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THE SELECTIVE INTERACTIONS OF DISPERSAL, DORMANCY, AND SEED SIZE AS ADAPTATIONS FOR REDUCING RISK IN VARIABLE ENVIRONMENTS

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A variety of critical life history functions must be integrated in the production of seeds (Stebbins 1974). Because these multiple functions interact in important ways, they evolve as coadapted syndromes. We consider here three seed traits that interact as adaptations to reduce the impact of environmental variation: the production of between-year seed banks, dispersal, and seed size. Whereas dormancy and dispersal permit escape from unfavorable conditions in time (Cohen 1966; Marks 1974; Sarukhán 1974) and in space (Platt 1975, 1976; Comins et al. 1980; O'Dowd and Hay 1980; Howe and Smallwood 1982), larger seeds provide seedlings with a store of provisions that improve their chances of becoming established under unfavorable conditions (Salisbury 1942; Baker 1972; Gross 1984; Stanton 1984, 1985; Winn 1985; Wulff 1986). Because they represent different ways of dealing with similar problems, the evolution of any one of them depends on the levels of the other two.

In the empirical literature, correlations between dispersal, dormancy, and seed size are usually considered in the context of biophysical constraints and then only in terms of two of these three characteristics. For example, it is often assumed that larger seeds will be less dispersible because of their greater mass (Salisbury 1975; Fenner 1985). Likewise, it has been suggested that because small seeds cannot successfully emerge from deep burial, they have evolved a light requirement for germination. This light requirement incidentally leads to the production of between-year seed banks (Thompson and Grime 1979; Cook 1980). Occasionally, adaptive population-dynamic interactions have been proposed to explain correlations obtained in surveys; for example, it has been suggested that shared population-dynamic functions might result in an inverse correlation between dormancy and dispersal (Werner 1979; Venable and Levin 1983).

A few theoretical studies have investigated how the joint evolution of two of these three seed traits might be driven by shared population-dynamic functions. Venable and Lawlor (1980) considered the optimal germination fraction in re-

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sponse to a given dispersal strategy under density-independent selection. They found trade-offs between dormancy and dispersal for dealing with temporal uncertainty: increasing dispersal increases the optimal germination fraction. S. Levin et al. (1984) demonstrated similar substitutable effects under density-dependent conditions. Templeton and Levin (1979) and Brown and Venable (1986) considered the joint evolution of dormancy and traits that result in trade-offs between fitness mean and variance. These authors found that between-year seed banks favor increased specialization to the more favorable subsets of environmental conditions. Conversely, increasing specialization to favorable conditions selects for more between-year dormancy. As we explain below, changes in seed size can result in the shifts in specialization studied by Templeton and Levin (1979) and Brown and Venable (1986). We extend these analyses by simultaneously considering selective interactions between dormancy, dispersal, and seed size.

THE POPULATION-DYNAMIC CONSEQUENCES OF SEED SIZE

Although the population-dynamic consequences of dormancy and dispersal have been extensively discussed in the literature, the consequences of seed size are perhaps less well known and merit brief consideration before we present our model. Several studies of early-successional plants have shown that open, mesic conditions are favorable for seedling establishment and that small and large seeds alike can establish. This has been documented at both among-species (Gross and Werner 1982) and within-species levels (Gross 1984; Stanton 1984). Thus, in open, moist conditions the expected reproductive yield (in terms of biomass) should be more or less independent of seed size (fig. 1*a*). Likewise, a number of studies have shown that shaded conditions under perennial vegetation or litter are unfavorable for seedling establishment and only larger seeds can successfully establish. This has also been demonstrated for differences in seed size among species (Grime and Jeffrey 1965; Gross and Werner 1982; Gross 1984) and within species (Gross 1984; Winn 1985). Thus, under shaded conditions, the expected reproductive yield, taking into account mortality, is an increasing function of seed size (fig. 1*b*). For a given reproductive yield, many small or a few large seeds can be produced (fig. 1*c*). Thus, in the favorable open patches, the production of large seeds is a waste of energy and nutrients, since the same success could be had with a smaller seed and more small seeds could be produced. Therefore, in open patches, the number of seeds produced per seed sown is a decreasing function of seed size (fig. 1*d*). In the unfavorable patches in the shade of perennial vegetation or litter, seed yield per seed is an increasing function of seed size despite the trade-off between seed size and seed number (fig. 1*e*).

Thus, in habitats partly covered by perennial vegetation and partly open as a result of some sort of periodic disturbances (see Platt 1975; Gross and Werner 1982; Reader and Buck 1986), small-seeded plants have more-variable reproductive success in space and time (Gross and Werner 1982; Gross 1984; Winn 1985). Large-seeded plants have some survival and fecundity in the shade but produce fewer seeds in the open because of the trade-off between seed size and seed number.

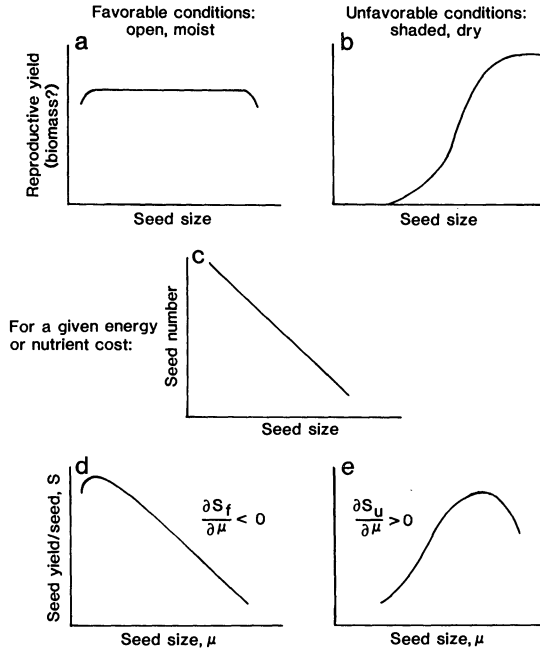


FIG. 1.—The fitness consequences of seed size assumed in this paper. *a*, Under favorable (open, moist) conditions reproductive yield is more or less independent of seed size. *b*, Under unfavorable conditions (shaded, dry) only large-seeded plants can establish and reproduce. *c*, For a given energy or nutrient cost, seed size is inversely related to seed number. *d*, Under favorable conditions, *a* and *c* result in the number of seeds produced per seed sown being a decreasing function of seed size. *e*, Under unfavorable conditions, the number of seeds produced per seed sown is an increasing function of seed size despite *c*.

These basic fitness consequences of seed size with regard to shade follow from the ideas initially proposed by Salisbury (1942) for plants of predominantly mesic habitats. Baker (1972) surveyed seed size in the California flora and concluded that larger seeds may be favored in arid habitats as well. He suggested that more provisions may allow seedlings to develop a larger root system before suffering the transpirational losses associated with photosynthesis (cf. Schimpf 1977). In arid conditions, the magnitude of these transpirational losses may be critical in determining survival. Although Baker's hypothesis has not been pursued experimentally to the same extent as Salisbury's, laboratory and field experiments on *Desmodium paniculatum* have shown that larger seeds produce longer roots even before shoot emergence and exhibit higher drought tolerance than do small seeds (Wulff 1986). The same basic fitness consequences illustrated in figure 1 are generated if moist and dry conditions are substituted for the favorable and unfavorable conditions.

Thus, the fitness consequences of seed size outlined in figure 1 have been fairly well documented for the effects of shading and are also appropriate for drought although the mechanisms here are less well documented. The fitness conse-

quences of seed size outlined in figure 1 provide basis for our models of selective interaction of seed size, dispersal, and dormancy. We recognize that other selective factors may result in fitness varying in more complicated ways with seed size, but shade and drought are clearly among the more important selective factors affecting seed size.

