

Delayed Germination and Dispersal in Desert Annuals: Escape in Space and Time

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Summary. A model is developed to consider the interplay between dispersibility and delayed germination in desert annuals. The model explores the effect of low levels of dispersal, considered realistic for annual plants, on optimal germination fraction. The model also demonstrates the effect of the amount and accuracy of “predictive” (responsive to the environment) dormancy on the optimal innate germination fraction (not responsive to environmental conditions).

Optimal germination fraction is found to be very sensitive to changes in dispersibility especially at the limited dispersibilities that are realistic for annual plants. As dispersibility increases, optimal germination fraction increases. If plants make two kinds of seeds with differing dispersibility, reproduction is maximized if the low dispersal seeds have delayed germination and the high dispersal seeds have quick germination. If dormancy mechanisms permit seeds to germinate when environmental conditions allow successful maturation, and remain dormant when environmental conditions do not permit successful maturation, what fraction of seeds should remain dormant under predicted good conditions as a hedge against inaccurate prediction of the environment? If environmental cues that break dormancy are uncorrelated with environmental conditions that permit successful maturation, predictive dormancy has little or no effect on the optimal innate germination fraction. When predictive dormancy lowers the probability of germinating when environmental conditions preclude successful maturation, the optimal innate germination fraction increases with increasing germination control by predictive dormancy. With a moderate degree of germination control by predictive dormancy, the optimal innate dormancy is still sensitive to changes in dispersal in the low dispersal ranges characteristic of annual plants.

Evidence is presented from plant species that have both dispersal and germination dimorphisms to support the predicted correlation of high germination fractions with high dispersal.

Introduction

The evolution of life histories is a subject that has provoked considerable discussion in recent years, and life histories have come to be viewed as interacting suites of adaptations. One line of inquiry has explored the effect of environmental uncertainty and variability in shaping survivorship and fecundity schedules (e.g.

Murphy 1968; Schaffer 1974; Hastings and Caswell 1979). For annual plants, seeds attain tremendous significance as the only link to the future. This contrasts with perennials whose vegetative perennation buffers them from the negative impact of bad seed years. For annuals, only two strategies are possible when unsuitable conditions arise: escape in space or escape in time. Annuals may escape spatially to new ephemeral patches via seed dispersal or they may escape in time by fractional or delayed seed germination. Clearly, the spatial and temporal patterns of habitat suitability will determine the relative merit of escape in space or time.

This paper explores how the germination fraction of annual plants in variable environments may evolve in response to their ability to disperse seeds and in response to environmentally induced or enforced dormancy. A relatively high innate dormancy provides a hedge against unsuitable environmental conditions in the local environment and would be expected in plants with poor dispersibility. Plants with the ability to disperse seeds to a large number of different environments may reach a few suitable habitats even though most habitats may be unsuitable. In such cases it would be advantageous to have a relatively low innate dormancy since high fecundity in the few successful sites would likely outweigh the failures of the many seeds germinating elsewhere. On the other hand, even with poor dispersability it would be advantageous to reduce the innate dormancy if dormancy could be environmentally enforced under unsuitable conditions.

Some of these possibilities have been developed in models of optimal germination by Cohen (1966, 1967) and MacArthur (1972). Cohen (1966) constructed a model of desert annuals that optimize their reproduction in randomly varying environments by fractional germination such that a proportion of seeds is subjected to the current environment and a proportion remains dormant as a hedge against unsuitable conditions. Some statistical comments on Cohen's model by MacArthur (1972) suggest a way to construct a model that explicitly considers the effect of dispersal on optimal germination. MacArthur uses the arithmetic mean of reproduction in environments of different quality as a fitness criterion rather than Cohen's geometric mean. However, MacArthur's discussion leaves some unanswered questions concerning the appropriate use of geometric and arithmetic means as fitness criteria in life history models.

The biological basis for choosing one of these over the other will be developed more explicitly in this paper in the context of spatial and temporal patterns of habitat suitability and dispersal. To make these models more generally applicable and more biologically realistic, low levels of seed dispersal will be emphasized as will the recognition that the amount of germination is not genetically fixed, but may be subject to considerable environmental

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modification. Environmental modification of the amount of germination will be termed “predictive” germination or conversely predictive dormancy under the assumption that plants have evolved germination responses that correlate germination with ensuing good conditions for maturation.

As with other ecological optimization models, specific genetic mechanisms and constraints are not considered. Thus, elaborate assumptions about unknown genetic mechanisms are avoided and the models indicate the direction selection should lead, given a certain set of ecological constraints. Evolving populations may or may not approach such optima depending on the specific form of genetic constraints. The optimal solutions do represent evolutionarily stable strategies since, if the optimal life history is attained, no alternative life history will be able to replace it.

I. Optimal Germination Fraction. No Dispersal (Cohen's Model)

In Cohen's (1966) simplest model he explored the relationship of optimal germination fraction to the quality of an unpredictable environment. He modeled an annual plant, the seeds of which either germinate or postpone germination and suffer some mortality. Cohen included a parameter describing seed mortality in the soil. However, when MacArthur discussed this model he omitted seed mortality to simplify the exploration of other variables on optimal germination strategy. We will follow MacArthur in ignoring the straightforward and intuitive effect of seed mortality. With this simplification, Cohen's model becomes:

$$\lambda_c = (GS + 1 - G)^p (1 - G)^q$$

where λ_c is the finite rate of increase or annual growth multiple, G is the fraction of seeds germinating, S is the seed set of a successful plant, p is the probability of a “good year” and q is the probability of a “bad year”. Good and bad years are defined in terms of survival from germination to maturity. In a good year each seed which germinates is assumed to reach maturity and produce S seeds; to these new seeds we must add those still in the soil that did not germinate, so the seed pool is increased by the factor $(GS + 1 - G)$. Conversely, in a bad year none of the seeds which germinate reach maturity and the seed pool is reduced by the factor G . In this formulation the germination fraction (G) is a constant that does not vary with the environment, thus there is no predictive germination possible. Cohen shows that maximizing the finite rate of increase, λ , yields the optimal innate germination fraction as:

$$\hat{G} = \frac{Sp - 1}{S - 1}.$$

For S larger than about 20, the prediction of this simple model is that when predictive germination is not possible the optimal germination fraction roughly equals p , the probability of “good” years.

II. Dispersal and Germination General Considerations

A. Arithmetic vs. Geometric Mean as Fitness Criteria

Cohen's model uses the geometric mean of population increase in good and bad years. A clear understanding of the biological

implications of using the geometric vs. arithmetic mean is a prerequisite to understanding the dispersal model developed in this paper. MacArthur (1972) points out that in Cohen's formulation, p and q are not probabilities but are the exact a posteriori fractions of a single sequence of good and bad years. Cohen's treatment ignores the fact that, when p and q are treated as probabilities, there is a finite probability that all years could be good, all bad, or any intermediate combination. The probabilities of the possible combinations are given by a binomial distribution. MacArthur summarized the large number of possible outcomes by calculating their expected value or arithmetic mean. When the exponents in Cohen's formula for the geometric mean of good and bad years are allowed to vary in a binomial fashion, the expected value of Cohen's formula is MacArthur's λ :

$$\lambda_m = p(GS + 1 - G) + q(1 - G). \quad (1)$$

This expected finite rate of increase is the *arithmetic average* of all the possible combinations of good and bad years weighted by the probabilities of each sequence and its reproductive consequences. In effect, a series of years, randomly assigned as good and bad, is replicated a large number of times and an arithmetic average is taken of all the replicates. For $pS > 1$, this function is maximized when the germination fraction (G) equals one. This is a peculiar result since a population would go extinct when it hit the first bad year and all germinating seeds died.

