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## GERMINATION BIOLOGY AND THE ECOLOGY OF ANNUAL PLANTS

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*Abstract.*—We derive spatially explicit population models for the interaction between a species of annual plant and a community of perennial species. The models are used to explore the conditions for persistence of the annual in both a constant and a stochastic environment. In both types of environment a seed's response to the presence of established perennial plants is found to affect strongly the conditions for persistence. Sensitivity analysis of a parameterized version of the model indicates the importance of germination and mortality parameters in allowing persistence. In the parameterized model large changes in fecundity have little effect on the condition for persistence. The implications of these results for the distribution of annual plants and the forces structuring communities of short-lived plants in successional habitats are discussed.

There is extensive literature describing the germination responses of seeds to changes in temperature (Popay and Roberts 1970*a*, 1970*b*; Baskin and Baskin 1972; Mekenian and Willemsen 1975), the range of temperature fluctuations (Cohen 1958; Hussey 1958; Edwards 1968; Thompson et al. 1977; Rice 1985), light intensity (Kinzel 1926; Ratcliffe 1961; Wesson and Wareing 1969*a*, 1969*b*), light spectral composition (Gorski 1975; King 1975; Gorski et al. 1977; Silvertown 1980), and the concentrations of various chemicals (Kidd 1914; Kidd and West 1917; Edwards 1968; Popay and Roberts 1970*a*, 1970*b*). Many of these responses can be interpreted as ways of preventing germination in a hostile environment (Baskin and Baskin 1971, 1974; Fenner 1985). For example, Rice (1985) has demonstrated that in *Erodium botrys* (Cav.) Bertol. and *Erodium brachycarpum* (Godr.) Thell. germination is dependent on the range of temperature fluctuations that a seed experiences. Rice then measured temperature range in a number of distinct microsites (i.e., under litter, bare ground, and mounds created by pocket gophers). The probability of germination increased with increasing temperature range, as did the net reproductive rate. These results suggest the importance of germination cuing in preventing germination in deleterious conditions.

The recent flurry of activity in theoretical plant ecology has brought a wide range of plant biology into a theoretical framework. There are models incorporating neighborhood competition (Weiner and Conte 1981; Pacala and Silander 1985; Pacala 1986*a*, 1986*b*, 1987), local dispersal (Shmida and Ellner 1985; Pacala 1986*a*), random environments (Fagerström and Ågren 1979; Chesson 1982; Ågren

and Fagerström 1984; Ellner 1984), and resource competition (Tilman 1982, 1988). One area of plant ecology conspicuous by its absence from this list is the germination biology described above. Although a number of studies have explored the effect of dormancy on population dynamics and coexistence (MacDonald and Watkinson 1981; Chesson 1982; Ellner 1984; Comins and Noble 1985; Pacala 1986a), none has attempted to incorporate the details of a seed's germination response to the presence of established plants. In this article, we present a series of models incorporating this biology.

Before we present the models, it is necessary to consider the habitats occupied by annual plants. These may be crudely characterized according to the disturbance regime. At one extreme are habitats where microsites are available for colonization in every year (Symonides 1979; Watkinson 1981). As Grubb (1986, p. 210) remarks, "Collectively they [the perennial species] form a 'matrix' in the 'interstices' of which the short-lived species come and go." At the other extreme are habitats where between large-scale disturbances there are virtually no microsites available for colonization (e.g., temperate successions where vertebrate herbivores have been excluded; Southwood et al. 1988). In habitats that contain perennial plants, there are large competitive differentials because annual plant seedlings are often competitively subdominant to established perennials (Fenner 1978; McConnaughay and Bazzaz 1987; Oliver 1988). This is a direct result of the size-dependent, asymmetrical nature of plant competition (Weiner and Thomas 1986). Consequently, there is an ecological problem because annual plants by definition reproduce and then die. This means that recruitment must occur from seed in every generation if the population is to persist. However, recruitment cannot occur in the presence of perennials. The role of germination biology in allowing annual plants to overcome this recruitment problem forms the basis of this article. Throughout the article we focus on this ecological problem and do not address evolutionary considerations, on which there is already considerable literature (Cohen 1966; Bulmer 1984; Ellner 1985a, 1985b; León 1985; Klinkhamer et al. 1987; Venable and Brown 1988).

The article is structured around a simple model of plant competition. This is elaborated to include details of germination biology and neighborhood competition in a constant environment. Finally, a simple stochastic environment is included in the model, and the results are contrasted with those obtained earlier. Parameter estimates for the models were obtained for the annual weed *Sinapis arvensis*. Sensitivity analysis of the parameterized models strongly suggests that germination biology is of crucial importance in determining the distribution of the *Sinapis*.

#### MODEL I—THE BASIC MODEL

The model introduced in this section was first used by Skellam (1951) in a pioneering study of plant competition. Skellam assumed that the environment consisted of a large number of cells or microsites suitable for the growth of a single plant. He further assumed that each plant produced  $F$  seeds and that these were distributed over the microsites according to a Poisson distribution. A frac-

tion  $d$  of the seeds die before germination. With these assumptions he derived the following population model:

$$\chi_{t+1} = 1 - e^{-(1-d)FEx_t},$$

where  $\chi$  is the proportion of microsites occupied by the plant population in generation  $t$  and  $t + 1$ . The parameter  $E$  is a coefficient of habitat suitability; see below. This model has a nonzero equilibrium point providing that

$$F > 1/(1 - d)E. \quad (1)$$

In a recent article Crawley and May (1987) rederive this result with the interpretation that  $E$  is the probability of a microsite's *not* containing an established perennial plant. Rewriting the model with the number of seeds as the dynamical variable, we obtain

$$S_{t+1} = FKE(1 - e^{-(1-d)S_t/K}), \quad (2)$$

where  $S$  is the number of seeds, the subscripts denote the successive generations, and  $K$  is the total number of microsites. This model is the simplest representation of plant competition in a spatially explicit environment and provides a baseline against which the effects of subsequent elaborations may be judged.

The parameter  $E$  was used by Skellam as a measure of habitat suitability and included both biotic and abiotic interactions. In this article, this parameter is interpreted as the probability of a microsite's *not* containing an established perennial plant. Thus, it is assumed that only seeds germinating in empty microsites are able to reproduce and that the established annual plants have no effect on perennial dynamics. With this interpretation, equation (1) gives the condition for persistence of an annual plant in a community of perennial plants; it is important to realize that because annuals have no effect on perennial dynamics, this is also the condition for coexistence (Ives and May 1985; Crawley and May 1987). The parameter  $E$  is determined by the details of perennial demography (Crawley and May 1987), abiotic disturbance (e.g., fire, drought, etc.), and herbivory (Silvertown and Smith 1989).

The condition for persistence, equation (1), is obtained from the finite per capita growth rate or finite rate of increase ( $R$ ) calculated using the identity

$$R \equiv \lim_{S_t \downarrow 0} \left[ \frac{S_{t+1}}{S_t} \right].$$

If when the population size is small a seed replaces itself, on average, with more than one seed in the next generation, the population will increase and persistence is possible. If, however, each seed replaces itself with less than one seed, the population will decline to extinction. Therefore, persistence is defined by the presence of viable seeds, and successful recruitment is not required in every year (see Model 2—Delaying Germination). Finite growth rates are widely used in the study of competition (Ågren and Fagerström 1984; Ellner 1984; Shmida and Ellner 1984; Comins and Noble 1985; Ives and May 1985).

