ESS Germination Strategies in Randomly Varying Environments. II. Reciprocal Yield-Law Models

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The study of ESS germination fractions in S. Ellner (1985, *Theor. Pop. Biol.* **27**, 000–000) is applied and extended in the case of annuals obeying the Reciprocal Yield Law. The effects of parameter changes on the value of the ESS germination fraction are determined in some limiting cases by analyses of approximations. Numerical solutions of the ESS criterion are used to check the robustness of the conclusions and the accuracy of the approximations. In general, the ESS germination fraction decreases with an increased survivorship of buried seeds and with increased "variability" of seed yields. However, different measures of "variability" are appropriate in different circumstances. To avoid the possibility of conflicting predictions depending on the measure of variability, it is suggested that tests of the theory be limited to co-occurring species, and to variability due to climatic fluctuations. The ESS theory based on the Reciprocal Yield Law is compared with D. Cohen's (1966, *J. Theor. Biol.* **12**, 119–129; 1968, *J. Ecol.* **56**, 219–228) density-independent theory of "optimal" germination. The theories differ qualitatively and quantitatively regarding the influence of mean yield, seed survivorship, and the frequency of favorable years on the predicted germination fraction. © 1985 Academic Press, Inc.

1. INTRODUCTION

This paper continues the theoretical study of seed germination strategies in randomly varying environments begun in Ellner (1985). In that paper—hereafter referred to as (I)—a simple model of annual plant population dynamics was presented, and analyzed to identify evolutionarily stable (ESS) values of the annual germination fraction G. Because the relationship between seedling density and final yield was specified qualitatively rather than exactly, the analysis was limited to studying qualitative relationships between population and environmental parameters (such as the frequency of years in which reproduction is impossible) and the ESS value of the germination fraction.

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In this paper a specific yield–density law is chosen, in order to examine relationships between the ESS germination fraction and measurable parameters of the yield–density law. The yield–density law used is the so-called "Reciprocal Yield Law" (RYL) first proposed by Shinozaki and Kira (1956):

$$Y(x) = \frac{K}{C + x}. \tag{1.1}$$

Here K, C are positive constants, x is initial seedling density, and Y is the per capita yield of seeds.

In Section 2 I outline the RYL model, and summarize the results of (I), specialized to the RYL. As in (I), the model describes annual plants with random year-to-year fluctuations in the parameters of the yield–density law. The annual germination fraction is assumed to be constant over time, but may vary between competing types in the population.

Even in this simple model, the ESS criterion is difficult to apply because it involves the (unknown) stationary distribution of population density for "resident" types. So, I resort to approximations; and, fortunately, an ounce of approximation is worth a pound of computation for the problem at hand. The approximations are (1) Bartlett's (1956, 1957) method for the case of "small fluctuations"; and (2) setting $C = 0$ in (1.1), so that total seed yield is independent of initial seedling density. These are applied separately and jointly in Sections 3 and 4. In Section 5, numerical solutions of the ESS criterion are used to examine the accuracy of the approximations, and to verify that they are a reliable guide to the behavior of the general model.

The final section summarizes the conclusions, and recasts them as testable predictions of inter- and intracommunity trends in germination. I also try to describe the sort of species to which the results should and should not be applied, and suggest extensions of the theory that would broaden its biological relevance and facilitate tests. A point-by-point comparison is made between the predictions of Cohen's (1966, 1968) density-independent theory of optimal germination, and the density-dependent theory in this paper and (I). The predictions of the theories are often diametrically opposed over substantial, biologically plausible ranges of the parameter values. This suggests that, in general, density-independent theories of life-history evolution in random environments may have limited applicability to density-regulated populations.

2. The Model

A. The Reciprocal Yield Law

A few words are in order about the Reciprocal Yield Law (RYL) and its generality. In (1.1), K is the asymptotic maximum total seed yield:

$K = \lim_{x \to \infty} x Y(x)$. The maximum per capita seed yield of germinated seeds is

$$b = K/C = \lim_{x \to 0} Y(x). \qquad (2.1)$$

These relationships are graphed in Fig. 1. Note that the total seed yield increases monotonically with increased initial density.

Experimental data on a variety of single-species populations suggest that the RYL usually applies to total yield (including seeds) if the initial seedling density is high enough that competition occurs, but density stress is absorbed by plasticity (reduced yield) rather than mortality (Harper, 1977). At high densities seeds may form a decreasing fraction of total yield (Harper, 1977), in which case the RYL would fail. The RYL also is not expected to hold at densities so high that competition causes increased mortality by self-thinning (Harper, 1977; White, 1980).

Watkinson (1980) synthesized experimental studies of single-species populations of annual plants into a general yield–density relationship for plant parts (such as seeds), which allows for possible density-dependent mortality. Watkinson's formula for the per capita seed yield is

$$Y(x) = \frac{\lambda}{(1 + (a + m)\,x)^\beta (1 + mx)^{1 - \beta}}$$

where x is the initial seedling density and λ, a, m, β are nonnegative constants related to the effects of competition on adult plant density and
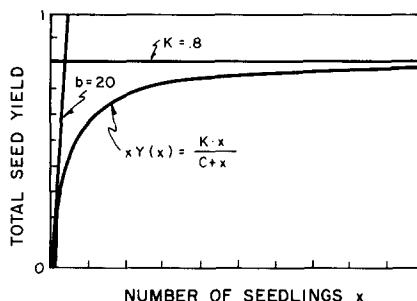

FIG. 1. Total yield as a function of initial seedling density in the Reciprocal Yield Law (1.1); $b = K/C = \lim_{x \to 0} Y(x)$.

weight, and to the allometry between the total weight and seed yield of adults. This model gives the RYL when $\beta = 1$ and/or $a = 0$. Values of $\beta \cong 1$ were reported by Watkinson (1980) for natural populations of *Vulpia fasciculata*, but greenhouse populations of *Agrostemma githago* had $\beta \cong 1.06$ and dynamic behavior inconsistent with RYL for seed number. $a = 0$ corresponds to pure "contest" competition: crowding affects survivorship to adulthood, but not the final yield of adults (Watkinson 1980). This sort of behavior seems unlikely.

Our use of the RYL to describe competition rests on the assumption that seeds in the population differ only in their germination characteristics, so that the seedling population is effectively monospecific. Weiner (1982) found that a competition model with RYL for seed number fit his experiments on *Trifolium incarnatum* and *Lolium multifloum* grown together in pots, but no other tests of RYL plant competition models have been carried out.

B. *Dynamics and Assumptions*

The model describes competition between morphs of an annual plant species that differ only in their germination fraction. The biological rationale for the model, and its limitations, are discussed in (I). With RYL seed yield, the population dynamics are

$$X_i(t+1) = X_i(t)\left[\frac{G_i K_t}{C_t + \sigma_t} + s(1 - G_i)\right]$$

$$i = 1, 2,...; \quad t = 0, 1, 2,..., \tag{2.2}$$

where $X_i(t)$ is the density of type-i seeds immediately prior to germination in year t; G_i is the annual germination fraction of type-i seeds; $\sigma_t = \sum_i G_i X_i(t)$ is the total density of germinated seeds in year t; and $s(0 < s < 1)$ is the annual survivorship of dormant (ungerminated) seeds.

The parameters K_t and C_t of the Reciprocal Yield Law are assumed to depend on some environmental parameter α_t that can vary over time, as follows.

ASSUMPTION 1.

$$K_t = \bar{K}(1 + \rho_k \alpha_t) \geqslant 0$$
$$C_t = \bar{C}(1 - \rho_C \alpha_t) > 0 \tag{2.3}$$

where $(\alpha_t)_{t=0}^{\infty}$ is a sequence of independent, identically distributed random variables with mean 0 and variance 1. The parameters $\bar{K}, \bar{C}$ are positive, and

$$\rho_K \geqslant 0, \qquad \rho_C \geqslant -\rho_k. \tag{2.4}$$

In this setup, K, C are the means of K_t and C_t, and ρ_K, $|\rho_C|$ are their coefficients of variation (standard deviation/mean). $\rho_C \geqslant -\rho_K$ is equivalent to total yield being an increasing function of α_t at all densities, so α_t represents some measure of environmental "favorability" in year t. The motivation for Assumption 1 is discussed below.

Assumption 1 introduces a lot of notation, but all the parameters of the RYL in (2.3) can be related to biological properties of the species, and these relationships make it easy to interpret the mathematical results. $\bar{K}$ is the mean of the high-density total seed yield, and $\bar{K}/\bar{C}$ is roughly the mean low-density per capita seed yield (actually, the per capita yield in the mean environment $\alpha = 0$). ρ_K is the coefficient of variation of high-density seed yields; it can be thought of as measuring the year-to-year variability in the capacity for seed production by an entire, dense population.

ρ_C turns out to be a measure of the variability of low-density seed yields, relative to the variability of high-density yield. If $\rho_C = 0$,

$$Y(x) = \frac{\bar{K}(1 + \rho_K \alpha_t)}{\bar{C} + x},$$

so the coefficient of variation of yield is the same at all seedling densities x. If $\rho_C < 0$ low-density yields are less variable high-density yields, and the reverse holds if $\rho_C > 0$. At the minimum value $\rho_C = -\rho_K$, (K_t/C_t) is constant over time, so low-density yields have small fluctuations which decrease to zero in the limit of zero density. An increase in ρ_C increases the variability of yields at all densities, but the increase is largest at low density an becomes vanishingly small at high densities.

In an environment with many variables changing from year to year, the values of ρ_C and ρ_K will depend on how the sensitivity of plants to each variable is affected by crowding. For example, if seed yield is limited by light at high densities and by water at low densities, with rainfall varying greatly from year to year but insolation more or less constant, ρ_K will be small and ρ_C large. If abbreviated growth seasons frequently prevent seed-set at high density, but uncrowded plants develop more rapidly and always set seed, ρ_K will be large and ρ_C will be near $-\rho_K$ (low variability at low density).

A technical assumption is necessary so that the results of (I) can be applied:

ASSUMPTION 2. (a) $K_t \leqslant K_M$ with probability 1, where K_M is some constant.

(b) $E[C_t^{-1}]$ and $E[\ln K_t | K_t > 0]$ are finite.

A rescaling reduces by one the number of parameters in the model. Redefining $X \to X/\bar{K}$, (2.2) becomes

$$X_i(t+1) = X_i(t) \left[\frac{G_i(1 + \rho_K \alpha_t)}{\omega(1 + \rho_C \alpha_t) + \sum_i G_i X_i(t)} + s(1 - G_i) \right] \qquad (2.5)$$

where $\omega = \bar{C}/\bar{K}$. All parameters in (2.5) are dimensionless, so in analyzing (2.2) we will be trying to see how the ESS germination fraction varies as a function of s, ω, ρ_K, ρ_C, and the distribution of α_t.

C. The Story So Far

The first step in analyzing (2.2) is to apply the general results in (I). Those results characterize ESS germination fractions, identify circumstances in which some extended dormancy is favored (i.e., $G = 1$ is not an ESS), and describe the behavior of the ESS germination fraction as the survivorship of ungerminated seeds decreases to 0.

A single-morph population with germination fraction G has dynamics

$$X_G(t+1) = X_G(t) \left[\frac{GK_t}{C_t + GX_G(t)} + (1 - G)s \right]. \qquad (2.6)$$

$X_G(t)$ has one of two possible long-term behaviors, depending on the sign of

$$v(G) = E[\ln (Gb_t + (1 - G)s)], \qquad (2.7)$$

where $b_t = K_t/C_t$. $v(G)$ is the log of $X_G(t)$'s geometric mean growth rate in the limit of zero density ($X_G(t) = 0$ in (2.6)). If $v(G) \leqslant 0$, $X_G(t)$ converges to 0 with probability 1, and $X_G(t)$ converges in distribution to a unique stationary distribution on $(0, \infty)$ whenever $v(G) > 0$. Thus $v(G) \leqslant 0$ and $v(G) > 0$ correspond to extinction and persistence of the population, respectively. For $v(G) > 0$, the stationary process obtained by letting $X_G(0)$ have the stationary distribution will be denoted $\tilde{X}_G(t)$.