To see why the geometric mean yields a superior model in this simple case, consider what happens in a single habitat over a single sequence of T years. With p as the probability of good years, some proportion of years will actually be good. This actual proportion of good and bad years, a and b , may deviate from the probabilities p and q (according to a binomial distribution), but in a single sequence of T years there are no replicates. After T years $(GS + 1 - G)^a (1 - G)^b$ will represent the actual growth for that population. Taking the T^{th} root to convert to a per year basis yields Cohen's equation with a and b substituted for p and q . So even with a more careful probabilistic phrasing of the problem, and with no replicates of our habitat patch, Cohen's solution involving the geometric mean is nearly correct except that his optimal solution has a variance; a and b vary in a binomial fashion around their means p and q . If a population experiences one set of conditions at a time, a fraction of the seeds should remain dormant as a hedge against uncertainty since a growth multiple of 0 results in extinction.

To this point we have considered only a single patch of habitat that experiences a sequence of good and bad conditions. Now consider a spatially variable environment consisting of a large number of such patches with independent weather regimes. What can now be expected to evolve? Within any one patch, the most successful germination fraction will be one that most closely approximates a , the actual proportion of good years in that patch. However, if reproduction summed over all patches is maximized, either in one year or over a number of years, the arithmetic mean of λ is maximized as in Eq. (1) since each patch is contributing additively to the overall λ . But dispersal has an essential role in such a model; if there is no dispersal between patches MacArthur's arithmetic mean is inappropriate for two reasons: 1) with no dispersal this maximization of reproduction summed over all patches is occurring in an unusual fashion because many populations are going extinct while unlimited geometric increase is occurring in a few patches with long runs of good years. If any type of density dependence were placed on these rare extraordinarily successful patches, the optimal germination fraction would be less

than one and in fact a metapopulation with Cohen's optimal germination fraction calculated using the geometric mean will have higher reproduction summed over all patches than one with $G=1$ calculated using MacArthur's arithmetic mean. 2) if patches were completely isolated with no dispersal between them, selection would occur independently in each patch and no mechanism can be invoked to justify maximization of reproduction summed over all patches.

On the other hand, if individual plants disperse their seeds across a large number of different patches, MacArthur's expected yearly growth rate which averages reproduction over a large number of independent Cohen "deserts" is an appropriate criterion of fitness. Selection does not occur independently in each patch and the effects of density in successful patches will be mitigated by dispersal. $\bar{G} \approx 1$ and unsuccessful patches (where local extinction occurs) are constantly being recolonized. The probability that all patches are bad at any one time is small and successful reproduction of seeds arriving at good patches mitigates the losses of those dying in bad patches.

In summary, there are conditions under which the expected value of λ or arithmetic average fecundity is inappropriate to model plant populations. But there are also conditions under which the geometric mean fecundity is inappropriate and the arithmetic mean must be used. Dispersal is the critical factor determining whether the arithmetic or geometric mean is the appropriate fitness criterion. The extreme alternatives are: (1) in an isolated single habitat patch with no dispersal the genotypes that will be most successful will have germination varying around $G=p$ with the patch to patch variance of germination fraction determined by the random nature of environmental conditions and the genetics that determine how long adaptations "remember" the past (geometric mean), and (2), environments where seeds are dispersed evenly to a large number of different patches every year, plants with germination fractions approaching 1 will leave more progeny as a result of windfall reproductive returns from the few seeds making it to good habitats (arithmetic mean).

The more probabilistic formulation of Cohen's result points to another interesting biological result. Evolution can be considered as a historical process whereby gene pools change but retain in their allele frequencies a memory of the past (Lewontin, 1966). Thus the variance of the a 's around p and the variance of the optimal germination fraction depends on how many years (T) we choose to average in calculating a , the proportion of good years. If $T=1$, the optimal germination frequency would be zero after a bad year and 1 after a good year. If T were very large, $\bar{G} \approx p$ with very little variation since the average over a large number of years is very stable. Most imaginable genetic systems would result in the current germination fractions being a weighted average of the past environments with the weights of the most recent past being much greater than those of the more distant past. Thus, the germination fraction that evolves in a single isolated patch will be a moving average of the actual unfolding of the weather probabilities p and q .

B. Realistic Patch Sizes and Dispersal

The dispersal model presented above (based on the arithmetic mean of reproduction in a number of patches) involves MacArthur's, "separate deserts each like the others except that its climate is determined independently", with each plant spreading its seeds equally among these "separate deserts". Using desert annuals as an example; let us consider the realism of such a

model. What are realistically sized patches of water availability, and how likely are they to be independent of one another? What are realistic dispersal distances and are they adequate to generate the germination optima suggested in the model?

Regarding dispersal, the important question is what proportion of seeds are deposited at various distances. There is much anecdotal evidence concerning dispersal in plants, however, documentation of spatial patterns of dispersal is rare. For species of annuals that have been documented, the bulk of the seeds remain very near the parent plant, even for those with good dispersal mechanisms. Only a small fraction of the seeds escape to any great distance (Levin and Kerster, 1974). Recorded dispersal distances are on the order of meters for the majority of seeds. Thus, patches must be small if seeds are to disperse to a large number of them and, even so, most seeds will not disperse a great distance.

Patches of water availability may be generated by local thunderstorms which are typical of deserts. Such storms may occur independently of one another in a fairly random manner, but they generate patches that are too large for significant numbers of seeds to disperse across a number of them as the model requires.

On a more local scale, small differences in surface topography and soil permeability may create tremendous variations in moisture conditions. A small depression a few feet across may catch a tremendous amount of runoff (Koller, 1969). Such small scale patches are likely to be relatively permanent but can be shown to create a shifting pattern of habitat suitability. If seeds can be "predictive" in their germination, they will not germinate when the environment is highly unsuitable. Intermediate, ambiguous environmental signals are more detrimental than totally unsuitable ones since they may trigger germination when the subsequent environment is unsuitable for maturation. Consider, for example a rise and a nearby depression in a desert. With moderate rain the seeds on the rise may germinate, but the seedlings may dry out and die, while seedlings have good growing conditions in the depression. With less rain, seeds on the rise will not germinate, but those in the nearby depression may germinate and die. In the first case, the seeds in the depression experience better conditions, while in the second case, seeds on the rise do. The better conditions in the first case result in present reproduction while the better conditions in the second case permit future reproduction when there is even more rain.

A scheme of this sort involves patch sizes suitable for dispersal of a proportion of a plant's seeds out of the parental patch and provides for habitat suitability to shift around. However, the assumption of even dispersal among such patches is unrealistic for plants. We will instead consider that only a fraction of a plant's seeds escapes the parental patch and only this fraction experiences numerous variable environments.