The model assumes that the spatial distribution of seeds is accurately described by a Poisson distribution. Recent theoretical work by Pacala and Silander (1985)

suggests that this is a reasonable assumption. However, empirical work indicates that the seed rain and seed banks are often spatially aggregated (Rabinowitz and Rapp 1980; Thompson 1986; Bigwood and Inouye 1988). Aggregation may be modeled using the negative binomial distribution. Replacing the zero term from the Poisson distribution with the appropriate term from the negative binomial, we obtain

$$\chi_{t+1} = 1 - \left[ 1 + \frac{(1-d)FE\chi_t}{\kappa} \right]^{-\kappa},$$

where  $\kappa$  is the clumping parameter (the distribution becomes more aggregated as  $\kappa \rightarrow 0$ ). The condition of persistence in this model is

$$F > 1/(1-d)E,$$

which is the same as the condition for persistence in the Poisson model. Thus, changing the spatial distribution of the seed rain or the seed bank has no effect on persistence. The spatial distribution of the superior competitors has a profound effect on coexistence but not the distribution of the subdominant species (Pacala 1986a). This is a generic result of spatial competition models (Ives and May 1985; Comins and Hassell 1987).

#### MODEL 2—DELAYING GERMINATION

The simple model introduced in the previous section assumes all viable seeds germinate in the next growing season. Although this is true for some plants (e.g., *Vulpia fasciculata*; Watkinson 1981), many annuals exist primarily as seeds in large belowground seed banks that persist between years. The simplest way of incorporating this biology into a population model is to assume that the probability of seed germination is less than one so that the population forms a between-year seed bank (MacDonald and Watkinson 1981). Throughout the article we use the term *seed bank* as shorthand for between-year seed bank; we do not consider the effects of forming a short-term seasonal or within-year seed bank (see Silvertown 1988). A population model incorporating a seed bank has the following structure:

$$S_{t+1} = (1-d)(1-g)S_t + FKE\{1 - \exp[-(1-d)gS_t/K]\}. \quad (3)$$

In this model, it is assumed that the probability of a seed's dying before germination in each time interval is  $d$  and that, of those seeds that survive, the probability of germination is  $g$ . The finite growth rate for a population with this structure is

$$R = (1-d)[1 + g(FE - 1)]. \quad (4)$$

When  $g$  is less than one, the population is said to form a seed bank. It is clear from figure 1 that the formation of a seed bank makes persistence more difficult. This result occurs because delaying germination does not increase the probability of a seed's germinating in an empty microsite and so cannot increase the finite rate of increase ( $R$ ). In fact, there is a cost in forming a seed bank that results

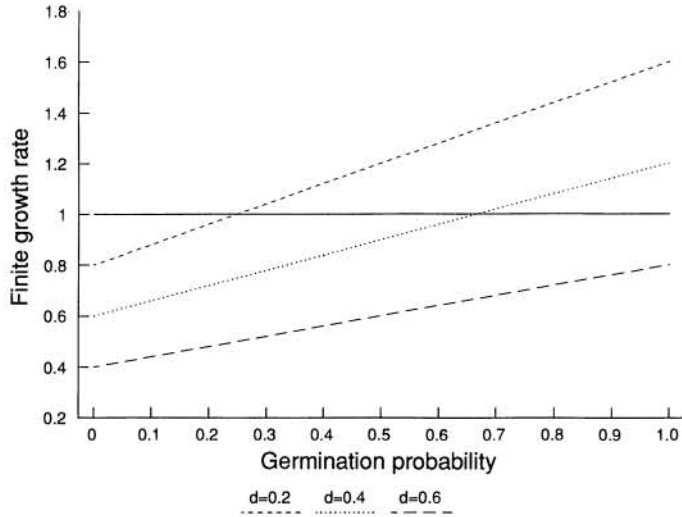


FIG. 1.—The relationship between finite growth rate ( $R$ ) and the probability of germination for eq. (4). Decreasing the germination rate results in a reduction of the finite growth rate, which makes coexistence more difficult. Other parameter values are  $E = 0.1$ ,  $F = 20$ .

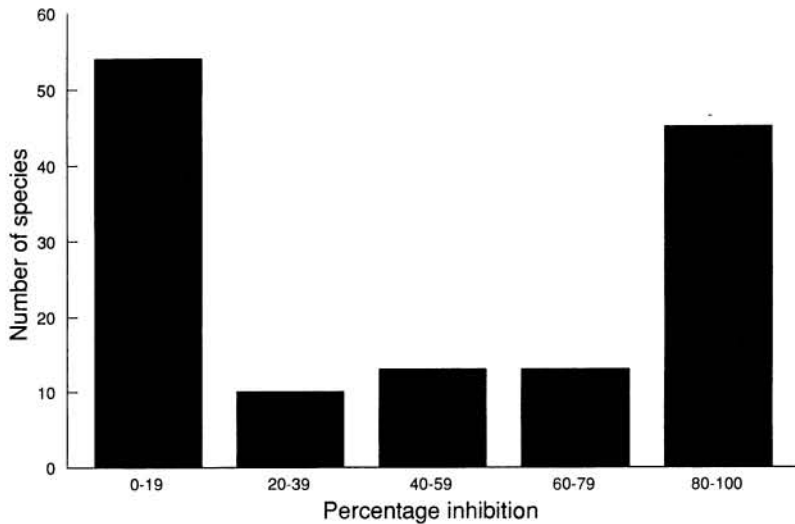


FIG. 2.—Frequency distribution of the percentage inhibition of germination by a leaf canopy, % inhibition =  $(1 - \% \text{ germination under a leaf canopy} / \% \text{ germination in diffuse white light}) \times 100$ . Data from Gorski (1975), King (1975), Gorski et al. (1977), and Rees (1989).

from the death of seeds before germination. To see this, note that the condition for persistence is

$$(1 - d)[1 + g(FE - 1)] > 1.$$

When  $g = 1$  this condition reduces to  $F > 1/(1 - d)E$ , which is equation (1). Therefore, it is clear that at best the formation of a seed bank has no effect on persistence (i.e.,  $d = 0$ ,  $g < 1$ ) and in general (i.e.,  $d > 0$ ) makes it more difficult.

#### MODEL 3—SIMPLE GERMINATION BEHAVIOR

The previous model assumes that germination biology may be summarized by a single parameter ( $g$ ). However, experimental work has demonstrated that the probability of a seed's germinating depends on the presence of established plants (Gorski 1975; King 1975; Gorski et al. 1977; Silvertown 1980; Rice 1985; Farmer and Spence 1987; Benech Arnold et al. 1988; Van Tooren and Pons 1988). The main result from this broad body of experimental work is that the presence of established plants inhibits seed germination; this may occur through changes in the red-far red ratio of the incident radiation, the range of temperature fluctuations, or a reduction in soil nitrogen levels. Where comparative data are available, the distribution of percentage inhibition appears to be of an all-or-nothing nature (fig. 2). Among the species studied by Gorski et al. (1977), 58% of the uncultivated species showed strong (80%–100%) inhibition of germination by a leaf canopy, whereas only 10% of the cultivated species had a similar response, which suggests the importance of germination inhibition in natural populations.