POPULATION-DYNAMIC FUNCTIONS SHARED BY DISPERSAL, DORMANCY, AND SEED SIZE

At least three population-dynamic functions are shared by dispersal, dormancy, and seed size in species occurring in spatially and temporally varying environments. Dispersal permits plants to average their demographic success spatially, thus escaping the risk of low success in any one site while sacrificing the chance of having all seeds in the occasional high-yield site (e.g., Kuno 1981). Between-year seed-bank dormancy allows plants to average their success over time, reducing opportunity and risk (Cohen 1966; León 1985). Increasing seed size also reduces spatial and temporal variance in reproductive success; rather than producing many seeds in a few open sites, large-seeded plants are more likely to produce some seeds in a greater variety of sites.

In addition to this bet-hedging or risk-reducing function, the three seed properties can also help plants to escape crowding. Since high density in an annual plant is the direct result of high local seed production in the preceding year, most seeds find themselves in patches of high density. Even random dispersal results in a net flow to areas of lower density. Dispersal is favored by natural selection in a temporally and spatially varying environment if fitness is higher in areas of low density (Comins et al. 1980; Motro 1982; S. Levin et al. 1984). Likewise, dormancy can be favored as a way to escape crowding. Most seeds are produced at times of high density and in temporally and spatially varying environments; between-year dormancy tends to take them to times of lower seed density (Ellner 1985*a,b*). Small seeds result in high seed yield in a few open patches, but low seed set in closed patches. This local high yield is not so valuable if all the seeds must compete for a limited number of safe sites. Plants may be able to escape some of the effects of intraspecific crowding by producing larger seeds, resulting in some seed production in a greater variety of microsites.

The third shared population-dynamic function is escape from sib competition. Even if the expected reproductive success is the same in all patches at all times, dispersal can be favored by kin selection (Hamilton and May 1977; Comins et al. 1980; Schoen and Lloyd 1983). If a seed has the same chance of obtaining a safe site near the parent or at some distance, taking the site near the parent is more likely to remove some fitness from a relative than taking a distant site. Similarly, even in a constant but spatially structured habitat, kin selection can favor dormancy or larger seeds because they result in a greater dispersion of kin in space or time (cf. Ellner 1986).

It is possible to make models to explore the selective interaction of seed size, dormancy, and dispersal for any one of these population-dynamic functions in isolation from the others. The model presented below is frequency- and density-independent and thus explores the risk-reducing or bet-hedging function in isola-

tion from the other two. The other two functions will be considered in a subsequent paper.

THE MODEL

Consider a spatially and temporally variable environment. In a given patch at the start of a growing season, a fraction G of the seed bank germinates. A proportion R of the seeds that do not germinate survive until the start of the next growing season; thus, $1 - R$ is the mortality cost of dormancy. Let the vector $\mathbf{S} = (S_1, \dots, S_m)$ denote the expected seed yield of a germinating seed, in each of m different possible environmental conditions, $i = 1, \dots, m$, that occur with probability $\mathbf{p} = (p_1, \dots, p_m)$.

Assume that n patches experience environmental conditions independently. Let S_{ij} denote that germinating seeds in patch j are experiencing seed yield S_i . Let ρ_j be the probability that a seed is in patch j (or the proportion of all seeds that are in patch j) at the start of a given growing season ($\rho_1 + \dots + \rho_n = 1$). Following a growing season, a fraction D of the seeds produced by each plant disperses. For now, imagine that dispersing seeds are evenly distributed over all patches, including their patch of origin. Dispersing seeds may encounter additional sources of mortality. Perhaps some of the places they land do not support growth of the species in question or perhaps the dispersal agent itself inflicts some mortality. Let a be the survival during dispersal; that is, $1 - a$ is a mortality cost experienced only by dispersing seeds. Thus, in a given year, the per capita population growth will be

$$\lambda = [1 - D(1 - a)] \sum_{j=1}^n \{\rho_j [GS_{ij} + R(1 - G)]\}, \quad (1)$$

where, taking dormancy into account, $GS_{ij} + R(1 - G)$ is the seed yield per seed in patch j . In equation (1), this seed yield is averaged over all patches, weighting each patch according to the proportion of the global seed bank that it contains. The per capita seed yield is further discounted by $1 - D(1 - a)$ to account for the dispersal-related mortality.

Expression (1) is the finite rate of increase following one growing season for which we have specified the environmental conditions and the proportion of the global seed bank found in each patch. The average growth rate consists of all the different possible values of equation (1), each weighted by its probability of occurrence. The different possible values of (1) are determined by the environmental conditions in each patch and by the proportion of the global seed bank in each patch.

If the patches experience the different environmental conditions independently, then a multinomial distribution describes the way in which the m different environmental conditions can occur among the n patches. During a given growing season, the probability of a particular vector of environmental conditions (drawn from $i = 1, \dots, m$) in the n different patches is

$$g_u = \prod_{j=1}^n p_{i(j)},$$

where $u = 1$ to $m!/(m - n)!$ indexes the specific vector of environmental conditions and $p_{i(j)}$ is the probability that environmental condition i occurs in patch j .

Let f_t be the probability of occurrence of a particular frequency distribution of seeds among patches, \mathbf{p}_t , where $t = 1$ to z indexes the specific distribution. Since this might actually be a virtually continuous set of vectors, assume that as an approximation we have divided it into z different classes. Thus, the probability that a particular vector of environmental conditions occurs with a particular distribution of seeds among patches is

$$q_{tu} = f_t g_u. \quad (2)$$

This is the probability of occurrence of a specific λ .

Because we are assuming density independence, individual selection will maximize the average growth rate of the population (Fisher 1958; Charlesworth 1980). As León (1985) has shown, the correct fitness criterion for this process is the geometric mean, which for our case is

$$W(\cdot) = \prod_{u=1}^{m!/(m-n)!} \prod_{t=1}^z \lambda(\cdot)^{q_{tu}}, \quad (3)$$

where (\cdot) is shorthand for $(D, G, S, \mathbf{p}, a, R)$.

We assume that dispersibility, seed-bank dormancy, and seed size are genetically variable and that selection favors the values of D , G , and S that maximize fitness, $W(\cdot)$, subject to the following constraints. Both D and G can take on any value from 0 to 1 ($0 \leq D, G \leq 1$). Seed size determines the reproductive schedule, S , in keeping with the biology in figure 1 (i.e., an increase in seed size increases the expected seed yield in unfavorable conditions at the expense of reduced yield in favorable conditions). Actually we could assume that the reproductive schedule is determined by any of a variety of other characteristics (e.g., timing of germination, mesophytic or xerophytic leaf anatomies, root-to-shoot ratios) that increase the seed yield of germinating seeds in one environmental condition while sacrificing seed yield in other environmental conditions (for further discussion of this point, see Brown and Venable 1986). Formally, let $F(S) = 0$, where

$$\begin{aligned} \partial F(S)/\partial S_i &> 0, & \partial^2 F(S)/\partial^2 S_i &< 0, \\ \partial^2 F(S)/\partial S_i \partial S_j &> 0, & S_i &\geq 0, \end{aligned}$$

for $i, j = 1, \dots, m$ and $i \neq j$. The constraint function on S defines a quasi-convex fitness set (Levins 1968).

The fitness function given by expression (3) is not very tractable. The number of terms is large, and the distribution of seeds among patches, \mathbf{p} , is a complex function of dispersal, dormancy, seed size, frequency of environmental conditions, and the survival probabilities of dormant and dispersing seeds. However, two special cases are straightforward and instructive: when there is only one patch, and when there are an infinite number of patches.