III. The Models

A. Effects of Dispersal on Optimal Germination Fraction

The fraction of a plant's seeds remaining in the parent patch will experience one set of conditions at a time. Their reproduction is best described by the Cohen model which considers the geometric average of a series of multiplied growth factors. For the sake of simplicity we will assume a very stable genetic system so that T is large and a is held tightly around p due to spatial and temporal averaging. Thus p can be substituted for a with little loss of accuracy and much gain in ease of presentation.

The seeds that disperse out of the parental patch will experi-

ence both good and bad conditions depending on where they land. Reproduction of the dispersing fraction is described by MacArthur's model [Eq. (1)] which considers the arithmetic average over all these spatial patches. Let us define D as the proportion of the seeds on an adult plant that disperses out of the parental patch. We will assume that only newly produced seeds borne on adult plants can disperse. That is, seeds already in the soil are not redistributed. Even though we specify a proportion D of newly produced seeds that disperse, the fraction D^1 of all seeds that disperse will be somewhat less since there are some non-dispersing seeds in the soil. Though D is a constant, D^1 is affected by the size of the seed reserve from the past and hence the germination fraction. With this in mind we can now construct the following model:

$$\lambda_{\text{total}} = D^1 \lambda_m + (1 - D^1) \lambda_c$$

or

$$\lambda_{\text{total}} = D^1 [G(pS - 1) + 1] + (1 - D^1)(GS + 1 - G)^p (1 - G)^{1-p} \quad (2)$$

where λ_m and λ_c are MacArthur and Cohen's growth multiples as defined and discussed earlier and D^1 is the dispersing fraction of all seeds corrected for the non-dispersing seeds in the soil.

The corrected dispersal fraction, D^1 , can be calculated in the following way. First, we must calculate the expected number of seeds next year from one seed this year. Then we must determine which of these expected seeds are dispersing and divide the expected number of dispersing seeds by the expected total number of seeds. The expected number of seeds next year from one this year is $(1 - G) + pGS(1 - D) + pGSD$. This includes the seeds that don't germinate, $1 - G$; offspring of germinating seeds that don't escape the parental patch, $pGS(1 - D)$; and offspring of germinating seeds that do escape the parental patch $pGSD$. This includes all possible fates. Only $pGSD$ seeds are expected to disperse. After collecting terms, this ratio of dispersed to total seeds reduces to:

$$D^1 = \frac{pGSD}{G(pS - 1) + 1}$$

as the dispersal fraction corrected for the seeds in the soil.

Substituting this expression for D^1 in Eq. (2) and setting

$$\frac{\partial \lambda}{\partial G} = 0$$

yields the following equation:

$$D = \frac{\frac{pS}{\hat{G}S + 1 - \hat{G}} - 1}{pS \left[\frac{\hat{G}[pS - \hat{G}S + 1 - \hat{G}]}{(\hat{G}(pS - 1) + 1)(\hat{G}S + 1 - \hat{G})} + \frac{1 - \hat{G}}{(\hat{G}(pS - 1) + 1)^2} - \frac{(1 - \hat{G})^p}{(\hat{G}S + 1 - \hat{G})^p} \right]} \quad (3)$$

This model generates the combinations of G 's and D 's that maximize the expected reproduction of individuals that have a fraction of seeds restricted to the home patch and a fraction escaping to a variety of other patches. This model differs from both Cohen's and MacArthur's in that it contains a term for dispersibility and thus permits the level of dispersal to be explicitly set at any desired level. This is an advance over MacArthur's model since we can now model low levels of dispersal that are realistic for plants.

Optimal germination fraction calculated for a given dispersal

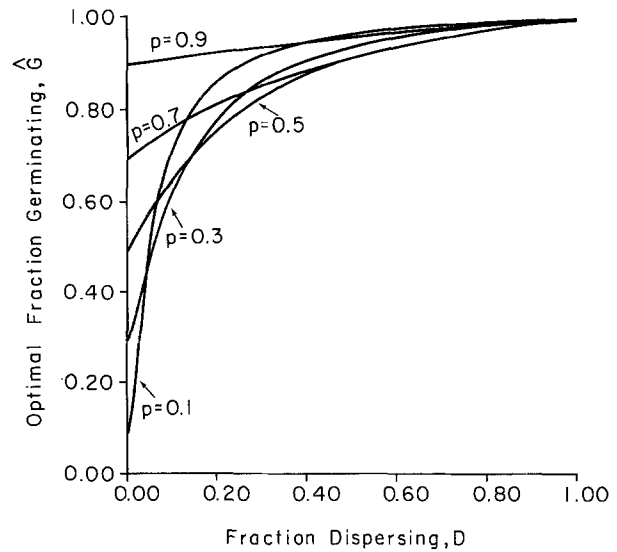


Fig. 1. Effect of dispersal on optimal germination fraction. Each curve represents a different environment characterized by the probability of experiencing good conditions (p). 50 seeds per successfully reproducing adult (S). See Eq. (3)

fraction, D , from Eq. (3) are shown in Fig. 1 for various values of p and q , the probabilities of good and bad environments. In the case of no dispersal, where the plots of optimal germination fraction versus dispersal fraction intersect the ordinate, this model reduces to Cohen's model. Likewise at the point where $D=1$, the model reduces to MacArthur's model where $\hat{G}=1$.

The most important consequence of this analysis is that *with a low dispersal fraction ($D < 0.15$), optimal germination is very sensitive to changes in dispersal*. This implies that low levels of seed dispersal, such as are reported in most plant dispersal literature, may be adequate to significantly affect the optimal germination fraction. This is especially true when the frequency of good environments is relatively low ($p=0.1$). Thus, the *sensitivity of optimal germination to dispersal should be more pronounced where high quality environments occur relatively infrequently (low p)*.

Notice that at low levels of dispersal (e.g. $D < 0.05$) the optimal germination fraction is higher for plants in better environments (see Fig. 1). At slightly higher dispersal levels (e.g. $0.10 < D < 0.30$) the plants in lower quality environments ($p=0.1$) have the higher optimal germination frequency. Since \hat{G} is the germination fraction that maximizes $\lambda_{\text{total}} = (1 - D^1)\lambda_c + D^1\lambda_m$, it will be a compromise between the germination fraction maximizing λ_m and that maximizing λ_c . If G is shifted toward 1, λ_m increases, but if G is shifted toward p , λ_c increases. Since \hat{G} is adjusted to maximize λ_{total} , its position depends on the relative contribution of dispersing and non-dispersing seeds to λ_{total} . In a poor environment (e.g. $p=0.1$), λ_c will be low since plants in any one patch will have relatively few opportunities to reproduce there. Optimal germination fraction rises steeply with dispersal since λ_m is important relative to λ_c , and high germination fractions increase λ_m . In good environments (e.g. $p=0.9$), more seeds will be able to mature and reproduce successfully in the parental patch (high λ_c) and the relative contribution to λ_{total} of the dispersers and non-dispersers will not be so different. \hat{G} will rise more slowly with increasing dispersal. For the extreme case where $p=1$ and all years are good everywhere, seeds will be equally successful whether they disperse or not and \hat{G} will not change at all with dispersal.

