83	E	580	66.4	25.30	17.82
		L	123	57.7	15.50	9.70
	83/84	E	2646	54.7	5.59	3.05
		L	92	51.1	4.40	2.25
	84/85	E	76	25.0	26.60	6.65
		L	365	42.2	24.70	10.26
	85/86	E	205	15.1	65.05	9.83
		L	260	48.5	24.04	11.65

^a b_x , the average fecundity of plants surviving to reproduce; $l_x b_x$, the expected fecundity of an emerging seedling (i.e., the product of survival and fecundity).

erated from these data using a simple model that allows plants to germinate early (October–November) or late (December–January) and to have a proportion of seeds remaining dormant between years (i.e. a combination of the within- and between-year dormancy models presented above). Seed yields were calibrated by the proportion of seeds produced in one yr that could be accounted for in the next year (germinating seed densities plus seed bank densities) to correct seed yield per germinating seed for seed mortality between the April seed production and the following germination season. The proportion of early germination and the proportion of seeds remaining dormant between years were arbitrarily varied through the full range of possible values, and the geometric mean fitness for each species was calculated (Fig. 5).

This analysis provides several insights not readily apparent in the original data. First, it appears that fitness is much more sensitive to changes in the within- and between-year timing of germination in *Schismus* than it is in *Plantago* because the fitness topography for *Plantago* is flatter. This difference in the shape of the fitness topography results from the greater seasonal and between-year variation in reproductive success of *Schismus* cohorts. *Schismus* cohorts ranged from an