Where there is only one patch, that is, $n = 1$, all seeds experience the same set of environmental conditions, i , in a given year with probability p_i , and all seeds are

in the one patch, $\rho_1 = 1$. Substituting these assumptions into the fitness function (3) yields

$$W(\cdot) = [1 - D(1 - a)] \prod_{i=1}^m [GS_i + R(1 - G)]^{p_i}. \quad (4)$$

Expression (4) is the fitness criterion used by Cohen (1966) to investigate the optimal germination fraction in a temporally varying environment.

Alternatively, assume that there are an infinite number of patches and that, at least initially, all patches are occupied. If the number of patches is infinite, exactly the fraction p_i of the patches experiences environmental condition i every year, without fail. Although seeds may be distributed unequally among patches, the fraction of seeds experiencing environmental condition i , ρ_i , is also exactly p_i . Since neither the proportion of patches nor the proportion of seeds experiencing each environmental condition varies from year to year, λ (expression 1) is constant. The fitness function (3) reduces to

$$W(\cdot) = [1 - D(1 - a)] \sum_{i=1}^m p_i [GS_i + R(1 - G)], \quad (5)$$

which is the fitness criterion advocated by MacArthur (1972) when he argued that arithmetic-mean fitness is the appropriate criterion in an infinite environment with local variability.

GLOBAL TEMPORAL VARIANCE AND THE RISK-REDUCING PROPERTIES OF SEED SIZE, DISPERSAL, AND DORMANCY

Spatial and temporal variation can be considered at several levels, which are important to distinguish if we are to understand how the population-dynamic functions of seed size, dormancy, and dispersal interact. *Local temporal variance* is the temporal variation in demographic success in a single patch, j , that is, in $GS_{ij} + R(1 - G)$, whereas *global temporal variance* is temporal variation in the total demographic success of all patches, that is, in expression (1). Spatial variation refers to the variation in demographic success from patch to patch at any time.

The risk-reducing properties of dispersal, dormancy, and seed size evolve only in response to global temporal variance. This can be seen from an examination of our risk-reduction model for the biologically unrealistic but nevertheless instructive case in which $n = \infty$. In this case, there is no global temporal variance (λ is constant from year to year), though there could be considerable spatial variance and local temporal variance. Since λ does not vary, its geometric mean equals its arithmetic mean (see eq. 5) and the values of dormancy, dispersal, and seed size that maximize arithmetic-mean fitness will evolve regardless of any temporal or spatial variance generated in the process. For example, cost-free dispersal is selectively neutral (when $a = 1$, dispersal cancels out of eq. 5). If dispersal has a mortality cost, selection always operates against it (eq. 5 is a monotonically

declining function of dispersal when $a < 1$). In the absence of global temporal variation, dormancy is not favored either ($G^* = 1$ as long as $\sum_{i=1}^m p_i S_i > R$; that is, for all species that are not in the process of becoming extinct). Likewise, the seed size corresponding to the S vector with the highest arithmetic mean will be favored.

These results hold only for the risk-reducing or bet-hedging properties of dormancy, dispersal, and seed size. Dormancy, dispersal, and seed size can have density-escaping properties in the absence of global temporal variance as long as there is local temporal and spatial variance (S. Levin et al. 1984; Ellner 1985*a,b*). The three seed traits can evolve in response to sib competition in the absence of any environmental variance as long as sib competition is greater locally than elsewhere (e.g., Hamilton and May 1977).

But to understand the risk-reducing properties of dispersal, dormancy, and seed size we must focus on global temporal variance and the factors that contribute to it. Global temporal variance is influenced by the multinomial variance in the proportion of patches experiencing each set of environmental conditions, $i = (1, \dots, m)$. This multinomial variance decreases with increasing number of patches until, as we have seen, when $n = \infty$ there is no global temporal variance. Positive spatial autocorrelation of environmental conditions results in an increase in global temporal variance over that expected for the same number of patches under the assumption of independence. The global temporal variance also increases with the magnitude of the local temporal variance as long as $n < \infty$. In the extreme, when there is no local variance (i.e., $GS_{ij} + R(1 - G)$ is constant from year to year), there is only one kind of year and thus no global temporal variance. Finally, global temporal variance increases with increasingly unequal distribution of seeds among patches. As the distribution becomes more unequal, the population fluctuations in a small number of patches will largely determine global temporal variance.

Dormancy directly reduces local temporal variance at the expense of arithmetic-mean fitness. In a single patch, a greater between-year seed bank lowers fitness in favorable years (in which $S_i > R$) by holding back seeds that could have yielded more seeds (the maximum contribution of dormant seeds is R less than or equal to 1). However, a between-year seed bank increases fitness in unfavorable years (in which $S_i < R$). Unlike other forms of delayed reproduction, seed dormancy does not permit growth or increased learning or experience, which might increase future reproduction.

Dispersal increases the evenness of the spatial distribution of seeds among patches (changes in germination and seed size do this only indirectly). Most seeds are produced in patches with higher than average densities; thus, uniform dispersal results in a net movement of seeds to patches with lower than average density (in the extreme, if $D = 1$, all patches have the same seed density at the beginning of each year; $p_j = 1/n$). Unlike dormancy, in the absence of a survival cost, dispersal reduces variance without reducing the arithmetic-mean fitness (thus, if global temporal variance exists and dispersal has no survival cost, it will always be favored; $D^* = 1$).

Increasing seed size directly lowers the local temporal variance since it im-

proves performance under unfavorable conditions while decreasing seed yield in favorable conditions. The lowered variance may have a cost in lowered mean, but the constraint on seed size differs from that on dormancy.

THE SUBSTITUTABILITY OF DISPERSAL, DORMANCY, AND SEED SIZE

Dormancy, seed size, and dispersal (with a mortality cost) all reduce year-to-year variance in fitness at the expense of reduced arithmetic-mean fitness. This balance of cost and benefit creates selective correlations among dormancy, dispersal, and seed size. To see why, assume that all three are at an equilibrium determined by the balance between their contributions to mean and variance. If one of them, say dispersal, is arbitrarily increased, then global temporal variance and mean are reduced. This reduces the benefit of the other two seed properties for hedging against variance while creating a greater opportunity for them to increase the arithmetic-mean fitness. Thus, the optima of the other two variance-reducing traits tend to shift toward values that favor the mean, that is, less dormancy and smaller seeds in this example.

To demonstrate these ideas, we ran computer simulations for a given set of conditions to determine the fitness-maximizing values of D , G , and S . Then we arbitrarily varied one of these and determined how the fitness-maximizing values of the other two changed in response (figs. 2, 3, 4). To determine the fitness-maximizing values of D , G , and S , 1000 generations of population growth were simulated and the geometric-mean growth rate was calculated. This number of generations was found to give repeatable results. The process was repeated for different combinations of D , G , and S , searching for the combination with the highest geometric-mean fitness. After determining the optimum in this way, one of D , G , or S was arbitrarily shifted to each of several values and the corresponding fitness-maximizing values of the other two were determined by the same process.

For the simulations, we assumed two sets of environmental conditions, $i = 1$ and 2, 11 patches, and

$$\begin{aligned} R &= 0.9, & p_1 &= 0.1, \\ a &= 0.6, & p_2 &= (1 - p_1) = 0.9, \\ F(S) &= 0.5 [1 - (S_1/25)^2]^{1/2} - S_2 = 0. \end{aligned}$$

Note that environmental condition 1 is favorable and environmental condition 2 is unfavorable.