The compromise nature of \hat{G} has important implications for the possible relationship between germination and dispersal in species with dimorphic seeds. If information were available to a plant as to which of its seeds would be the good dispersers, it could adjust its germination accordingly and not be forced to compromise. Thus, *plants with seed dispersal polymorphisms due to size or shape are expected to have corresponding germination polymorphisms* with non-dispersing seeds having fractional germination and dispersers having quick germination. In the present model, this would lead to higher λ_{total} , all else being equal. Specifically, the fraction of $(1-D)$ seeds should have \hat{G}_c approximately equal to p , whereas the dispersing fraction D should have $\hat{G}_m = 1$.

B. Effects of Predictive Germination on Optimal Germination Fraction with no Dispersal

Up to now the models have not explicitly considered the possibility of seeds adjusting their germination to cues indicative of environmental quality. Deserts may exhibit variable and seemingly random weather patterns but they are not truly unpredictable. Predictive germination strategies are well known for many plants (Juhren et al. 1956; Koller 1956, 1972, 1969; Lahari 1961, 1962; Mayer and Poljakoff-Mayber 1975; Mott 1972, 1974; Went 1948, 1949). First the effects of incorporating predictive germination into Cohen's simple model (which ignores dispersal) will be explored. Both the amount and accuracy of predictive dormancy will be permitted to vary (see Fig. 2).

A distinction must be made between the actual quality of the environment and the environmental quality predicted by the plant. The environment will either supply adequate moisture for maturation and seed set and thus be actually "good" (G_a), or not provide adequate moisture and be "bad" (B_a). Likewise, the seeds can either germinate in response to some signal indicating that the environment is likely to be good (G_p) or not germinate in response to some signal that the environment will be bad (B_p). There are four possible combinations of actual and predicted environments ($G_p \cap G_a$), ($G_p \cap B_a$), ($B_p \cap G_a$), ($B_p \cap B_a$). If the actual environment is moist enough for maturation and seeds germinate, the seed pool is multiplied by $(GS + 1 - G)$. This occurs with probability $u = P(G_p \cap G_a)$. The worst environment is that where an inadequate moisture supply is predicted to be adequate and seeds germinate and die. This error occurs with probability $v = P(G_p \cap B_a)$ and results in reducing the seed pool by a factor G . If seeds do not germinate because the environment is predicted as bad, the seed pool is multiplied by 1 regardless of whether the environment was actually good ($B_p \cap G_a$), or actually bad ($B_p \cap B_a$). This is in keeping with the assumption of no mortality for those seeds not germinating. We will designate the probability that the environment is predicted to be bad and no germination occurs as $w = P(B_p) = P(B_p \cap G_a) + P(B_p \cap B_a)$. For the case of no dispersal, this gives rise to the following equation:

$$\lambda_c = (GS + 1 - G)^u (1 - G)^v (1)^w. \quad (4)$$

Differentiating and setting $\frac{\partial \lambda}{\partial G} = 0$ yields

$$\tilde{G} = \frac{uS - (u + v)}{(S - 1)(u + v)} \quad (5)$$

as the optimal germination fraction. Predictive dormancy, w , can increase as is represented in Fig. 2 by increasing the area covered by hatch marks. The accuracy of prediction is determined for

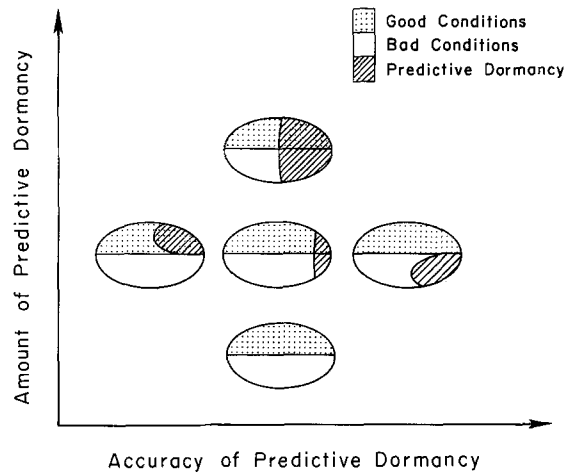


Fig. 2. The Venn diagrams partition all possible environmental conditions in two ways: 1) "actual" good (stippled) and bad (unstippled) conditions for survival of germinated seedlings to reproductive maturity and 2) "predicted" good (unhatched) and bad (hatch marks) conditions for maturation of seedlings. When the environment is predicted to be bad, seeds remain dormant (predictive dormancy). The amount of predictive dormancy is determined by the area covered by hatch marks reflecting the proportion of all possible environments in which seeds can be expected to remain predictively dormant. The accuracy of predictive dormancy reflects how well the predicted bad conditions coincide with actual bad conditions. (see text, p. 276).

a fixed value of w , by whether the dormancy is occurring when actual conditions are good or when actual conditions are bad. In the figure this is represented by superimposing predictive dormancy on good conditions or bad conditions. In the probabilistic terminology used above, the accuracy of prediction is varied by varying the partition of w into its two components, $P(B_p \cap B_a)$ and $P(B_p \cap G_a)$. These two components reflect whether the dormancy occurs when plants could mature or when-germinating plants would die. Their relative probabilities $\frac{P(B_p \cap B_a)}{P(B_p \cap G_a)}$ describe the accuracy of prediction. The magnitude of w can be considered as the amount, as apposed to the accuracy, of predictive dormancy (move vertically on Fig. 2).

Notice \hat{G} now becomes \tilde{G} , which is the optimal fraction to germinate when the environment is predicted to be good, i.e. $\hat{G} | G_p$, since predictive ability allows plants not to germinate when the environment is predicted to be bad, i.e. $\hat{G} | B_p = 0$. \tilde{G} is an inherent aspect of the germination strategy of the plant and as such can be considered an evolved constant. It is an aspect of what Harper (1957, 1977) calls innate dormancy that is characteristic of genotypes and species. \tilde{G} could be measured as the germination fraction under favorable environmental conditions. Our predictive dormancy ($\hat{G} | B_p = 0$) is similar to Harper's enforced dormancy which he defines as dormancy imposed and maintained by environmental conditions. The actual germination fraction changes constantly with changing environmental signals.

Selection is expected to adjust the partition of dormancy into its innate and predictive components so as to maximize λ . It should be clear that an increase in predictive dormancy increases λ only as long as it is relatively effective at allowing seeds to escape unsuitable environmental conditions. As the amount of prediction continues to increase a point is reached at which dor-

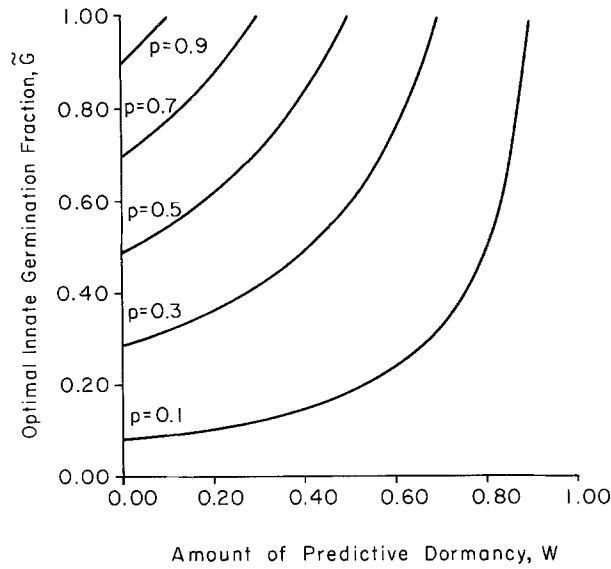


Fig. 3. Effect of predictive dormancy (w) on optimal germination fraction (\tilde{G}) when predictions are always correct. Each curve represents a different environment characterized by the probability of experiencing good conditions (p). 50 seeds per successfully reproducing adult (S). No dispersal. See Eq. (5)