It is therefore necessary to modify the previous model to allow different germination probabilities in unoccupied microsites and in those occupied by perennials. If we assume that unoccupied microsites occur independently at random in each time interval and that the probability of germinating in an unoccupied microsite is  $g_u$  and the probability of germination in a microsite occupied by an established perennial plant is  $g_o$ , we obtain the following model:

$$S_{t+1} = (1 - d)(1 - \Omega)S_t + FKE[1 - \exp(-(1 - d)g_u S_t/K)], \quad (5)$$

where  $\Omega = g_u E + g_o(1 - E)$ . For persistence we require

$$(1 - d)[1 - g_o(1 - E) + g_u E(F - 1)] > 1. \quad (6)$$

Equation (6) can be rearranged to show the minimum fecundity required for persistence. If this fecundity is less than the corresponding fecundity derived from model 1, it shows that the germination biology promotes persistence. The exact conditions that dictate whether a specific germination biology is advantageous are complex and not susceptible to precise biological interpretation. However, the following necessary conditions can be derived:  $g_u > g_o$  and  $g_u > d/[1 - (1 - d)E]$ . The first condition requires that germination be inhibited by established perennial plants. The second provides a limit on the cost of forming a seed bank, as a result of seed mortality before germination, that can be made good by the inhibition of germination in microsites containing perennials.

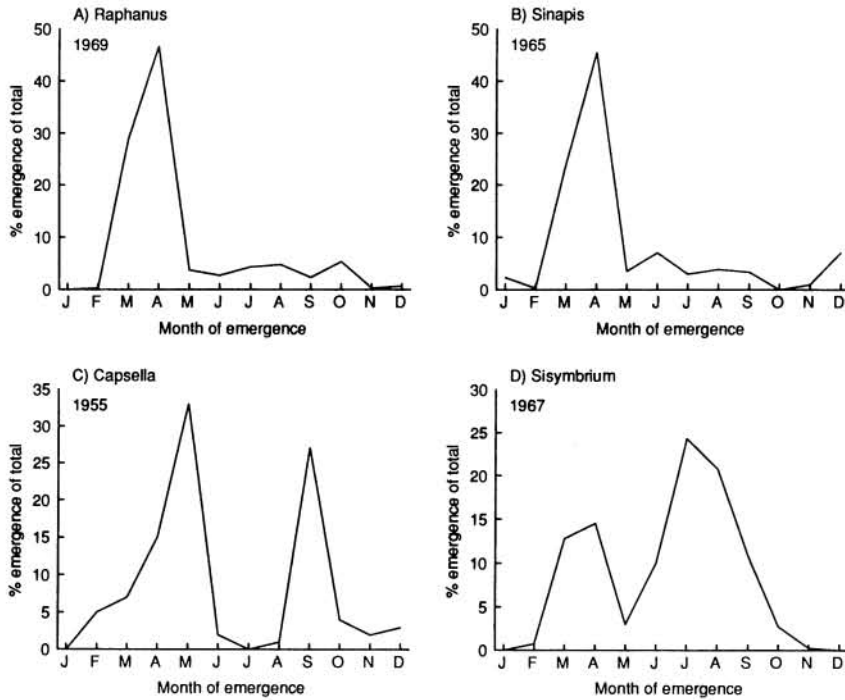


FIG. 3.—Variation in the time of emergence of (A) *Raphanus raphanistrum* L., (B) *Sinapis arvensis* L., (C) *Capsella bursa-pastoris* L., (D) *Sisymbrium officinale* L. Data from Roberts (1964) and Roberts and Boddrell (1983).

In a similar way a comparison can be performed with model 2. If we set  $g = g_o(1 - E) + g_uE$  so that the fraction of seeds that germinate in a time interval is equal, we ensure that the cost of forming a seed bank as a result of seed mortality is the same in both models, and we obtain the condition,  $g_u > g_o$ . When this is true, the germination is inhibited by the presence of perennial plants, and this promotes persistence.

The data presented in figure 2 suggest, to a rough approximation, that for the uncultivated species,  $g_o < 0.2 g_u$ , which assumes  $g_o$  and  $g_u$  can be estimated by the probability of germination under a leaf canopy and in diffuse light, respectively. Therefore, the germination biology described above can promote persistence subject to the conditions given above. It is worth repeating that it is not delaying germination per se that promotes persistence (Model 2—Delaying Germination) but the seed's germination response to the presence of established plants.

#### MODEL 4—COMPLEX GERMINATION BEHAVIOR

In the simple germination behavior model, it was assumed that seeds could respond to the presence of perennial plants and that as a result the probability of germination was reduced. However, in these simple models it was assumed that germination was synchronous such that the probability of germination was unaf-

TABLE I  
CONDITIONAL GERMINATION PROBABILITIES

Parameter	Conditional Probability
$g_{pe}$	Germinating early with a perennial
$g_{pl}$	Germinating late with a perennial
$g_e$	Germinating early without a perennial
$g_l$	Germinating late without a perennial or a seedling from the early cohort
$g_{le}$	Germinating late without a perennial but with a seedling from the early cohort

ected by the presence of seedlings. However, it is well established that for most seed populations there is considerable variance in the timing of germination (Popay and Roberts 1970*b*; Roberts and Neilson 1980; Marks and Prince 1981; Roberts and Boddrell 1983; fig. 3). As a result of this variability, it is possible that seedlings from early germinating seeds will alter the recruitment probability of seeds in the soil. This effect has been documented in the field in two experimental studies (Inouye 1980; Graham and Hutchings 1988). The simplest way of incorporating variance in germination time into a population model is to divide seedlings into two cohorts—early and late. The germination probabilities are given in table 1.

As in the earlier models, a fraction  $d$  of the seeds die in each time interval before germination. All seeds that germinate with a perennial are assumed to die before reproduction. The expected number of seeds that germinate in an unoccupied microsite is

$$\begin{aligned} \xi[\text{germ}|\sigma \text{ seeds}] &= \sum_{i=1}^{\sigma} \binom{\sigma}{i} g_e^i (1 - g_e)^{\sigma-i} \left[ i + \sum_{j=0}^{\sigma-i} \binom{\sigma-i}{j} g_{le}^j (1 - g_{le})^{\sigma-i-j} \right] \\ &\quad + (1 - g_e)^{\sigma} g_l \sigma \\ &= \sum_{i=1}^{\sigma} \binom{\sigma}{i} g_e^i (1 - g_e)^{\sigma-i} [i + g_{le}(\sigma - i)] + (1 - g_e)^{\sigma} g_l \sigma \\ &= g_{le} [1 - (1 - g_e)^{\sigma}] \sigma + (1 - g_{le}) g_e \sigma + (1 - g_e)^{\sigma} g_l \sigma. \end{aligned}$$

Combining unoccupied microsities with those occupied by perennial plants, we see that the expected number of seeds that germinate is

$$\xi[\text{germ}|\sigma \text{ seeds}] = \sigma\theta + \sigma\phi r^{\sigma},$$

where for notational convenience  $\phi = E(g_l - g_{le})$ ,  $r = (1 - g_e)$ ,  $g_p = 1 - (1 - g_{pe})(1 - g_{pl})$ , and  $\theta = (1 - E)g_p + E\{g_e + g_{le} - g_e g_{le}\}$ . If we assume that the spatial distribution of the seed bank can be described by a Poisson distribution, we can calculate the expected number of seeds that germinate given that there are  $(1 - d)S_t$  seeds.

