
Article:

Rees, M. and Long, M.J. (1993) The Analysis and Interpretation of Seedling Recruitment Curves. American Naturalist, 141 (2). pp. 233-262. ISSN 0003-0147

Vol. 141, No. 2 The American Naturalist February 1993

THE ANALYSIS AND INTERPRETATION OF SEEDLING RECRUITMENT CURVES

Mark Rees and Michael J. Long

Department of Biology and Centre for Population Biology, Imperial College at Silwood Park,
Ascot, Berks SL5 7PY, United Kingdom

Submitted February 14, 1991; Revised January 29, 1992; Accepted February 6, 1992

Abstract.—We present statistical methods appropriate for the analysis of seedling recruitment data. The techniques are applied to the data collected by H. A. Roberts and his colleagues. The main result of this analysis is that seed banks do not in general decay according to a negative exponential pattern and that a wide range of recruitment patterns occur. We explore the effects of unobserved mortality on age-specific recruitment. We also demonstrate the difficulty of interpreting age-specific patterns of recruitment in terms of the behavior of individual seeds. This difficulty is a result of unobserved seed mortality and between-seed variability, either of which can qualitatively change the shape of the recruitment curve. A simple model of the recruitment process is presented, and it is demonstrated that density dependence can generate spurious patterns of age-specific recruitment.

Understanding patterns of seed survivorship is of fundamental importance for the management of weed populations (Roberts 1963) and the study of plant population and community ecology (Pacala 1986; Rees and Long 1992). Indeed, the early studies of Chepil (1946, p. 345) demonstrated that the number of seedlings emerging in successive years differed greatly between species, and he concluded that "the relative period of seed dormancy is one of the greatest single factors contributing to the seriousness of a weed."

In 1989 Lonsdale published a forum paper in *Oikos* discussing the interpretation of seed survivorship curves and drawing attention to the apparently anomalous behavior of seed populations. He noted that populations of established plants often show a wide range of survivorship curves whereas, on the basis of studies by Roberts (Roberts 1964, 1979, 1986; Roberts and Neilson 1980; Roberts and Boddrell 1983), seed populations are regarded as almost always following log-linear or Deevey type II decay curves (Harper 1977; Begon and Mortimer 1981; Fenner 1985; Watkinson 1986; Silvertown 1987). Lonsdale (1989) suggested that the most likely explanation of this pattern is that Roberts's data were inadequate to reject the null hypothesis of exponential decay. However, it should be noted that Roberts demonstrated nonexponential patterns of seedling emergence in several papers (e.g., Roberts and Feast 1972, 1973; Roberts and Neilson 1980; Roberts and Boddrell 1983).

Seed survivorship curves are often studied indirectly, and the pattern of seed bank decay is inferred from the distribution of seedling emergence through time,

Am. Nat. 1993. Vol. 141, pp. 233–262.

although a number of studies have assessed the number of viable seeds present in successive years (e.g., Roberts 1962; Roberts and Dawkins 1967). In these studies the pattern of seedling emergence often closely mimics the decline in the number of viable seeds. The observed patterns of recruitment reflect the underlying processes of germination, which may or may not result in successful establishment, and seed mortality. Germination is only partially observable, through those seedlings that successfully establish, and mortality is completely unobserved, making it difficult to determine which contributes most to the observed patterns. However, Cook (1980) puts forward a number of plausible arguments that suggest that germination is the dominant process. Observed age-dependent (nonexponential) recruitment is the result of one or a combination of the following processes: (1) age-dependent germination; (2) age-dependent mortality; (3) age-dependent establishment success of those seeds that germinate; (4) changes in the abiotic or biotic environment; (5) between-individual variability in the probability of recruitment; and (6) density-dependent germination or mortality. The fifth and sixth mechanisms are not usually considered by biologists and yet may explain many of the observed distributions.

In this article we first present statistical methods appropriate for the analysis of seedling recruitment data and then apply these techniques to the data collected by H. A. Roberts and his colleagues. The patterns of recruitment observed in this large data set (145 species) are then described. Particular attention is focused on inferences that can be made from this population level data to the behavior of individual seeds. Where possible, methods for distinguishing the different mechanisms generating age dependence are discussed.

THE ANALYSIS OF SEEDLING RECRUITMENT CURVES

Data Collection

Freshly collected seeds were mixed with the upper 7.5 cm of steam-sterilized sandy clay loam confined in open-ended 23-cm-diameter cylinders sunk in the ground outdoors and netted to exclude birds. There were two replicate cylinders per species, each containing usually 1,000 seeds. On three occasions each year the soil layer containing the seeds was mixed to its full depth to simulate cultivation. All seedlings were recorded and removed soon after they appeared. Recording continued usually for 5 yr; the soil was dug up and the number of viable seeds remaining was determined. For most species, separate experiments were begun in each of 3 different years with freshly collected seeds. Between 1953 and 1986 data were obtained for 145 species of annual and perennial plants (Roberts 1964, 1979; Roberts and Neilson 1980; Roberts and Boddrell 1983).

Therefore, for each species we have a pattern of seedling emergence times describing the number of recruits in each year of the experiment. In this article we consider the pattern of emergence of the aggregate data set obtained by summing over all replicates, giving for each species a single set of seedling emergence times. From these data the pattern of age-specific recruitment can be determined through the techniques outlined below.

Background Theory

For each species four parametric survival distributions were fitted and the goodness of fit assessed with χ^2 tests; the distributions were the exponential, compound exponential, Weibull, and log logistic. The log-normal distribution was not fitted because of the complexity of the survivor function, the difficulty in distinguishing it from the exponential distribution, and its sensitivity to the grouping of small emergence times (Cox and Oakes 1984). These distributions are continuous, and, although germination is a continuous process, data analyzed in this article are considered over yearly intervals and hence discrete versions of the continuous distributions are used. A continuous distribution is defined by $f(t)$, the probability density function that gives $F(t)$, the cumulative density function ($F(t) = \int_0^t f(t)\,dt$). The discrete distribution is obtained from $F(t)$ by

$$\pi_i = F(i) - F(i - 1)\,,$$

$i = 1, 2, \ldots, n$, where π_i is the probability of recruitment in year i. The age-specific recruitment rate or hazard is given by

$$R_i = \frac{\pi_i}{1 - F(i - 1)}\,.$$

The recruitment rate in year i is the number of seedlings observed in year i divided by the total number of seedlings observed in year i or at any time thereafter. This concept needs interpretation.

The measured quantity in the experiments is the number of seedlings observed in each year. However, ignoring possible density and seasonal effects, the recruitment process is a combination of not just the age-specific germination but also age-specific mortality (the probability in each year that a seed becomes nonviable) and age-specific establishment (the probability that a seed that germinates is observed as a seedling). If there is no death and establishment success is independent of seed age, then all seeds will eventually germinate (though not necessarily in the lifetime of the experiment), and the age-specific recruitment rate will equal the age-specific germination rate.

Unfortunately, in reality there will be some death that by its nature is unobserved—by observing seedlings one cannot determine the number of seeds that are viable. Moreover, if one tried to recover all remaining viable seeds at the end of the experiment, then that would only give an estimate of the maximum number of seeds that died and not when they died.

When there are viable seeds present at the end of the experiment, it is not possible to calculate the recruitment rate directly from the number of seedlings observed over the duration of the experiment. The approach used in the analysis, presented below, is to extrapolate the results beyond the end of the experiment, until all seedlings that would have been recorded have been recorded, by fitting a probability distribution to the observed figures. The recruitment rate can then be calculated from the resulting fitted distribution. It is important to note that the recruitment rate does not indicate the number of seeds that will germinate but