The first requirement for evolutionary stability is that $v(G) > 0$, in which case G will be called *viable*. The second requirement is that rare invaders fail to become established in the population. In (I), noninvasibility was shown to be equivalent to

$$H(G) \stackrel{\text{def}}{=} H_G \left[\frac{\tilde{X}_G(t+1)}{\tilde{X}_G(t)} \right] = s \qquad (2.8a)$$

for $0 < G < 1$, and $G = 1$ is noninvasible if

$$H(1) = H_1 \left[\frac{\tilde{X}_1(t+1)}{\tilde{X}_1(t)} \right] \geqslant s. \qquad (2.8b)$$

Here $H_G[\,\cdot\,]$ is the harmonic mean with respect to the joint distribution of $(\tilde{X}_G(t), K_t, C_t)$; the harmonic mean of a random variable Z is $H[Z] = 1/E[1/Z]$. $G = 0$ can never be an ESS, since $v(0) = \ln s < 0$.

In (I) it was shown that the ESS germination fraction considered as a function of s has essentially three possible behaviors as $s \to 0$, depending on the sign of $v(1)$ and on whether $H(1) > 0$ or $H(1) = 0$. For seed yield given by the Reciprocal Yield Law,

$$H(1) = (E[C_t/K_t] + E[X_1(t)]\, E[1/K_t])^{-1}. \tag{2.9}$$

Since $E[\tilde{X}_1(t)] \leqslant K_M$ and C_t is bounded above, it follows from (2.9) that

$$H(1) = 0 \qquad \text{if and only if } E[1/K_t] = +\infty. \tag{2.10}$$

The classification of possible behaviors therefore may be summarized as follows:

   (a)   If $v(1) < 0$ or $E[1/K_t] = +\infty$, some dormancy is always favored (any ESS germination fraction is < 1).

   (b)   If $v(1) > 0$ and $E[1/K_t] < +\infty$, $G = 1$ is an ESS if $s \leqslant H(1)$, and some dormancy is favored if $s > H(1)$.

In general any ESS germination fraction must be $\leqslant 1 - P_0$, where P_0 is the frequency of zero-yield years, $P_0 = P[K_t = 0]$. If $v(1) < 0$ (which is always the case if $P_0 > 0$), there will be no viable morphs (hence no ESSs) for s near 0.

Intuitively, (a) and (b) say that a low survivorship of dormant seeds can favor 100% germination even if yields are variable, unless yields are so variable that some dormancy is necessary to prevent frequent severe "crashes" in population density and/or a steady decrease to extinction.

D. *Why Assumption 1?*

To see why something like Assumption 1 is necessary, consider the (biologically implausible) case $K_t = C_t + x_0$, with $x_0 > 0$ and K_t, C_t satisfying the assumptions of (I). In this case, low-density and high-density yields are negatively correlated: b_t is high when K_t is low. At intermediate densities there is little variability in yields, and at density x_0 there is none at all. The stationary distribution of a resident with germination fraction $G = 1$ is $X_1(t) = x_0$ with probability 1 (Ellner, 1984, Appendix). Consequently $G = 1$ is an ESS, regardless of the value of s and the amount of variability in K_t or C_t: an invader with germination fraction $G < 1$ has low-density growth rate $\ln(G + (1 - G)s) < 0$, and therefore fails to invade. If we want the model to behave reasonably, this sort of situation must be ruled out.

Assumption 1 is a simple way to ensure that low- and high-density yields are not negatively correlated. As discussed above, the model with Assumption 1 still is flexible enough to describe a variety of ecological situations. Some variants on Assumption 1 were used before settling on the present version, and while the results differed in notation, the biological interpretations were always the same.

3. Approximate Solution for "Small" Fluctuations

Because the ESS criterion cannot be solved analytically, our strategy is to study limiting cases by approximation, and to check the general validity of the conclusions by numerical solutions for selected parameter values. This section is devoted to the first approximation, obtained by using Bartlett's method (Bartlett 1956, 1957; Bartlett *et al.*, 1960) to estimate $H(G)$ in the case of "small" fluctuations in K_t and C_t. Bartlett's method has been expounded in detail recently (Nisbet and Gurney, 1982) and applied to invasibility analyses (Turelli, 1978, 1981; Turelli and Petry, 1980), so we concentrate on the assumptions and results.

A. *The Approximation*

We introduce a parameter ε measuring the "size" of the fluctuations by setting

$$\rho_K = \varepsilon \gamma_K$$
$$\rho_C = \varepsilon \gamma_C \tag{3.1}$$

for some $\gamma_K \geqslant 0$, $\gamma_C \geqslant -\gamma_K$. The coefficients of variation of K_t and C_t are then both of order ε. In the approximation, ε is treated as a small parameter and terms of order ε^3 or smaller are discarded.

If there are no environmental fluctuations ($\varepsilon = 0$), $X_G(t)$ has a stable equilibrium at $\max(\bar{X}_G, 0)$, where

$$\bar{X}_G \overset{\text{def}}{=} \frac{\bar{K}}{1 - s + sG} - \frac{\bar{C}}{G}. \tag{3.2}$$

$\bar{X}_G$ will be positive if and only if $G(\bar{K}/\bar{C}) + s(1 - G) > 1$, so $\bar{X}_G > 0$ is roughly equivalent to G being viable.

If there are "small" fluctuations in K_t and C_t, fluctuations of $X_G(t)$ about $\bar{X}_G$ are also "small," in the following sense. Set $x(t) = (X_G(t) - \bar{X}_G)/\bar{X}_G$. For ε sufficiently small and $X_G(t)$ in its stationary distribution, $|x(t)| < 1$ holds

with probability one and $E[x(t)^n]$ is of order ε^n for any $n \geqslant 2$ (this is proved in Appendix 1). We can therefore estimate

$$H(G)^{-1} = E_G\left[\frac{X_G(t)}{X_G(t+1)}\right] = E_G\left[\frac{1+x(t)}{1+x(t+1)}\right]$$

$$= E_G[(1+x(t))(1-x(t+1)+x(t+1)^2 - \cdots)]. \quad (3.3)$$

The distribution of $X_G(t)$ is assumed to be stationary, so $E_G[x(t)^m] = E_G[x(t+1)^m]$. Also, by the Schwarz inequality $E[x(t)^n x(t+1)^m]$ is of order ε^{n+m} for $n + m \geqslant 2$. Therefore to order ε^2

$$H(G)^{-1} = 1 + E_G[x(t)^2] - E_G[x(t)\,x(t+1)]. \quad (3.4)$$

$E_G[x(t)^2]$ and $E[x(t)\,x(t+1)]$ may be estimated to order ε^2 by linearizing the dynamics of $x(t)$ about 0 and calculating the stationary moments of the linearized process; this is carried out in Appendix 1. The resulting approximation to $H(G)^{-1}$, accurate to order ε^2, is

$$H(G)^{-1} = 1 + \frac{(1-d)^2}{1+d+\omega G^{-1}(1-d)^2}\,(\rho_K + \omega G^{-1}(1-d)\,\rho_C)^2 \quad (3.5)$$

where

$$d = s(1-G), \qquad \omega = \bar{C}/\bar{K}. \quad (3.6)$$

Using the right-hand side of (3.5) in place of $H(G)^{-1}$ gives the approximate ESS criterion:

(1) $G = 1$ is an ESS for $0 < s \leqslant s^*$, where

$$s^* = \left(1 + \frac{(\rho_K + \omega\rho_C)^2}{1+\omega}\right)^{-1} \quad (3.7)$$

(2)   For $s > s^*$, $G \in (0, 1)$ is an ESS if and only if

$$s\left(1 + \frac{(1-d)^2}{1+d+\omega G^{-1}(1-d)^2}\,(\rho_K + \omega G^{-1}(1-d)\,\rho_C)^2\right) = 1. \quad (3.8)$$

B. *The Case $C_t \equiv 0$.*

Equation (3.8) is a mess, but it is a tractable mess. The most convenient starting point for analysis is the case $C_t \equiv 0$, i.e., $\omega = 0$. In the approximate ESS criterion $G = 1$ is then an ESS for $0 < s \leqslant s^*$, where

$$s^* = (1 + \rho_K^2)^{-1}. \quad (3.9)$$

For $s > s^*$, $G \in (0, 1)$ is an ESS if and only if

$$s \left(1 + \rho_K^2 \frac{(1 - s + sG)^2}{(1 + s - sG)} \right) = 1. \tag{3.10}$$

The question on the floor is: How does the value of ESS respond to changes in s and ρ_K? The answers may depend on whether $\rho_K > 1$ or $\rho_K < 1$. In the former case the approximation is not valid, so we assume $\rho_K < 1$.

Substituting $G = 0$ and 1 into (3.10) shows that for $s > s^*$, (3.10) has at least one solution $\hat{G} = \hat{G}(s, \rho_K) \in (0, 1)$. The left-hand side of (3.10) is differentiable and increasing in G, s, and ρ_K, so long as $\rho_K < 1$. $\hat{G}(s, \rho_K)$ is therefore unique, and $\hat{G}$ is continuously decreasing in both s and ρ_K except where $\hat{G} = 1$. Thus, for small fluctuations in K_t and $C \equiv 0$, an increased survivorship of dormant seeds and/or an increase in the coefficient of variation of K_t will favor a decreased germination fraction—exactly as intuition would suggest.

Taking ρ_K fixed and varying s, $\hat{G}$ has the behavior shown in Fig. 2. $\hat{G} = 1$ for $s \leqslant (1 + \rho_K^2)^{-1}$, and $\hat{G}$ decreases to 0 as s increases to 1. The limiting slope near s^* is (via the Implicit Function Theorem) $\partial \hat{G}/\partial s = -(1 + \rho_K^2)^3/(3\rho_K^2)$. That is, when s^* is smaller (ρ_K larger), the initial increase in $(1 - \hat{G})$ is less rapid.

The behavior of $\hat{G}$ near $s = 1$ can be found by rewriting (3.10) in the form

$$\rho_K^2 \frac{(\sqrt{1 - s} + s(G/\sqrt{1 - s}))^2}{1 + s - sG} = \frac{1}{s}. \tag{3.11}$$
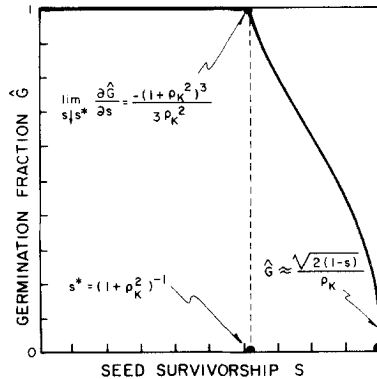

FIG. 2. $\hat{G}$ as a function of seed survivorship s in the small-fluctuations approximation with $C_t \equiv 0$ ($\omega = 0$). The plotted curve is for $\rho_K = 0.8$.

Since $\hat{G} \to 0$ as $s \to 1$, (3.11) implies

$$\lim_{s \to 1} \frac{\hat{G}(s, \rho_K)}{\sqrt{1-s}} = \frac{\sqrt{2}}{\rho_K}. \tag{3.12}$$

These results are summarized in Fig. 2.