$$\begin{aligned} \xi[\text{germ}|(1 - d)S_t \text{ seeds}] &= \sum_{i=0}^{\infty} \frac{e^{-(1-d)S_t/K} [(1 - d)S_t/K]^i}{i!} (\theta i + \phi r^i) \\ &= [(1 - d)S_t/K][\theta + \phi r e^{-(S_t/K)(1-d)(1-r)}]. \end{aligned}$$

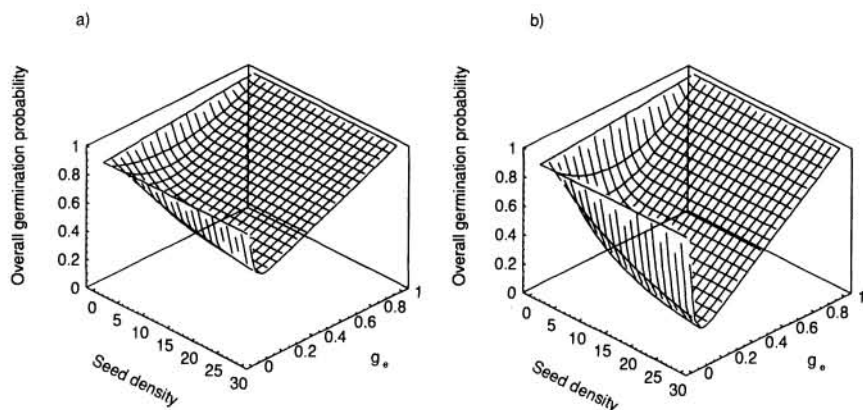


FIG. 4.—Density-dependent seed germination as a result of the interaction between seeds and seedlings. *a*,  $g_{le} = 0.5$ ; *b*,  $g_{le} = 0.1$ . In both cases  $g_1 = 0.9$ ,  $d = 0$ .

The next step is the derivation of the expected fecundity. If we assume that all seeds that germinate in a microsite with a perennial die, we need to consider only the unoccupied microsities. The probability of at least one seed's germinating is

$$p(> 0 \text{ seedling} | \sigma \text{ seeds}) = 1 - (1 - g_e)^\sigma (1 - g_1)^\sigma.$$

From this expression the expected fecundity of a microsite can be calculated:

$$\xi(\text{fecundity} | \sigma \text{ seeds}) = FE(1 - \lambda)^\sigma,$$

where  $\lambda = (1 - g_e)(1 - g_1)$ . As in the calculation of the expected number of seeds that germinate, we now calculate the expected fecundity:

$$\begin{aligned} \xi[\text{fecundity} | (1 - d)S_t \text{ seeds}] &= \sum_{i=0}^{\infty} \frac{e^{-(1-d)S_t/K} [(1-d)S_t/K]^i}{i!} FE(1 - \lambda)^i \\ &= FE(1 - e^{-(1-d)S_t/K(1-\lambda)}). \end{aligned}$$

Combining these results, we arrive at the following population model:

$$S_{t+1} \approx (1 - d)(1 - \theta - \phi r e^{-[(1-d)S_t/K](1-\lambda)}) S_t + FKE(1 - e^{-(1-d)S_t/K(1-\lambda)}).$$

The finite growth rate is

$$R = (1 - d)[1 - (1 - E)g_p + E(g_e + g_1 - g_e g_1)(F - 1)]. \quad (7)$$

This expression is independent of  $g_{le}$ , the probability of germinating in a microsite with no perennial but with a seedling from the first cohort. This result occurs because the finite growth rate is calculated at low densities where seed-seedling interactions are unimportant. Note also that the condition for persistence in this complex model is formally equivalent to the simpler model with just two germination parameters, equation (5).

A second unexpected feature of this model is that although the seeds cannot

directly detect the presence of other seeds, let alone the density of seeds in a microsite, the probability of seed germination is density-dependent (fig. 4). When there is no variation in germination time ( $g_e = 1$  or  $g_e = 0$ ), the probability of germination is density-independent. Thus, the essential ingredients generating density dependence are variability in emergence time and the interaction between seedlings and buried seed. Density-dependent germination has been found in a number of studies (Palmlblad 1968; Linhart 1976; Inouye 1980; Bergelson and Perry 1989). In Bergelson and Perry's study, the rate of germination was found to be dependent on the number of seeds in a microsite regardless of their specific identity.

Density-dependent germination will disrupt the assumed Poisson distribution of seeds in the seed bank and so could invalidate the analytical results. However, Monte Carlo simulation studies strongly suggest that the analytical condition for persistence (eq. [7]) is correct. This result was expected since the spatial distribution of the annual has no effect on the condition for persistence (see model 1).

#### MODEL 5—NEIGHBORHOOD COMPETITION

It has been demonstrated by a number of workers that the relationship between plant fecundity ( $F_c$ ) and the weight or number of neighbors is a nonlinear decreasing function (Weiner 1982; Pacala and Silander 1985; Goldberg 1987; McConaughay and Bazzaz 1987; Miller and Werner 1987). The relationship is often well described by the simple hyperbolic function

$$F_c = \frac{F}{1 + \alpha i}$$

or an exponential function,

$$F_c = Fe^{-\alpha i},$$

where  $F$  is the fecundity of a plant with no neighbors,  $i$  is the number of neighbors, and  $\alpha$  is a decay parameter.

In the present context we have considered the case in which perennial plants reduce microsite quality, for example, by shading or nutrient uptake. Before we include this biology in the model, it is necessary to specify the spatial arrangement of microsites. In keeping with previous workers, we assume that microsites are arranged in a hexagonal packed square such that each microsite has six nearest neighbors (Comins 1982; Comins and Noble 1985; Crawley and May 1987). If unoccupied microsites occur independently at random, then the probability of a microsite's having  $i$  perennial neighbors is given by the usual binomial expression

$$P_1(i) = \binom{6}{i} (1 - E)^i E^{6-i}.$$

Thus, the expected fecundity of a microsite is

$$\xi(\text{fecundity}) = \sum_{i=0}^6 \binom{6}{i} (1 - E)^i E^{6-i} G(i), \quad (8)$$

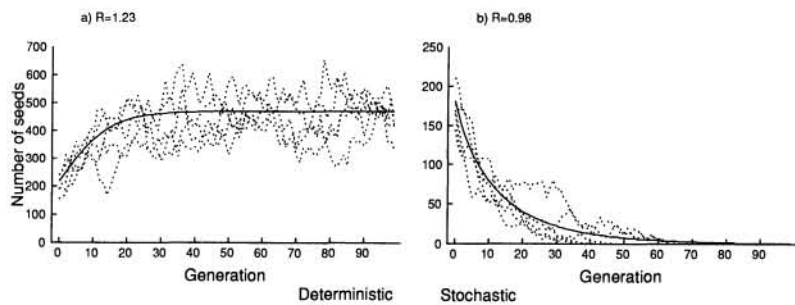


FIG. 5.—The results of two simulation experiments. The relationship between microsite quality and the number of perennial neighbors is described by the hyperbolic function with  $\alpha = 1$ . The *solid line* is obtained from the deterministic analytical model, eq. (5); the *dotted lines* are from spatially explicit Monte Carlo simulations. *a*,  $F = 50$ , which gives a finite growth rate of 1.23, thus the population persists. *b*,  $F = 30$ , which gives a finite growth rate of 0.98 and results in extinction. Parameter values common to both simulations:  $E = 0.1$ ,  $g_o = 0.25$ ,  $g_u = 0.75$ ,  $d = 0.1$ ,  $K = 400$ .