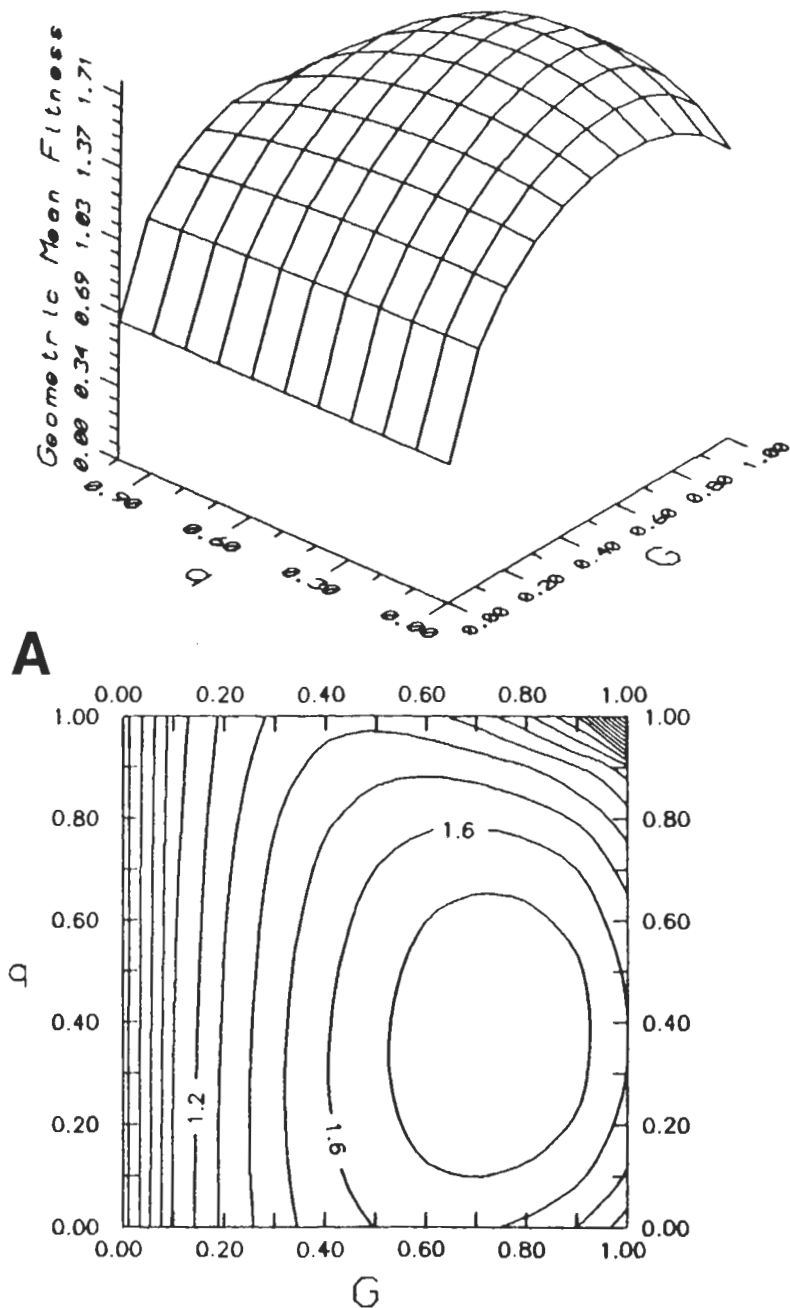
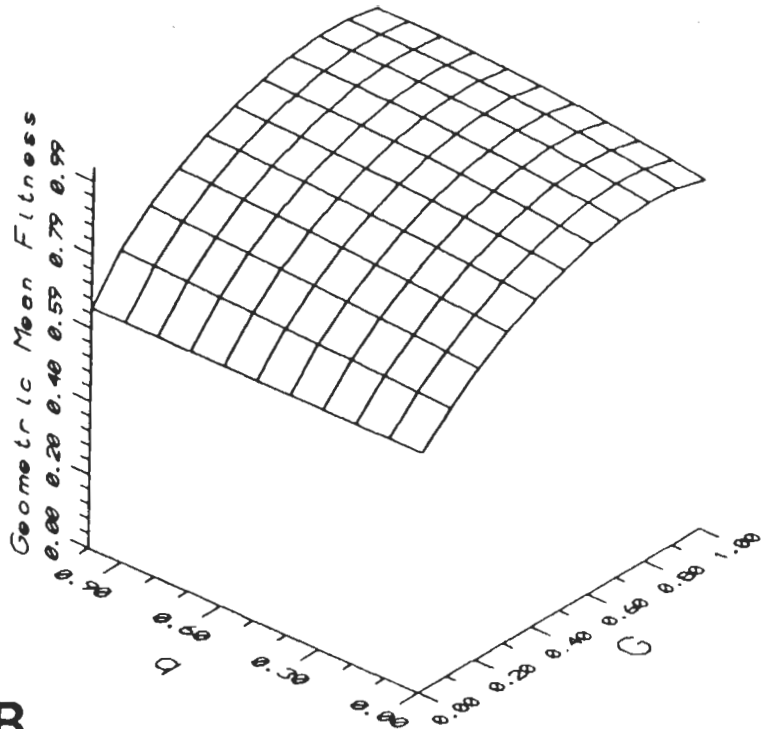
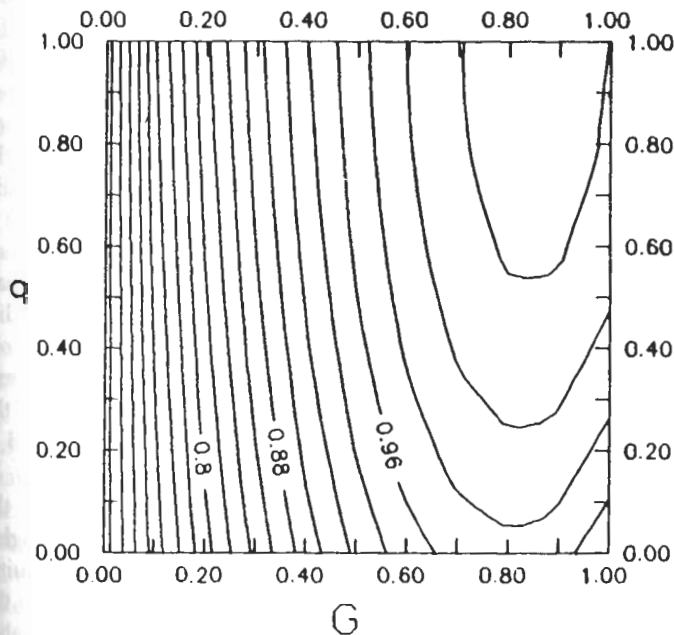


Figure 5. Fitness topographies and corresponding fitness contour maps generated from 4 yr of field data on the expected fecundity of germinating seedlings for early and late cohorts of (A) *Schismus barbatus* and (B) *Plantago patagonica* and a simple model combining within- and



B



between-year dormancy. The survival between years of nongerminating seeds was assumed to be 65% for these calculations (see Section II,D for details).