Equation (3.10) is quadratic in G, and so can be solved explicitly. In Fig. 3, solutions to (3.10) are compared with numerical solutions of the exact ESS criterion. As expected, the approximation is quite accurate for ρ_K small, and $\hat{G}$ is a nearly linear function of $\sqrt{1-s}$ for s near 1. As ρ_K increases the approximation becomes less accurate, the size of the discrepancy depending on the distribution of α_t (Figs. 3a vs 3b). An important feature of (3.10) seen in Fig. 3 is that even very small fluctuations can favor a low germination fraction, so long as seed survivorship is near 1.

C. *The General Case*

Returning to Eq. (3.8), we have two more parameters to deal with, but the situation is not much more complicated. As before, we report the behavior of $\hat{G}$ for ρ_K, ρ_C sufficiently small, which in this case is $\rho_K + \omega |\rho_C| < 1$. And, in order that $\bar{X}_G$ be positive for some G (a requisite for the approximation) we assume $\omega < 1$.

Differentiation (followed by debilitating amounts of algebra) discloses that the left-hand side of (3.8) is increasing in $G, s, \rho_K,$ and ρ_C. Substituting $G = 1$ and $G = \omega(1-s)(1 - \omega s)^{-1}$ into (3.8) shows that (3.8) has a solution $\hat{G}$, which is necessarily unique.
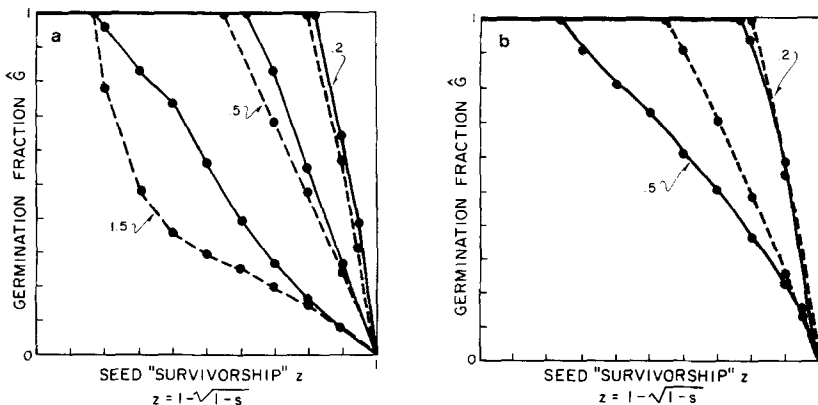

FIG. 3. Exact values of $\hat{G}$ (solid curve) compared with the small-fluctuations approximation (dashed), for two possible values of K_t: (a) $P[K_t$ takes larger value$] = 0.2$, $\rho_K = 0.2, 0.5,$ or 1.5; (b) $P[K_t$ takes larger value$] = 0.75$, $\rho_K = 0.2$ or 0.5.

$\hat{G}$ therefore remains well-defined, and is decreasing in s, ρ_K, and ρ_C. The methods applied to (3.10) carry over without difficulty to describe the behavior of G as a function of s (Fig. 4). $G = 1$ for $s < s^*$ (defined in Eq. (3.7)), and as s increases, $\hat{G}$ decreases with negative initial slope. Near $s = 1$ the behavior of $\hat{G}$ is again square-root-like:

$$\lim_{s \to 1} \frac{\hat{G}(s)}{\sqrt{1-s}} = \frac{\sqrt{2}}{\rho_K + \omega\rho_C}. \tag{3.13}$$

Note that when C_t is constant ($\rho_C = 0$), the behavior near $s = 1$ does not depend on the value of ω.

As before, G decreases with increased seed survivorship s and with increased variability of yield (ρ_K or ρ_C). The effect of ω on $\hat{G}$ is more complicated. Near $s = 1$, (3.13) shows that $\partial\hat{G}/\partial\omega$ has the sign of $-\rho_C$. On the other hand, $\partial\hat{G}/\partial\omega$ has the sign of $\rho_K - (4 - \omega)\rho_C$ near $s = s^*$. Thus if ρ_C is positive but $\rho_C \ll \rho_K$ (so low-density yields are just slightly more variable than high-density yields), an increase in ω will favor more germination if seed survivorship is low ($s \approx s^*$), and less germination if seed survivorship is high ($s \approx 1$).

The complicated interaction between ρ_C and ω occurs because ω influences both the mean and the variability of achieved seed yields. An increase in ω decreases low-density yields; this by itself would moderate population fluctuations by slowing the population's increase after a run of bad years, which favors increased germination. However, if low-density yields are more variable than high-density yields ($\rho_C > 0$), the extra time spent at low density might actually magnify the population fluctuations, resulting in a lower ESS germination fraction.
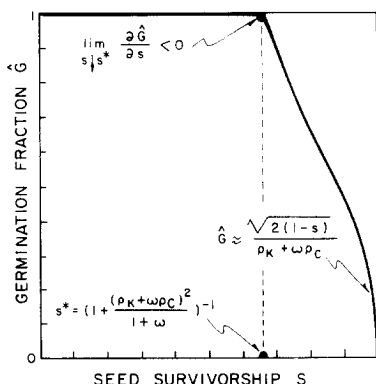

FIG. 4. $\hat{G}$ as a function of seed survivorship s in the general small-fluctuations approximation. The plotted curve is for $\rho_K = 0.6$, $\rho_C = 0.6$, $\omega = 0.4$.

Similarly, the value of ω influences the relative importance of ρ_C and ρ_K. Low densities rarely occur if $\omega \ll 1$, so the variability of low-density yields is unimportant (i.e., the ρ_C terms in (3.8) and (3.14) are negligible).

4. THE "SATURATION" CASE: $C_t \equiv 0$

A second useful approximation is obtained by setting $C_t \equiv 0$ in the basic model (2.1). The dynamics of a single-morph population are then

$$X_G(t+1) = K_t + s(1-G) X_t. \tag{4.1}$$

This describes a "saturated" habitat in which the available resources are fully utilized by the germinated seeds, regardless of how many germinate.

Analysis of the saturation case is possible because (4.1) is first-order autoregressive, and (as is well known) has stationary distribution

$$\tilde{X}_G(t) \sim \sum_{n=0}^{\infty} d^n K_{t-n}, \tag{4.2}$$

where $d = s(1-G)$ and $\{K_t\}_{t=-\infty}^{\infty}$ are independent random variables each having the distribution of K_1. The ESS criterion still cannot be solved explicitly, but we can use (4.2) to determine the asymptotic behavior near $s = 0$ and $s = 1$. In other words, we can redo Section 3B *without* the assumption of small fluctuations and see how the results change.

The analysis is similar in spirit to that of the small-fluctuations case, but technically much more involved. In this section, the behavior of the saturation case is discussed, and contrasted with the small-fluctuations approximation. The proofs are in Appendixes 2 and 3.

The main results for the saturation case are summarized in Fig. 5. For any seed survivorship s, the ESS criterion $H(G) = s$ has at least one solution $\hat{G}(s)$. Extensive numerical simulations with a variety of distributions of K_t suggest that $H(G)$ is monotonically decreasing in G. If so, the ESS $\hat{G}(s)$ is unique, and G is decreasing in s with $G(s) \to 0$ as $s \to 1$. These properties are henceforth assumed to be true.

The asymptotic behavior near $s = 1$ is quite interesting: it is exactly the same as in the small-fluctuations approximation to the saturation case (Fig. 2). This occurs because $X_G(t)$ has coefficient of variation

$$\rho_X = \sqrt{\frac{1-s+sG}{1+s-sG}} \rho_K \tag{4.3}$$

(obtained easily from (4.2)). As $s \to 1$ and $\hat{G}(s) \to 0$, $\rho_X \to 0$ and so the "small-fluctuations" approximation becomes increasing accurate. Thus for s
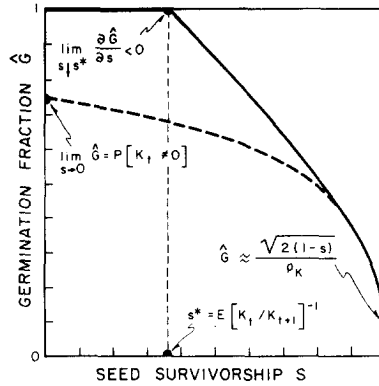
FIG. 5. $\hat{G}$ as a function of seed survivorship s in the saturation case. Solid line: $K_t > 0$ with probability 1. Dashed line: $K_t = 0$ with probability $P_0 > 0$.

near 1, the value of $\hat{G}$ depends only on the seed survivorship (s) and the coefficient of variation of total yield (ρ_K). A larger ρ_K (a more "variable" environment) favors a decreased germination fraction.

The behavior of $\hat{G}$ as s decreases to 0 depends on whether or not zero-yield years occur. If they do, some dormancy is favored regardless of the seed survivorship, with $\lim_{s \to 0} \hat{G}(s) = P[K_t \neq 0]$. Thus if seed survivorship is low, the germination fraction is proportional to the frequency of years with nonzero yield. This is similar to Cohen's (1966) result for the density-independent case, but here it holds only near $s = 0$, and only if the "unfavorable" years have $K_t = 0$ exactly rather than K_t small and positive (see below).

If zero-yield years do not occur, then 100% germination is an ESS for $s \leqslant s^*$, where

$$s^* = E[K_t/K_{t+1}]^{-1} = H[K_t]/E[K_t] \tag{4.4}$$

(recall that $H[K_t] = 1/E[1/K_t]$). Thus $E[K_t/K_{t+1}]$, rather than ρ_K, is the appropriate measure of environmental variability when seed survivorship is low. A "variable" environment ($E[K_t/K_{t+1}]$ high, $\hat{G}$ low) is one in which next year is likely to be much worse than this year, or much better. A very similar shift between measures of environmental variability was found by Levin *et al.* (1984) in a model of optimal dispersal rates in patchy habitats.

The relationship between ρ_K and $E[K_t/K_{t+1}]$ is clarified by writing

$$\rho_K^2 = E\left[\frac{(K_t - \bar{K})^2}{\bar{K}^2}\right],$$

$$E[K_t/K_{t+1}] = 1 + E\left[\frac{(K_t - \bar{K})^2}{K_t \bar{K}}\right]. \tag{4.5}$$

Here ρ_K^2 and $E[K_t/K_{t+1}]$ are both expressed as "standardized" variances of K_t, with the difference that $E[K_t/K_{t+1}]$ is weighted so as to emphasize fluctuations below $\bar{K}$.

The shift between different measures of variability has some interesting and possibly counterintuitive consequences. Figure 6 shows the ESS germination fraction in a "good year"/"bad year" model, $K_t = 0.5$ or 10 with probabilities $(1-p)$ and p, respectively. Intuitively, one might expect $\hat{G}$ to be largest when the chance of a "good" year is highest. And, if per capita seed yields were density-independent (but random) as in the model analyzed by Cohen (1966, 1968), $\hat{G}$ would in fact be approximately proportional to p (Cohen, 1966).

In Fig. 6, $\hat{G}$ is increasing in p near $s = 1$, since ρ_K is decreasing in p for $p \geqslant 0.01$. But as s decreases, there is a striking convergence of the ESS values for the extreme environments $p = 0.1$ and $p = 0.9$. This is not a coincidence. In the case of two non-zero possible K values, $E[K_t/K_{t+1}]$ depends only on the probability that the K values in two successive years are different, $P_d = 2p(1-p)$:

$$E[K_t/K_{t+1}] = 1 + P_d[(K_1/K_2) + (K_2/K_1) - 2].$$

P_d is maximized at $p = 0.5$, so germination at low values of s is minimized. At $p = 0.1$ or 0.9, next year is likely to be like this year, so more germination is favored.