where  $G(i)$  is a function describing the effect of perennial neighbors on microsite quality. Unfortunately, when  $G(i) = F/(1 + \alpha i)$ , the sum, equation (8), cannot be brought to a closed form except when  $\alpha = 1$ . The expected fecundity for the hyperbolic model with  $\alpha = 1$  is

$$\xi(\text{fecundity}) = F \left[ \frac{1 - E^7}{7(1 - E)} \right]. \quad (9)$$

For the exponential function the expected fecundity is given by

$$\xi(\text{fecundity}) = F[(1 - E)e^{-\alpha} + E]^6. \quad (10)$$

In order to construct a model in which perennial neighbors reduce microsite quality, we substitute the fecundity term,  $F$ , in equation (2), (3), or (5) by the expected fecundity given by equation (9) or (10). Thus the effect of neighborhood competition can be simply incorporated into the models. Comparing environments where perennials reduce microsite quality with those where they do not indicates that persistence will be more difficult for a given set of germination parameters when there is neighborhood competition. Output from a model with realistic germination biology (eq. [5]), Poisson seed distribution, and neighborhood competition is shown in figure 5. In each case the analytical model accurately predicts the simulation results.

The incorporation of neighborhood competition into the model results in plant fecundity that varies from microsite to microsite. The comparison of an environment where the number of perennial neighbors is constant around each microsite with one where the number of neighbors varies indicates that between-microsite variability may promote coexistence even though, in both environments, the average number of neighbors is the same. This occurs because the average plant fecundity is greater than the fecundity of a plant in the average environment

(Jensen's inequality; Feller 1966). The average fecundity can be approximated by Taylor-expanding  $F_c$  about the mean number of neighbors and by taking expectations, which gives

$$\xi(\text{fecundity}) \approx F_c(\bar{i}) + \frac{\sigma_i^2}{2} \frac{d^2 F_c}{di^2} \Big|_{\bar{i}},$$

where  $\bar{i}$  and  $\sigma_i^2$  are the mean and variance in the number of neighbors, respectively. For the exponential function, this gives

$$\xi(\text{fecundity}) \approx F \exp(-\alpha \bar{i}) + \frac{F \alpha^2 \sigma_i^2}{2} \exp(-\alpha \bar{i}).$$

The first term on the right-hand side is the fecundity of a plant with the average number of perennial neighbors; the second term is positive and proportional to the variance in the number of neighbors, which demonstrates that variance in microsite quality promotes persistence relative to the average environment.

One could incorporate other sources of microsite variability resulting from, say, differences in abiotic conditions or the size distribution of microsites (McConnaughay and Bazzaz 1987) into the model by using the same mathematical framework. Note that in this model the expected fecundity of a plant is constant from year to year; models incorporating variation from year to year are presented in the next section.

#### RANDOM ENVIRONMENTS

In all the models considered so far, the environment is assumed to be constant from year to year, although not from microsite to microsite. However, many annual plants live in successional environments where the fraction of sites available for colonization ( $E$ ) varies through time. Until recently the incorporation of such stochastic variation into population models was a formidable mathematical task. However, Ellner (1984) provides a recipe for the analysis of stochastic population models. He considers models in the framework

$$S_{t+1} = H(S_t, E_t), \quad (11)$$

where  $S_t$  is the population size,  $E_t$  the random environmental condition in year  $t$ , and  $H(\cdot)$  is a function that maps the number of seeds in generation  $t$  to  $t + 1$ . In order to determine whether a population is persistent, Ellner (1984) used the condition of "stochastic boundedness" developed by Chesson (1982):

$$\lim_{\epsilon \rightarrow 0} \sup_t P[S_t < \epsilon] = 0. \quad (12)$$

This condition can be viewed as requiring that  $S_t$  does not spend "too much time" near zero (Chesson 1982). For the class of models presented in this article, Ellner (1984) has demonstrated that the persistence criterion for  $S_t$  is

$$\xi[\ln R(E_t)] > 0, \quad (13)$$

where  $\xi[\ ]$  is the expected value with respect to the random variable  $E_t$ . This

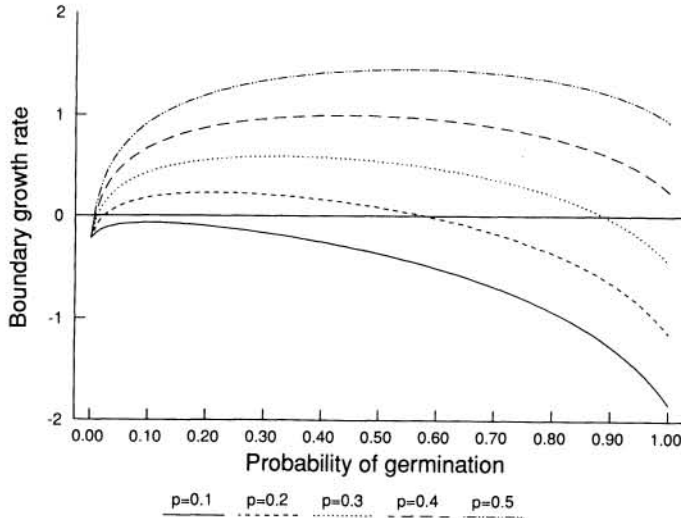


FIG. 6.—Boundary growth rate ( $v_0$ ) as a function of the probability of a seed's germinating. The boundary growth rate is calculated from eq. (14) with eq. (4) to specify the finite rate of increase. Parameter values:  $d = 0.2$ ,  $F = 100$ ,  $E_d = 1$ ,  $E_u = 0.001$ .

quantity is denoted  $v_0$ . When this criterion is met, condition (12) is satisfied and the population is persistent in the sense of stochastic boundedness (i.e., the probability of extinction is zero). However, if the condition is not met, then extinction is certain. The finite rate of increase is  $R$ , and so the condition for persistence may be stated as requiring that the average of the logarithm of  $R$  be greater than zero. Note that when  $E_t$  is constant, the condition, equation (13), reduces to  $R > 1$ , which is the condition for persistence in a constant environment.

In the simplest successional environment virtually all microsites will be available for colonization after a large-scale disturbance ( $E \approx 1$ ), whereas if there is no disturbance virtually all sites will be occupied by perennial plants ( $E \approx 0$ ). If disturbances occur independently at random with probability  $p$ , then

$$v_0 = p \ln[R(E_d)] + (1 - p) \ln[R(E_u)], \quad (14)$$

where  $E_d$  is the probability of a microsite's being unoccupied in a year with a disturbance, and  $E_u$  is the probability of a microsite's being unoccupied in a year when there is no disturbance.