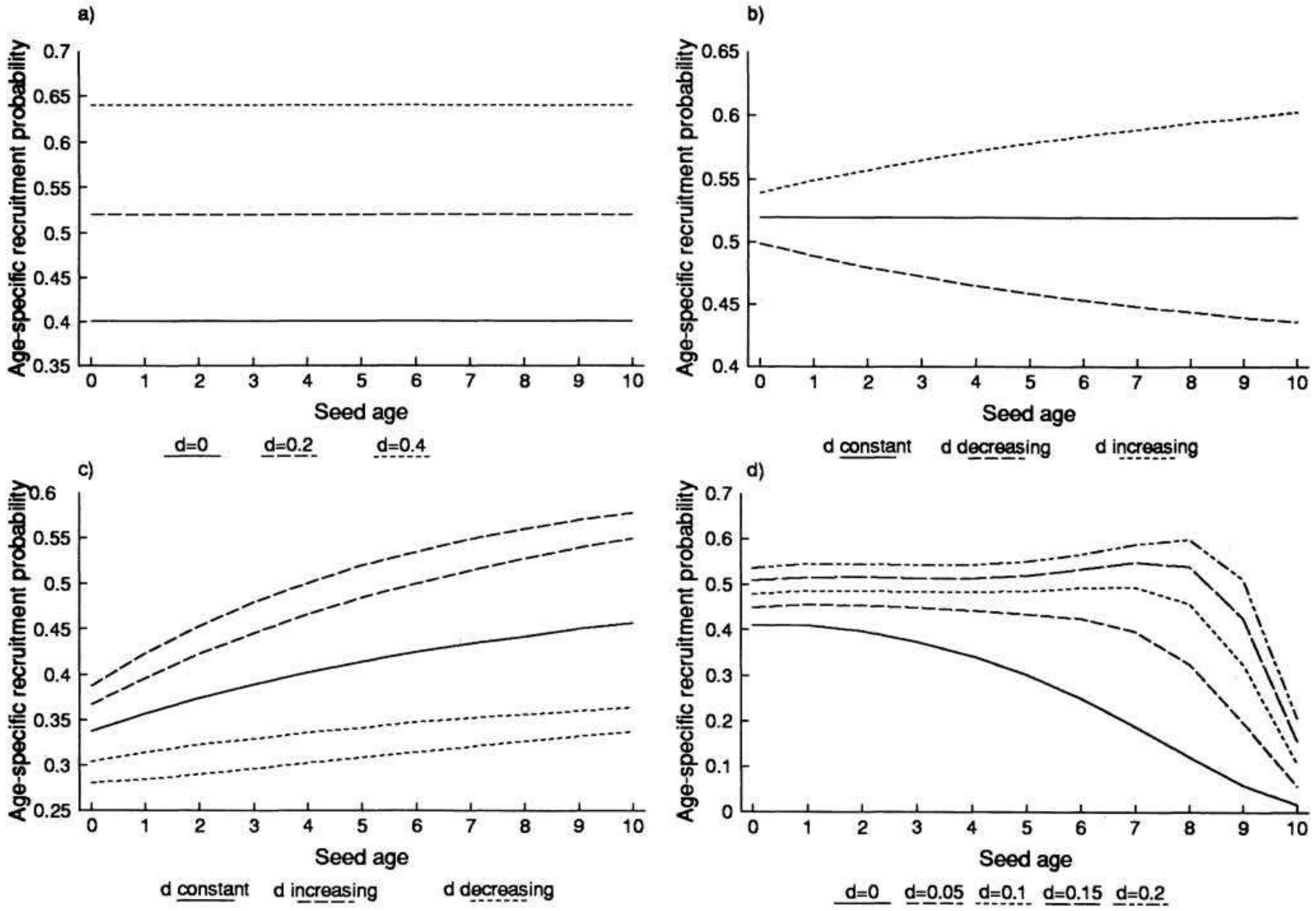

FIG. 1.—Age-specific recruitment patterns for (*a*) constant germination and mortality, (*b*) constant germination and age-specific mortality, (*c*) increasing germination and age-specific mortality, and (*d*) decreasing germination and constant mortality.

indicates, of those seeds that become seedlings, what fraction will be observed in a given year.

Before discussing the properties of the probability distributions that were used, it is beneficial to look at how changes in age-specific germination and mortality affect recruitment, under the assumption that age-specific establishment success is constant; the mathematical results are presented in Appendix A. In the simplest case in which germination (g) and seed mortality (d) are independent of seed age, age-specific recruitment is constant ($d + g - dg$) and the pattern of seedling emergence follows a negative-exponential distribution. Thus, if one has two populations, with the same germination rate but different constant death rates, then the population with the higher death rate has the higher recruitment rate (fig. 1*a*). This is because the seeds that germinate do so earlier.

If the germination rate is constant and the death rate increases/decreases with age then the recruitment rate will similarly increase/decrease (fig. 1*b*). However, when the germination rate increases with age, the recruitment rate increases irrespective of the death rate (fig. 1*c*). Unfortunately, when the germination rate decreases with age, the resulting recruitment rate follows no simple rule. Even with a constant death rate, it is possible for the recruitment rate to increase in places, and the overall recruitment curve may be nonmonotonic (fig. 1*d*). This makes interpretation of the observed recruitment curves in terms of germination and mortality parameters difficult.

A summary of the properties of the distributions fitted is presented below. In each case the parameter ρ has the dimension of the reciprocal of time and κ is dimensionless. The distributions were chosen to provide a wide range of possible recruitment patterns; examples of the discrete versions are presented in figure 2.

Exponential Distribution

This distribution is defined by a single parameter ρ, the mean is $1/\rho$, and

$$F(t) = 1 - e^{-\rho t}, f(t) = \rho e^{-\rho t}, \pi_i = e^{-\rho i}(e^{\rho} - 1), R_i = 1 - e^{-\rho}.$$

The hazard is constant, implying that the probability of recruitment does not vary with age (fig. 2*a*). The underlying discrete distribution is a geometric distribution.

Compound Exponential Distribution

When each recruitment time is exponentially distributed but the rate varies randomly between individuals, the resulting distribution is a compound exponential. If the distribution of recruitment rates follows a gamma distribution then the resulting distribution is

$$f(t) = \frac{\kappa(\kappa/\rho)^{\kappa}}{(t + \kappa/\rho)^{\kappa+1}}, F(t) = 1 - \frac{(\kappa/\rho)^{\kappa}}{(t + \kappa/\rho)^{\kappa}}$$

and

$$\pi_i = (\kappa/\rho)^{\kappa}\left[\frac{1}{(i - 1 + \kappa/\rho)^{\kappa}} - \frac{1}{(i + \kappa/\rho)^{\kappa}}\right], R_i = 1 - \left(1 - \frac{1}{i + \kappa/\rho}\right)^{\kappa}.$$

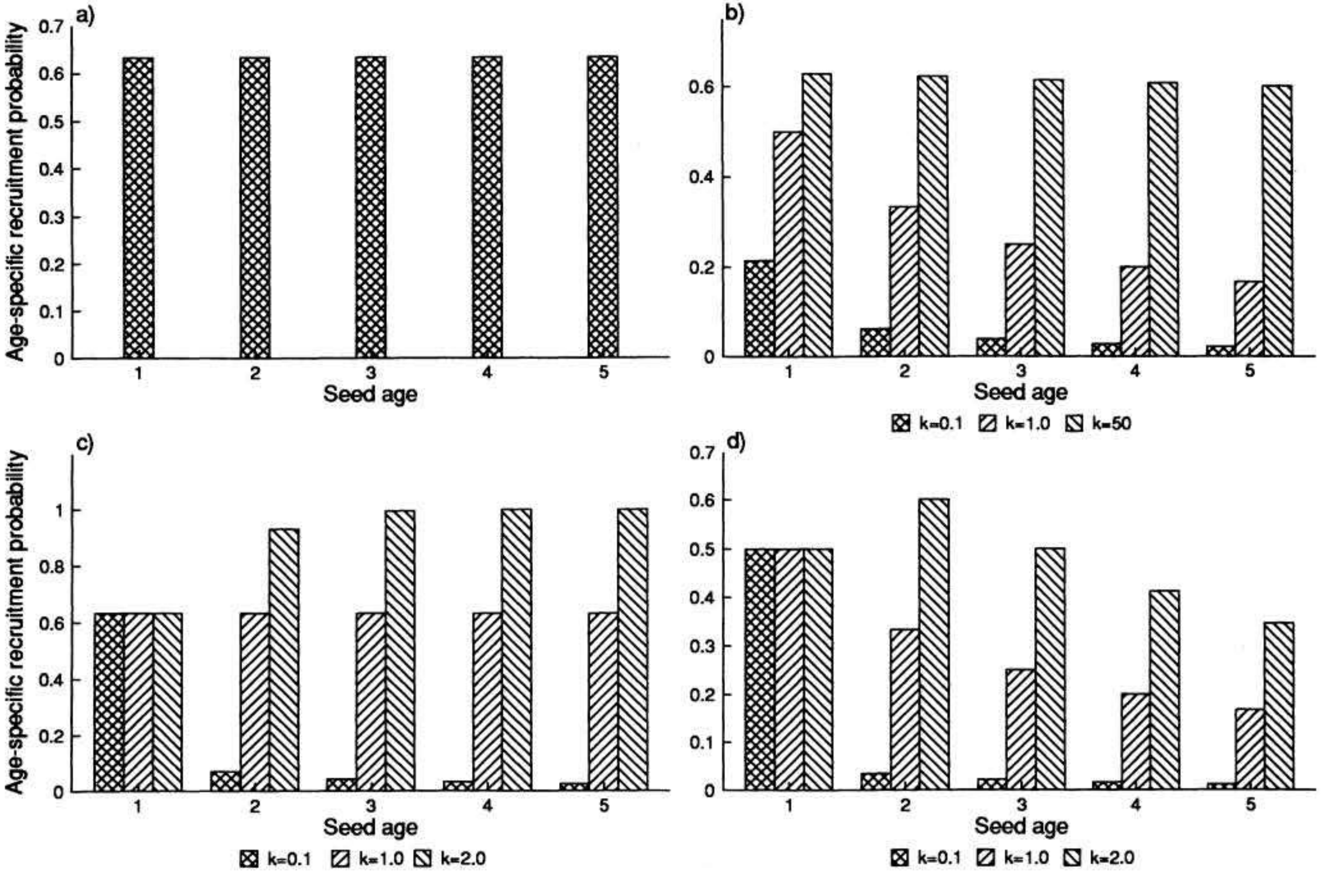

FIG. 2.—Age-specific recruitment probabilities for (*a*) exponential distribution, (*b*) compound exponential, (*c*) Weibull distribution, and (*d*) log logistic distribution. In each case $\rho = 1$.