The curves cross in Fig. 6 because p affects both ρ_K and the distribution of α_t. However, if the distribution of α_t is fixed and ρ_K is increased (recall $K_t = \bar{K}(1 + \rho_K \alpha_t)$), $E[K_t/K_{t+1}]$ also increases and the environment is "more variable" in both measures. The expected result is a decreased germination fraction at all values of s, and this is supported by the numerical studies in the next section.
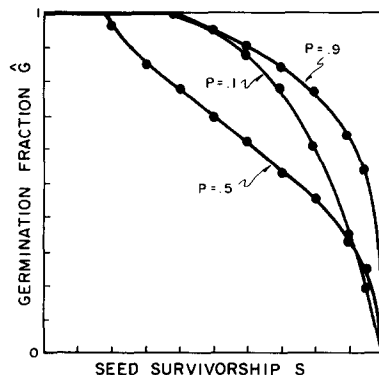

FIG. 6. $\hat{G}$ as a function of seed survivorship s in the saturation case with $K_t = 0.5$ or 10, $p = P[K_t = 10]$.

5. Numerical Studies

It is time to return to the general model, still asking how changes in ρ_K, ρ_C, ω, s, and the distribution of $\alpha(t)$ affect the ESS value of G. The approximations provide a set of answers for special cases, and in this section we use numerical calculations of ESSs to see if the general model behaves similarly. The focus here is still on the model: biological interpretation is in the Discussion.

Based on the small-fluctuations and saturation approximations, we expect that

   (a)   The small-fluctuations approximation will become accurate as $s \to 1$ even if fluctuations in K_t and C_t are large; therefore $\hat{G} \sim \sqrt{2(1-s)/(\rho_K + \omega\rho_C)}$ for s near 1.

   (b)   In general, $\hat{G}$ will be decreasing in s, ρ_K, and ρ_C.

   (c) $\hat{G}$ will be decreasing in $E[K_t/K_{t+1}]$; this effect will be strongest when s is small, and the asymptotic behavior near $s = 1$ will be controlled by $(\rho_K + \omega\rho_C)$ as per (a).

   (d) $\partial\hat{G}/\partial\omega$ will have the sign of $-\rho_C$ near $s = 1$; near $s = s^*$, $\partial\hat{G}/\partial\omega > 0$ if $\rho_C \leqslant 0$ but $\partial\hat{G}/\partial\omega$ will be < 0 if ρ_C is sufficiently large and positive. An increase in ω will also make $\hat{G}$ more sensitive to changes in ρ_C.

   (e) $\hat{G}$ will approach $P[K_t \neq 0]$ from below as $s \to 0$.

Values of $\hat{G}$ were obtained by generating pseudorandom $\alpha(t)$'s and estimating $H(G)$ by its time-average over a single realization of $X_G(t)$. Reported values are the means of three independent estimates using 1200–2000 generations; standard errors of the means were invariably $\leqslant 0.02$, indicating that the estimates are quite reliable. A unique solution (within the resolution of the calculations) of the ESS criterion $H(G) = s$ was always found, unless yields were so low that all morphs were nonviable. Spot-check simulations confirmed that the calculated ESSs resisted invasion by morphs having germination fractions $\hat{G} \pm 0.05$, and also were able to invade and competitively exclude any other morphs. If the ESS *can* invade any other morph, then $H(G) - s$ must have the sign of $(\hat{G} - G)$ (Appendix 4, Proposition A4.1), and this was true in all our computations.

Two sorts of distributions of $\alpha(t)$ were used. In the first, $\ln K_t$ had the triangular density

$$f_K(x) = \begin{cases} \dfrac{1}{M}\left(1 - \dfrac{|x-a|}{M}\right) & |x-a| \leqslant M \\[2mm] 0 & |x-a| > M \end{cases} \tag{5.1}$$

This is similar to a lognormal, but (unlike a lognormal) satisfies

Assumption 2. Conveniently, M and a are uniquely determined by $\bar{K}$ and ρ_K (and vice versa). Increasing ρ_K with $\bar{K}$ fixed increases $E[K_t/K_{t+1}]$ also, so conjecture (c) cannot be checked with K_t log-triangular. For this we used discrete distributions of (K_t, C_t), with two or three possible values. To emphasize the conjectured linearity of $\hat{G}$ in $\sqrt{1-s}$ near $s = 1$, $z = 1 - \sqrt{1-s}$ was used in place of s as the measure of seed survivorship. We notate $z^* = 1 - \sqrt{1-s^*}$, the largest value of z at which $G = 1$ is an ESS.

The effects of s and ρ_K are checked in Table I. $\hat{G}$ decreases in s and ρ_K as expected, and the near-linearity of $\hat{G}$ in z near 1 is apparent (if $\hat{G}$ were exactly linear, the values at $z = 0.6$, 0.8, 0.9, 0.95 would form a geometric series with ratio $\frac{1}{2}$: $\hat{G}(0.8) = \frac{1}{2}\hat{G}(0.6)$, etc.). The small-fluctuations approximation does surprisingly well at $\rho_K = 1$, considering the size of the fluctuations. At $\rho_K = 1$, K_t varies over two orders of magnitude and the first and third quartiles (which bracket the central 50% of the probability) differ by a factor of 22.7. The approximation is poor at $\rho_K = 2$ and nonsensical at $\rho_K = 3$; and, unfortunately, the accuracy at $\rho_K = 1$ can also be poor for other distributions of K_t.

Table II shows the effects of ρ_C. As expected, $\hat{G}$ is decreasing in ρ_C and the effect is more pronounced at $\omega = 0.3$ than at $\omega = 0.1$. The same data indicate the effects of changing ω. At $\rho_C = 0.15$, the small fluctuations results have $\hat{G}$ increasing in ω near $s = s^*$ and decreasing in ω near $s = 1$, and at $\rho_C = -1$ $\hat{G}$ should increase with ω at all values of s. Both of these occur, which is nor surprising given the accuracy of the small-fluctuations approximation. However, the same trends also occur at larger values of ρ_K(not shown) at which the approximation is no longer accurate. At $\rho_C = 0$ (Table III) $\hat{G}$ increases with ω at all values of s, but the asymptotic behavior near $s = 1$ does not depend on the value of ω (as expected).

TABLE I

EFFECTS OF ρ_K AND s ON ESS VALUES OF G

| ρ_K | z^* | $z = 1 - \sqrt{1-s}$ | | | | | |
		0.2	0.4	0.6	0.8	0.9	0.95
0.2	0.81(0.81)	1(1)	1(1)	1(1)	1(1)	0.61(0.60)	0.32(0.32)
0.5	0.55(0.56)	1(1)	1(1)	0.90(0.91)	0.51(0.48)	0.27(0.26)	0.14(0.13)
1	0.25(0.30)	1(1)	0.82(0.73)	0.57(0.44)	0.27(0.24)	0.14(0.13)	0.07(0.07)
2	0.05(0.21)	0.79(0.35)	0.53(0.17)	0.33(0.15)	0.15(0.10)	0.07(0.06)	0.04(0.03)
3	0.03(0.05)	0.65(0.03)	0.41(0.01)	0.23(0.04)	0.10(0.06)	0.05(0.04)	0.02(0.02)

Note. K_t log-triangular with $\omega = 0.05$, $\rho_C = 0$. Values in parentheses are the small-fluctuations approximations.

TABLE II

Effects of ρ_C and ω on ESS Values of G

ρ_C	ω	z^*	$z = 1 - \sqrt{1-s}$					
			0.2	0.4	0.6	0.8	0.9	0.95
0.15	0.4	0.31(0.33)	1(1)	0.88(0.79)	0.56(0.45)	0.26(0.23)	0.12(0.12)	0.06(0.06)
−1	0.4	0.55(0.55)	1(1)	1(1)	0.92(0.88)	0.54(0.44)	0.27(0.23)	0.13(0.12)
0.15	0.1	0.30(0.30)	1(1)	0.83(0.73)	0.54(0.44)	0.27(0.24)	0.13(0.13)	0.07(0.06)
−1	0.1	0.32(0.35)	1(1)	0.92(0.86)	0.64(0.54)	0.34(0.27)	0.16(0.14)	0.08(0.07)

Note. K_t log-triangular with $\rho_k = 1$. Values in parentheses are the small-fluctuations approximations.

When ρ_C is positive and large compared with ρ_K (low-density yields much more variable than high-density yields), an increase in ω is expected to favor less germination. This behavior is seen in Table IV, even at parameter values where the small-fluctuations approximation fails (the log-trangular was not used in Table IV because it is highly skewed right, so ρ_C large and positive makes C_t nonpositive).

The remaining conjectures have to do with the behavior as $s \to 0$, in particular the shift from ρ_K to $E[K_t/K_{t+1}]$ and $P[K_t = 0]$ as the key measures of environmental variability. In the saturation case $\omega = 0$, the shift occurs as in Fig. 5. As ω is increased, however, the saturation approximation becomes inaccurate (Table V). The approximation fails if C_t is not negligible compared to $GX_G(t)$ in the denominator of the yield-function. At $p = 0.9$ in Table V, $\omega = 0.195$ might as well be $\omega = 0$, but at $p = 0.1$ population densities are low enough that the results for $\omega = 0.14$ and $\omega = 0$ are quite different. As $s \to 1$ the saturation approximation always becomes accurate, since the population densities becomes so large that C_t is negligibly small in comparison.

TABLE III

Effect of ω on ESS Values of G

ω	z^*	$z = 1 - \sqrt{1-s}$					
		0.2	0.4	0.6	0.8	0.9	0.95
0	0.24(0.29)	1(1)	0.82(0.71)	0.57(0.44)	0.28(0.24)	0.14(0.13)	0.07(0.07)
0.3	0.32(0.34)	1(1)	0.89(0.82)	0.61(0.47)	0.29(0.24)	0.14(0.13)	0.07(0.07)
0.6	0.40(0.38)	1(1)	1(0.93)	0.63(0.51)	0.29(0.25)	0.14(0.13)	0.07(0.07)

Note. K_t log-triangular with $\rho_K = 1$, $\rho_C = 0$. Values in parentheses are the small-fluctuations approximations.

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TABLE IV

Effects of ω on ESS Values of G

ω	z^*	$z = 1 - \sqrt{1-s}$					
		0.2	0.4	0.6	0.8	0.9	0.95
0.01	0.79(0.80)	1(1)	1(1)	1(1)	0.97(0.98)	0.57(0.57)	0.30(0.31)
0.5	0.48(0.51)	1(1)	1(1)	0.73(0.76)	0.40(0.36)	0.23(0.19)	0.13(0.10)
1	0.33(0.37)	1(1)	0.81(0.81)	0.52(0.33)	0.30(0.19)	0.18(0.11)	0.09(0.06)
2	0.20(0.23)	1[a]	0.58[a]	0.41[a]	0.25[a]	0.15(0.05)	0.10(0.03)

Note. $K_t = 1.2$ or 0.8 with equal probability $\rho_K = 0.2$, $\rho_C = 0.95$. Values in parentheses are the small-fluctuations approximations.

[a] No solution to small-fluctuations approximation.

If ρ_K is increased with the distribution of α_t fixed, $E[K_t/K_{t+1}]$ increases also, so less germination should be favored. Table VI is an example of this, and similar results were obtained with a variety of parameter values and distributions of α_t. This is an important result for tests of the model, because there is no possibility of conflicting predictions depending on whether ρ_K or $E[K_t/K_{t+1}]$ is used to measure environmental variability.