For this constraint set and these environmental parameters, the fitness-maximizing values of dispersal, dormancy, and seed size are $D^* = 0.45$, $G^* = 0.47$, and $S_1^* = 22.0$. As predicted above, in the vicinity of this optimum, arbitrarily increasing any of the three variance-reducing traits selects for a lower level of the other two (figs. 2, 3, 4). Note, however, that one trait may do most of the responding and that, as the syndrome is forced farther away from the three-dimensional optimum, one of the two responding traits may even shift direction and begin to increase. Presumably, when this occurs, the point has been reached at which some counterbalancing fitness cost has become greater than the bet-

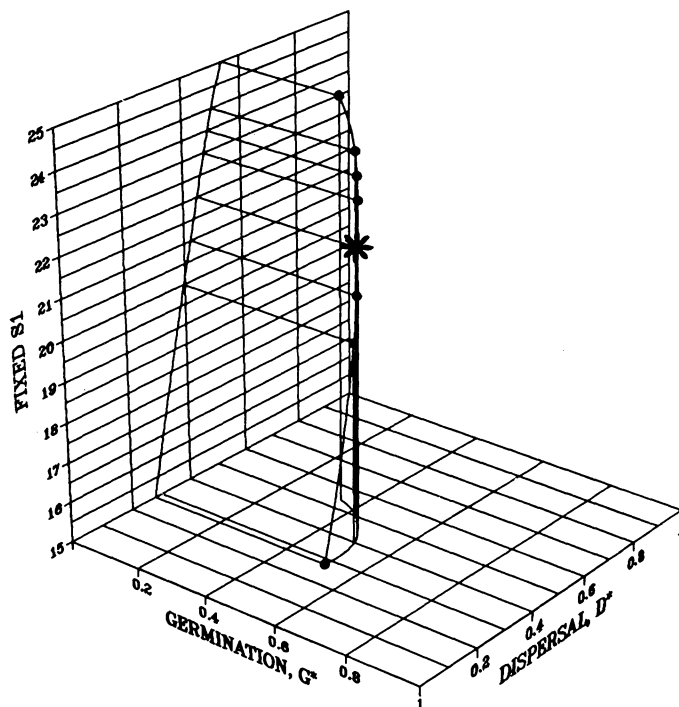


FIG. 2.—Correlated responses to seed size. Optimal germination, G^* , and dispersal, D^* , for different fixed values of S_1 (an inverse function of seed size). The asterisk is the three-dimensional optimum (G^* , D^* , S_1^*), and the other points are two-dimensional optima for different arbitrary values of S_1 . Projections of the optima onto the G - D plane and the S_1 - D plane are shown for perspective. To obtain the optimum for a given value of S_1 , 1000 generations of population growth were simulated and the geometric-mean growth rate was calculated. This process was repeated for different combinations of D and G , searching for the combination with the highest fitness for that value of S_1 . See the text for a list of parameter values and the constraint function used in the simulations.

hedging benefit of the negative correlation. For example, as dispersal is arbitrarily increased from the optimum, dormancy and seed size both decline initially, though seed size declines more than dormancy (fig. 3). As dispersal continues to increase, dormancy eventually starts to increase. Since a decrease in seed size favors an increase in dormancy and vice versa, the responses of seed size and of dormancy to increasing dispersal dampen one another. Although this counterbalancing selective force partly accounts for the shift in dormancy, other factors must be at work as well since dormancy eventually starts to increase with dispersal even if seed size is held constant. This may be explained as follows. The increase in dispersal is arbitrary, moving the seed syndrome away from its three-dimensional optimum for the given environment. Initially, seed size and dormancy compensate for this shift and the decline in population growth rate is slight. Eventually though, the population growth rate declines to a significant extent and

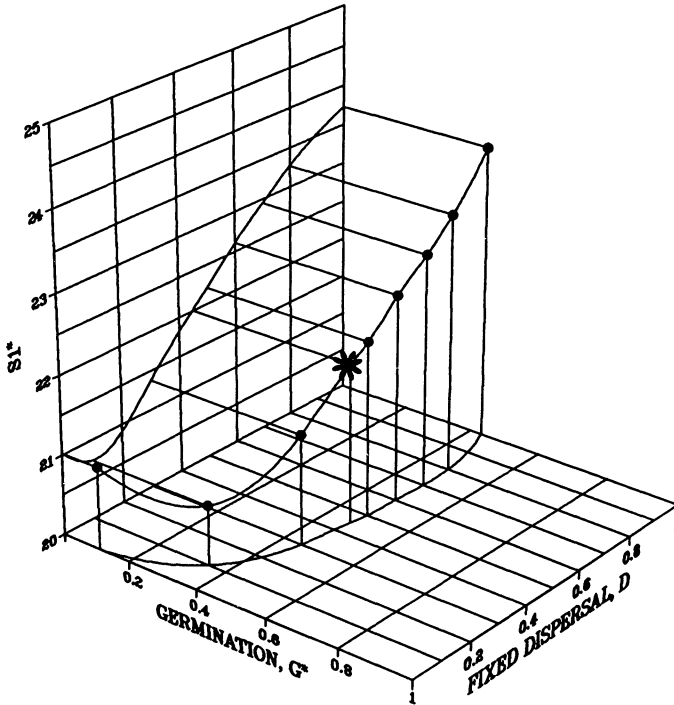


FIG. 3.—Correlated responses to dispersal. Optimal germination, G^* , and S_1^* (which is an inverse function of seed size) for different fixed values of dispersal, D . The asterisk is the three-dimensional optimum (G^* , D^* , S_1^*), and the other points are two-dimensional optima for different arbitrary values of D . Projections of the optima onto the G - D plane and the S_1 - D plane are shown for perspective. To obtain the optimum for a given value of D , 1000 generations of population growth were simulated and the geometric-mean growth rate was calculated. This process was repeated for different combinations of G and S_1 , searching for the combination yielding the highest fitness for that value of D . See the text for a list of parameter values and the constraint function used in the simulations.

this deteriorating situation is compensated for by an increase in dormancy. The details of these shifts in correlation probably depend on the specific environment and constraint function.

Our main point here is that the shared function of risk reduction results in selective correlations among the seed traits and that these are negative in the vicinity of the optimum (though, as one of the seed traits continues to be pushed away from the optimum, one of the others may eventually shift directions).

THE COMPLEMENTARITY OF DISPERSAL, DORMANCY, AND SEED SIZE

Because dispersal, dormancy, and seed size reduce global temporal variance via different mechanisms, different kinds of environmental changes may preferentially select for one or another of them. Below, we report how the seed syndrome

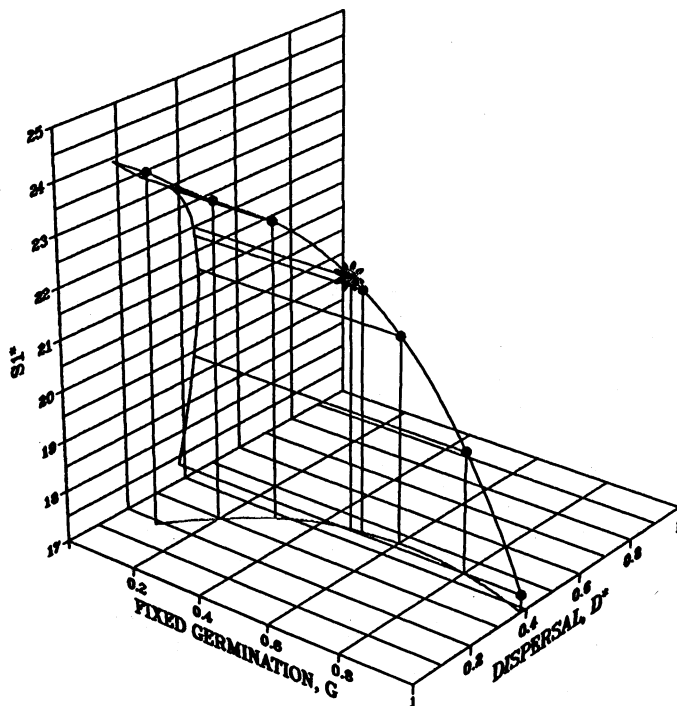


FIG. 4.—Correlated responses to germination. Optimal dispersal, D^* , and S_1^* (which is an inverse function of seed size) for different fixed values of germination, G . The asterisk is the three-dimensional optimum (G^* , D^* , S_1^*), and the other points are two-dimensional optima for different arbitrary values of G . Projections of the optima onto the G - D plane and the S_1 - D plane are shown for perspective. To obtain the optimum for a given value of G , 1000 generations of population growth were simulated and the geometric-mean growth rate was calculated. This process was repeated with different combinations of D and S_1 , searching for the combination yielding the highest fitness for that value of G . See the text for a list of parameter values and the constraint function used in the simulations.

responds to changes in the number of independent environmental patches, the probability of favorable environmental conditions, the dispersal radius, and spatial and temporal correlations of patch conditions.