average of 0–221 seeds per adult, while *Plantago* cohorts ranged from 4.4–65 seeds per adult. It is tempting to attribute this difference between species to the variance-reducing properties of larger seeds (Venable and Brown, 1988) (0.08 mg for *Schismus* versus 0.8 mg for *Plantago*). Another prediction generated by the positions of the fitness optima is that selection should favor a percentage of early (i.e., risky) germination greater for *Plantago* than for *Schismus*. The observed germination schedule is in general agreement with this prediction; *Plantago* had more early germination than did *Schismus* in 3 of 4 yr. The positions of the optima also suggest that *Schismus* should have greater between-year dormancy than should *Plantago*. The closest estimate of between-year dormancy available for this study is the proportion of viable seeds in the seed bank that do not germinate by the end of the germination season. The grand mean of this is 15% for *Plantago* and 37% for *Schismus*, indicating general agreement with the prediction.

These simulations searched for the best constant partition into early and late germination, yet the actual partition varies considerably between years (Table 1). Whether the observed plasticity in germination time is capable of increasing fitness can be ascertained by calculating the geometric mean population growth rate using the actual variable partition into early and late germination and comparing it to that for the best constant partition. When this is done, the mean growth rate for *Schismus* with variable germination time is 2.18 compared to 1.78 calculated for the "optimal" constant partition into early and late germination (for *Plantago* the respective growth rates are 1.12 versus 1.03). These differences suggest that the observed variation in the proportion of early germination is adaptive in that it tends to correlate germination with the best time for successful establishment and reproduction. This "predictive germination" is, however, less than perfect; if all germination is assigned to the cohort with highest expected fecundity, growth rates are higher yet (2.43 and 1.18 for *Schismus* and *Plantago*, respectively). Apparently these species can use cues that permit them to adaptively modify germination time from year to year. The information, however, is not perfect; it is not beneficial to germinate only at the predicted best time. The imperfect nature of predictive germination can be seen in the *Schismus* data, where the majority of the seeds actually germinated in the less successful cohort in 2 yr.

Thus, the simple models discussed in this chapter can aid in the interpretation of empirical data on seed behavior and generate insights into the nature of seed banks. They also suggest further data requirements. For *Schismus* and *Plantago* there is clearly a need for data on the proportion of seeds remaining dormant between years and their viabilities.

Venable (1985) and Silvertown (1988), reanalyzing published experi-

mental and field data, have shown a reasonable fit of empirical data to model predictions (very reasonable considering the simplicity of the models and the shortcomings of the data sets for this purpose). For two seed heteromorphic annuals (*Heterotheca latifolia* and *Gymnarrhena micrantha*) Venable (1985) found that dormancy, seed bank survival, and variation in reproductive success of germinating seeds favored seed heteromorphism and the production of a between-year seed bank when fitted to a model similar to those in Eqs. (1) and (2). Silvertown (1988) analyzed two species for within-year timing of dormancy and found that *Bromus tectorum* had population dynamics at one site that should favor multiple cohorts, while *Avena sterilis* dynamics favored only fall germination. These predictions mimic actual germination pattern for these two species. He applied a model of between-year dormancy to demographic data for 10 annual species (*Androsace septentrionalis*, *Avena barbata*, *Bromus tectorum*, *Carrichtera annua*, *Emex australis*, *Erophila verna*, *Sorghum intrans*, *Avena sterilis*, *Medicago polymorpha*, and *Spergula vernalis*); the model correctly predicted the dormancy characteristics of the first 7 species. A study by Freas and Kemp (1983) demonstrated that two Chihuahuan Desert winter annuals that receive low amounts of unreliable rain (i.e., unfavorable conditions) had innate dormancy ($G < 1$), while a summer annual that receives more abundant and predictable rainfall (i.e., favorable conditions) did not ($G = 1$). All three species exhibited plasticity in germination fraction, with germination increasing with the amount of rain above a threshold of ~ 15 mm. The basic models presented here could be combined or made more elaborate for comparison with data sets from organisms with more complicated life histories.