If there are zero-yield years (Table VII) $\hat{G}$ comes close to the expected

TABLE V

Effects of p and ω on ESS Values of G

ω	p	z^*	$z = 1 - \sqrt{1-s}$					
			0.2	0.4	0.6	0.8	0.9	0.95
0	0.1	0.05(0.06)	0.87[a]	0.59[a]	0.25(0.06)	0.09(0.07)	0.04(0.04)	0.02(0.02)
	0.5	0.02(0.30)	0.61(1)	0.45(0.73)	0.33(0.45)	0.21(0.24)	0.11(0.13)	0.07(0.07)
	0.9	0.05(0.69)	0.90(1)	0.82(1)	0.71(1)	0.47(0.69)	0.32(0.38)	0.18(0.20)
0.14	0.1	0.39(0.07)	1(0.10)	0.99(0.05)	0.22(0.07)	0.08(0.07)	0.04(0.04)	0.02(0.02)
	0.5	0.07(0.32)	0.63(1)	0.45(0.79)	0.34(0.47)	0.20(0.25)	0.12(0.13)	0.07(0.07)
	0.9	0.06(0.70)	0.91(1)	0.82(1)	0.70(1)	0.49(0.71)	0.30(0.39)	0.18(0.20)
0.195	0.1	[b]	[c]	[c]	[c]	0.08(0.07)	0.04(0.04)	0.02(0.02)
	0.5	0.09(0.33)	0.63(1)	0.47(0.81)	0.34(0.47)	0.20(0.25)	0.12(0.13)	0.07(0.07)
	0.9	0.06(0.71)	0.91(1)	0.82(1)	0.71(1)	0.49(0.72)	0.32(0.39)	0.18(0.20)

Note. $K_t = 1$ or 100, $p = P[K_t = 100]$; $\rho_K = 2.72$ ($p = 0.1$), 0.98 ($p = 0.5$), 0.33 ($p = 0.9$). Values in parentheses are the small-fluctuations approximations.

[a] No solution to small-fluctuation approximations

[b] $G = 1$ nonviable, so z^* is undefined.

[c] No morph is viable, so there is no ESS.

TABLE VI

EFFECTS OF ρ_K ON ESS VALUES OF G WITH $\alpha_t = (B_t - 0.3)/\sqrt{0.21}$.

		$z = 1 - \sqrt{1 - s}$					
ρ_K	z^*	0.2	0.4	0.6	0.8	0.9	0.95
0.1	0.92(0.91)	1(1)	1(1)	1(1)	1(1)	1(1)	0.68(0.66)
0.5	0.61(0.58)	1(1)	1(1)	1(0.94)	0.55(0.50)	0.28(0.26)	0.14(0.14)
1	0.31(0.31)	1(1)	0.88(0.76)	0.54(0.46)	0.26(0.24)	0.13(0.13)	0.07(0.07)
1.5	a	b	0.34(0.40)	0.23(0.26)	0.14(0.15)	0.08(0.08)	0.04(0.04)

Note. $B_t \sim$ Binomial $(1, 0.3)$. $\omega = 0.1$; $\rho_C = 1$. Values in parentheses are the small-fluctuations approximations.

[a] $G = 1$ is nonviable, so z^* is undefined.

[b] No morph is viable, so there is no ESS.

value $P[K_t \neq 0]$, but does not quite reach it because all morphs are non-viable when s is small. The difference between K_t "small" and $K_t = 0$ is very important near $s = 0$, but near $s = 1$ it is inconsequential and the small-fluctuations approximation is accurate as usual.

In summary, the expectations based on the approximations seem to be valid, unless ω is large enough to significantly reduce the mean population density.

TABLE VII

EFFECT OF ZERO-YIELD YEARS ON ESS VALUES OF G

		$z = 1 - \sqrt{1 - s}$					
Set	z^*	0.2	0.4	0.6	0.8	0.9	0.95
L	a	b	0.62(0.38)	0.33(0.25)	0.15(0.14)	0.08(0.08)	0.04(0.04)
L_0	a	b	b	0.27(0.23)	0.13(0.13)	0.07(0.07)	0.04(0.04)
M	0.18(0.23)	0.97(1)	0.74(0.54)	0.48(0.33)	0.21(0.18)	0.10(0.10)	0.05(0.05)
M_o	a	0.75(1)	0.63(0.53)	0.45(0.32)	0.21(0.18)	0.10(0.10)	0.05(0.05)
H	0.08(0.49)	0.87(1)	0.67(1)	0.49(0.76)	0.39(0.39)	0.16(0.20)	0.09(0.10)
H_0	a	0.73(1)	0.63(1)	0.47(0.75)	0.39(0.38)	0.16(0.20)	0.08(0.10)

Note. $\rho_C = -0.5$, $\omega = 0.2$, $K_t = 1$, 10, or 100 with probabilities (0.6, 0.2, 0.2) set L, (0.2, 0.6, 0.2) set M, (0.2, 0.2, 0.6) set H. Sets L_0, M_0, H_0 are the same except that $K_t = 0$, 10, or 100. Values in parentheses are the small-fluctuations approximations.

[a] $G = 1$ is nonviable, so z^* is undefined.

[b] No morph is viable, so there is no ESS.

6. DISCUSSION

A. *Predictions and Possible Tests of the Theory*

The results have complicated, but much of the action can be summarized in two general principles:

(i) If the seed survivorship $s \approx 1$, or if environmmental fluctuations are small, the ESS germination fraction varies in response to parameter changes as predicted by the asymptotic behavior as $s \to 1$ of the small-fluctuations approximation

$$\hat{G} \sim \frac{\sqrt{2(1-s)}}{\rho_K + \omega\rho_C} = \frac{\bar{K}\sqrt{2(1-s)}}{\sigma_K + \sigma_C}$$

where σ_K^2, σ_C^2 are the variances of K_t and C_t.

(ii) At lower values of s, $\hat{G}$ is decreased by parameter changes increasing the severity of population fluctuations in the absence of dormancy (i.e., increasing $H(1)$).

The situation at low values of s is the more complicated because the entire distribution of (K_t, C_t) is important, not just the means and variances. Near the saturation case ($\omega \ll 1$), the controlling parameters are $E[K_t/K_{t-1}]$ and $P[K_t = 0]$, as in Fig. 5. But even at moderate values of ω the saturation approximation may be inaccurate (e.g., Table V).

For tests of the theory, these complexities should be avoided. One possible way is to do a within-community comparison limited to species that are (a) crowded, and (b) all respond to some overriding environmental variable, but differ in their sensitivity to it. "Crowded" is $\omega \approx 0$: total yield is limited by crowding, and the addition of more seedlings would not increase the total final seed yield. Constraint (b) is that α_t be the same for all species: what's good for one must be good for all. In these circumstances, the germination fraction is predicted to decrease with increased seed survivorship and with an increased coefficient of variation of total yield.

Needless to say, the predictions should be expected to hold only in a statistical sense (such as rank-correlation) in a sample of many species. It is also necessary that the model be appropriate for the population dyamics. The year-to-year variability must occur uniformly over the community, and should be more or less independent between years. If the variability is localized (e.g., gaps in established perennial vegetation) or has long-term periodicities (e.g., a clearing followed by succession) a different model is called for. The model also takes no account of seeds' possible responses to environmental variability. As discussed in (I), the model's predictions may be very different if variable germination fractions are allowed and future

environmental conditions can be predicted with some accuracy at the time of germination.

In all likelihood, then, the data collected for a test will mandate reanalysis of a modified model. If we have done our job properly, that should pose no great difficulties to anyone who has come this far and has not shirked the Appendices. The methods developed here have set the stage for an analysis of more realistic models tailored to specific communities or qualitative aspects of germination behavior. Further developments depend on close collaboration between theoretician and fieldworker, so that model, species, data, and tests are matched.

B. *Comparison with the Density-Independent Theory*

Cohen's (1966, 1968) pioneering studies of optimal germination used a model differing from ours in only one essential way: the per capita seed yields in his model are density-independent. General life history theory is mostly based on density-independent models (e.g., Cole, 1954; Lewontin, 1965; Schaffer, 1974a; Caswell, 1982), including the "bet-hedging" theory of life history evolution in varying environments (Schaffer, 1974b; Stearns, 1976). A comparison between this paper's model and Cohen's consequently is of general theoretical interest as an example of the limitations of density-independent theory. Assertions about Cohen's model in this section are proved by Cohen (1966, 1968) or in Appendix 2 of (I), or else are easily obtained by similar methods (so proofs are omitted).

In Cohen's (1966, 1968) model the population dynamics are

$$X_G(t+1) = X_G(t)[GY_t + (1-G)s] \tag{6.1}$$

with $Y_t = \bar{Y}(1 + \rho_Y \alpha_t)$. $\bar{Y}_t$ is the per capita seed yield in year t, having mean $\bar{Y}$ and coefficient of variation ρ_Y. Equation (6.1) is a reparametrization of Cohen's model, to allow a direct comparison with this paper's results. I will be calling Cohen's model the "DI" (density-independent) model, and this paper's model the "RYL" (reciprocal yield law) model.

In the DI model, the optimal germination fraction (G^*) is the value of G that maximizes

$$E[\ln(GY_t + (1-G)s)];$$

this is equivalent to maximizing the geometric mean growth rate of the population. With Reciprocal Yield Law seed yields, population size settles into steady-state fluctuations. The ESS germination fraction in the RYL model ($\hat{G}$) *minimizes* the geometric mean growth rate of invaders with a different germination fraction: they all decrease to extinction. Because of these differences, the DI and RYL models make qualitatively (as well as

quantitatively) different predictions of relationships between the germination fraction and other measurable population parameters:

(1) *Mean yield.* In the DI model, an increase in the mean per capita yield $\bar{Y}$ causes G^* to increase (unless $G^* = 1$ already). In the RYL model, either an increase or a decrease in $\hat{G}$ may result from an increase in $\bar{K}$ (which is equivalent to a decrease in ω). With small fluctuations or seed survivorship near 1, $\hat{G}$ will increase if low-density yields are more variable than high-density yields ($\rho_C > 0$) and will decrease if the reverse is true.

(2) *Coefficient of variation of seed yield.* Here the models agree: increasing ρ_Y decreases G^*, and increasing ρ_K or ρ_C decreases $\hat{G}$.

(3) *Seed survivorship.* Increased seed survivorship decreases both G^* and $\hat{G}$, but the limiting values as $s \to 1$ can be very different. For example, suppose that in the DI model Y_t takes possible values $Y \gg 1$ and $y \ll 1$ with probabilities p and $1 - p$, respectively (so p = probability of a "good" year). A comparable situation in the RYL model is $K_t = Y$ or y with the same probabilities and $C_t \equiv 0$ (so total yield = Y or y).

Near $s = 0$ the models agree: the "best" germination fraction approaches p (if $y = 0$) or 1 (if $y > 0$) as $s \to 0$. Near $s = 1$ however, the models disagree:

$$\text{DI:} \qquad \lim_{s \to 1} G^*(s) = \frac{pY - 1}{Y - 1} \approx p.$$

$$\text{RYL:} \qquad \lim_{s \to 1} \hat{G}(s) = 0.$$

Why the discrepancy? In the DI model, an increase in s only affects s. In the RYL model it also makes the habitat more crowded and lowers the achieved per capita yields at any fixed G. As a result, a lower germination fraction is favored. As $s \to 1$ with any fixed G, the mean population density becomes infinite and the coefficient of variation decreases to 0, so $\hat{G} \to 0$.

In general, as s varies between 0 and 1, $\hat{G}(s)$ varies between $P[K_t \neq 0]$ and 0. The DI model may have much smaller changes in $G^*(s)$. For example, if $y = 0$ in the example above,

$$G^*(s) = \frac{pY - s}{Y - s} \approx p,$$

so $G^*(s)$ is only very weakly dependent on s.