The distribution has a long tail when κ is small and tends to the exponential as $\kappa \rightarrow \infty$. The hazard is a monotone and is decreasing (fig. 2*b*).

Weibull Distribution

The Weibull distribution with scale parameter ρ and index κ has

$$F(t) = 1 - \exp[-(\rho t)^{\kappa}], f(t) = \kappa\rho(\rho t)^{\kappa-1}\exp[-(\rho t)^{\kappa}],$$

$$\pi_i = \exp[-(\rho i - \rho)^{\kappa}] - \exp[-(\rho i)^{\kappa}], R_i = 1 - \exp[-\rho^{\kappa}(i^{\kappa} - (i - 1)^{\kappa})].$$

The hazard is either constant ($\kappa = 1$) or monotonic increasing ($\kappa > 1$) or decreasing ($\kappa < 1$) (fig. 2*c*).

Log Logistic Distribution

This distribution allows a nonmonotonic hazard; the distribution is defined by

$$f(t) = \frac{\kappa t^{\kappa-1}\rho^{\kappa}}{[1 + (t\rho)^{\kappa}]^2}, F(t) = 1 - \frac{1}{1 + (t\rho)^{\kappa}},$$

$$\pi_i = \frac{1}{1 + (\rho i - \rho)^{\kappa}} - \frac{1}{1 + (\rho i)^{\kappa}}, R_i = 1 - \frac{[1 + (\rho i - \rho)^{\kappa}]}{[1 + (\rho i)^{\kappa}]}.$$

If $\kappa < 1$ the hazard is decreasing; if $\kappa > 1$ the hazard of the continuous distribution has a single maximum (fig. 2*d*).

The patterns of age-specific recruitment or hazard translate directly into patterns of survivorship often used by biologists (Southwood 1978). A constant hazard or age-specific rate implies a Deevey type II survivorship curve. If the hazard is increasing then the probability of recruitment increases with age resulting in a Deevey type I survivorship curve. Decreasing hazards imply a type III curve. Nonmonotonic hazards result in a hybrid survivorship curve that is S-shaped. This occurs because initially the probability of recruitment is low and so relatively few recruits are recorded. The probability of recruitment then increases resulting in the survivorship curve's declining, and finally as the probability of recruitment declines the curve flattens out.

Parameter Estimation and Assessment of the Goodness of Fit

The parameters, ρ and κ, defining the distributions were estimated by maximum likelihood. This involves obtaining an expression for the probability of observing the data and then maximizing this to obtain the parameter estimates (Edwards 1972). Suppose we observe the emergence of N seedlings grouped into five fixed intervals of a 1-yr duration. The number of seedlings observed in year i is G_i, and

$$N = G_1 + G_2 + G_3 + G_4 + G_5.$$

The unconditional probability that a seedling recruits in year i is $\pi_i(\underline{x})$, where $\underline{x}$ is a vector of unknown parameters. Since the experiments were terminated after 5 yr the fitted distributions were truncated. This involved dividing each term, $\pi_i(\underline{x})$, by the probability that recruitment occurs during the experiment. The likelihood function (*lik*) is a multinomial probability regarded as a function of $\underline{x}$, that is,

$$lik(\underline{x}) = N! \prod_{i=1}^{5} \frac{1}{G_i!} \left[\frac{\pi_i(\underline{x})}{F(5;\underline{x})} \right]^{G_i} .$$

By maximizing this expression we obtain the maximum likelihood estimates of the parameters defining the distribution. The maximization was carried out numerically with the downhill simplex method (Nelder and Mead 1965).

An alternative approach to fitting a truncated distribution is to use the data from the viability trial carried out after the experiments had run for 5 yr. These data provide an estimate of the number of seedlings that could have recruited after the experiment was terminated. This could be incorporated into the likelihood function by including a term that is the probability of recruitment at some time after the end of the experiment (i.e., $\pi_6(\underline{x}) = 1 - F(5; \underline{x})$). The likelihood function is then of the form

$$lik = N'! \prod_{i=1}^{6} \frac{1}{G_i!} \pi_i(\underline{x})^{G_i} ,$$

where G_6 is the number of seedlings observed in the viability trial and $N' = N + G_6$. This approach was not used because it assumes that seedlings observed in the viability trial come from the same recruitment process as those from the rest of the experiment. This seems unlikely for a number of reasons: (1) the probability of successful establishment is increased when the soil is spread thinly during the viability trial and (2) because the soil is spread out germination occurs rapidly so that fewer seeds lose viability before having a chance to germinate. For these reasons the data from the viability trial were not incorporated into the likelihood function.

Since the distributions were fitted to a large number of species it was necessary to apply a correction that reduced the probability of rejecting the null hypothesis when it is in fact true. When fitting a distribution to k species, we perform k independent tests of the same hypothesis. Let α^* be the significance level for each test. Then the probability of at least one significant test is $1 - (1 - \alpha^*)^k$. The overall significance level is then

$$\alpha = 1 - (1 - \alpha^*)^k .$$

Using this significance level we may correct for the large number of tests performed (Elandt-Johnson and Johnson 1980).

Comparison of the Fitted Distributions

The shape of the hazard function was determined by the least significant χ^2 value with the significance levels 5%, 1%, and 0.1%. However, for those species in which none of the four fitted distributions adequately described the pattern of seedling emergence, assuming a 0.1% corrected significance level, no attempt was made to determine the shape of the hazard. In those species in which two or more nonexponential distributions provided a similar fit to the data the shape of the hazard function is given for each distribution (see App. B). In cases in which the exponential and a nonexponential distribution provide a similar fit the hazard was said to be constant. For the log logistic distribution the shape of the hazard function was determined by inspection of the fitted hazards. This was necessary because if the continuous hazard function has a maximum in the first year of the experiment then the fitted hazards in each yearly interval may be monotonic as a result of grouping the data.

When comparing two distributions in which one is a special case of the other a likelihood ratio test may be applied to determine whether the extra parameters that were fitted provide a statistically significant improvement in the fit of the distribution (Elandt-Johnson and Johnson 1980; Cox and Oakes 1984). This allows comparison of (1) the exponential and compound exponential and (2) the exponential and Weibull distributions. Specifically, if $lik_e(\hat{\rho})$ and $lik(\hat{\rho}, \hat{\kappa})$ are the maximized likelihoods of the exponential and nonexponential models, respectively, then the statistic

$$\chi^2 = -2 \ln\left[\frac{lik_e(\hat{\rho})}{lik(\hat{\rho}, \hat{\kappa})}\right]$$

is approximately χ^2 distributed with 1 df, assuming the distribution is in fact exponential. This test was only applied in cases in which the nonexponential distribution was not significantly different from the observed pattern of recruitment at the 5% corrected level.

RESULTS

In *Geranium pratense* and *Myrrhis odorata* virtually all the seedlings emerged during the first year of the experiment. For 29 species none of the four fitted distributions adequately described the pattern of seedling emergence, assuming a corrected significance level of 0.1%, and so the shape of the age-specific recruitment curve could not be determined. In these species the pattern of age-specific recruitment shows no simple pattern (fig. 3). Among the 114 species for which the pattern of seedling emergence could be described adequately all four patterns of age-specific recruitment were observed (i.e., constant, increasing, decreasing, and nonmonotonic).

Previously data of this type have been analyzed with semilog plots. Figure 4 contains plots of the logarithm of the number of recruits against time. Such plots are not very informative; compare parts *a* and *b* of figure 4, in which the plots look very similar. In figure 4*a* the age-specific probability of recruitment is constant, whereas in figure 4*b* the probability declines from 0.6577 to 0.2852. In figure 4*c* and *d* the species show increasing and nonmonotonic age-specific recruitment probabilities, although again the observed patterns are very similar.

Descriptive Properties of the Distributions

Of the four distributions the exponential, with its single adjustable parameter, is the least successful at describing the observed patterns of recruitment (fig. 5).