Number of Patches

For the constraint function on seed size given above and a 0.1 probability of favorable conditions, we varied the number of patches from 3 to 50. This environmental change results in selection for increased dispersal, decreased dormancy, and a reduction in seed size (fig. 5). Increasing the number of patches results in the global growth rate being less dependent on the vagaries of a particular patch; that is, there is less year-to-year variation in the proportion of favorable patches (conditions are likely to be favorable in a subpopulation somewhere). This lessening of the overall level of uncertainty favors less dispersal, more germination, and

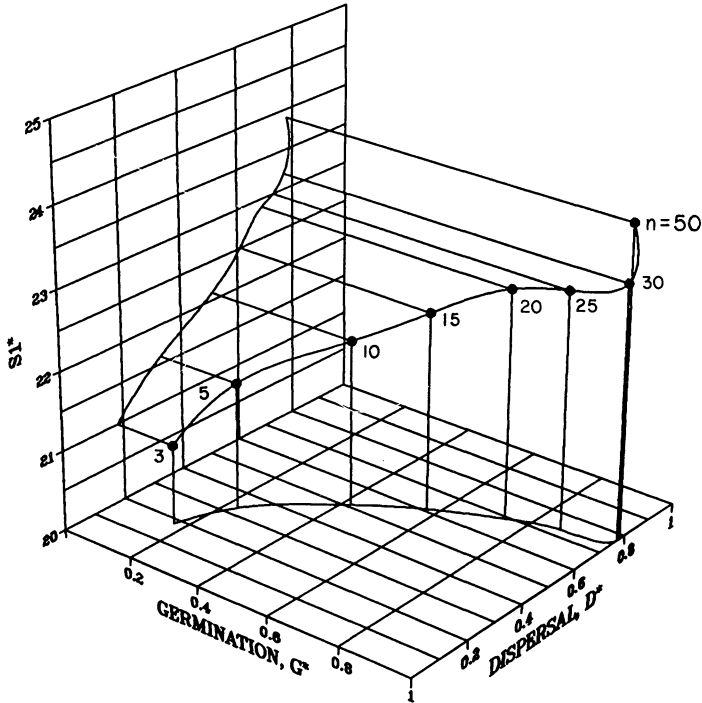


FIG. 5.—The effect of increasing the number of patches, n , on optimal S_1 (an inverse function of seed size), germination, G , and dispersal, D . Projections of the three-dimensional optima onto the G - D plane and the S_1 - D plane are shown for perspective. To obtain the optimum for a given number of patches, 1000 generations of population growth were simulated and the geometric-mean growth rate was calculated. This process was repeated for different combinations of D , G , and S_1 , searching for the combination yielding the highest fitness for that number of patches. See the text for a list of parameter values and the constraint function used in the simulations.

greater specialization to favorable conditions (smaller seeds). Yet, an increase in the number of patches also makes dispersal a more effective tool for dealing with uncertainty (since dispersal moves seeds to the temporarily favorable subpopulations). The net result is selection for an increase in dispersal (fig. 5). Dormancy and seed size decrease not only because of lowered uncertainty resulting from more patches, but also as a correlated response to the evolutionary increase in dispersal.

As the number of patches continues to increase, the potential fitness gains from increased dispersal diminish. Although the mortality cost of increased dispersal, $1 - a$, remains constant when n (the number of patches) is large, there is less and less global temporal variance (risk) to escape, and, as a result, optimal dispersal eventually decreases. As we have already seen (see discussion of eq. 5, above), when the number of patches approaches infinity, year-to-year variance approaches zero and dispersal loses its variance-reduction value.

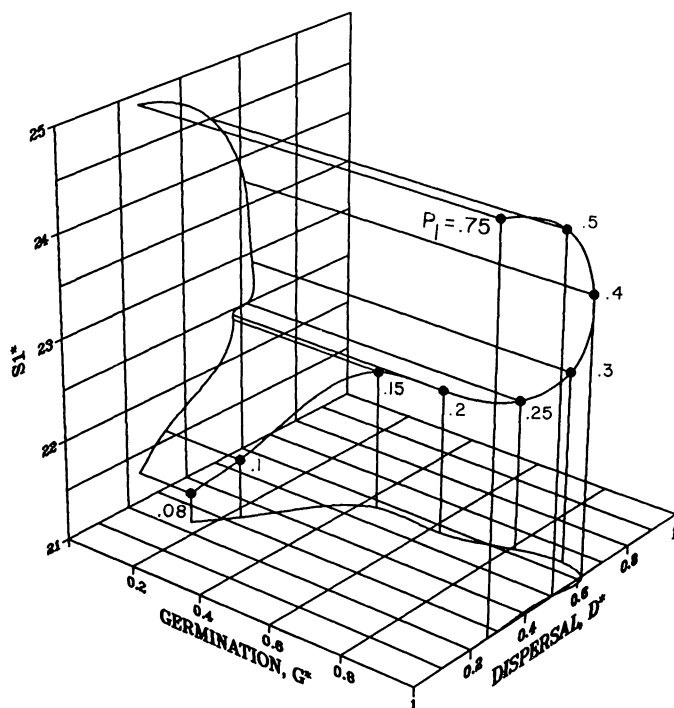


FIG. 6.—The effect of increasing the probability of favorable conditions, p_i , on optimal S_1 (an inverse function of seed size), germination, and dispersal. Projections of the three-dimensional optima onto the G - D plane and the S_1 - D plane are shown for perspective. To obtain the optimum for a given probability of favorable conditions, 1000 generations of population growth were simulated and the geometric-mean growth rate was calculated. We repeated this process for different combinations of D , G , and S_1 , searching for the combination yielding the highest fitness for that probability of favorable conditions. See the text for a list of parameter values and the constraint function used in the simulations.

The Probability of Favorable Conditions

Increasingly favorable environments can be modeled by increasing the probability of favorable conditions, p_i . In arid environments, this may be interpreted as increasing the frequency of wet conditions, and in disturbed habitats, as increasing the frequency of openings in perennial vegetation. We simulated five patches that experience no temporal or spatial autocorrelation and assumed that dispersing seeds are evenly distributed over all patches.

As the probability of favorable conditions increases from 0.08 to 0.75, the optimal dormancy decreases, the optimal seed size decreases, and optimal dispersibility at first increases, then decreases (fig. 6). Since plants more frequently encounter favorable conditions, selection favors increased specialization on them, which in our model means smaller seeds.

Between-year dormancy is advantageous only at times and places where the expected seed set of germinating seeds is less than the survival of seeds in the soil.