(4) *Frequency of favorable years.* Continuing with the example above: a higher frequency of "good" years in the DI model always favors a higher

germination fraction. In the RYL model this is not the case. Figure 6 provides a numerical example: as the probability of a favorable year increases from 0.1 to 0.5, the ESS germination fraction decreases, except near $s = 1$. This is not a freak occurrence. Near saturation and away from $s = 1$, G is lowest when successive years are likely to be very different (because G is a decreasing function of $E[K_t/K_{t+1}]$). If most years are bad ($p \approx 0$), or most years are good ($p \approx 1$), $\hat{G}$ will be low. This is a marked difference from the DI model, in which 100% germination is predicted if all years are favorable ($Y_t > 1$ with probability 1).

More generally, suppose that there are n possible environment states occurring with probabilities $p_1, p_2, ..., p_n$. If the frequency of the "best" environment-states (largest α) is increased, with the frequencies of the others relative to each other held constant, the optimal germination fraction in the DI model always increases. In the RYL model, $\hat{G}$ may either increase or decrease (this may be proved for the saturation case by noting that ρ_K and $E[K_t/K_{t+1}]$ may decrease or increase). As before, $\hat{G}$ will decrease if "best" years are infrequent, and much better than the other years.

The significance of these differences is not in the details, but in the greater variety of possible behaviors of the RYL model (depending on the parameter values). This is important for empirical tests, since interspecific or interpopulation comparisons that disagree with the DI theory may be perfectly consistent with the RYL or some other density-dependent model.

Of course, a density-independent model can be used to check quantitatively the optimality (or evolutionary stability) of a life history trait in a real population, because the density effects are manifested in the measured vital rates (see Hastings, 1978; Charlesworth, 1980; and especially Caswell and Werner, 1978, for elaboration of this point). To check if a species' germination fraction is optimal, one would estimate seed survivorship and the probability distribution of per capita seed yield. From these, the DI model predicts an "optimal" germination fraction, which can be compared with the actual germination fraction.

This sort of quantitative test of life history optimality is rare, because lots of laboriously acquired data are needed (Stearns, 1976; Stearns and Crandall, 1981; Ellner and Beuchat, 1984). Most often, an unquantified model is used to generate qualitative predictions (as in this paper), and data are said to support the theory if the sign is right (parameter X really is lower in species Y than in species Z, etc.). Density-independent models are not a priori applicable in this sort of theory-building, and the differences between the DI and RYL theories show very clearly that the addition of density dependence can substantially change or even reverse the predictions of density-independent life history theory.

APPENDIX 1: SMAL-FLUCTUATIONS APPROXIMATION

In this appendix Bartlett's method is used to derive the "small-fluctuation" approximations to $E[x(t)^2]$ and $E[x(t)\,x(t+1)]$ used in Section 3. The notation of Section 3 is retained. The method involves fixing all model parameters *except* ε (recall $\rho_K = \varepsilon\gamma_K$, $\rho_C = \varepsilon\gamma_C$), including the distribution of $\{\alpha_t\}_{t=0}^{\infty}$, and deriving approximations valid to order ε^2 as $\varepsilon \to 0$. The first step is to show that for ε sufficiently small, $|x(t)| < 1$ and $E[x(t)^n]$ is of order ε^3 for $n \geqslant 3$.

The dynamics of a single-morph population have the form

$$X_G(t+1) = F(X_G(t), \alpha_t) \tag{A1.1}$$

where

$$F(x, \alpha) = \frac{G\bar{K}(1 + \alpha\rho_K)\,x}{\bar{C}(1 + \alpha\rho_C) + Gx} + s(1 - G)\,x. \tag{A1.2}$$

For ρ_K, ρ_C sufficiently small, any "constant-environment" iteration $y_{t+1} = F(y_t, \alpha)$ has an equilibrium globally stable on $(0, \infty)$, at

$$\bar{X}(\alpha) = \frac{\bar{K}(1 + \rho_K\alpha)}{1 - s + sG} - \frac{\bar{C}(1 + \rho_C\alpha)}{G} > 0. \tag{A1.3}$$

In Ellner (1984) it was shown for a more general model that the stationary distribution of $X(t)$ has support contained in $[x_*, x^*]$, where

$$
\begin{aligned}
x_* &= \text{ess inf } \bar{X}(\alpha_t) \\
x^* &= \text{ess sup } \bar{X}(\alpha_t).
\end{aligned}
\tag{A1.4}
$$

Hence in the stationary distribution $|x(t)| \leqslant (x^* - x_*)/\bar{X}_G$. To satisfy Assumption 1, α_t must have support in some finite interval $[-M, M]$; and $\partial\bar{X}/\partial\alpha > 0$, so

$$(x^* - x_*) \leqslant \bar{X}(M) - \bar{X}(-M) = 2\varepsilon M\left(\frac{\bar{K}\gamma_K}{1 - s + sG} - \frac{\bar{C}\gamma_C}{G}\right) \tag{A1.5}$$

Since $\gamma_K \geqslant \gamma_C$, (A1.5) implies $(x^* - x_*) \leqslant 2\varepsilon M\gamma_K\bar{X}_G$, whence $|x(t)| \leqslant 2\varepsilon M\gamma_K$. Hence for ε sufficiently small $|x(t)| < 1$ and $E[x(t)^n]$ is of order ε^n, as desired.

We can now apply Bartlett's approximation to (2.1). The right-hand side is expanded in a Taylor series in $X_G(t)$ and α_t about $(\bar{X}_G, 0)$, and $\bar{X}_G$ subtracted from both sides. Both sides are then divided by $\bar{X}_G$, which gives

$$
\begin{aligned}
x(t+1) = {}&(d + G^{-1}\omega(1-d)^2)\,x(t) \\
&+ (1-d)(\rho_k - \omega G^{-1}(1-d)\,\rho_C)\,\alpha_t + \cdots.
\end{aligned}
\tag{A1.6}
$$

$\partial^{i+j}F/\partial x^i\,\partial\alpha^j$ is of order ε^j (since ρ_K, ρ_C are of order ε), and $x(t)^i$ is of order ε^i; hence (A1.6) omits only terms of order ε^2 or smaller. Squaring both sides of (A1.6), dropping terms of order ε^3 or smaller, taking expectations (and recalling $E[x(t)\,\alpha(t)] = E[x(t)]\,E[\alpha(t)] = 0$, $E[\alpha(t)^2] = 1$), we have

$$E[x(t+1)^2] \cong (d + G^{-1}\omega(1-d)^2)^2\,E[x(t)^2]$$
$$+ \,(1-d)^2(\rho_K - \omega G^{-1}(1-d)\,\rho_C)^2 \qquad (A1.7)$$

accurate to order ε^2. Since $E[x(t+1)^2] = E[x(t)^2]$, (A1.7) implies

$$E[x(t)^2] \cong \frac{(1-d)^2}{1-(d+G^{-1}\omega(1-d)^2)^2}\,(\rho_K - \omega G^{-1}(1-d)\,\rho_C)^2. \quad (A1.8)$$

Multiplying through (A1.6) by $x(t)$ and taking expectations,

$$E[x(t)\,x(t+1)] = (d + G^{-1}\omega(1-d)^2)\,E[x(t)^2], \qquad (A1.9)$$

again accurate to order ε^2. Substituting (A1.8) and (A1.9) into (3.4) gives the approximation (3.5) to $H(G)^{-1}$, accurate to order ε^2.

APPENDIX 2:   ANALYSIS OF THE SATURATION APPROXIMATION

Setting $C_t \equiv 0$ violates the technical assumptions of (I) and this paper, and simulations show that the ESS criterion (2.7) is not always valid in that case. The analysis here uses the results derived for $C_t > 0$, with (4.2) in place of the true stationary distribution. Because (4.2) is a good approximation to the stationary distribution for C_t positive but small, this procedure gives a good approximation to the true ESS.

First item on the agenda is the existence of ESSs. In this case $X_1(t+1) = K_t$, so

$$H(1) = H[K_{t+1}/K_t] = E[K_t/K_{t+1}]^{-1}$$
$$= (\bar{K}E[1/K_t])^{-1}.$$

Applying the results of Section 2C, $G = 1$ is therefore an ESS for $s \leqslant s^*$, where

$$s^* = E[K_t/K_{t+1}]^{-1}, \qquad (A2.1)$$

and for $s > s^* G \in (0, 1)$ is an ESS if and only if

$$s^{-1} = E\left[\frac{\sum_{n=0}^{\infty} d^n K_{t-n}}{K_{t+1} + \sum_{n=0}^{\infty} d^{n+1} K_{t-n}}\right]. \qquad (A2.2)$$

Note that $s^* > 0$ so long as $E[1/K_t]$ is finite.

LEMMA A2.1. *The function*

$$E(d) = E\left[\frac{\sum_{n=0}^{\infty} d^n K_{t-n}}{K_{t+1} + \sum_{n=0}^{\infty} d^{n+1} K_{t-n}}\right]$$

is continuous on $(0, 1)$, *and is* > 1 *unless* $\rho_K = 0$.

Proof. The integrand is pointwise in $(0, 1/d)$, so continuity follows by Dominated Convergence. $E(d)$ is $E[Y_t/Y_{t+1}]$ for the process $Y_{t+1} = K_t + dY_t$ with stationary initial distribution. The proof of Theorem 5.1 of Chesson (1982) is easily adapted to show that $E[Y_t^{-\varepsilon}] < +\infty$ for $\varepsilon > 0$ sufficiently small. Since $x^{-\varepsilon} > |\log x|$ for $x > 0$ sufficiently small this implies $E[\ln Y_t^-] < +\infty$, and $Y(t) \leqslant K_M/(1-d)$ by (4.2) so $E[\ln Y_t^+] < +\infty$ also. By stationarity $E[\ln Y_{t+1}] = E[\ln Y_t]$, so $E[\ln(Y_t/Y_{t+1})] = 0$. By Jensen's Inequality therefore $E[Y_t/Y_{t+1}] > 1$ unless K_t is constant.

PROPOSITION A2.2. (a) *For any* $s \in (0, 1)$, *there is at least one ESS value of* G.

(b) *For any* $G \in (0, 1 - P_0)$ *there is a unique value of the seed survivorship* $\hat{s}(G)$ *at which* G *is an ESS, and* $\lim_{G \to 0} \hat{s}(G) = 1$.

Proof. (a) For $s \leqslant (\bar{K}E[1/K_t])^{-1}$, $G = 1$ is an ESS. For s larger, the ESS criterion is $s^{-1} = E(d)$. As $G \to 0$, $d \to s$ and so

$$E(d) \to E(s) = E\left[\frac{\sum_{n=0}^{\infty} s^n K_{t-n}}{K_{t+1} + \sum_{n=0}^{\infty} s^{n+1} K_{t-n}}\right] < s^{-1}.$$

Therefore $E(d) < s^{-1}$ for G near 0. As $G \to 1$, $d \to 0$ and

$$E(d) > E\left[\frac{K_t}{K_{t+1} + \sum_{n=0}^{\infty} d^{n+1} K_{t-n}}\right]. \tag{A2.3}$$

By Monotone Convergence, as $d \to 0$ the expectation in (A2.3) $\to E[K_t/K_{t+1}] = \bar{K}E[1/K_t] > s^{-1}$. For G near 1 therefore $E(d) > s^{-1}$, so by the continuity of $E(\cdot)$ at least one G satisfies $s^{-1} = E(d)$, and so is an ESS.