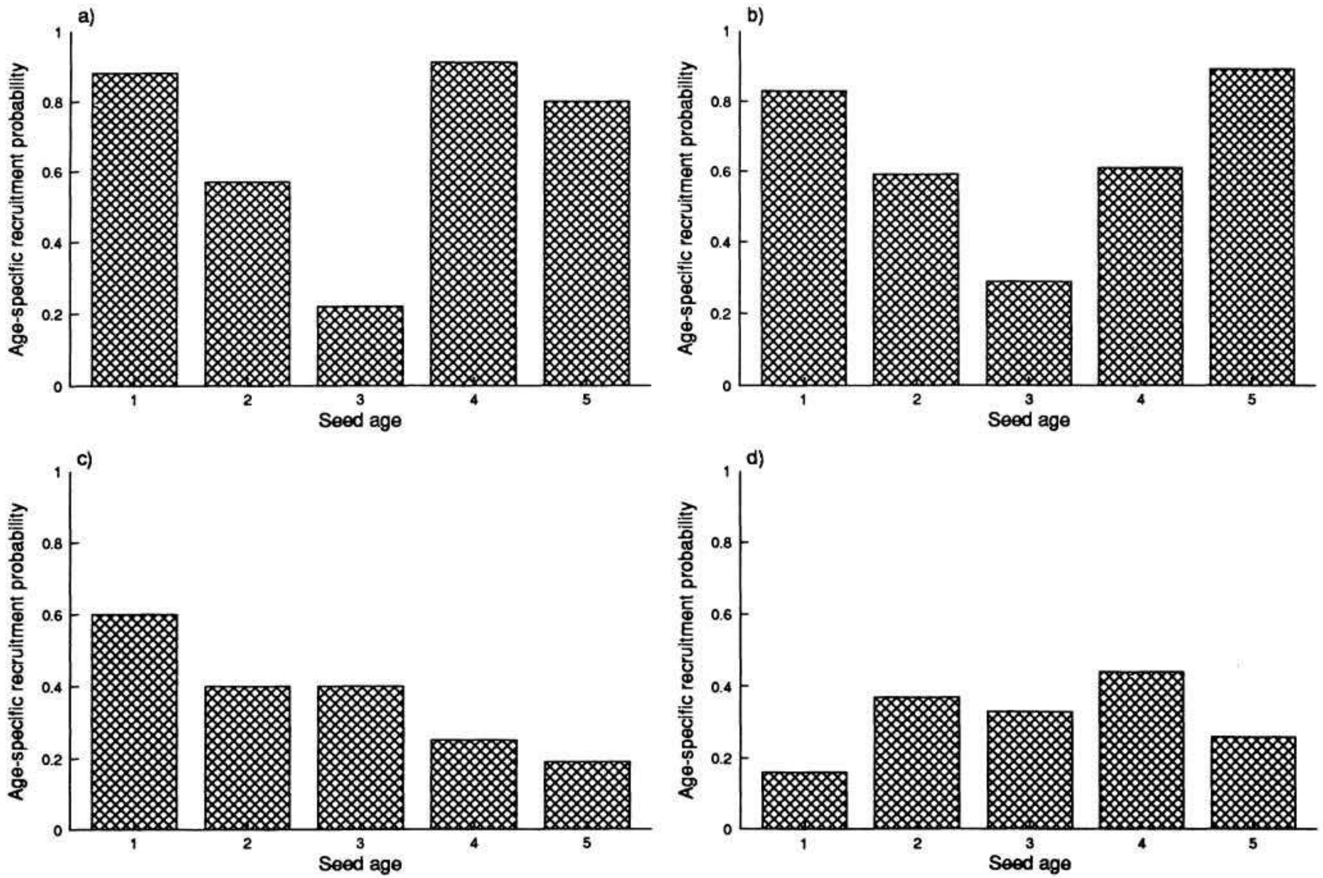

FIG. 3.—Empirical seedling recruitment curves for (*a*) *Leontodon hispidus*, (*b*) *Euphorbia helioscopia*, (*c*) *Polygonum persicaria*, and (*d*) *Aphanes arvensis*. Age-specific recruitment probabilities were calculated using the number of seedlings observed in the postexperiment viability trial as an estimate of the number of seedlings that would have emerged after year 5.

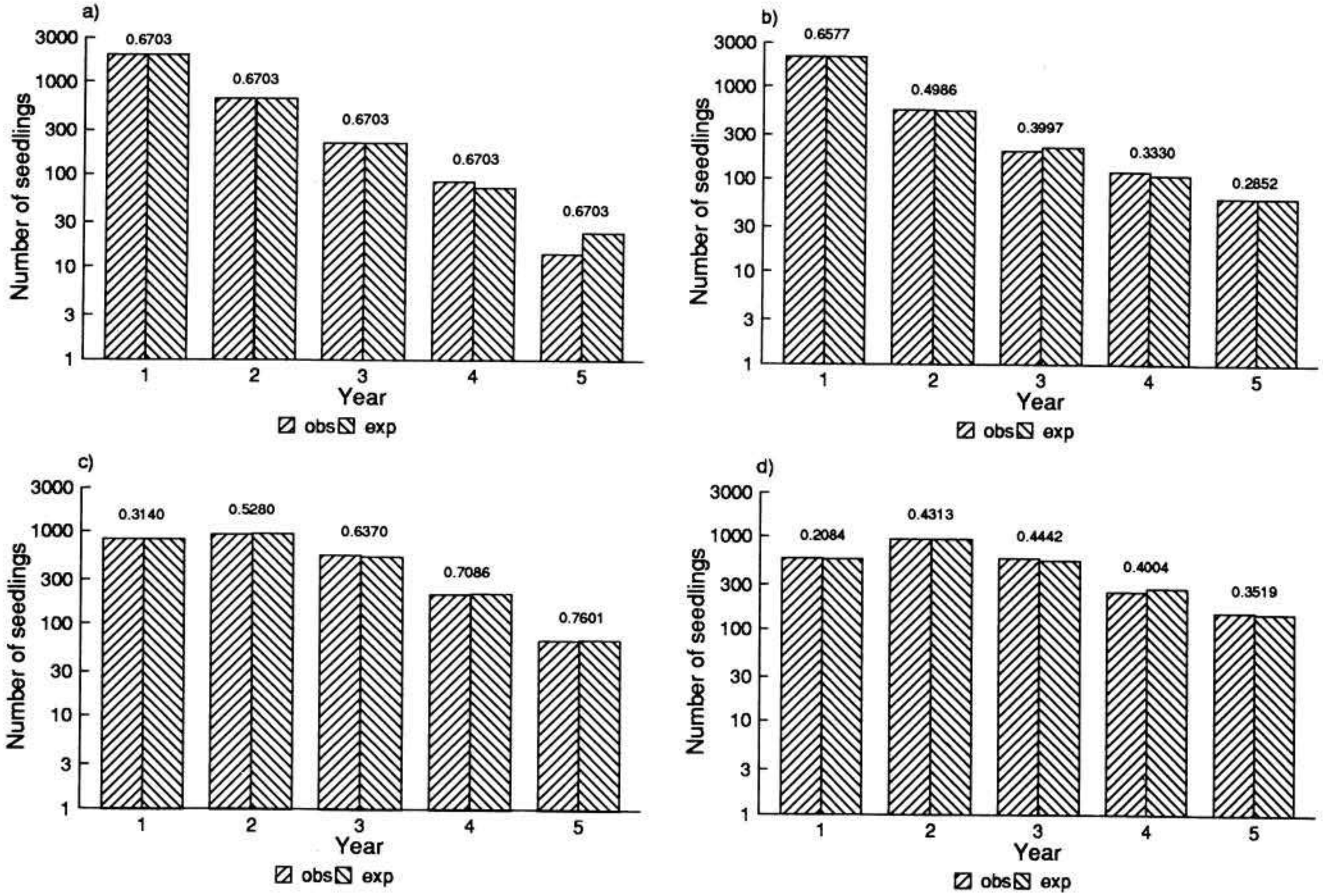

FIG. 4.—Observed and expected seedling recruitment distributions. The figures above the bars are the age-specific recruitment probabilities. (*a*) *Geranium pusillum*, fitted distribution exponential $\chi^2_3 = 6.08$, $P > .10$; (*b*) *Rumex sanguineus*, fitted distribution compound exponential $\chi^2_2 = 2.80$, $P > .30$; (*c*) *Veronica arvensis*, fitted distribution Weibull $\chi^2_2 = 1.81$, $P > .30$; (*d*) *Vicia hirsuta*, fitted distribution log logistic $\chi^2_2 = 3.64$, $P > .20$.