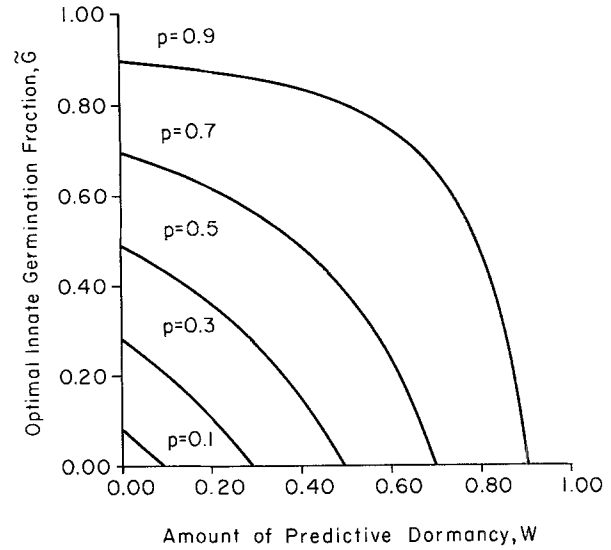


Fig. 4. Effect of predictive dormancy (w) on optimal germination fraction (\tilde{G}) when predictions are always incorrect. Each curve represents a different environment characterized by the probability of experiencing good conditions (p). 50 seeds per successfully reproducing adult (S). No dispersal. See Eq. (5)

mancy causes seeds to miss good environmental conditions as well as unsuitable ones, and λ no longer increases. The amount and accuracy of prediction at this point are determined by the specific constraints of the particular system under consideration. Rather than develop this model quantitatively, we will show how optimal germination for the innate component of germination fraction (\tilde{G}) can be calculated for any given amount and accuracy of predictive dormancy.

Figures 3, 4, and 5 give the results for three possible mappings of germination onto environments. In each figure the amount of predictive dormancy (w) varies in different environments. Each environment is represented by a constant proportion of actual good and bad years, $p/q = P(G_a)/P(B_a) = C$. Figures 3 and 4 show the opposite extremes of accuracy of prediction.

In Fig. 3, the accuracy of prediction is assumed to be perfect, that is, $P(B_p \cap G_a) = 0$. An increase in $w = P(B_p \cap B_a)$, the predictive dormancy, results in a decrease in $v = P(G_p \cap B_a)$, the probability of germinating and dying, but has no depressing effect on $u = P(G_p \cap G_a)$, the probability of germinating and reproducing. Thus, good years are always predicted correctly as being good and the only mistakes are possibly perceiving bad years as good. Under these conditions, as w increases, the optimal germination fraction (\tilde{G}) increases as well. The increase of \tilde{G} with w seems reasonable since correctly predicting bad years and avoiding them by remaining dormant removes some of the uncertainty involved in germination. \tilde{G} won't have to be kept low as a hedge against uncertainty.

Figure 4 illustrates the opposite and unlikely extreme in which the seeds are always mistaken when they predict an unsuitable environment. Accuracy of prediction $\frac{P(B_p \cap B_a)}{P(B_p \cap G_a)}$ equals zero which means that these seeds are always wrong when they predict bad years. As $w = P(B_p \cap G_a)$ increases, $u = P(G_p \cap G_a)$ decreases, but $v = P(G_p \cap B_a)$ remains constant. Everytime the environment is actually bad, seeds germinate and die. However, they do occasionally predict bad years and remain dormant when the environment is actually good. As might be expected, increasing such erroneous

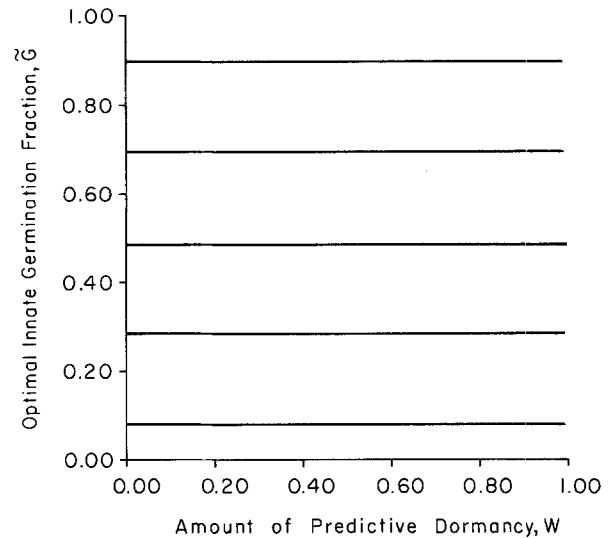


Fig. 5. There is no effect of predictive dormancy (w) on optimal germination fraction (\tilde{G}) when predictions are statistically independent of environmental quality. Each curve represents a different environment characterized by the probability of experiencing good conditions (p). 50 seeds per successfully reproducing adult (S). No dispersal. See Eq. (5)

predictions lowers the probability of successful reproduction and \tilde{G} is lowered as a hedge against this uncertainty. Figures 3 and 4 represent opposite extremes of accuracy and any less extreme degree of accuracy will result in an intermediate optimal germination fraction for a given probability of good years.

An important intermediate case is shown in Fig. 5. This is the transitional case where increasing the amount of predictive dormancy (w) causes neither an increase nor a decrease of optimal G . This result occurs when prediction is uncorrelated with actual

environmental conditions. As w increases, the ratio of u (the probability of germination and reproduction) to v (the probability of germination and death) remains equal to the ratio of the probabilities of good to bad environments $\frac{u}{v} = \frac{p}{q}$. In other words, if the probability of germinating given a good environment equals the probability of germinating given a bad environment, increasing the tendency to predict has no effect on optimal innate germination fraction. The conditions that give rise to this transitional case are elaborated more fully in Appendix I.

In summary, the effect of predictive dormancy (w) on optimal innate germination fraction (\tilde{G}) depends on the accuracy of prediction. If the accuracy of prediction is better than random, increasing the predictive dormancy (w) will increase the optimal innate germination fraction (\tilde{G}). This is intuitive since keeping \tilde{G} low is a hedge against mistakenly germinating and dying. More specifically, if the probability of germinating and reproducing increases relative to the probability of germinating and dying such that u/v is greater than p/q (the ratio of the probabilities of actual good to bad environments), \tilde{G} will increase as w increases. If the reverse situation holds such that as predictive dormancy (w) increases, the ratio u/v is less than the ratio of actual good to bad environments (p/q) the optimal germination fraction (\tilde{G}) will decrease.