(b) Pick $G \in (0, 1 - P_0)$. Conditioning on whether or not $K_{t+1} = 0$,

$$E(d) = s^{-1} P_0/(1 - G) + (1 - P_0) E\left[\left(d + \frac{K_{t+1}}{\sum_{n=0}^{\infty} d^n K_{t-n}}\right)^{-1} \bigg| K_{t+1} > 0\right]$$

so $\tag{A2.4}$

$$sE(d) = \frac{P_0}{1 - G} + (1 - P_0) E\left[\left(1 - G + \frac{K_{t+1}}{s \sum_{n=0}^{\infty} d^n K_{t-n}}\right)^{-1} \bigg| K_{t+1} > 0\right].$$

As $s \to 0$ the integrand decreases pointwise to 0, so by Dominated Convergence the right-hand side of $(A2.4) \to P_0/(1-G) < 1$. Therefore $E(d) < s^{-1}$ for s near 0. As $s \to 1$, $E(d) \to E(1-G) > 1$ by the last Lemma, so $E(d) > s^{-1}$ for s near 1 and by continuity $E(d) = s^{-1}$ for at least one s. To prove s unique, note that

$$dE(d) = 1 - E\left[\frac{K_{t+1}}{K_{t+1} + \sum_{n=0}^{\infty} d^n K_{t-n}}\right]$$

$$= 1 - E\left[\frac{K_t}{\sum_{n=0}^{\infty} d^n K_{t-n}}\right].$$

The ESS criterion $s^{-1} = E(d)$ is therefore equivalent to

$$G = E\left[\frac{K_t}{\sum_{n=0}^{\infty} d^n K_{t-n}}\right] \tag{A2.5}$$

for $0 < G < 1$. The integrand in (A2.5) is pointwise decreasing in s, so any G is an ESS for at most one value of s. Since $K_t \leqslant K_M$ almost surely, (A2.5) implies that any ESS satisfies

$$G \geqslant E\left[\frac{K_t}{\sum_{n=0}^{\infty} d^n K_M}\right] = (1-d)(\bar{K}/K_M). \tag{A2.6}$$

Setting $s = \hat{s}(G)$ in (A2.6) and letting $G \to 0$, we must have $d = \hat{s}(G)(1-G) \to 1$, hence $\hat{s}(G) \to 1$.

The last proposition is frustratingly close to a proof that $\lim_{s \to 1} \hat{G}(s) = 0$. The missing piece is the following conjecture, which is supported by numerous simulations: For fixed s and $\rho_K > 0$, $H(G)$ is monotonically strictly decreasing in G. This is a statement about first-order autoregressive processes and ought to be well-known, but I have been unable to find or supply a proof. If you can, please write.

Assuming the conjecture, writing the ESS criterion as $s^{-1}H(G) = 1$ shows that $G(s)$ unique and decreasing in s. Since $G(s)$ takes all values in $(0, 1 - P_0)$, this implies $\lim_{s \to 1} \hat{G}(s) = 0$.

Turning now to the behavior as $s \to 0$: If $E[1/K_t] = +\infty$, conditioning on K_{t+1} in (A2.2) gives

$$s^{-1} = \frac{P_0}{s(1-\hat{G})} + (1-P_0) E\left[\frac{\sum_{n=0}^{\infty} \hat{d}^n K_{t-n}}{K_{t+1} + \sum_{n=0}^{\infty} \hat{d}^{n+1} K_{t-n}} \,\middle|\, K_{t+1} \neq 0\right],$$

where $\hat{d} = s(1-\hat{G})$ and $P_0 = P[K_t = 0]$. Hence

$$1 - \hat{G} = P_0 + (1-P_0) E\left[\frac{\sum_{n=0}^{\infty} \hat{d}^{n+1} K_{t-n}}{K_{t+1} + \sum_{n=0}^{\infty} \hat{d}^{n+1} K_{t-n}} \,\middle|\, K_{t+1} \neq 0\right]. \tag{A2.7}$$

As $s \to 0$ the integrand in (A2.7) decreases pointwise to 0, so

$$\lim_{s \to 0} \hat{G}(s) = 1 - P_0 \qquad (A2.8)$$

(if ESSs are not unique, (A2.8) applies to any choice of $\hat{G}$).

If $E[1/K_t]$ is finite, then necessarily $P_0 = 0$, and $\hat{G} = 1$ for $0 < s < s^*$; therefore (A2.8) still holds. If in addition K_t is bounded away from 0 then the initial slope at $s = s^*$ can be obtained by an asymptotic expansion

$$G(s) = 1 - \beta \varepsilon - \gamma \varepsilon^2 + \cdots \qquad (A2.9)$$

where $\varepsilon = (s - s^*)$. W seek β, which requires expansion of (A2.5) to order ε^2. Near s^*, $d = s(1 - G) = (s^* + \varepsilon)(\beta \varepsilon + \gamma \varepsilon^2 + \cdots) = s^* \beta \varepsilon + \beta \varepsilon^2 + \gamma s^* \varepsilon^2$, so all terms of order ε^2 are obtained by expanding (A2.5) in d to order d^2. For d sufficiently small and K_t bounded away from 0, $\sum_{n=1}^{\infty} d^n(K_{t-n}/K_t) < 1/2$ with probability 1, so we may expand

$$
\begin{aligned}
E\left[\frac{K_t}{\sum_{n=0}^{\infty} d^n K_{t-n}}\right] &= E\left[\frac{1}{1 + \sum_{n=0}^{\infty} d^n(K_{t-n}/K_t)}\right] \\
&= E\left[\frac{1}{1 + d(K_{t-1}/K_t) + d^2(K_{t-2}/K_t) + \cdots}\right] \\
&= 1 - dE[K_{t-1}/K_t] - d^2 E[K_{t-2}/K_t] \\
&\quad + d^2 E[(K_{t-1}/K_t)^2] + \cdots \qquad (A2.10) \\
&= 1 - (d + d^2)\, \bar{K} E[1/K_t] + d^2 E[K_t^2]\, E[K_t^{-2}] + \cdots.
\end{aligned}
$$

Substituting (A2.9) and (A2.10) into (A2.5) and equating like-order coefficients, we obtain

$$\frac{\partial G}{\partial s}(s^*) = -\beta = -(s^*)^2(s^* R - 1), \qquad (A2.11)$$

where $R = E[K_t^2]\, E[K_t^{-2}]$.

PROPOSITION A2.3. *If the distribution of α_t is fixed, $E[K_t/K_{t+1}]$ is increasing in ρ_K.*

Proof. $E[K_t/K_{t+1}] = E[(1 + \rho_K \alpha_t)^{-1}]$. $\alpha_* = \text{ess inf } \alpha_t$ is negative and finite, and ρ_K must lie in $[0, -\alpha_*^{-1}]$ (otherwise $K_t < 0$ has positive probability). For $\rho_K \in (0, -\alpha_*^{-1})$, difference quotients for the derivative of

$(1 + \rho_K \alpha_t)^{-1}$ as a function of ρ_K can be uniformly bounded pointwise, so by Dominated Convergence

$$\frac{d}{d\rho_K} E[(1 + \rho_K \alpha_t)^{-1}] = -E[\alpha_t (1 + \rho_K \alpha_t)^{-2}].$$

The last integrand has negative second derivative as a function of α_t, so an application of Jensen's Inequality (recalling $E[\alpha_t] = 0$) completes the proof.

APPENDIX 3:   THE SATURATION CASE NEAR $s = 1$

In this appendix we show that the small-fluctuations approximation to $H(G)^{-1}$ in Eq. (3.5) is accurate to order $(1 - d)^2$ in the saturation case.

In the saturation case, $X_G(t + 1)$ depends linearly on $X_G(t)$ and α_t, so the linearization in (A1.6) is exact:

$$x(t + 1) = dx(t) + (1 - d) \rho_K \alpha_t. \tag{A3.1}$$

The stationary distribution for $x(t)$ is therefore

$$x(t) \sim (1 - d) \rho_K \sum_{n=0}^{\infty} d^n \alpha_{t-n} \tag{A3.2}$$

where $\{\alpha_t\}_{t=-1}^{-\infty}$ is an independent copy of $\{\alpha_t\}_{t=0}^{\infty}$. The proof consists of bounding the moments of $x(t)$, in order to justify the expansion of $H(G)^{-1}$ in (3.3) and to identify the terms of order $(1 - d)^3$ or smaller.

LEMMA A3.1. $E[x(t)^k]$ is of order $(1 - d)^{I((1+k)/2)}$, where $I(x)$ is the greatest integer $\leqslant x$.

Proof.   It clearly suffices to consider the case $\rho_K = 1$. Then

$$E[x(t)^k] = (1 - d)^k E\left[\left(\sum_{n=0}^{\infty} d^n \alpha_{t-n}\right)^k\right]$$

$$= (1 - d)^k E\left[\sum_{i=1}^{k} \sum_{n_i=0}^{\infty} d^{n_1 + n_2 + \cdots n_k} \alpha_{n_1} \alpha_{n_2} \cdots \alpha_{n_k}\right]$$

$$= (1 - d)^k \sum_{i=1}^{k} \sum_{n_i=0}^{\infty} d^{n_1 + n_2 \cdots n_k} E[\alpha_{n_1} \alpha_{n_2} \cdots \alpha_{n_k}]. \tag{A3.3}$$

$E[\alpha_t] = 0$, so by independence any term in which a particular subscript appears only once contributes 0 to the sum. The terms which do contribute are thus all of the form

$$d^{n_1 m_1 + n_2 m_2 + \cdots n_k m_k} E[\alpha_{n_1}^{m_1} \alpha_{n_2}^{m_2} \cdots \alpha_{n_k}^{m_k}] \tag{A3.4}$$

where $(m_1, m_2, ..., m_k)$ is a k-tuple of integers satisfying $\sum_{j=1}^{k} m_j = k$ and each $m_j = 0$ or is $\geqslant 2$. Let A_k denote the collection of all such $(m_1, ..., m_K)$, and N_k the cardinality of A_k. Each term of the form (3.4) is $\leqslant d^{n_1 m_1 + \cdots + n_k m_k} U^k$ in absolute value, where $U = \text{ess sup}(|\alpha_t|)$; hence

$$|E[x(t)^k]| \leqslant U^k (1-d)^k \sum_{A_k} \sum_{i=1}^{k} \sum_{n_i=0}^{\infty} d^{n_1 m_1 + n_2 m_2 + \cdots n_k m_k}$$

$$= U^k (1-d)^k \sum_{A_k} \prod_{m_j \neq 0}^{\infty} \frac{1}{(1-d^{m_j})}$$

$$= U^k \sum_{A_k} \prod_{m_j \neq 0}^{\infty} \frac{(1-d)^{m_j}}{(1-d^{m_j})} \leqslant U^K \sum_{A_k} \prod_{m_j \neq 0}^{\infty} (1-d)^{m_j - 1}$$

$$= U^k \sum_{A_k} (1-d)^{(k - \sum_{m_j \neq 0} 1)}. \tag{A3.5}$$

All m_j that $\neq 0$ are $\geqslant 2$, so at most $I(k/2)$ can be nonzero; hence $(k - \sum_{m_j \neq 0} 1) \geqslant k - I(k/2) = I((1+k)/2)$. Therefore

$$|E[x(t)^k]| \leqslant U^k N_k (1-d)^{I((1+k)/2)}. \tag{A3.6}$$

We now need to estimate N_k. N_k is less than the number of nonnegative integer k-tuples $(x_1, x_2, ..., x_k)$ such that $\sum_{j=1}^{k} x_j = k$, which is the number of distinct orderings of k one's and $(k-1)$ zeros, namely $\binom{2k-1}{k}$. Applying Stirling's formula, it is easily shown that $N_k \leqslant 6^k$ for $k > 1$. Consequently

$$|E[x(t)^k]| \leqslant U^k 6^k (1-d)^{I((1+k)/2)}$$

$$\leqslant \{36 U^2 (1-d)\}^{I((1+k)/2)}, \tag{A3.7}$$

which proves the Lemma. For $\rho_K \neq 1$, by (A3.2) the bound becomes

$$|E[x(t)^k]| \leqslant \rho_K^k \{36 U^2 (1-d)\}^{I((1+k)/2)}. \tag{A3.8}$$

COROLLARY A3.2.   *Let* $\bar{E}[z] = E[z \cdot 1_{\{|x(t+1)| < 1/2\}}]$. *If* $E[z^2]$ *is finite; then*

$$|E[z] - \bar{E}[z]| \leqslant A E[z^2]^{1/2} (1-d)^3, \tag{A3.9}$$

where A *is a constant not depending on* z *or* d.