Having developed the appropriate theory, we can now study the models developed in the previous sections but in a stochastic environment, starting with equation (3), which describes a population that can form a seed bank. Earlier (Model 2—Delaying Germination) it was demonstrated that simply delaying germination and so forming a seed bank made persistence more difficult. Calculating the boundary growth rate from equation (14) using equation (4) to define the finite rate of increase, we obtain figure 6. This calculation clearly shows that high rates of germination make persistence more difficult in contrast to the constant

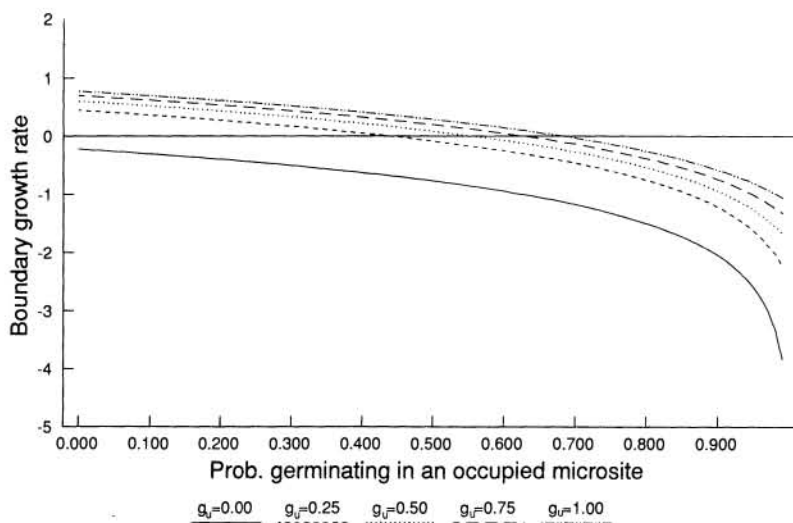


FIG. 7.—The boundary growth rate as a function of the probability of germinating in an occupied microsite. Decreasing the probability of germination in an occupied microsite makes coexistence easier. Parameter values:  $p = 0.2$ ,  $d = 0.2$ ,  $F = 100$ ,  $E_d = 1$ ,  $E_u = 0.001$ .

environment model. This result occurs because when the germination rate was high, the population rapidly declined in years when there was no large-scale disturbance. A lower germination rate results in slower decay of the seed bank, which allows the population to persist in the years between disturbances. Cohen (1966) has presented a similar result for a density-independent model of the evolution of dormancy in a random environment. By maximizing the geometric rate of increase, Cohen determined the germination rate that would be favored by natural selection; this is equivalent to maximizing the boundary growth rate.

Both Cohen's model and the one presented above assume that the germination biology of a species can be summarized by a single parameter ( $g$ ). As discussed earlier (model 3), this is unlikely to be the case. The assumption that seeds can detect the presence of established plants gives the model defined by equation (5). The condition for persistence in this model is

$$\sum_{i=1}^2 p_i \ln[(1-d)(1-g_0)(1-E_i) + E_i g_u (F-1)] > 0, \quad (15)$$

where  $p_i$  is the probability of a year of type  $i$  and  $E_i$  is the probability of a microsite's being unoccupied in a year of type  $i$ .

Incorporation of germination biology allows the seeds to detect the presence of established perennial plants and hence to determine the conditions for successful recruitment. As expected, this biology strongly promotes persistence (see fig. 7) because the seeds avoid germinating in the years between large-scale disturbances.

TABLE 2  
TABLE OF PARAMETER VALUES FOR *SINAPIS*

Parameter	Estimate	Source
$F_d$	771	Seedling estimator from disturbed site
$F_u$	24	Seedling estimator from undisturbed sites
$d$	.2	Roberts and Boddrell (1983)
$g_u$	.15	Field germination experiment
	.17	Greenhouse experiment
	.17	Roberts and Boddrell (1983)
$g_o$	.03	Greenhouse experiment

#### AN APPLICATION

In this section we attempt to apply some of the models developed earlier in the article. In order to predict whether a species will persist in a particular environment we need to estimate the finite rate of increase ( $R$ ). In general,  $R$  is a function of the average fecundity of an individual and the appropriate germination and mortality parameters. The average fecundity can be estimated by sowing seeds or planting seedlings into the community and then estimating the number of seeds produced per seed or seedling. This is an estimate of the expected fecundity of a seed or seedling (see Model 5—Neighborhood Competition). If a seedling estimator is used, this approach will overestimate the fecundity per seed because early mortality between germination and establishment is ignored.

For *Sinapis arvensis* L., average fecundity was estimated using a seedling estimator. Seedlings were planted in a recently disturbed and two undisturbed sites at Silwood Park, Berkshire (National Grid reference SU 945690), and the average fecundity per seedling estimated (for a detailed site description, see Southwood et al. 1988). The seedlings, in the recently disturbed site, formed part of a factorial field experiment in which competition and herbivory were experimentally manipulated. From this experiment it was possible to estimate the fecundity of a *Sinapis* seedling in an interspecific neighborhood that contained a wide range of annual and perennial plants (see Model 5—Neighborhood Competition). The experiment also demonstrated that mollusk herbivory resulted in a 30% decrease in plant fecundity. In the undisturbed sites each seedling was completely surrounded by established perennial plants that resulted in the average fecundity's being greatly reduced (see table 2).

The probability of seed mortality was estimated from data collected by H. A. Roberts (Roberts and Boddrell 1983). In these experiments Roberts sowed a known number of *Sinapis* seeds into steam-sterilized soil and then recorded the number of seedlings that emerged in each month for 5 yr. Three times every year the soil was disturbed to simulate cultivation. At the end of 5 yr a germination trial was conducted to determine the number of viable seeds present in the soil. It is assumed that in the first winter of the experiment a fraction  $d$  of the seeds die and in the second winter a further fraction  $d$  of the remaining seeds die. In this way an expression for the sum of all seeds that die during the course of the

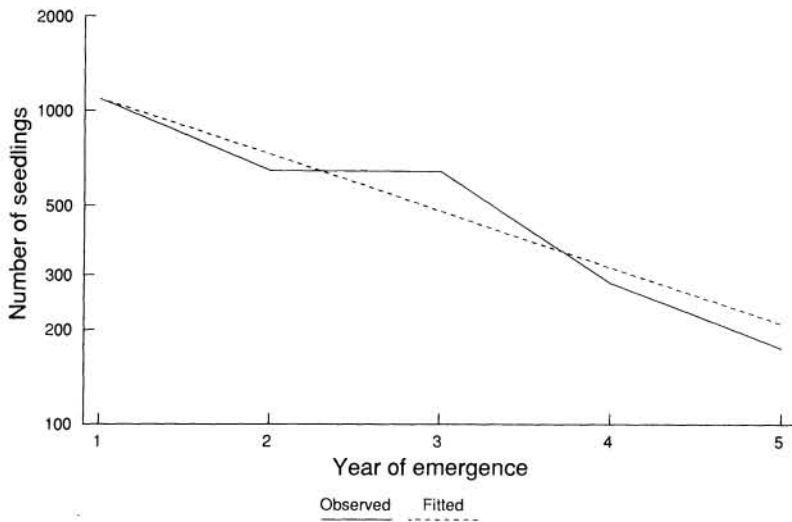


FIG. 8.—Seedling emergence pattern for *Sinapis*; see text for details. Data from Roberts and Boddrell (1983).

experiment may be found. By equating this expression with the number of seeds that do not germinate during the experiment or germination trial, we can obtain an upper estimate of  $d$ . With these assumptions we obtain the following expression:

$$N_1 = G_0[1 - (1 - d)^5] - \sum_{i=1}^4 G_i[1 - (1 - d)^{5-i}],$$

where  $N_1$  is the number of seeds that do not germinate,  $G_0$  is the number of seeds sown,  $G_1$  is the number of seedlings that emerge in the first year, and so on. This equation was solved numerically to obtain an estimate of the probability of seed mortality. This is an overestimate because some seeds may have been viable at the end of the experiment and yet failed to germinate and because not only those seeds that die but also those that germinate and fail to recruit are included.