III. How Seed Banks Affect the Way Selection Operates on Other Traits

The basic models presented in the previous section can be used to explore how seed banks affect and are affected by other traits. For example, we can demonstrate that natural selection in high seed-yield years may have a disproportionate impact on the direction of evolutionary change (Templeton and Levin, 1979; Brown and Venable, 1986). This occurs because the large influx of seeds in such years constitutes a population memory of selective events. Up to now the seed yield per germinating seed, S_i , has varied depending on the environment (i.e., it takes different values in different year types with different environmental conditions), but it has not been able to evolve. However, the values of this demographic parameter were important for determining how the within- and among-year timing of germination evolved.

Now let the seed yield per germinating seed be a function of some trait with heritable variation that is selected for under favorable environmental conditions but selected against under unfavorable conditions (e.g., low root/shoot ratio). For visualization, consider only two year types, favorable and unfavorable. We can plot the seed yield per germinating seed in favorable years on the x axis and the yield in unfavorable years on the y axis of a two-dimensional graph (Fig. 6). Seed yield, which varies under different conditions, would be represented as a point on this graph (for more year types it would be a point in some higher dimensional space). For illustration, let root/shoot ratio be a heritable trait that affects the seed yield per seed in the manner depicted in the curve drawn in Fig. 6. According to this curve (which we will call a "constraint set"), a higher root/shoot ratio gives a higher seed yield per germinating seed in unfavorable (e.g., dry) conditions. This would occur because greater allocation to roots makes it less likely for plants to die from desiccation. However a high root/shoot ratio would lower seed yield per germinating seed in favorable (wet) conditions because nutrients and energy that could have been creating more leaf area (resulting in more photosynthesis, growth, and ultimately seed set) were unnecessarily allocated to roots. We can now let root/shoot ratio evolve (resulting in changes in seed yield in favorable and unfavorable years) subject to the constraint set in Fig. 6.

It is possible to describe the slope of the constraint curve illustrated in Fig. 6 for the root/shoot ratio (and thus seed yields) of highest fitness

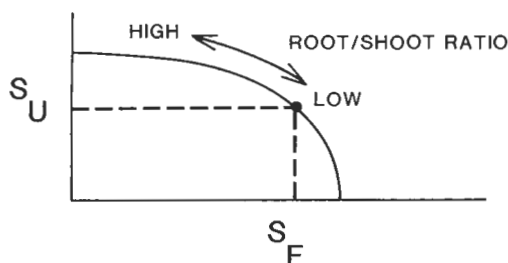


Figure 6. The constraint set for different feasible root/shoot ratios is plotted on axes of seed yield per germinating seed in favorable (S_F) and unfavorable (S_U) conditions. A higher root/shoot ratio results in higher seed yield per seed in unfavorable (dry) years because greater allocation to roots makes it less likely for plants to die from desiccation. It results in lower seed yield per seed in favorable (wet) years because nutrients and energy that could have been allocated to photosynthetically active tissue are unnecessarily allocated below ground. A particular root/shoot ratio is represented by a point on the curve. Evolution of root/shoot ratio is represented by movement along the curve of feasible root/shoot ratios.

for a given set of parameters (germination fraction, probability of favorable and unfavorable years, etc.). Then we can determine how this slope changes with a change in germination fraction (see Brown and Venable, 1986, for the mathematical details). As dormancy is increased (more and more seeds diverted into the seed bank), the slope becomes more negative, resulting in a lower root/shoot ratio and an increase in adaptation to favorable years.

But notice that the seed yields per germinating seed in the different environmental conditions experienced in different years also determine whether selection favors between-year dormancy. Thus the production of seed banks affects selection on traits like root/shoot ratios that in turn determine how selection operates on dormancy. This coevolutionary dynamic has been explored in detail by Brown and Venable (1986).

I will use this principle of selective interactions between seed banks and other traits to explore seed size, seed banks, and dispersal as an adaptive syndrome. To consider dispersal we must add complexity to the model. Consider a species or population distributed over a number of patches that have varying environmental conditions in space and time. In any single year, plants in some patches are experiencing favorable conditions while plants in others are experiencing unfavorable conditions (e.g., due to local disturbance or local predation). Also, conditions in each patch vary over time. There could actually be many different environmental conditions but for simplicity I will discuss only "favorable" and "unfavorable" conditions that result in high versus low expected seed yield per germinating seed.