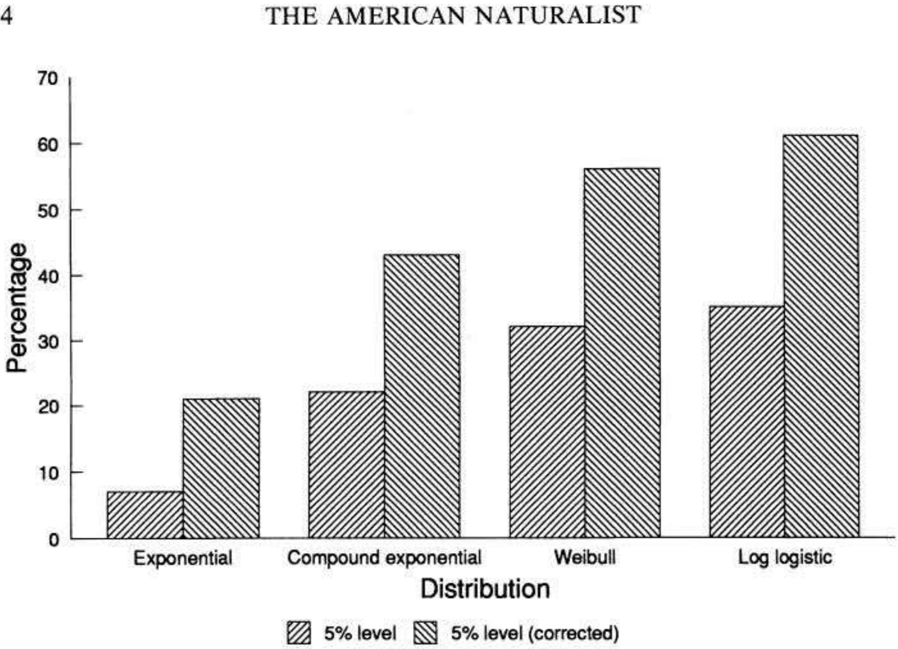

FIG. 5.—Percentage of the fitted distributions that are not significantly different at the 5% level and 5% corrected level.

Only 23% of the fitted distributions were not significantly different at the 5% corrected level, indicating that in general the probability of recruitment is age-dependent. In contrast the log logistic distribution provided an accurate description of 61% of the species. The compound exponential and Weibull distributions were intermediate in their descriptive powers (fig. 5). This pattern reflects the flexibility of the hazard function; the exponential distribution has a constant hazard, the compound exponential has a constant or decreasing hazard, the Weibull has constant, decreasing, or increasing hazards, and the log logistic has decreasing or nonmonotonic hazards.

Patterns of Recruitment

The frequency distribution of the four types of age-dependent recruitment, as determined by the least significant χ^2 value, is given in figure 6*a*. The pattern of age-specific recruitment is largely independent of how the data are chosen. Considering all the species for which the hazard could be determined or only those species in which the pattern of recruitment is accurately described at the 5% level or 5% corrected level produces virtually identical distributions of the hazard (fig. 6*a*). Approximately 14% of the species have constant hazards, 15% are increasing, 44% are decreasing, 21% are nonmonotonic, and 6% are undetermined, being equally well described by two different types of hazard.

The distribution of hazards, for cases in which likelihood-ratio tests can be used to differentiate between constant hazards and increasing or decreasing hazards, is given in figure 6*b*. In this case 15% of the species have constant hazards at the 5% level and 28% at the 5% corrected level. This increase in the percentage

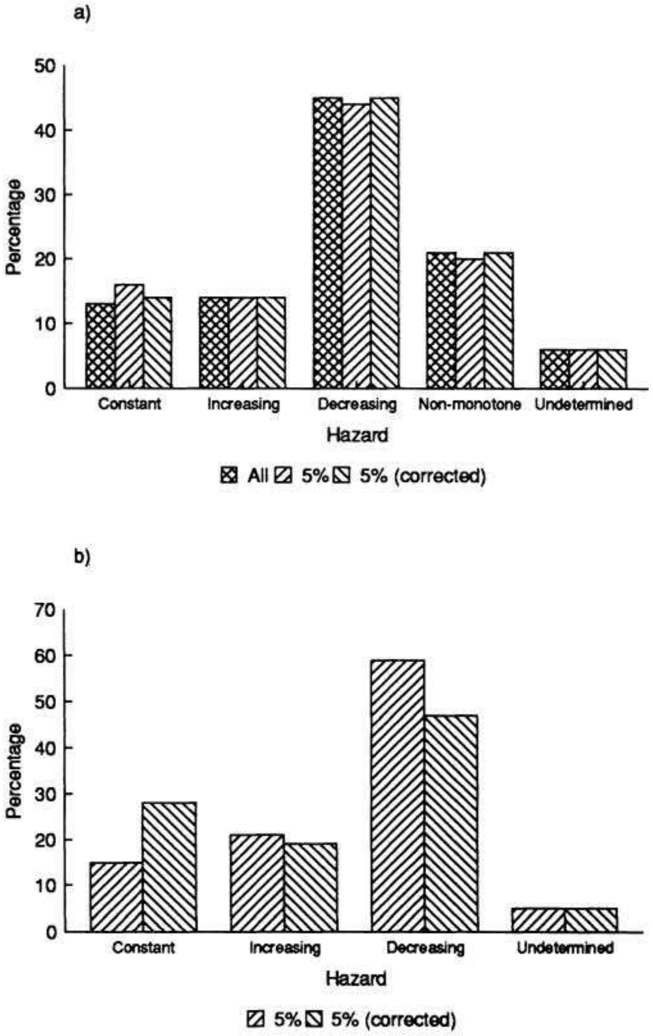

FIG. 6.—The distribution of hazards. (*a*) The hazard is determined by the least significant χ^2. (*b*) The hazard is determined using a likelihood ratio test.

of species with constant hazards reflects the exclusion of those species with nonmonotonic hazards and also the more rigorous determination of the shape of the hazard function. Approximately 20% of species have increasing, and 53% decreasing, hazards. However, the hazard observed for a particular species should not be treated as if graven in stone; changing the depth of incorporation or the cultivation regime could well alter the observed pattern (this possibility is currently being explored).

For the Compositae, Cruciferae, Leguminosae, Umbelliferae, and Scrophulariaceae there are enough species to allow the distribution of hazards within each family to be determined (see fig. 7). The Compositae show similar patterns to

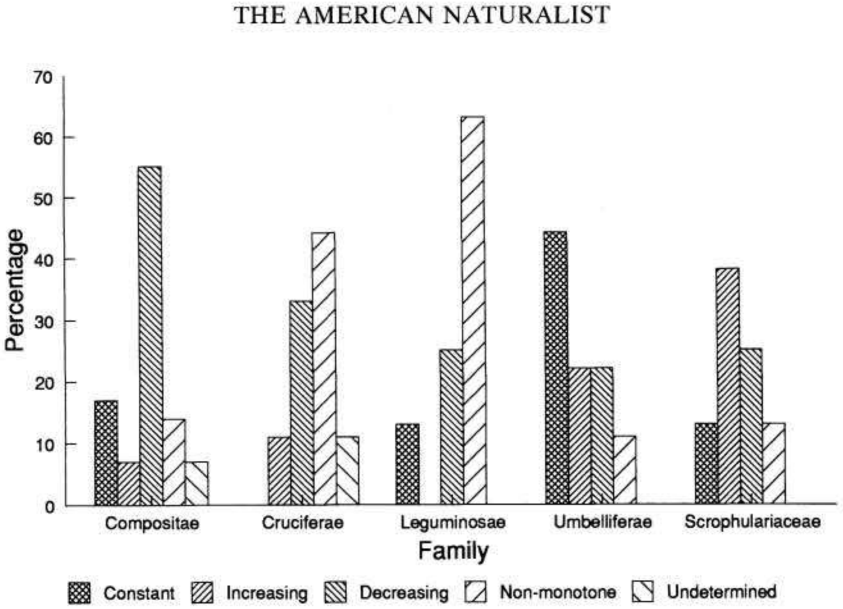

FIG. 7.—The distribution of hazards using all the data available for the Compositae (n = 29), Cruciferae (n = 9), Leguminosae (n = 8), Umbelliferae (n = 9), and Scrophulariaceae (n = 7).

those in the overall data set. The Umbelliferae, in contrast, have a higher proportion of species with constant hazards. The Cruciferae, Leguminosae, and Scrophulariaceae appear to have a larger proportion of increasing and nonmonotonic hazards. However, the data from these families must be interpreted with some caution because of the relatively small sample sizes involved.

Interpreting Population-Level Patterns of Recruitment

It is often assumed that by studying population level patterns we may infer the behavior of individuals within the population. Thus, if age-dependent patterns of recruitment are observed at the population level it is assumed that these are the result of individuals' experiencing different recruitment probabilities as they age (Lonsdale 1989). This need not be the case. If each individual has a constant probability of recruitment but this probability varies between individuals then at the population level we will observe a declining age-specific rate of recruitment. This occurs because initially the population consists of individuals with high and low probabilities of recruitment. However, as time proceeds the individuals with high probabilities of recruitment will be selectively removed from the population, leaving only those individuals with low probabilities of recruitment, resulting in a decrease in the probability of recruitment at the population level. There is abundant evidence that the probability of germination varies from seed to seed; this may be the result of environmental heterogeneity or genetic or somatic polymorphisms (see Silvertown 1984 for a review with many examples). In Appendix C we prove that the hazard of the compound exponential distribution is always decreasing no matter what the distribution of recruitment probabilities. This may provide a partial explanation for the high proportion of species with decreasing hazards. It must be remembered that the observed patterns are for aggregate cohorts. If each cohort declined exponentially but at a different rate then the net result would be a declining hazard in the aggregate data set; this hypothesis is currently being explored. In Appendix C we also demonstrate that a mixture of decreasing hazards always gives a decreasing hazard at the population level.