C. Effects of Prediction and Dispersal on Optimal Germination Fraction

Dispersal can now be introduced into the predictive germination model. The new formula for $\lambda_{\text{total}} = (1 - D^1)\lambda_c + D^1\lambda_m$ can be readily constructed from our previous models. Equation (4) is the formula for λ_c when prediction is possible. Since we are assuming that when seeds remain dormant with probability $w = P(B_p)$, the seed pool is neither decreased nor increased, Eq. (1) now becomes $\lambda_m = u(GS + 1 - G) + v(1 - G) + w$. In this equation, the probability of seeds remaining predictively dormant, is multiplied by 1, indicating that when seeds remain dormant, the seed pool neither increases nor decreases. The following equation allows the amount of dispersal to vary and is analogous to Eq. (2) in which predictive germination was not possible:

$$\lambda_{\text{total}} = D^1[u(GS + 1 - G) + v(1 - G) + w] + (1 - D^1)(uGS + 1 - G^v)(1 - G)^v. \quad (6)$$

In a manner analogous to the case for no prediction, D^1 is calculated to be $\frac{uDG\tilde{S}}{u(G\tilde{S} - G) - vG + 1}$. This was calculated by knowing D , the fraction of new seeds that disperse, and calculating the expected number of dispersing seeds and the total expected number of seeds to give the fraction of all seeds that disperse.

Substituting for D^1 , differentiating and setting $\frac{\partial \lambda}{\partial \tilde{G}} = 0$ yields:

$$D = \frac{\frac{v}{(\tilde{G} + 1)} + \frac{u(S - 1)}{(\tilde{G}S + 1 - \tilde{G})}}{uS \left\{ \frac{\tilde{G}}{u\tilde{G}S - u\tilde{G} - v\tilde{G} + 1} \left[\frac{v}{(\tilde{G} - 1)} + \frac{u(S - 1)}{\tilde{G}S + 1 - \tilde{G}} \right] + \frac{1}{(u\tilde{G}S - u\tilde{G} - v\tilde{G} + 1)^2} - \frac{1}{(\tilde{G}S + 1 - \tilde{G})^v(1 - v)^v} \right\}} \quad (7)$$

where \tilde{G} is an implicit function of D .

This is the most general elaboration of our model to be discussed and includes all previous models as special cases. Setting

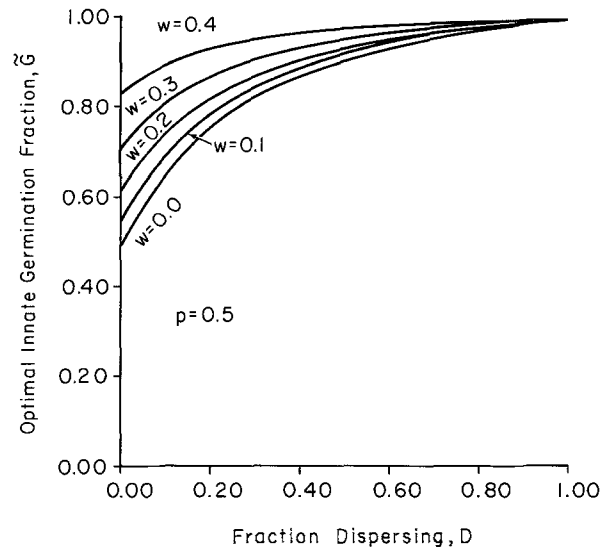


Fig. 6. Effect of predictive dormancy (w) on the relationship between optimal innate germination and dispersal, when predictions are always correct. Each curve represents a different amount of predictive dormancy (w). As w increases the lines flatten out and the \tilde{G} intercept increases. The probability of good years (p) equals 0.5. There are 50 seeds per successfully reproducing adult (S). See Eq. (7)

$w=0$ and $u+v=1$ yields the model in Eq. (2) for no prediction but allowing for fractional dispersal. Setting $D=0$ gives the predictive germination model of the previous section where dispersal was not possible. Setting $w=0$ and $D=1$ gives MacArthur's solution while setting $w=0$ and $D=0$ yields Cohen's model. Now we will explore the new situation where all parameters may vary between 0 and 1.

Figures 6, 7, and 8 illustrate the relationship between dispersal and germination (holding $p=0.5$). In Fig. 6 the decision to remain dormant is always accurate. This accuracy is reflected in the fact that increases in predictive dormancy (w) cause a decrease in the probability of germinating and dying (v) but have no depressing effect on the probability of germinating and reproducing (u).

For low dispersal fractions (realistic for most plant species) the effect of increasing w (which in this case is the probability of accurate prediction of bad years) is to increase the optimal germination fraction. Again, this makes sense because retaining a fraction $1 - G$ of dormant seeds is a hedge against a bad environment. To the extent that bad environments can be escaped by predictive dormancy, the hedge becomes counterproductive by holding back seeds that could be reproducing.

In the earlier model with dispersal but no prediction, we saw that as the quality of the environment improved, \tilde{G} became less sensitive to changes in dispersal. If patches had a high probability of good conditions there was not a great reproductive gain from dispersal. The compromise value of \tilde{G} favored the non-dispersers more than it did when the environment was poor. This effect can be seen again in the present model where both dispersal and prediction are possible. Here environmental conditions experienced by seedlings can be "improved" by prediction. As predictive ability increases, \tilde{G} becomes less sensitive to dispersal.

Figure 7 shows the opposite and unlikely extreme of prediction accuracy. In this case, predictive dormancy is always wrong and seeds never remain predictively dormant when the environment is bad. When they predict bad conditions, the environment is always

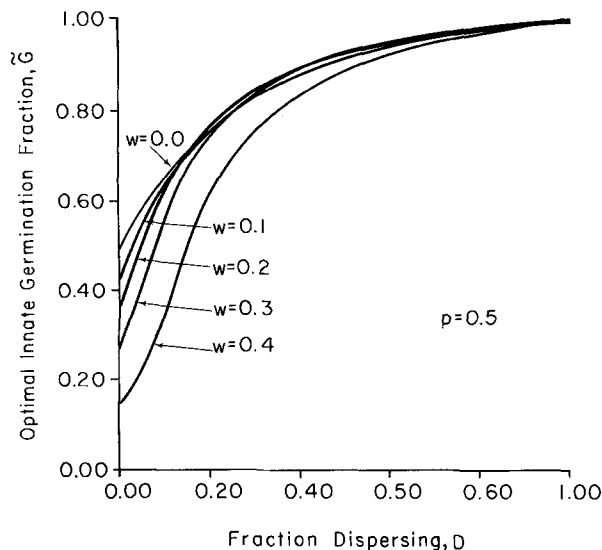


Fig. 7. Effect of predictive dormancy (w) on the relationship between optimal innate germination and dispersal, when predictions are always incorrect. Each curve represents a different amount of predictive dormancy (w). As w increases the slopes increase and the \bar{G} intercepts decrease. The probability of a good year (p) equals 0.5 and there are 50 seeds per successfully reproducing adult (S). See Eq. (7)