Larger seed size is favored in conditions of shading or drought, which are unfavorable for the establishment and growth of plants (e.g., Baker, 1972; Gross, 1984; Wulff, 1986b). Small seeds are superior in moist open habitats where seed size is less critical for establishment, and where more seeds per unit energy or nutrients can be produced. Thus we can draw a constraint set for the evolution of seed size similar to that previously used for root/shoot ratio (Fig. 7). The basic expression describing population growth in a patch is almost the same as was used in Section II, B to model the evolution of between-year seed bank dormancy:

$$[GS_{ij} + R(1 - G)]$$

The extra subscript on S_i indicates that seed yield per germinating seed experiencing environmental conditions i is occurring in patch j . Summing over all patches ($j = 1, \dots, n$) we have

$$\lambda = \sum_{j=1}^n \{p_j [GS_{ij} + R(1 - G)]\} \quad (3)$$

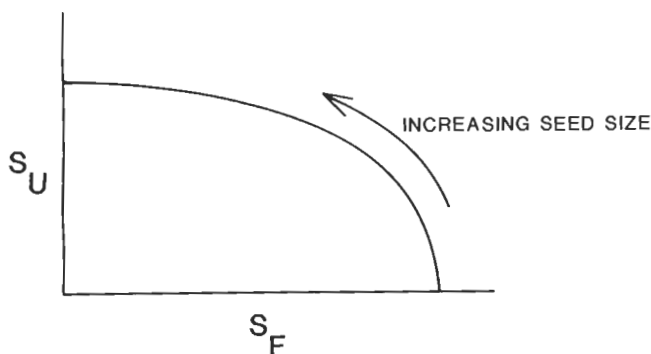


Figure 7. The constraint set for different feasible seed sizes plotted on axes of seed yield per germinating seed in favorable (S_F) and unfavorable (S_U) conditions. Larger seeds are assumed to result in higher seed yield per seed in unfavorable conditions while small seeds are assumed to result in higher seed yield per seed in favorable (open, moist) conditions.

where λ equals the finite rate of increase during a growing season for which we have specified the environmental conditions in each patch and the proportion of the seed bank in each patch. The proportion of the seed bank in each patch is designated by p_j . Finally, consider that there might be some dispersal-related mortality. If a is the survival of dispersing seeds and D is the proportion of seeds dispersing out of the parental patch, then the average number of seeds produced in all patches must be discounted by $1 - D(1 - a)$:

$$\lambda = [1 - D(1 - a)] \sum_j \{p_j[GS_{ij} + R(1 - G)]\} \quad (4)$$

Because this equation is the population growth rate for only 1 yr with a particular set of conditions, we must take the geometric average over all possible λ , each weighted by its probability of occurrence p_i .

Because of the difficulty of calculating geometric mean λ , a simpler procedure is to establish a number of patches in the computer and simulate population growth for any particular set of model parameters. Seed size can be varied by varying values of S_F and S_U , which are assumed to be determined by seed size, along a constraint set like that in Fig. 7. Dispersibility is determined by the proportion of seeds leaving the parental patch. Dispersing seeds could either be uniformly spread among all patches after suffering some dispersal related mortality, or they could be restricted to a few neighboring patches. To find the seed syndrome that yields the highest fitness in a particular environment, one searches for the three-dimensional adaptive peak by simultaneously

varying dispersibility, germination fraction, and seed size and calculating the geometric mean fitness after 1000 yr. Then different environmental parameters (such as the probability of favorable conditions or the pattern of spatial and temporal autocorrelation) can be varied one at a time to see in what direction the optimal three-dimensional seed syndrome shifts (see Venable and Brown, 1988, for more details on the simulations).

This procedure provides several important insights as to how selection simultaneously operates on seed size, dormancy, and dispersal. First, the risk-reducing properties of dispersal, dormancy, and seed size in variable environments are partly substitutable. That is, for a given set of environmental conditions, if one of the seed traits is arbitrarily shifted from the optimum, correlated selective pressures are generated on the other two traits to compensate. For example, if seed size is arbitrarily increased, a shift toward less between-year dormancy and less dispersibility is favored. The implication of this is that the optimal germination fraction (and thus the production of seed banks) depends on the dispersibility and the size of the seeds.