The probability of a seed's germinating in an unoccupied microsite ( $g_u$ ) was determined using data from three separate experiments. First, seeds were sown at a range of densities into a recently disturbed experimental site at Silwood Park. The number of seedlings that emerged from the seeds was determined by destructive sampling; this approach allowed the probability of recruitment to be determined. Second, *Sinapis* seed was buried in a greenhouse experiment, and the probability of germination was determined by careful examination of the exhumed seeds (Rees and Brown 1991). The experiment was run over the period when most germination occurs in the field (see fig. 3). Third, we used the seedling emergence data collected by H. A. Roberts (Roberts and Boddrell 1983; see fig. 8). As a result of mortality, the number of seeds present in the soil is unknown except at the beginning and end of the experiment. If we assume that mortality acts before germination and that the probability of a seed's dying is  $d$ , then the

probability of a seed's germinating in the first year of the experiment is  $(1 - d)g_u$  where  $g_u$  is the probability of a seed's germinating. In general, the probability of a seed's germinating in year  $i$  is

$$(1 - d)g_u(1 - d - g_u + dg_u)^{i-1}, \quad i = 1, 2, 3, 4, 5.$$

Unfortunately, this probability distribution is defective because the sum of the terms does not equal unity. To overcome this problem we use a correction term,  $c$ , which is defined as

$$\begin{aligned} c &= \sum_{i=1}^5 (1 - d)g_u(1 - d - g_u + dg_u)^{i-1} \\ &= \frac{(1 - d)g_u[1 - (1 - d - g_u + dg_u)^5]}{d + g_u - dg_u}. \end{aligned}$$

By multiplying each term in the distribution by the inverse of the correction term, we obtain a distribution that sums to unity. The resulting probability distribution is of the form

$$P_1(i) = \frac{\theta}{[1 - (1 - \theta)^5]} [1 - \theta]^{i-1}, \quad i = 1, 2, 3, 4, 5,$$

where  $\theta = d + g_u - dg_u$ , such that  $P_1(i)$  is the conditional probability of a seed's germinating in year  $i$  given that it germinates in the first 5 yr. This is a truncated geometric distribution, defined by a single parameter,  $\theta$ ; this parameter is the probability of a seed's either germinating or dying. The compound parameter,  $\theta$ , may be estimated from the seedling emergence data even though seed mortality is unobserved. If we observe the emergence times of  $S$  seedlings, say  $x_1, x_2, \dots, x_S$ , then the log likelihood of  $\theta$  given the data is

$$L(x_1, x_2, \dots, x_S; \theta) = S \ln(\theta) + \ln(1 - \theta) \sum_{i=1}^S (x_i - 1) - S \ln(1 - (1 - \theta)^5).$$

By solving the equation  $dL/d\theta = 0$  for  $\theta$ , we obtain the maximum likelihood estimate of  $\theta$ , denoted  $\hat{\theta}$ . A detailed discussion of the use of the truncated geometric distribution is given by Chapman and Robson (1960) and Robson and Chapman (1961). Using the estimate of  $d$  obtained above, we can then obtain an estimate of  $g_u$ :

$$\hat{g}_u = \frac{\hat{\theta} - \hat{d}}{(1 - \hat{d})},$$

where  $\hat{d}$  is the estimated value of  $d$ ; because  $\hat{d}$  is an overestimate,  $\hat{g}_u$  is underestimated.

The probability of germinating in an occupied microsite ( $g_o$ ) was estimated from a greenhouse experiment in which *Sinapis* seeds were buried under an established sward of *Holcus lanatus* L. The seeds were recovered, and those with split testas were assumed to have germinated (Rees and Brown 1991). All parameter estimates are given in table 2. The finite rate of increase for *Sinapis* in a continually

disturbed environment ( $E \approx 1$ ) is

$$R \approx (1 - d)[1 + g_u(F_d - 1)], \quad (16)$$

which uses the parameter estimates from table 2; if we assume that  $g_u = 0.17$ , this gives  $R = 106$ . That is, on the average each seed replaces itself with 106 seeds. Clearly the population will increase rapidly when rare. However, the environment at Silwood is successional with irregular large-scale disturbances. Large-scale disturbances occur primarily as a result of plowing. In the first year after plowing, the vegetation is dominated by annuals; however, within 3–4 yr there is 100% cover by perennial plants, and annual plants have been completely excluded (Rees 1989). Thus, the appropriate persistence criterion is given by equation (15). Assuming that most microsites are occupied by perennials in a year with no large-scale disturbance (i.e.,  $E_u \approx 0$ ) and most microsites are available for colonization after a large-scale disturbance (i.e.,  $E_d \approx 1$ ), then for persistence,

$$p \ln[R(E_d, F_d)] + (1 - p) \ln[R(E_u, F_u)] > 0,$$

where  $p$  is the probability of a large-scale disturbance;  $F_d$  and  $F_u$  are the per capita fecundities in disturbed and undisturbed years, respectively; and  $R(E_d, F_d)$  and  $R(E_u, F_u)$  are the corresponding finite rates of increase. Setting this equation to zero and solving for  $p$ , we can calculate the critical probability required for persistence. The critical probability is given by

$$p_{\text{crit}} = \frac{-\ln[R(E_u, F_u)]}{\ln\left[\frac{R(E_d, F_d)}{R(E_u, F_u)}\right]}.$$

A small value of  $p_{\text{crit}}$  indicates that infrequent disturbances are required for persistence; whereas a large value, near one, indicates that frequent disturbances are necessary. Thus a species with a small value of  $p_{\text{crit}}$  will be able to persist at many sites and so will be widely distributed. On the other hand, a species with a large value of  $p_{\text{crit}}$  will be able to persist only in those favorable sites where disturbances occur frequently. In this way, the relative impact of demographic processes on patterns of distribution may be assessed.

Table 3 shows the critical average times between large-scale disturbances required for persistence under various conditions. It is clear from table 3 that the reduction in fecundity caused by mollusk herbivory is unlikely to be important in determining the distribution of *Sinapis* in successional environments. An interesting observation that supports the idea that changes in fecundity have little effect on the distributions of annual weeds comes from classical biological control. In a recent review, Crawley (1989, p. 218) notes, "The most obvious category of plants absent from the list of successes are the annual weeds of arable agriculture." In all cases the herbivores released were folivores or predispersal frugivores that could potentially reduce plant fecundity, and in all cases control failed.