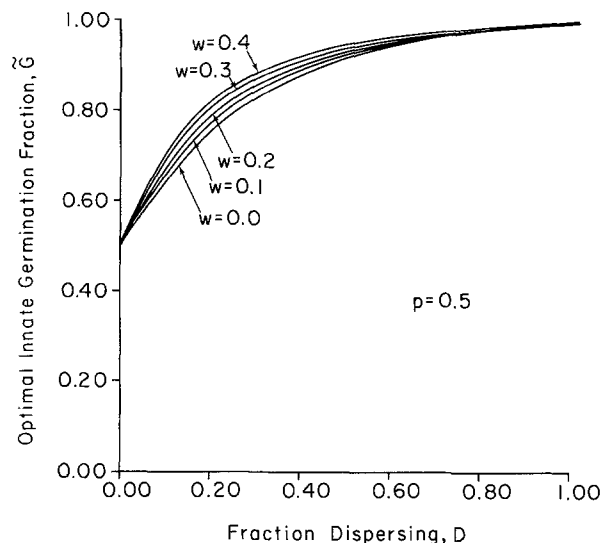


Fig. 8. Effect of predictive dormancy (w) on the relationship between optimal innate germination and dispersal, when predictions are statistically independent of environmental quality. Each curve represents a different amount of predictive dormancy (w). The probability of a good year (p) equals 0.5 and there are 50 seeds per successfully reproducing adult (S). See Eq. (7)

good. In terms of the model this means that as predictive dormancy (w) increases, the probability of germinating and reproducing (u) decreases while the probability of germinating and dying (v) remains unchanged. Thus, Fig. 7 shows the result of increasing the ability to predict inaccurately. Increasing such inaccurate predictiveness (w) lowers the optimal innate germination fraction (\bar{G})

for the relatively low dispersal fractions. This makes sense because bad prediction is causing the seeds to remain dormant when the environment is actually good so that germinating seeds have a higher probability of meeting bad conditions. Lower \bar{G} provides a seed reserve as a hedge against this increased uncertainty.

If the predictive ability is random in the sense that the probability of correctly predicting bad years equals the expected frequency of bad years, the model exhibits the behavior illustrated in Fig. 8. It can be seen that for the condition $D=0$ the optimal germination fraction ($\bar{G}=\bar{G}_p$) remains unchanged by increasing predictive dormancy. However, at intermediate levels of dispersal, the optimal germination fraction depends somewhat on the value of w . This effect is not nearly as great as when prediction is either accurate or inaccurate.

Unless predictive germination removes uncertainty altogether ($v=0$), optimal germination fraction remains sensitive to changes in dispersal. This finding underlines the role of uncertainty in producing the sensitivity of optimal germination to dispersal. Also notice that the accuracy of predictive dormancy has more effect on optimal innate germination fraction than the amount of predictive dormancy. In Fig. 8 a wide range of variation in w (the amount of prediction) has little effect on the germination-dispersal interaction. The relatively dramatic differences between Figs. 6, 7, and 8 are the effects of changing assumptions about the accuracy of prediction.

IV. Empirical Evidence and Discussion

One of the key predictions from these models is that differences in plant dispersal (at realistically low levels) generate different optimal germination strategies. This prediction is unaltered even with moderate amounts of predictive dormancy in response to environmental conditions. One test of this idea is to compare germination rates among closely related plants with differences only in dispersal. An even better opportunity presents itself in the form of plants that make two types of seeds, one of which has greater dispersal potential. In this case, the different dispersal types come from the same individuals, and this removes the confounding effects on dispersal of phylogenetic and ecological differences.

Table 1 presents a list of species producing two dispersal morphs on each plant. Dispersal differences are inferred either from the presence vs. absence of dispersal structures such as wind dispersed or adhesive pappus or by considerable differences in size and weight of seeds. The available germination data on the seed types comes from laboratory tests of the rate and percent of seed germination (Becker 1912; Burt 1977; Zohary 1962). *These data indicate a strong tendency for low dispersal seeds to have delayed germination and high dispersal seeds to have quick germination, as was predicted by the model.*

In addition to the two morphs representing low and high dispersal strategies, the two morphs may be viewed as aspects of a single strategy. The models assume that all plants have a fraction of seeds that do not disperse and a fraction that disperse to other patches and that \bar{G} or \bar{G} represents a compromise germination strategy since the optimal G for dispersers is 1 and some lower fraction for the non-dispersers. If information is available to a plant as to which of its seeds will be the dispersing fraction and which the non-dispersing fraction, optimal germination of the dispersers and non-dispersers should diverge. Table 1 illustrates examples where the dispersing and non-dispersing fraction have actually evolved these predicted germination differences.

Table 1. All species listed here have two types of seeds with differences in both dispersal and germination. N and F signify whether the seed type is dispersed nearer or farther from the parent than the other type. D and Q signify which seed type has delayed or quick germination relative to the other seed type. Dispersal is inferred from presence versus absence of dispersal structures such as barbed or plumed pappus for animal or wind dispersal respectively. If dispersal differences are inferred from substantial differences in size and weight of propagules, symbols are marked with an asterisk (*). Data compiled from Becker (1912), Burt (1977), and Zohary (1968) as described on p. 273, 279

Species of Compositae	Dispersal		Germination	
	Outer	Inner	Outer	Inner
<i>Dimorphotheca pluvialis</i>	N	F	slightD	Q
<i>Xanthocephalum</i>	N	F	D	Q
<i>gymnospermoides</i> (= <i>Gutierrezia</i> g.)				
<i>Heterotheca latifolia</i> (= <i>H. lamarckii</i>)	N	F	D	Q
<i>Chamaecrista heterophylla</i>	N	F	Q	Q
<i>Bidens bipinnata</i>	similar		D	Q
<i>Sanvitalia procumbens</i>	N	F	D	Q
<i>Verbesina encelioides</i>	N	F	slightD	Q
<i>Synedrella nodiflora</i>	N	F	D	Q
<i>Heterospermum xanthii</i>	N	F	D	Q
<i>Galinsoga parviflora</i>	N	F	Q	D
<i>Layia platyglossa</i> subsp. <i>campestris</i> (= <i>L. elegans</i>)	N	F	slightD	Q
<i>L. platyglossa</i>	N	F	D	Q
<i>L. heterotricha</i>	N	F	D	Q
<i>Achyrochaena mollis</i>	N	F	D	Q
<i>Chrysanthemum segetum</i>	N*	F*	D	Q
<i>C. coronarium</i>	N*	F*	D	Q
<i>C. viscosum</i>	N*	F*	D	Q
<i>C. frutescens</i>	N*	F*	D	Q
<i>Coleostephus myconis</i> (= <i>Chrysanthemum m.</i>)	N*	F*	D	Q
<i>Chardinia xeranthemoides</i>	N	F	D	Q
<i>Leontodon taraxacoides</i>	N	F	D	Q

Species of Cruciferae	Dispersal		Germination	
	Upper	Lower	Upper	Lower
<i>Cakile maritima</i>	F	N	Q	D
<i>Rapistrum rugosum</i> (with capsule wall)	F	N	D	Q
(without capsule wall)	F	N	Q	D
<i>Sinapis arvensis</i>	N	F	D	Q
<i>S. alba</i>	N	F	D	Q
<i>Hirshfieldia incana</i>	N	F	D	Q
<i>Brassica tournefortii</i>	N	F	D	Q

The relationship between optimal germination fraction and dispersal depends on several elements of the model which merit brief review. Uncertain environments are critical to the existence of this relationship. If habitats are always benign or if plants exhibit perfect predictive germination abilities, successful maturation is assured and there is no need for a genetically determined hedge against bad conditions in the form of fractional germination. Instead, the innate germination fraction should be uniformly high regardless of seed dispersibility.