While the three seed traits are partly substitutable adaptations to variable environments, they are also complimentary in that they reduce risk in slightly different ways. Different environmental changes often preferentially favor one trait over another. Selection favoring one trait may elicit a correlated response in the other two traits, in addition to any other direct selective effects on them. For example, if the number of patches is increased, there is less overall risk [variability in Eq. (4)] from which to escape. With only one patch, the environment is either favorable or unfavorable in a given year; but with many patches, it is more likely to be favorable in some places and simultaneously unfavorable in others. Less overall risk favors less dispersal, less dormancy, and smaller seed size. Yet the presence of more patches with different environmental conditions creates a further opportunity for dispersal to lower risk by evening out the distribution of seeds among the varying patches. The net effect is selection for more dispersal. Because this further reduces variability in λ and risk, there is correlated selection for even further reduction in dormancy and seed size.

We also can explore how selection impinges on the seed syndrome when the probability of favorable conditions is increased, when the distance traveled (in terms of patches) by dispersing seeds is varied, and when the spatial and temporal autocorrelations of environmental variability are varied (Table 2; see Venable and Brown, 1988, for more details).

One important implication of selective trade-offs among seed traits is that it may be necessary to study traits in an integrated fashion. For example, in surveys of seed size, seed banks, and dispersal in which

Table 2
 Risk-reducing responses of seed size, dormancy, and dispersal to different environmental changes^a

Environmental change	Selective effect on seed syndrome ^b		
Increasing the number of patches	Dispersal ↑	Dormancy ↓	Seed size ↓
Increasing the probability of favorable conditions	Dispersal*	Dormancy ↓	Seed size ↓
Decreasing the effective dispersal radius	Dispersal ↓	Dormancy ↑	Seed size ↑
Increasing positive spatial autocorrelation	Dispersal ↓	Dormancy ↑	Seed size ↑
Increasing positive temporal autocorrelation	Dispersal ↓	Dormancy ↓	Seed size ↑

^aSee Venable and Brown, 1988.

^b ↑, Increases; ↓, decreases; *, dispersal increases with variance in environmental conditions.

attempts are made to explain patterns in terms of habitat factors or growth habits of the plants, there is a considerable amount of unexplained variance. Perhaps some of the variance can be accounted for by variation in correlated traits that share the job of risk reduction.

It is important to realize that the selective correlations discussed above are the result of fitness interactions due to the fact that they all reduce risk. Usually correlations between seed traits such as dispersal, dormancy, and seed size are discussed in terms of biophysical constraints. For example, it has been suggested that large seeds are less dispersible because of their greater weight or inertia (Salisbury, 1975; Fenner, 1985). Likewise, a correlation between seed bank production and seed size has been proposed based on the following scenario involving biophysical constraints. Small seeds are unable to emerge from great burial depth and as a result they often have evolved a light requirement for germination that leads to the production of a between-year seed bank (Thompson and Grime, 1979; Cook, 1980). The models presented here demonstrate that, regardless of any weight constraints, large seeds should be less dispersive because seed size and dispersal are complementary ways of reducing risk. Small seeds should have greater dormancy independently of any problems involved with burial. The question now concerns the importance of biophysical constraints in determining trait correlations as opposed to selection for trait correlations resulting from interacting population dynamic effects, such as traits sharing in risk reduction.

IV. Density Dependence and Kin Selection

By restricting my attention to density-independent models, I have focused on seed banks, dispersal, and seed size as avenues of adaptation to risk. These seed traits can also function as adaptations to escape the effects of local crowding or to escape the effects of competition with siblings (via kin selection). Crowding and sibling competition (which must be modeled using game theoretical approaches or explicitly genetic models because of their density/frequency-dependent nature) can also give rise to fitness interactions between seed traits. It can be shown that the density-escaping properties of seed banks, seed size, and dispersal can evolve even in the absence of uncertainty [in the sense of year-to-year variation in λ averaged over all patches; Eq. (4)] as long as there is local spatial and temporal variation in environmental conditions, and thus opportunities to escape the effects of crowding. The selective interactions are similar but not identical to the ones generated for the risk-reducing function of seed size, dispersal, and dormancy (J.S. Brown and D.L. Venable, unpublished data). These three seed traits can also evolve to escape the effects of sibling competition even in the absence of environmental variation, as long as there is some spatial structure to the environment (J.S. Brown and D.L. Venable, unpublished data). This occurs because, under competitive conditions, to germinate here and now rather than elsewhere or later is more likely to remove some fitness from a relative even if a germinating seed has the same expected fitness near the parent as elsewhere (or now, as at some future date). These matters are considered in Venable and Brown (1988). Ellner (1985a,b) analyzes the case for seed banks evolving to escape the effects of density and global uncertainty in a single patch environment. Levin *et al.* (1984) explore the interaction of dispersal and seed banks evolving to escape the effects of density in a globally risk-free environment. Hamilton and May (1977), Comins *et al.* (1980), and Schoen and Lloyd (1983) all examine how dispersal can evolve via kin selection even if the expected fecundity is the same in all patches at all times. Ellner (1987a) does the same for the evolution of a seed bank.