As the probability of encountering favorable conditions increases, fewer and fewer seeds encounter such unfavorable conditions and selection favors less between-year dormancy.

The value of dispersal lies in moving seeds away from places that are going to be unfavorable and into ones that are going to be favorable. This occurs less frequently as either favorable or unfavorable conditions become rare. Thus, the value of dispersal depends more on the variation in the favorability of conditions than on the average favorability. With only two types of conditions, dispersal contributes most to fitness at intermediate probabilities of favorable conditions.

Limited Dispersal Radius

The seeds of most plants travel only short distances on the average (Levin and Kerster 1974). To explore the effects of a limited dispersal radius we used the same constraint function on seed size as above, $p = 0.1$, 25 patches, and varied the radius of dispersal in the following way. Non-dispersing seeds still remain in the home patch, but dispersed seeds are uniformly distributed to the nearest r neighboring patches on either side (where r is the radius of dispersal) as well as to the patch of origin. This results in a peak of dispersal in the parental patch and a tail of dispersal of radius r , like that commonly reported for many plant species (Howe and Smallwood 1982). The patches were arranged linearly with the last patch wrapping around to the first, resulting in a circular one-dimensional environment. We varied the dispersal radius from zero (all seeds stay in the parental patch) to 12 (dispersing seeds uniformly distributed to all 25 patches).

Decreasing the radius of dispersal selects for a lower proportion of seeds dispersing, more dormancy, and larger seed size (fig. 7). Decreasing the radius of dispersal makes dispersal a less effective tool for spreading risk spatially. Since risk (global temporal variance) is increased, increases in dormancy and seed size are favored for their risk-reducing properties (i.e., escape in time and resistance via seed size become more necessary in the face of reduced escape in space).

Spatial Autocorrelation

Another assumption of the model up to now is that conditions occurring in one patch do not correlate with those occurring in the neighboring patches. To explore the effect of spatial autocorrelation of environmental conditions, we used the same constraint function on seed size, 25 patches, a dispersal radius of 6, and conditioned the probability of favorable conditions on those of neighboring patches. In each year, the probability of favorable conditions in the first patch was fixed at $p = 0.1$. If the first patch experienced favorable conditions, the probability that the neighboring patch experienced favorable conditions was varied from 0.1 (no spatial autocorrelation) to 0.9 (high spatial autocorrelation). The probability of favorable conditions in all the other patches was similarly contingent on the conditions of their neighboring patches. If a patch experiences unfavorable conditions, the probability of its neighbor's experiencing favorable conditions was set at less than 0.1 according to the formula

$$p_{F|U} = \bar{p}_F(1 - p_{F|F})/(1 - \bar{p}_F), \quad (6)$$

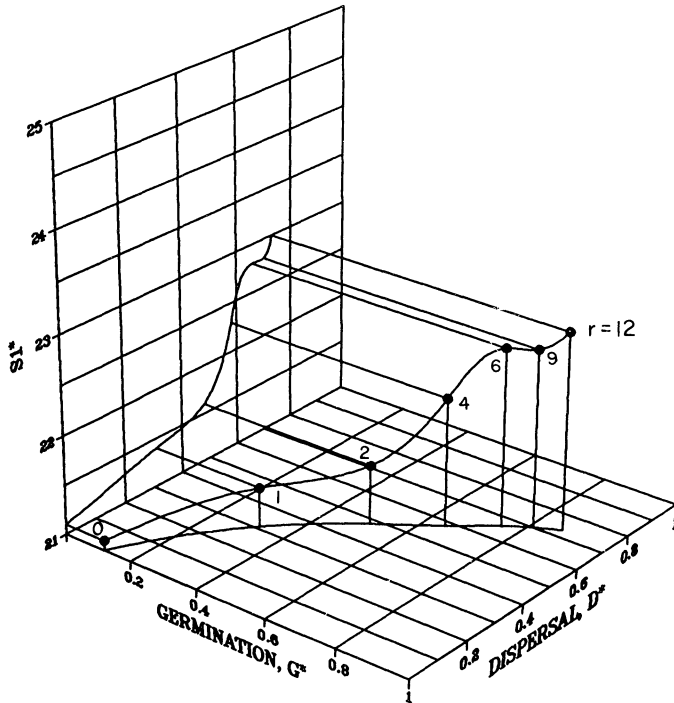


FIG. 7.—The effect of increasing the radius of dispersal, r (see text for definition), on optimal S_1 (an inverse function of seed size), germination, and fraction of seeds dispersing. Projections of the three-dimensional optima onto the G - D plane and the S_1 - D plane are shown for perspective. To obtain the optimum for a given radius of dispersal, 1000 generations of population growth were simulated and the geometric-mean growth rate was calculated. We repeated this process for different combinations of D , G , and S_1 , searching for the combination yielding the highest fitness for that radius of dispersal. See the text for a list of parameter values and the constraint function used in the simulations.

where \bar{p}_F is the overall probability of favorable conditions and $p_{F|F}$ is the probability of favorable conditions if the neighboring patch is favorable. This formula keeps these contingent probabilities of favorable conditions balanced so that the overall probability of a favorable year remains 0.1 despite increasing spatial autocorrelation.

In the simulations, increasing spatial autocorrelation of environmental conditions favors decreased dispersibility, increased dormancy, and increased seed size (fig. 8). Increasing spatial autocorrelation makes it more likely that most patches are favorable or unfavorable in any given year. This makes the average condition vary more from year to year, which increases risk (i.e., the global temporal variance). The increase in risk factors increased seed size, dormancy, and dispersal. Yet, because most patches are either favorable or unfavorable in any given year, dispersal mostly moves seeds to similar patches at the expense of dispersal-related mortality. If dispersal moves seeds only to neighboring patches (limited

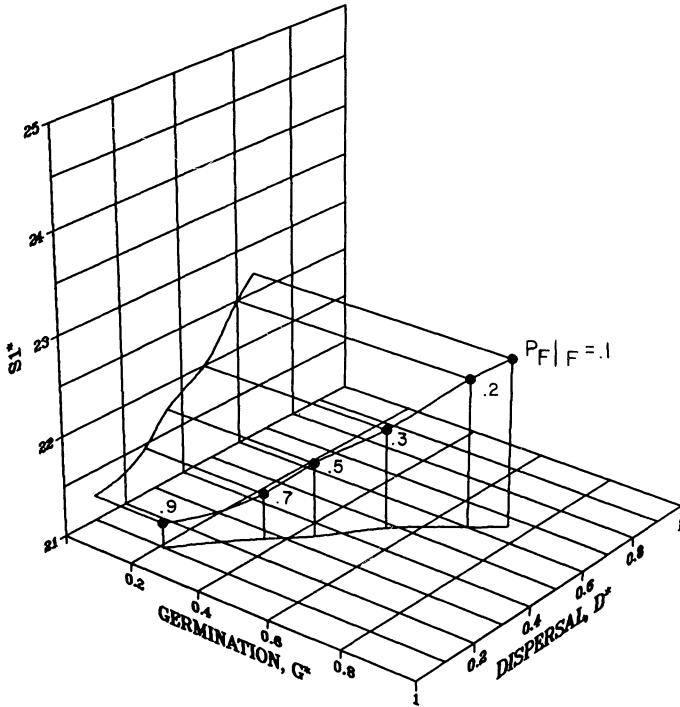


FIG. 8.—The effect of increasing spatial autocorrelation on optimal S_1 (an inverse function of seed size), germination, and dispersal. $p_F|F$ is the probability of favorable conditions in a patch given that conditions were favorable in the neighboring patch (higher values mean greater spatial autocorrelation). The probability of favorable conditions in a patch given unfavorable conditions in the neighboring patch was balanced such that the overall probability of favorable conditions does not change with increasing spatial autocorrelation. Projections of the three-dimensional optima onto the G - D plane and the S_1 - D plane are shown for perspective. To obtain the optimum for a given degree of spatial autocorrelation, 1000 generations of population growth were simulated and the geometric-mean growth rate was calculated. We repeated this process for different combinations of D , G , and S_1 , searching for the combination yielding the highest fitness for that degree of spatial autocorrelation. See the text for a list of parameter values and the constraint function used in the simulations.

dispersal radius), this problem is accentuated since neighboring patches within dispersal distance are even more likely to be similar to the patch of origin. Thus, the value of dispersal for reducing risk diminishes with spatial autocorrelation even though the overall level of risk is increasing. In our simulations, the net effect was selection for reduced dispersibility and increased dormancy and seed size.