It should also be noted that increasing the fraction of microsites available for colonization in years when there is no large-scale disturbance ( $E_u$ ) has little effect

TABLE 3  
CRITICAL AVERAGE TIMES BETWEEN DISTURBANCES (yr) REQUIRED FOR PERSISTENCE ( $1/p_{crit}$ )

$F_d$	$E_u$ ( $g_o = 0.17$ )			$E_u$ ( $g_o = 0.03$ )		
	0.00	0.001	0.01	0.00	0.001	0.01
930*	13 (18)	13 (18)	14 (21)	20 (38)	20 (39)	24 (53)
612†	12 (17)	12 (17)	13 (20)	19 (35)	19 (36)	22 (48)

NOTE.—The main table entries assume the maximal seed mortality probability,  $d = 0.2$ ; the values in parentheses assume a more realistic value,  $d = 0.1$ , in line with experimental estimates (Rees and Brown 1991). Other parameter estimates are  $g_u = 0.17$ ,  $E_d = 1$ ,  $F_u = 24$ .

\* Fecundity with mollusks excluded.

† Fecundity with mollusks present.

on the critical mean time between disturbances, which indicates that reproduction in undisturbed years has little effect on the condition of persistence. Increasing the proportion of available microsites in an undisturbed year will reduce the effect of neighborhood competition with perennial plants and hence increase the average fecundity of the annual. Analysis of equation (10) has shown that if  $E_u \leq 0.01$ , there is no significant difference (less than 5%) in average fecundity, and so a constant value was used ( $F_u = 24$ ).

The values in parentheses in table 3 indicate the effect of reducing the probability of seed mortality from the maximal value of 0.2 to 0.1: this has a dramatic effect on the critical mean time between disturbances required for persistence in all cases. Ignoring seed germination behavior (i.e., setting  $g_o = g_u$ ) also results in a substantial reduction in the critical mean time between disturbances, when  $d = 0.2$ . This effect is even more dramatic when the probability of seed mortality,  $d$ , is reduced. Therefore, germination biology and patterns of seed mortality are likely to have profound effects on the distribution of *Sinapis*.

#### DISCUSSION

In any theoretical study it is important to determine which of the results reflect the simplification inherent in the model and which are biologically important. Perhaps the strongest criticism of the models presented is the failure to include indirect effects (Werner and Chesson 1985). Indirect effects occur owing to interactions with other species in the community not included in the model. For example, changing the disturbance regime may result in the extinction of a species of annual; this in turn will change the expected fecundity of the study species as a result of interspecific competition and so alter the condition for persistence. This seems the most likely type of indirect effect. However, in *Sinapis* this may be relatively unimportant because the condition for persistence is only weakly dependent on changes in fecundity.

The results obtained for *Sinapis* suggest that in successional environments the

germination and seed mortality parameters are critical in determining whether a population will be persistent. Comparative studies (M. Rees, unpublished manuscript) that demonstrate a link between the rate of seed bank decay and a plant's distribution (the number of 10-km squares occupied in Britain or 2-km squares in Kent) suggest that the results obtained for *Sinapis* may be representative of a larger group of weed species. This does not mean that plant fecundity is unimportant in allowing persistence. For example, in environments where there are always a proportion of sites available for colonization, changes in fecundity have a profound effect on the finite rate of increase (see eq. [16]). In such habitats, species with low seed survival, high germination rates, and limited spatial dispersal may occur, and high adult fecundity may be very important in maintaining a finite rate of increase greater than unity.

Throughout the article we have focused on the mechanisms that allow annual plants to persist in communities dominated by perennials. An important related problem concerns how coexistence occurs within guilds of annual plants. The condition for persistence, equation (14), is a necessary condition for coexistence: if a species cannot persist in the habitat, then it cannot enter the community. Of the species that can persist, competitive interactions, perhaps mediated by herbivores or pathogens, with annual plants already present in the system will determine whether coexistence occurs. Classical competition theory assumes that niche differentiation for essential trophic resources is necessary for coexistence (Harper 1977; Tilman 1982, 1988). For autotrophic plants it is difficult to see how, in a homogeneous habitat, differential use for essential trophic resources (e.g., light, water, carbon dioxide, and mineral nutrients) could allow a large number of species to coexist (Grubb 1977). This idea is supported by many experimental studies that demonstrate that competitive interactions in a homogeneous environment are destabilizing, which results in extinction (Harlan and Martini 1938; Trenbath 1974; Harper 1977; Law and Watkinson 1987; Pacala and Silander 1990), with the important exception of interactions involving a legume and a nonlegume, presumably because legumes and nonlegumes use different nitrogen sources (Pacala 1986a). Assuming that plants within a guild use the same set of trophic resources, Goldberg and Werner (1983) predicted that on a per gram basis plants should be equivalent in their competitive effects on neighbors; this prediction has been confirmed by a number of experimental studies (Goldberg 1987; Miller and Werner 1987; Gaudet and Keddy 1988).

In order to obtain coexistence in theoretical models, it is necessary to make the environment spatially or temporally variable so that each species has times or places where it is a successful competitor (Chesson 1982, 1986; Tilman 1982, 1988; Pacala and Crawley 1992). In a variable environment, dispersal in time or space is necessary for coexistence. For each species we may consider two aspects of its ecology: its competitive ability and dispersal ability.

A species' competitive ability is in part determined by the abiotic environment, morphology, and physiology, but it also has a germination component. The time of germination is important in determining competitive ability because of the size-dependent asymmetrical nature of plant competition. In a particular environment it is often possible to reverse the outcome of competition by changing the

planting date. Perhaps the best example of this comes from the study of competition between a variety of annual weeds and wheat (Firbank et al. 1985; Firbank and Watkinson 1986). From a number of studies, the competition coefficients, which describe the competitive interactions in terms of species equivalents, were estimated: the coefficients range from 0.41 to 1.5 for the effect of wheat on the weeds and 0.06 to 1.63 for the effect of the weeds on wheat. Law and Watkinson (1989) suggest that the switch from competitive dominance to subdominance is largely the result of variation in the relative emergence time of the crop and the weeds. These results strongly suggest that competitive ability of established plants is not strictly determined by abiotic conditions.

A species' dispersal ability is largely determined by seed characteristics that allow a species to sample a wide range of environments and so colonize places where it will be competitively dominant. The germination biology described in the main body of the article allows seeds to differentiate between favorable and unfavorable microsites and so increase the probability of successful recruitment.

Only when all species germinate synchronously might it be possible to separate these components of a plant's ecology. However, in general when there is asynchronous germination, the two components will be confounded. Therefore, germination biology plays an important role in determining not only whether a plant colonizes a particular microsite but also whether it is competitively dominant. This means that when studying annual plant systems it is essential to explore the effects of seed characteristics on dispersal and competitive ability. Therefore, germination biology may play an important role in allowing annual plants to persist in successional environments and also foster coexistence within guilds of annual plants in these habitats.

Another community pattern that requires a knowledge of germination biology is the early dominance and subsequent decline of annual plants during succession (Tilman 1982, 1988 and references therein). Perhaps the simplest explanation of this pattern is based on a knowledge of seed germination behavior and plant competition. Annuals will dominate early succession because they have high relative growth rates; however, the perennials will be competitively dominant in the long term because they are larger and so can reduce resource levels to below those necessary for annual plant growth (Tilman 1988). As a result of this competitive differential, there will be strong selection for mechanisms that prevent germination under established perennial plants, which will result in the germination biology discussed earlier. Therefore, the proximal ecological explanation for the decline of annual plants during succession may be the inhibition of germination as a result of the establishment of perennials rather than resource competition. Inhibition of seed germination results in the formation of large seed banks that together with higher relative growth rates could explain the dominance of annuals in early succession.

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