In an important series of papers Vaupel and co-workers (Vaupel et al. 1979; Vaupel and Yashin 1983; Vaupel 1990) have investigated the demographic implications of variability between individuals. The approach is to assume that the hazard of an individual of age t is

$$h(t, q) = qh(t),$$

where q is a random variable representing the variability between individuals and $h(t)$ is the hazard of an individual when $q = 1$. In this framework they demonstrate that variability can create or remove age dependence or nonmonotonicity depending on the nature of the individual hazard and the magnitude of the variability. These specific results have been generalized by Hoem (1990, p. 126) who has shown that "any nonstochastic hazard function in a model without unobserved heterogeneity can be represented alternatively as the unconditional hazard for a model with multiplicative unobserved heterogeneity and with a freely chosen heterogeneity distribution (with finite mean). All such mixing distributions are observationally equivalent to each other and to the original nonheterogeneity model." This means that it is impossible to determine the individual-level hazard from observational, population-level data. This difficulty is related to the normal variance components model, in which it is impossible to divide variation into within- and between-individual components if there is only one observation per individual (Hougaard 1984). However, if the individual-level hazard is constant then unobserved variability can only produce, at the population level, declining hazards. Thus, if the population-level hazard is increasing or nonmonotonic then this cannot be the result of variability and age independence; the individual hazard must be age-dependent, assuming there is no density dependence in the system (see below).

Density Dependence versus Age Dependence

In this section a simple model of a declining cohort is introduced and the effects of density-dependent germination on population-level patterns of recruitment investigated. The model incorporates two well-documented aspects of germination biology: (1) there is often considerable spread in the timing of seedling emergence (Roberts and Neilson 1980; Roberts and Boddrell 1983) and (2) the presence of established plants can affect the probability of germination (Gorski 1975; King 1975; Rice 1985). In the model, it is assumed that germination occurs in two cohorts—autumn and spring. The probability of a seed's germinating in the spring depends on the presence of established seedlings from the autumn cohort. The probability of germinating in the autumn is g_a, and the probability of germinating in the spring is g_s with no established seedling and g_{sa} with an established seedling from the autumn cohort. In each case the probability of germination is independent of seed age. When $g_{sa} < g_s$ seedlings from the autumn cohort inhibit the germination of seeds in spring. With these assumptions the average number of seedlings observed in a microsite at the end of the germination period, given that σ seeds were initially present, can be calculated:

$$\begin{aligned} E[\text{germ} \mid \sigma \text{ seeds}] &= \sum_{i=1}^{\sigma} \binom{\sigma}{i} g_a^i (1 - g_a)^{\sigma - i} \left[i + \sum_{j=0}^{\sigma - i} \binom{\sigma - i}{j} g_{sa}^j (1 - g_{sa})^{\sigma - i - j} j \right] \\ &\quad + (1 - g_a)^{\sigma} g_s \sigma \\ &= \sum_{i=1}^{\sigma} \binom{\sigma}{i} g_a^i (1 - g_a)^{\sigma - i} [i + g_{sa}(\sigma - i)] + (1 - g_a)^{\sigma} g_s \sigma \\ &= g_a \sigma + \{[1 - (1 - g_a)^{\sigma}] g_{sa} \sigma - g_{sa} g_a \sigma\} + (1 - g_a)^{\sigma} g_s \sigma , \end{aligned}$$

where $E[\ ]$ is the mathematical expectation (i.e., average value). This expression has three components: (1) the average number of seeds that germinate in the autumn cohort; (2) the average number of seeds that germinate in spring with established seedlings from the autumn cohort; and (3) the average number of seeds that germinate in spring if there are no established seedlings from the autumn cohort. Assuming there are K microsites and that the seeds are distributed over the microsites according to a Poisson distribution, we can calculate the average number of seeds that germinate in each microsite given that S_i seeds were initially present,

$$\begin{aligned} E[\text{germ} \mid S_i \text{ seeds}] &= \sum_{j=0}^{\infty} \frac{\exp(-S_i/K)(S_i/K)^j}{j!} \{(1 - g_{sa}) g_a j \\ &\quad + [1 - (1 - g_a)^j] g_{sa} j + (1 - g_a)^j g_s j\} \\ &= (S_i/K)[g_a + g_{sa}(1 - g_a) \\ &\quad + (1 - g_a)(g_s - g_{sa}) \exp(-g_a S_i/K)] . \end{aligned}$$

Multiplying this expression by K we obtain the total number of seeds that germinate. It is assumed that the probability of seed germination in each cohort is density-independent. Two important results emerge from the model.

First, the overall probability of seed germination can be density dependent, even though germination in each cohort is density independent (i.e., seeds cannot directly detect the presence of other seeds, let alone their density). The ingredients generating density dependence are variation in germination time ($0 < g_a < 1$ and $0 < (g_s, g_{sa}) < 1$) and the interaction between established plants and seeds; germination is negatively density-dependent if established plants inhibit germination ($g_s > g_{sa}$) and positively density-dependent if germination is stimulated ($g_s < g_{sa}$). Density-dependent germination has been found in a number of studies (Palmblad 1968; Qadir and Abbasi 1971; Linhart and Pickett 1973; Linhart 1976; Bergelson and Perry 1989).

Second, this density dependence can generate spurious age dependence as a result of the reduction in seed density during a germination experiment. If germi-

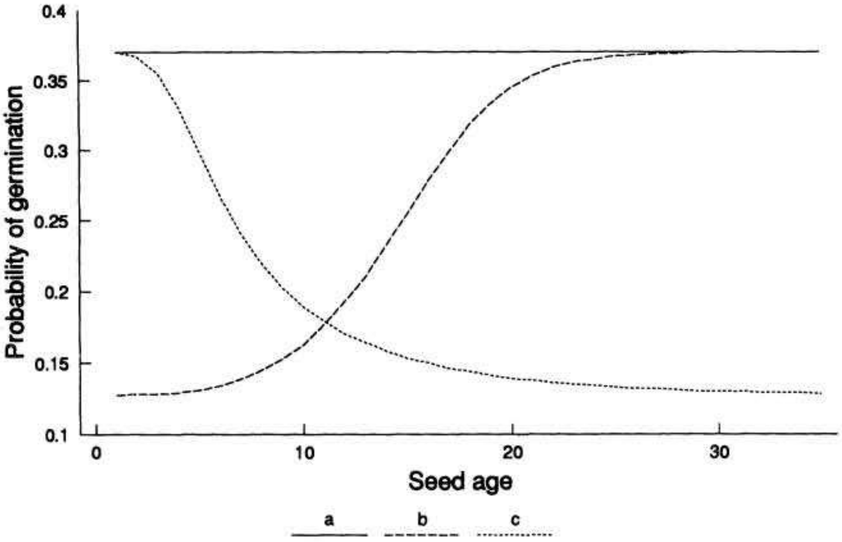

FIG. 8.—Spurious age-dependent germination as a result of density dependence generated by the interaction between seeds and established seedlings. (*a*) Germination is density independent, $g_s = g_{sa} = 0.3$; (*b*) germination is negatively density dependent, $g_s = 0.3$, $g_{sa} = 0.03$; (*c*) germination is positively density dependent, $g_s = 0.03$, $g_{sa} = 0.3$. Other parameter values: $K = 100$, $g_a = 0.1$.

nation is negatively density-dependent then the probability of germination appears to increase with seed age. In contrast, when germination is positively density-dependent the probability of germination appears to decrease with seed age (fig. 8). Density-dependent seed mortality can also generate spurious age dependence; if seed mortality is negatively density-dependent then age-specific recruitment probability appears to increase with seed age, whereas positive density dependence results in the probability of recruitment's declining.

It is therefore possible to observe density- and age-dependent patterns of germination at the population level when neither is present at the level of the individual seed. Unlike the combination of age independence and variability, density dependence can produce increasing or decreasing patterns of age-dependent recruitment. It should be noted that because each seedling was removed soon after establishing that density dependence generated via the mechanism presented above is unlikely to be observed in the data set presented in the main body of the article. However, in other situations in which seedling establishment occurs this type of density dependence has been observed (Inouye 1980; Graham and Hutchings 1988).