Temporal Autocorrelation

If a patch experiences favorable conditions one year, it may have a higher than average probability of experiencing favorable conditions the next year. We simulated temporal autocorrelation using 11 patches, uniform dispersal, and an overall probability of favorable conditions, $p = 0.1$. In the first year, patches were

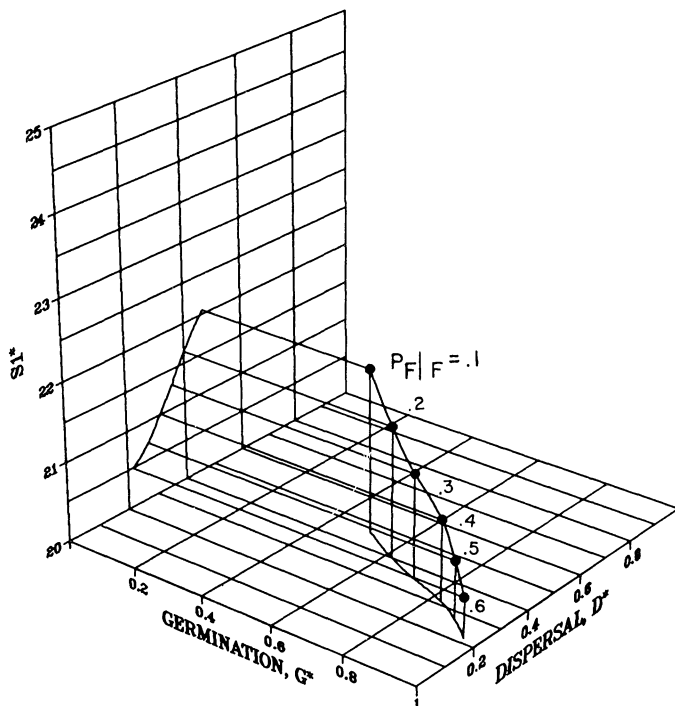


FIG. 9.—The effect of increasing temporal autocorrelation on optimal S_1 (an inverse function of seed size), germination, and dispersal. $p_{F|F}$ is the probability of favorable conditions in a patch given that conditions were favorable in that patch in the preceding year (higher values mean greater temporal autocorrelation). The probability of favorable conditions in a patch given unfavorable conditions in that patch in the preceding year was balanced such that the overall probability of favorable conditions does not change with increasing temporal autocorrelation. Projections of the three-dimensional optima onto the G - D plane and the S_1 - D plane are shown for perspective. To obtain the optimum for a given degree of temporal autocorrelation, 1000 generations of population growth were simulated and the geometric-mean growth rate was calculated. We repeated this process for different combinations of D , G , and S_1 , searching for the combination yielding the highest fitness for that degree of temporal autocorrelation. See the text for a list of parameter values and the constraint function used in the simulations.

independently assigned favorable or unfavorable conditions with a probability of $p = 0.1$. In subsequent years, the probability of favorable conditions depended on whether patches had experienced favorable or unfavorable conditions in the preceding year. As with the simulations for spatial autocorrelations, the probabilities of favorable conditions given a favorable preceding year and given an unfavorable preceding year were balanced to maintain the overall probability at $p = 0.1$ (see eq. 6).

In the simulations, as the probability of favorable conditions given favorable conditions in the preceding year increases from 0.1 (no temporal autocorrelation) to 0.9 (high positive temporal autocorrelation), dormancy and dispersal decrease, and seed size increases (fig. 9). Since there is no spatial autocorrelation, year-to-

year variance in average patch conditions does not increase as it did in the preceding section. Thus, the global temporal variance in the proportion of patches experiencing each year type does not increase with temporal autocorrelation. Yet, the long-term average success in each patch varies more. Therefore, some patches will be consistently more favorable than others, at least for a while. The problem facing plants is to get into these better patches and stay there, at least for a while. Most seeds will eventually be in the better patches because of mortality in the unfavorable ones and population growth in the favorable ones. As site favorability becomes more predictable, selection favors less dispersal, and less dormancy follows because most seeds are in reliably favorable sites. The increase in seed size is somewhat counterintuitive. Presumably, the direct selective effect of more predictability, that is, favoring smaller seeds, is weaker than the countervailing indirect selective pressure resulting from lowered dormancy and dispersal.

DISCUSSION

Both theoretical and empirical investigations of how annual plants respond to environmental variability have tended to focus on only one trait at a time. By modeling the evolution of seed size, dormancy, and dispersal together we have been able to uncover ways in which they interact to increase fitness. Seed size, dormancy, and dispersal share three population-dynamic functions: risk reduction, escape from crowding, and escape from sib competition. In this paper, we explore the ways they interact to reduce risk in temporally and spatially variable environments. We have demonstrated that global temporal variance is necessary for the evolution of the risk-reducing properties of seed size, dispersal, and dormancy. Because all three traits can reduce global temporal variance, they are partly substitutable. This results in selective trade-offs among them such that if they are at the optimum for a particular environment, and if any one of the three seed traits is arbitrarily increased, selection will favor a corresponding reduction in the other two. For example, the optimal seed size depends on dispersibility and dormancy. We also have explained why the three seed traits are not completely substitutable: they reduce global temporal variance in slightly different ways. Thus, different kinds of environmental changes may preferentially favor one or another seed trait with the other two adjusting according to their fitness trade-offs with the first trait and with each other.

The selective trade-offs between dispersal, dormancy, and seed size have several implications. In the different habitats surveyed by Salisbury (1942), Baker (1972), and others (e.g., D. Levin 1974; Silvertown 1981), considerable variation in seed size was not explained by the suggested habitat or life history factors. Some of this variation may be due to interacting selective pressures such as those operating through dormancy and dispersal. For example, species that regularly produce large seed banks may produce smaller than average seeds for their habitats.

The selective trade-offs described here also have implications for the issue of constraint versus adaptation (Gould and Lewontin 1979). Correlations between dormancy, dispersal, and seed size are usually discussed in terms of biophysical constraints. Examples (mentioned in the introduction) include the trade-off be-

tween seed size and dispersibility caused by weight constraints and the relationship between seed size and dormancy resulting from the inability of small seeds to emerge from great burial depth. Selective trade-offs represent an adaptive reason for such correlations. Regardless of weight constraints, large seeds should usually be less dispersive. Small seeds should usually have greater dormancy independent of any problems involved with burial. Now that we are aware of selective dynamics that favor such correlations, for any given case the question becomes whether constraints or selective factors are more important in shaping correlations between seed properties. What if, for example, it had turned out that selection favored greater dispersal for larger, not smaller, seeds? Can not adaptations evolve to promote greater dispersal of large seeds (e.g., fleshy animal-dispersed seeds) and retard the dispersal of smaller seeds (perhaps by holding them together in a non-dispersing fruit)?