Proof. By the general Markov inequality $P[|x(t)| \geqslant 1/2] \leqslant 2^{12}E[x(t)^{12}]$, which combined with (A3.8) implies $P[|x(t)| \geqslant 1/2] \leqslant A^2(1-d)^6$ for some constant A not depending on d. Then by the Schwartz inequality

$$|E[z] - \bar{E}[z]| = |E[z \cdot 1_{\{|x(t+1)| \geqslant 1/2\}}]|$$
$$\leqslant E[z^2]^{1/2} E[1_{\{|x(t+1)| \geqslant 1/2\}}]^{1/2}$$
$$\leqslant E[z^2]^{1/2} A(1-d)^3$$

as desired.

For $(1-d)$ sufficiently small $X_G(t)/X_G(t+1) \leqslant 2$. Hence any ESS $G \in (0, 1)$ satisfies

$$s^{-1} = H(G)^{-1} = E[X_G(t)//X_G(t+1)]$$
$$= \bar{E}[X_G(t)/X_G(t+1)] + O(1-d)^3$$
$$= \bar{E}\left[\frac{1+x(t)}{1+x(t+1)}\right] + O(1-d)^3$$
$$= \bar{E}[(1+x(t))(1-x(t+1)+x(t+1)^2 \cdots)] + O(1-d)^3$$
$$= 1 + (\bar{E}[x(t+1)^2] - \bar{E}[x(t) x(t+1)])$$
$$\quad - (\bar{E}[x(t+1)^3] - \bar{E}[x(t) x(t+1)^2]) + \cdots + O(1-d)^3$$
$$= 1 + \sum_{m=2}^{\infty} (-1)^m \bar{E}[x(t+1)^{m-1}(x(t+1) - x(t))]$$
$$= + O(1-d)^3. \tag{A3.10}$$

Now $x(t+1) - x(t) = (1-d)(\rho_k \alpha_t - x(t))$, so $E[|x(t+1) - x(t)|^k]$ is $O(1-d)^k$. It therefore follows from Lemma A3.1 that $E[\{x(t+1)^{m-1}(x(t+1) - x(t))\}^2]$ is $O(1-d)^{m+1}$. This estimate plus Corollary A3.2 imply that replacing $\bar{E}$ by E in (A3.10) introduces an error of $O(1-d)^3$ or smaller. Therefore, to order $(1-d)^2$, any ESS $G \in (0, 1)$ satisfies

$$s^{-1} = 1 + \sum_{m=2}^{\infty} (-1)^m E[x(t+1)^{m-1}(x(t+1) - x(t))]. \tag{A3.11}$$

From (A3.1) it follows exactly as in Appendix 1 that

$$E[x(t+1)(x(t+1) - x(t))]$$
$$= E[x(t+1)^2] - E[x(t) x(t+1)] = \frac{(1-d)^2}{1+d} \rho_k^2. \tag{A3.12}$$

(A3.11) is therefore the small-fluctuations approximation to $H(G)^{-1}$ in (3.5), plus the terms for $m \geqslant 3$. But (arguing as above) $E[x(t+1)^{m-1}(x(t+1)-x(t))]$ is of order $O(1-d)^{l(1+m/2)}$, so the terms of (A3.11) for $m \geqslant 4$ are together of $O(1-d)^3$. A repetition of the argument of Lemma A3.1 shows that $E[x(t+1)^3]$ is of order $(1-d)^2$, so $E[x(t+1)^3(x(t+1)-x(t))]$ is also $O(1-d)^3$.

We have thus shown that in the saturation case, any ESS $G \in (0, 1)$ satisfies

$$s^{-1} = 1 + \frac{(1-d)^2}{1+d} \rho_K^2 + O(1-d)^3. \qquad (A3.13)$$

This rearranges to

$$\rho_K^2 \frac{(\sqrt{1-s} + s(G/\sqrt{1-s}))^2}{1+s-sG} (1 + O(1-d)) = s^{-1}. \qquad (A3.14)$$

Assuming $\hat{G} \to 0$ as $s \to 1$, (A3.14) implies that

$$\lim_{s \to 1} \frac{\hat{G}(s)}{\sqrt{1-s}} = \sqrt{2}/\rho_K,$$

as was claimed in Section 4.

APPENDIX 4: PROOFS FOR SECTION 5

Here we determine the behavior of $H(G)$ on the assumption that ESSs can invade other morphs, and show that s^* is larger for $\omega > 0$ than it is for $\omega = 0$, if $\rho_C \geqslant 0$.

PROPOSITION A4.1. *If an ESS $\hat{G}$ can invade any other $G \in (0, 1]$, then $(H(G) - s)$ has the sign of $(\hat{G} - G)$.*

Proof. We use the notation of (I); our assumptions are that $\rho(\hat{G}, g) < 0$ and $\rho(g, \hat{G}) > 0$ for any $g \neq \hat{G}$, and any ESS has $v(\hat{G}) > 0$. From (I, Section 3C) we know that $(H(G) - s)$ has the sign of $m(G) = (\partial \rho/\partial G_2)(G, G)$.

If $G > \hat{G}$ is viable then $\rho(G, G) = 0$, so there exists an $x \in (\hat{G}, G)$ at which $(\partial \rho/\partial G_2)(G, x) < 0$. Since $(\partial^2 \rho/\partial G_2^2) < 0$ (I, Proposition A1.1), this implies $m(G) = (\partial \rho/\partial G_2)(G, G) < 0$. Similarly $m(G) > 0$ if $G < \hat{G}$ is viable. If $G \in [0, 1)$ is nonviable, then $m(G) = v'(G)$ (I, Proposition A1.1 and Lemma A2.5). The viability of $\hat{G}$ implies $P[b_t = s] < 1$, so $v'' < 0$ on $[0, 1]$. Hence any nonviable $G > \hat{G}$ must have $m(G) = v'(G) < 0$, and $m(G) > 0$ for non viable $G < \hat{G}$. Finally, if $G = 1$ is non viable, $m(1) = \lim_{G \to 1} v'(G)$ (I, Lemma A2.5) which (since $\hat{G}$ is viable and $G = 1$ is not) must be < 0 as desired.

PROPOSITION A4.2. *If* $\rho_C \geqslant 0$, $v(1) > 0$, $E[1/K_t] < +\infty$ *and* $\omega > 0$, *then* $H(1) > E[K_t/K_{t+1}]^{-1}$.

Note. $v(1) > 0$ and $E[1/K_t] < +\infty$ are equivalent to s^* being defined and > 0; the conclusion is that s^* with $\omega > 0$ is larger than the value of s^* for $\omega = 0$.

Proof.

$$H(1)^{-1} = E\left[\frac{C_t + \tilde{X}_1(t)}{K_t}\right]$$

$$= E\left[\frac{\bar{C}(1 + \rho_C \alpha_t) + \tilde{X}_1(t)}{\bar{K}(1 + \rho_K \alpha_t)}\right]$$

$$= E\left[\frac{\bar{C} + \tilde{X}_1(t)}{\bar{K}(1 + \rho_K \alpha_t)}\right] + E\left[\frac{\bar{C}\rho_C \alpha_t}{\bar{K}(1 + \rho_K \alpha_t)}\right].$$

By Jensen's Inequality, for $\rho_C \geqslant 0$

$$E\left[\frac{\bar{C}\rho_C \alpha_t}{\bar{K}(1 + \rho_K \alpha_t)}\right] \leqslant \frac{\bar{C}\rho_C E[\alpha_t]}{\bar{K}(1 + \rho_K E[\alpha_t])} = 0. \qquad \text{(A4.1)}$$

Hence

$$H(1)^{-1} \leqslant E\left[\frac{\bar{C} + \tilde{X}_1(t)}{\bar{K}(1 + \rho_K \alpha_t)}\right] = (\bar{C} + E[\tilde{X}_1(t)])\, E[1/K_t], \qquad \text{(A4.2)}$$

the last equality holding by the independence of $\tilde{X}_1(t)$ and α_t. Since $\tilde{X}_1$ is stationary,

$$E[\tilde{X}_1(t)] = E[\tilde{X}_1(t+1)] = E\left[\frac{K_t \tilde{X}_1(t)}{C_t + \tilde{X}_1(t)}\right]. \qquad \text{(A4.3)}$$

The independence of α_t and $\tilde{X}_1(t)$ allows us to express the last expectation as a double integral with respect to the (unconditional) distributions of $\tilde{X}_1$ and α_t. The integrand has negative second derivative in both $\tilde{X}_1$ and α, so two applications of Jensen's Inequality give

$$E\left[\frac{K_t \tilde{X}_1(t)}{C_t + \tilde{X}_1(t)}\right] < \frac{\bar{K} E[\tilde{X}_1(t)]}{\bar{C} + E[\tilde{X}_1(t)]}. \qquad \text{(A4.4)}$$

Combining (A4.3) and (A4.4) we have

$$\bar{C} + E[\tilde{X}_1(t)] < \bar{K}.$$

Hence by (A4.2), $H(1)^{-1} \leqslant \bar{K}E[1/K_t] = E[K_t/K_{t+1}]$, which proves the proposition.

APPENDIX 5: Summary of Notation

(a) Model Parameters

K, C	Parameters of reciprocal yield law for per capita seed yield $Y(x)$ at density x (see Eq. (1.1))
b	$= K/C$, low-density per capita seed yield
K_t, C_t, b_t	Values of K, C, b in year t
$\bar{K}, \bar{C}, \bar{b}$	Mean values of K_t, C_t, b_t
ρ_K, ρ_C	Coefficients of variation (standard deviation/mean) of K_t, C_t
α_t	Random "environment quality" in year t: $K_t = \bar{K}(1 + \rho_K \alpha_t)$, $C_t = \bar{C}(1 - \rho_C \alpha_t)$
G	Annual germination fraction
s	Annual survivorship of dormant seeds
d	$= s(1 - G)$
ω	$= \bar{C}/\bar{K}$
P_0	$= P[K_t = 0]$

(b) Population Process and Equilibria

$X_G(t)$	Single-type population with germination fraction G (see Eq. (2.5))
$\tilde{X}_G(t)$	$X_G(t)$ with stationary initial distribution
$\bar{X}_G$	Equilibrium population size of $X_G(t)$ in the constant environment $\alpha_t \equiv 0$ (or equivalently, $\rho_K = \rho_C = 0$)
$\bar{X}(\alpha)$	Equilibrium population size of $X_G(t)$ in constant environment $\alpha_t \equiv \alpha$; so $\bar{X}_G = \bar{X}(0)$
$x(t)$	$= (\tilde{X}_G(t) - \bar{X}_G)/\bar{X}_G$.

(c) Special Functions

$v(G)$	$= E[\ln(Gb_t + (1 - G)s)]$
$E_G[\cdot]$	Expectation with respect to the joint stationary distribution of $(\tilde{X}_G(t), \alpha_t)$
$H_G[\cdot]$	Harmonic mean with respect to the joint stationary distribution of $(\tilde{X}_G(t), \alpha_t)$; i.e., $H_G[Z] = 1/E_G[1/Z]$
$H(G)$	$= H_G[\tilde{X}_G(t+1)/\tilde{X}_G(t)]$, the harmonic mean growth rate of $\tilde{X}_G(t)$.

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