DISCUSSION

The main empirical result from the analysis presented is that in general seed banks do not decay according to a negative exponential pattern. The exponential distribution provides an adequate description (using a corrected significance level of 5%) for only about 23% of the species analyzed. The widespread acceptance of the exponential model is largely a result of the difficulty in detecting nonexponential patterns of recruitment from semilog plots of seedling emergence against time. However, it should also be noted that Roberts demonstrated nonexponential patterns of recruitment on several occasions (e.g., Roberts and Feast 1972, 1973; Roberts and Neilson 1980; Roberts and Boddrell 1983), yet these results seem to have been ignored. Unfortunately other graphical procedures (Cox 1979; Cox and Oakes 1984), such as plotting the probability of recruitment against time, rely on knowing the total number of seedlings that would have been observed had the experiment been run indefinitely. An upper estimate of this figure can be obtained by assuming that all seedlings recorded in the viability trial would have successfully recruited. The use of least-squares regression analysis of the logarithm of seedling number against time is inappropriate for a number of reasons: (1) the data points are not independent, since, if 1,500 out of 2,000 seeds sown recruit in the first year then no more than 500 can recruit thereafter; (2) there is a considerable loss of efficiency (Cox and Hinkley 1968) resulting in parameter estimates with large standard errors, which makes rejecting the null hypothesis of exponential decay difficult; (3) the estimates may be biased because it is assumed that the likelihood of recruitment is known with equal confidence in each year. This is clearly not true when the number of seedlings observed declines rapidly through time.

These problems also plague studies of plant survivorship where semilog plots are a popular form of analysis (e.g., Sarukhan and Harper 1973). Indeed, reanalysis of much of these data has demonstrated that many survivorship curves previously thought to be negative exponential are in fact much better described by nonexponential models (M. Rees, unpublished manuscript). These problems stem from the difficulty in identifying nonexponential patterns from semilog plots. For a graphical analysis of survival data it is much better to plot the age-specific mortality probabilities against age or some function of age (Cox 1979) rather than the logarithm of the number surviving. Likewise, data on seed and pollen dispersal are often presented on semilog plots (e.g., Werner 1975), and the problems described above again apply.

A second theme arising from the results presented is the difficulty of interpretation. For example, nonmonotonic recruitment curves can be generated by (1) nonmonotonic germination and negligible seed mortality, (2) declining germination and age-independent seed mortality, and (3) increasing germination, any pattern of seed mortality, and between-individual variability, to name but three different mechanisms; of course other mechanisms are possible. This makes it difficult to give simple mechanistic interpretations of the observed patterns. It should also be emphasized that between-individual variability and unobserved seed mortality can create complex patterns of recruitment at the population level when the underlying individual behavior patterns are straightforward. For example, U-shaped age-specific patterns of recruitment can be produced by mixing two seed types, each with increasing age-specific rates. We have also demonstrated that density dependence can generate spurious patterns of age dependence. These difficulties can only be overcome by experimental studies that manipulate the frequency distribution of seed characteristics that affect the probability of recruitment (Lonsdale 1989) and the density of seeds sown. However, even in this type of study, it must be remembered that individual seeds will experience different environments and that this variability can affect the overall patterns of recruitment observed. One source of variability that can be assessed with the data already collected is the effect of between-cohort heterogeneity. This is currently being studied by fitting separate parameters to each cohort and comparing the individual cohort hazards with the pattern observed in the aggregate data set.

An earlier model showed the possibility of density-dependent effects in seed germination even though seeds cannot directly detect the presence of other seeds. This could have important consequences for population dynamics. When seedlings inhibit germination, germination becomes negatively density dependent, which prevents relatively high or low seedling densities from occurring and so can stabilize population dynamics. In contrast, we suspect that, when germination is stimulated by the presence of established seedlings, so generating positive density dependence, this could be destabilizing. However, further work is required to determine the importance of these effects.

Although at present there is a large body of theory predicting when dormancy will evolve (reviewed in Venable 1989) there appear to be no theoretical results predicting when a given pattern of age-specific recruitment will evolve. However, Templeton and Levin (1979) have explored the consequences of dormancy on the evolution of traits not directly related to seed germination behavior. They show that in a constant fitness model the presence of a seed bank does not affect the equilibrium gene frequencies, although the rate of approach to the equilibrium decreases as the average and variance in time to recruitment increases. To explore the effect of changing the recruitment hazard consider a species in which the age-specific recruitment follows a Weibull distribution (see Background Theory). Both the mean and variance in recruitment time increase as the hazard changes from increasing to decreasing (holding the rate parameter constant), and this will slow the rate of approach to a genetic equilibrium.

In heterogeneous environments the fate of alleles is determined by both the temporal sequence of fitnesses and the age-specific pattern of recruitment. Under these circumstances the presence of a seed bank provides the population with a store of information on the relative and absolute fitnesses over the past several years. The selective importance of a given year depends on the fraction of seeds that recruit. If few seeds recruit in a particular year then the selection in that year will be effectively filtered out of the evolutionary process. Thus, the outcome of natural selection can be altered by the pattern of age-specific recruitment (Templeton and Levin 1979). This is of great practical importance for the management of, for example, herbicide resistance in weed populations.

ACKNOWLEDGMENTS

It is our great pleasure to thank H. Roberts for providing the raw data on which this article is based and also for detailed constructive comments on earlier drafts.

APPENDIX A

EFFECT OF UNOBSERVED SEED MORTALITY RECRUITMENT

In this appendix we explore the interaction between unobserved seed mortality and germination on patterns of age-specific recruitment. It is assumed that in each year the germination occurs before the seed mortality. Let S_i be the number of viable seeds at the beginning of year i. A fraction, g_i, of the seeds germinate to give G_i seedlings. After germination a fraction, d_i, of the remaining seeds die, so that the number of seeds that die is D_i. Finally, let R_i be the age-specific recruitment rate in year i. The following simple equalities apply:

$$G_i = g_i S_i,\ D_i = (1 - g_i) d_i S_i,\ S_{i+1} = (1 - g_i)(1 - d_i) S_i ,$$

$$R_i = \frac{G_i}{\sum_{j=i}^{\infty} G_j} .$$

From these it follows that

$$S_{i+k} = \left[\prod_{j=1}^{k} (1 - g_{i+j-1})(1 - d_{i+j-1}) \right] S_i ,$$

and so

$$R_i = \frac{g_i}{\sum_{k=0}^{\infty} g_{i+k} \left[\prod_{j=1}^{k} (1 - g_{i+j-1})(1 - d_{i+j-1}) \right]} .$$

CASE 1.—If g and d are both age-independent, then the expression for R_i reduces to

$$\begin{aligned} R_i &= \frac{g}{\sum_{k=0}^{\infty} g \left[\prod_{j=1}^{k} (1 - g)(1 - d) \right]} \\ &= \frac{g}{\sum_{k=0}^{\infty} g (1 - g)^k (1 - d)^k} \\ &= g + d(1 - g) , \end{aligned}$$

so the recruitment rate is independent of seed age. That is, the pattern of seedling emergence follows a negative-exponential pattern.

CASE 2.—If g is constant but d is age-dependent, then

$$\begin{aligned} R_i &= \frac{g}{\sum_{k=0}^{\infty} g \left[\prod_{j=1}^{k} (1 - g)(1 - d_{i+j-1}) \right]} \\ &= \frac{1}{\sum_{k=0}^{\infty} (1 - g)^k m_{k,i}} , \end{aligned}$$

where

$$m_{k,i} = \prod_{j=1}^{k} (1 - d_{i+j-1}) .$$

Now if death is increasing with time, then $m_{k,i}$ decreases with time and thus R_i increases. Also if death decreases with time, then $m_{k,i}$ increases with time and thus R_i decreases. So if the germination rate is constant, the recruitment rate increases/decreases depending on whether the death rate increases/decreases.

Case 3.—If g increases with seed age and d is either age-dependent or age-independent, then we have the ratio R_{i+1}/R_i such that

$$\frac{R_{i+1}}{R_i} = \frac{G_{i+1} \sum_{j=i}^{\infty} G_j}{G_i \sum_{j=i+1}^{\infty} G_j}$$

$$= \frac{g_{i+1}(1 - g_i)(1 - d_i)}{g_i} + R_{i+1} .$$

Since $R_i > g_i$,

$$\frac{R_{i+1}}{R_i} > \frac{g_{i+1}(1 - g_i)(1 - d_i)}{g_i} + g_{i+1}$$

$$> \frac{g_{i+1}}{g_i} [1 - d_i(1 - g_i)] .$$

If the germination rate is increasing then $g_{i+1} > g_i$, so

$$\frac{1 - \frac{g_i}{g_{i+1}}}{1 - g_i} > 1 > d_i ,$$

$$\frac{g_{i+1}}{g_i} [1 - d_i(1 - g_i)] > 1 ,$$

$$\therefore \frac{R_{i+1}}{R_i} > 1 ,$$

demonstrating that the recruitment rate increases independently of the death rate.