Because the three seed traits reduce global temporal variance in slightly different ways and thus respond differently to environmental changes, we are encouraged to think about habitat patterns of seed size, dormancy, and dispersal together. If one trait is more successful at coping with a particular environmental change, the other traits may change more as a result of the indirect effects operating through correlated responses to the first trait than as a direct result of the environmental change itself. This kind of thinking brings us closer to studying reproductive biology in terms of structures integrating multiple functions through a process of coadaptation. With our current understanding of the population-dynamic effects of seed size, dispersal, and dormancy, further insights may be gained by considering, as we have here, how seed traits function as syndromes.

A number of specific predictions were generated by varying environmental parameters and observing the responses of seed traits in simulations. Increasing the number of patches may be thought of as an increase in spatial heterogeneity in the conditions experienced by a population, or as an increase in the independence of conditions in local subsites. This creates the possibility of reducing risk by dispersing among patches to find locally favorable conditions. The classic fugitive strategy of high dispersal, small seed size, and low dormancy is favored. This syndrome is expected for annual plants that experience many small (relative to potential dispersal distance) unsynchronized habitat disturbances.

We also generated predictions about adaptive seed responses to an increase in the frequency of favorable conditions. Favorable conditions in the scenarios we have constructed for annual plants are open patches of bare soil in mesic settings or moist conditions in arid environments. Since the model deals with density-independent risk reduction, we must add the caveat that the desert has not become so favorable that the habitat begins to close and competitive interactions begin to favor large-seeded, competitive plants. As the habitat begins to ameliorate in the above sense, plants should produce smaller, less dormant seeds. Adaptive change in dispersal in this scenario is more tied to variance in site quality, because the value of dispersal lies in moving seeds from unfavorable to favorable conditions rather than from favorable to favorable or from unfavorable to unfavorable conditions. If variance in site quality increases with environmental amelioration, greater dispersal is favored. If it decreases, less dispersal is favored.

Dispersal is in many ways the best tool for dealing with variability. Unlike dormancy and seed size, dispersal does not have an inherent cost other than the mortality cost we have assigned it, $1 - a$. Between-year dormancy inherently involves a cost of delayed reproduction in addition to any mortality cost, and changes in seed size inherently result in fitness trade-offs among the different environmental conditions.

Even though dispersal would seem to be the best tool for dealing with variability in the model, in nature we often observe dormancy and large seeds in annual plants; all annuals do not rely on dispersal alone to spread the risk of variable environments. Three factors that reduce the efficacy of dispersal in nature are mortality costs of transportation, inherent limitations on how far seeds can go, and correlations experienced in neighboring patches. In the model, there are no inherently bad places for seeds to land; all patches have the same probability of sooner or later becoming favorable. Dispersal to permanently inferior or unsuitable sites is accounted for by the dispersal-associated mortality term. Because dispersal to inherently unsuitable sites is a real hazard for most plant species, dispersal-related mortality should be set at high values for reasonable simulations.

Most recorded seed shadows indicate that seeds do not go very far (usually seeds travel a few meters to tens of meters). Such limited dispersal has the effect of making seed size and dormancy relatively more important adaptations for coping with environmental variation. Likewise, when neighboring habitats have fairly correlated environmental conditions, efficacy of dispersal is reduced below that found in our simplest models, since dispersal to a similar habitat is of little value. For example, Ellner and Shmida (1981) suggested that spatial autocorrelation in rainfall may be responsible for the relative lack of dispersal adaptations in plants of old-world deserts. If this is true for plants of North American deserts, the increased seed size reported by Baker (1972) may be at least partly due to a correlated selective response to low dispersibility.

In the simulations, dormancy and dispersal decreased with temporal autocorrelation. High temporal autocorrelation in a density-independent model implies that some strong density-independent mortality factor is operating every year in a reliable fashion, though its intensity may vary substantially spatially. In such circumstances, not much dispersal is required since the home patch is usually suitable next year, and not much dormancy is required for the same reason. Some dune annuals that reportedly do not produce seed banks may meet these criteria (Watkinson 1981).

We have assumed throughout the paper that the fraction of seeds germinating each year is a genetically determined strategy of a plant, and we have asked which one germination strategy is best. This assumes that plants cannot vary their germination strategy in response to cues indicative of favorable or unfavorable conditions or that such cues do not exist. This assumption can be easily relaxed by substituting the conditional probabilities of different environmental conditions given a particular cue into the model everywhere the (unconditioned) probabilities are found (see Cohen 1967; León 1985). When this substitution is made, a different optimal germination fraction will be associated with each cue, and cues associated reliably with favorable conditions for plant survival and reproduction will elicit

higher germination fractions. Seed size and dispersibility could be permitted to vary plastically as well, or they could be treated as genetically determined strategies not under environmental control. These modifications are mathematically straightforward and do not require any special elaboration here. It should be remembered, however, that predictive or plastic germination is an important aspect of seed behavior that provides an additional level of flexibility in dealing with variable environments.

For all of the cases simulated, interpreting the limited survey data in terms of our model predictions is difficult. First, different plants may experience the same environment differently. Two species in the same habitat may experience different numbers of patches, different patterns of spatial or temporal autocorrelation, etc. For example, two weeds in the same field with different vulnerabilities to weeding practices might experience large differences in all the environmental parameters we modeled. A second difficulty with the interpretation of survey data is that since the models make predictions about intraspecific evolution, they might best be tested by evolutionary ecological studies of a single species or of several closely related species. Interspecific comparisons are complicated because many other traits besides the ones of interest vary among species (though the microevolutionary dynamics explored in this paper ought to leave their mark at higher taxonomic levels if appropriate phylogenetic differences are factored out of the analysis; Felsenstein 1985). It must also be remembered that the models presented here consider fitness interactions with respect to the risk-reduction function of seed size, dormancy, and dispersal. These traits may also interact with respect to escape from crowding or sib competition. Interactions with regard to these functions will be explored in a separate paper, but their importance for actual case studies cannot be completely neglected. Fortunately, since the interactions for these other functions usually create similar selective correlations, predictions do not alter drastically, though the mechanisms do. Finally, our predictions of correlated seed responses are based on simulation models; thus, generalizing our predictions beyond the parameter values that we explored is difficult. Although many of the simulation results appear to be quite general, some specific results depend on the magnitude of counterbalancing selective effects. The net direction of selection in these cases may shift with changes in parameter values or in the form of the constraint function. Because all these issues limit our ability to test model predictions with survey data, we do not attempt any exhaustive review of observed patterns here. However, most of the model parameters are amenable (albeit with some difficulty) to empirical measurement. We hope that our outline of the issues and our predictions will stimulate the collection of population-dynamic data relevant to the evaluation of the adaptive significance of syndromes of seed traits.

SUMMARY

Seed size, dormancy, and dispersal share three population-dynamic functions in temporally and spatially varying environments: risk reduction or bet hedging, escape from crowding, and escape from sib competition. Here we developed a

model to explore the ways they may interact to reduce risk. We have shown that the risk-reducing properties of these three seed traits evolve only in response to global temporal variance. Thus, to understand how selection impinges on the seed traits, creating fitness interactions, we must understand the factors contributing to global temporal variance and how they are mitigated by the various seed traits. Since the traits interact to reduce variance, arbitrarily fixing any one trait at different values alters the fitness-maximizing values of the others, resulting in trade-offs among traits. We explore how changes in the number of independent environmental patches, the probability of favorable conditions, the radius of dispersal, and spatial and temporal autocorrelation of environmental conditions alter selection on the interacting syndrome of seed traits. We discuss the implications of these fitness interactions for our understanding of each of the seed traits in isolation, as well as for our understanding of seeds as reproductive structures integrating coadapted functions.

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