There is another critical factor responsible for the sensitivity of optimal germination fraction to dispersal changes. Dormancy is assumed to be safer than germination and growth under bad

conditions. This assumption can be violated either by decreasing the hazards of germination and maturation or by increasing the hazards of remaining dormant. Decreasing the hazards of germination and maturation is the same as removing environmental uncertainty mentioned above. Increasing the hazards of remaining dormant could result from high post-dispersal predation and parasitism.

Another assumption of the model is the absence of any correlation between neighboring patches in space. This is often likely to be an over-simplification. Correlation between neighboring patches that gradually diminishes with distance has the same effect as increasing the effective patch size and thus lowering *D*, dispersal relative to patch size. Correlation between neighboring patches means that greater dispersal distances are required to generate the same changes in optimal germination fraction.

Further progress in understanding the significance of life histories of annual plants including rigorous testing of the models presented here must entail detailed measurements of plant demographic response to patterns of spatial and temporal heterogeneity. One such test might involve closely related species of annual plants with differing dispersibilities or annuals with dimorphic seeds having differing dispersibilities. One would then estimate actual patch sizes in nature along with an estimate of their temporal duration. Measurements of seed dispersal patterns could then be used to estimate *D*, the proportion of seeds escaping the parental patch. One would then measure any difference in innate germination fraction between the two species or seed types and then use the models to determine whether the estimated dispersal differences were adequate to generate the observed germination differences.

Since the models are based on only a few relevant ecological parameters only first order estimates are expected from the models. However, the models can be falsified by a variety of findings. First, among species (or seed morphs, as in Table 1) with the predicted dispersal-germination differences, substantial germination differences may exist while only small differences in *D* (the proportion of seeds escaping the parental patch) exist despite differences in morphological dispersal structures. If this result were found repeatedly one would have to conclude that mechanisms other than those in the models were generating the correlations between dispersal structures and germination biology. Second, if species or seed morphs with the predicted germination-dispersal differences occur in patches that last longer than dormant seeds live in the soil, the germination differences could not represent a hedge against environmental change, thus invalidating the models as an explanation of the pattern. Third, for the models to be valid there must be substantial spatial and temporal variation in survivorship to maturity among species or seed morphs in which the predicted dispersal-germination differences are found. Furthermore, the variance in survivorship to maturity should be greater for the dispersing quick-germinating species or seed morphs. On the other hand, fractional germination should demonstrably reduce the probability of all seeds germinating and dying, but should also reduce the probability of all seeds germinating and surviving to reproduction. Fourth, related species or seed morphs with dispersal differences should have small or negligible differences in innate dormancy if germination is triggered by stimuli that successfully predict high survivorship. For species or seed types for which predictive dormancy is less successful at inhibiting germination under unsuitable conditions, innate dormancy should be greater for the low dispersal plants. For example, if water is the main stimulus triggering germination, low innate dormancy should exist where the water stimulus

reliably portends good conditions for survival to maturity (even with relatively poor seed dispersal). Thus the germination-dispersal relationship predicted in these models should be more pronounced and more frequently found in unpredictable environments.

Appendix I

The optimal innate germination fraction (\tilde{G}) is insensitive to changes in predictive dormancy (w) if the accuracy of prediction is such that seeds are as likely to predict bad weather and remain dormant given good weather as they are given bad weather. This can be demonstrated as follows.

Experimental manipulation of the model with predictive dormancy but no dispersal shows that increasing w (the predictive dormancy) has no effect on the optimal innate germination fraction (\tilde{G}) when increasing $w = \Delta u + \Delta v$ from zero obeys $\Delta u = \alpha p$ and $\Delta v = \alpha q$ where α is a constant. As w increases, u and v decrease in proportion to the probabilities p and q . This can be written as:

$$\frac{\Delta u}{\Delta v} = \frac{p}{q} \quad (a)$$

Since $p = P(G_a)$ and $q = P(B_a)$, then $\frac{p}{q} = \frac{P(G_a)}{P(B_a)}$. For any change from $w=0$ to $w = \Delta u + \Delta v$, $\Delta u = P(B_p \cap G_a)$ and $\Delta v = P(B_p \cap B_a)$ from our definition of w as the probability of predicting bad conditions when conditions are good plus the probability of predicting bad conditions when they are really bad. Substituting in Eq. (a) above to solve for the experimentally determined conditions for which an increase in w generates no change in \tilde{G} for the case with no dispersal yields,

$$\frac{P(B_p \cap G_a)}{P(B_p \cap B_a)} = \frac{P(G_a)}{P(B_a)}$$

or

$$\frac{P(B_p \cap G_a)}{P(G_a)} = \frac{P(B_p \cap B_a)}{P(B_a)}$$

By Bayes Theorem defining conditional probability this can be rewritten as,

$$P(B_p/G_a) = P(B_p/B_a)$$

which states that seeds are just as likely to predict bad weather and remain dormant given good weather as they are given bad weather. This implies that increasing w (the predictive dormancy) has no effect on the optimal innate germination fraction (\tilde{G}) when predictive dormancy is statistically independent of the actual weather, i.e. when predictions are uncorrelated with actual weather.

Appendix II

List of Symbols

- a the actual proportion of good years in a particular sequence of T years.
- b the actual proportion of bad years in a particular sequence of T years.
- B_a the event that a year actually has bad conditions (environment will not support maturation of germinating seedlings).

- B_p the event that seeds respond to the environment as if it were bad, whether it is or not (predicting that environmental conditions will be unsuitable).
- D the fraction of newly produced seeds that disperse from the parent plant out of the parental patch.
- D^1 the proportion of all seeds (both newly produced and those in the soil) that disperse out of the parental patch.
- G general term for germination fraction
- \tilde{G} the optimal germination fraction (used when predictive germination is not possible, thus representing fixed or innate germination).
- \tilde{G} the optimal innate component of germination fraction. Given that seeds can "predict" bad conditions and remain dormant, \tilde{G} is the optimal fraction that should germinate when good conditions are predicted.
- \tilde{G}_a the event that a year actually has "good" conditions (i.e. will support maturation of germinating seedlings).
- G_p the event that seeds respond to the environment as if it were good, whether it is or not (predicting that environmental conditions will be suitable for successful maturation).
- λ_c the finite rate of increase calculated by Cohen's model which uses the geometric mean to average fitness over different environments (appropriate with no dispersal).
- λ_m the finite rate of increase calculated by MacArthur's arithmetic mean (appropriate with dispersal to variable environmental patches).
- λ_{total} the finite rate of increase when some of the seeds do not disperse (Cohen model) and some disperse (MacArthur model) defined as a linear combination of the two models.
- p the probability of good conditions for survival of germinating seedlings to reproductive maturity ($p = P(G_a)$).
- q the probability of bad conditions for survival of germinating seedlings to reproductive maturity ($q = P(B_a)$).
- S the number of seeds produced by a successfully maturing plant.
- u the probability that conditions are actually good and seeds "predict" them to be good ($u = P(G_a \cap G_p)$) and germinate (p. 276).
- v the probability that conditions are actually bad and seeds predict them to be good ($v = P(B_a \cap G_p)$) and so germinate and die (p. 276).
- w the probability that seeds predict bad conditions whether they are or are not bad ($w = P(B_p) = P(B_p \cap G_a) + P(B_p \cap B_a)$), and no germination occurs (p. 276).

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Received June 10, 1979