V. Community Seed Bank Patterns

By restricting consideration to single species models, I have ignored how seed banks may contribute to the coexistence of species and conversely how coexisting species may contribute to the evolution of seed banks. Chesson (1986) has explored how factors such as seed banks can create a "storage effect" that permits coexistence in temporally varying

environments of species that would otherwise not coexist. The basic idea is that if interspecific competition mostly affects the seed yield component of the life cycle (but not the survival of dormant seeds), an annual can persist through many competitively (or abiotically) unfavorable years via a seed bank that is replenished in occasional years, when competition is escaped and when underlying abiotic variability is favorable. Thus a number of competing species can coexist if each can replenish its seed bank at some time when the other species are at low density.

Ellner (1987b), Cohen (1987), and Schmidha (personal communication) have considered how species interactions affect the evolution of dormancy strategies in what may be called "the community evolutionary stable strategy." The basic idea can be encapsulated in the following scenario. If a dominant species achieves its optimal dormancy strategy in a variable environment, it will tend to survive and reproduce more in some years and less in others. If a second species is competitively inferior, otherwise favorable years will be unfavorable for it because of the high density of the dominant species. Thus the optimal dormancy strategy of the second species will be shifted to utilize the temporal variation differently and have peak years that do not coincide with those of the dominant. If two species are coevolving in this way, one may become a low-risk species with a large seed bank, producing a few seeds even in the worst years and never very many in good years, because most of the seed bank remains dormant. The other species may then become a high-risk species that is only successful in a subset of very favorable years; the high germination fraction results in boom and bust years. This divergence in the use of temporal variation creates more times when each species escapes the competitive effects of the other. Models of this nature suggest that if competition is strong enough, the seed bank biology of similar species in similar environments, which might otherwise be expected to be convergent, may diverge. These ideas could be generalized to the community evolutionary stable strategy of seed size, dispersal, and dormancy syndromes for a set of species.

VI. Summary and Conclusions

Many questions regarding the ecology and evolution of seed banks are relatively easy to model and require fairly simple mathematics and programming skills. I have focused on the questions of the timing of germination within years, of when it is adaptive to produce a between-year seed bank and what proportion of seeds should remain dormant between years, of how the timing of germination within and among years

may be expected to vary with different environmental cues, of how fitness interactions are likely to provide links between seed bank ecology and other life history traits (e.g., root/shoot ratio, dispersibility, and seed size), of some of the implications of density dependence and kin selection for the evolution of seed banks, and of how interactions among species may affect community patterns of seed bank production.

Many interesting questions remain to be modeled, the most obvious being combinations of the factors discussed above. How does the presence of a between-year seed bank alter selection for within-year timing of dormancy? How do interspecific interactions favor different dormancy/dispersal strategies? How do various aspects of the perennial life cycle (e.g., vegetative reproduction) affect the evolution of dormancy/dispersal strategies?

Models can be made less heuristic and to mimic a particular system more closely. This can often be done without increasing conceptual complication, although a shift from analysis to simulation or to a bigger computer may be required. Some simple applications to particular annual plant species were analyzed and provided insights into the plants' seed bank biology and suggested new questions in need of empirical exploration.

A close interaction between theoretical and empirical studies will sharpen our insights of seed bank functions. The models presented here suggest numerous patterns and mechanisms to be tested empirically. For example, can the explicit consideration of dispersal and seed size significantly improve our ability to explain the ecological patterns of seed bank formation? Do seed bank species have traits that tend to specialize them more (compared to nonseed bank relatives) for favorable subsets of conditions? Are there density-dependent or individual-fecundity-dependent shifts in dispersal, dormancy, or seed size? To what extent can population dynamic data, fit to simple models, accurately predict actual patterns of within- and between-year timing of dormancy and predictive dormancy? Indeed, many of the interesting ecological patterns in seed bank production documented in the different chapters of this book beg for models of the possible mechanisms explaining them.

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