APPENDIX B

TABLE B1

SPECIES LIST AND χ^2 FOR EACH OF THE FITTED DISTRIBUTIONS

	Exponential	Compound Exponential	Weibull	Log Logistic	Hazard
Amaranthaceae:					
Amaranthus retroflexus	178.55^{***}	85.04^{***}	69.13^{***}	69.15^{***}	
Boraginaceae:					
Anchusa arvensis	82.65^{***}	44.63^{***}	57.06^{***}	30.20^{***}	
Myosotis arvensis	143.11^{***}	143.11^{***}	$11.72^{**,\mathrm{NS}}$	69.97^{***}	+ive***
Caryophyllaceae:					
Arenaria serpyllifolia	$23.18^{***,**}$	$12.14^{**,\mathrm{NS}}$	$14.55^{***,\mathrm{NS}}$	$8.07^{*,\mathrm{NS}}$	−ive
Cerastium fontanum	172.77^{***}	$11.21^{**,\mathrm{NS}}$	$14.14^{***,\mathrm{NS}}$	$10.90^{**,\mathrm{NS}}$	−ive***
Cerastium glomeratum	207.97^{***}	207.97^{***}	51.57^{***}	33.73^{***}	
Silene dioica	$25.23^{***,**}$	$21.03^{***,**}$	$22.70^{***,**}$	$13.98^{***,\mathrm{NS}}$	−ive
Silene latifolia	$16.37^{***,\mathrm{NS}}$	$16.37^{***,*}$	1.23^{NS}	$6.72^{*,\mathrm{NS}}$	+ive***,**
Spergula arvensis	28.37^{***}	3.30^{NS}	1.36^{NS}	4.63^{NS}	−ive***
Stellaria media	149.95^{***}	$8.88^{*,\mathrm{NS}}$	2.18^{NS}	$16.59^{***,*}$	−ive***
Chenopodiaceae:					
Atriplex prostrata	256.83^{***}	256.83^{***}	$18.36^{***,*}$	$18.09^{***,*}$	+ive,nm
Atriplex patula	318.00^{***}	318.00^{***}	48.87^{***}	$18.94^{***,*}$	nm
Chenopodium album	$17.59^{***,\mathrm{NS}}$	$17.59^{***,*}$	$10.17^{**,\mathrm{NS}}$	51.45^{***}	+ive$^{**,\mathrm{NS}}$
Chenopodium hybridum	$16.29^{***,*}$	3.13^{NS}	4.49^{NS}	3.88^{NS}	−ive***,*
Chenopodium polyspermum	53.03^{***}	$10.31^{**,\mathrm{NS}}$	$6.35^{*,\mathrm{NS}}$	$8.75^{*,\mathrm{NS}}$	−ive***
Chenopodium rubrum	27.69^{***}	26.08^{***}	$22.37^{***,**}$	29.32^{***}	−ive
Compositae:					
Anthemis cotula	474.44^{***}	474.44^{***}	40.97^{***}	$9.77^{**,\mathrm{NS}}$	nm
Arctium lappa	75.63^{***}	28.35^{***}	37.96^{***}	$13.19^{**,\mathrm{NS}}$	−ive
Arctium minus	3.30^{NS}				const$^{*,\mathrm{NS}}$(−ive)
Artemisia vulgaris	62.41^{***}	62.41^{***}	5.25^{NS}	$11.96^{**,\mathrm{NS}}$	+ive***
Carduus nutans	105.01^{***}	$6.42^{*,\mathrm{NS}}$	$6.70^{*,\mathrm{NS}}$	$6.46^{*,\mathrm{NS}}$	−ive***
Centaurea nigra	$15.63^{**,\mathrm{NS}}$	$.01^{\mathrm{NS}}$	$.23^{\mathrm{NS}}$	2.78^{NS}	−ive***,*
Centaurea scabiosa	$7.75^{*,\mathrm{NS}}$	1.45^{NS}	1.93^{NS}	$.67^{\mathrm{NS}}$	−ive$^{*,\mathrm{NS}}$
Chrysanthemum segetum	257.49^{***}	257.49^{***}	4.33^{NS}	38.90^{***}	+ive***
Cichorium intybus	3.68^{NS}	$.71^{\mathrm{NS}}$	$.38^{\mathrm{NS}}$	3.78^{NS}	const$^{\mathrm{NS}}$
Cirsium arvense	294.63^{***}	33.96^{***}	33.52^{***}	33.75^{***}	

Cirsium vulgare	456.32***	18.27^{***,NS}	13.86^{***,NS}	18.77***,*	−ive***
Crepis capillaris	14.26^{**,NS}	14.26^{***,NS}	12.19^{**,NS}	5.71^{NS}	nm
Galinsoga parviflora	16.70^{***,NS}	16.70***,*	16.64***,*	13.94^{***,NS}	const
Hieracium pilosella	9.40^{*,NS}	9.40^{**,NS}	8.95^{*,NS}	6.89^{*,NS}	const^{NS}
Hypochoeris radicata	101.36***	7.66^{*,NS}	6.70^{*,NS}	7.64^{*,NS}	−ive***
Lactuca serriola	6.48^{**,NS}	6.48^{*,NS}	1.13^{NS}	3.85^{NS}	+ive^{*,NS},nm
Lapsana communis	159.94***	70.92***	54.31***	76.58***	
Leontodon autumnalis	159.11***	54.59***	42.44***	55.71***	
Leontodon hispidus	376.63***	57.33***	57.15***	57.42***	
Leontodon taraxacoides	10.63^{*,NS}	6.02^{*,NS}	4.32^{NS}	11.31^{**,NS}	−ive^{*,NS}
Leucanthemum vulgare	38.06***	10.55^{**,NS}	6.32^{*,NS}	15.67^{***,NS}	−ive***
Matricaria matricarioides	15.05^{**,NS}	15.05^{***,NS}	7.35^{*,NS}	2.62^{NS}	nm
Matricaria recutita	39.82***	39.82***	5.87^{NS}	3.31^{NS}	+ive***,nm
Onopordum acanthium	58.62***	57.34***	49.47***	59.88***	
Picris hieracioides	148.51***	2.58^{NS}	3.13^{NS}	2.58^{NS}	−ive***
Senecio erucifolius	15.99***,*	4.52^{NS}	4.60^{NS}	5.13^{NS}	−ive^{**,NS}
Senecio jacobaea	53.66***	5.78^{NS}	4.63^{NS}	6.01^{*,NS}	−ive***
Senecio sylvaticus	10.89^{*,NS}	10.89^{**,NS}	10.03^{**,NS}	32.92***	const^{NS}
Senecio viscosus	18.98***,*	18.98***,*	15.94***,*	2.57^{NS}	nm
Senecio vulgaris	364.44***	.56^{NS}	.26^{NS}	1.07^{NS}	−ive***
Sonchus arvensis	231.88***	15.23^{***,NS}	19.41***,**	14.66^{***,NS}	−ive***
Sonchus asper	57.65***	4.76^{NS}	4.78^{NS}	4.78^{NS}	−ive***
Sonchus oleraceus	29.50***	27.21***	23.51***,**	43.20***	−ive
Taraxacum agg.	163.55***	8.42^{*,NS}	5.49^{NS}	8.88^{*,NS}	−ive***
Tripleurospermun inodorum	145.86***	43.47***	28.22***	41.09***	
Cruciferae:					
Alliaria petiolata	132.54***	132.54***	12.98***,*	7.70^{*,NS}	nm
Arabidopsis thaliana	12.20^{**,NS}	12.20^{**,NS}	.29^{NS}	3.33^{NS}	+ive***,nm
Barbarea vulgaris	14.04***,*	14.04^{***,NS}	13.32^{**,NS}	7.44^{*,NS}	−ive
Brassica nigra	365.10***	365.10***	91.97***	74.97***	
Capsella bursa-pastoris	41.35***	41.35***	37.72***	45.48***	
Cardamine hirsuta	344.06***	3.22^{NS}	3.89^{NS}	3.60^{NS}	−ive***
Coronopus didymus	113.28***	113.28***	13.17^{**,NS}	3.89^{NS}	nm
Lepidium campestre	9.98^{*,NS}	8.39^{*,NS}	9.27^{**,NS}	4.51^{NS}	−ive
Raphanus raphanistrum	302.98***	302.98***	28.21***	17.20***,*	nm
Rorippa islandica	117.36***	117.36***	24.72***	51.71***	
Sinapis alba	362.80***	362.80***	44.30***	5.69^{NS}	nm
Sinapis arvensis	71.49***	71.49***	64.86***	85.27***	
Sisymbrium officinale	52.18***	52.28***	44.26***	65.59***	
Thlapsi arvense	183.75***	183.75***	7.47^{*,NS}	13.45^{**,NS}	+ive***

(continued)

TABLE B1 (*Continued*)

	Exponential	Compound Exponential	Weibull	Log Logistic	Hazard
Dipsacaceae:					
Dipsacus fullonum	$.61^{NS}$	$.61^{NS}$	$.60^{NS}$	5.62^{NS}	const^{NS}
Euphorbiaceae:					
Euphorbia helioscopia	569.44^{***}	36.95^{***}	40.34^{***}	37.70^{***}	
Euphorbia peplus	247.76^{***}	3.70^{NS}	3.70^{NS}	3.70^{NS}	−ive***
Fumariaceae:					
Fumaria densiflora	719.92^{***}	719.92^{***}	49.24^{***}	$6.42^{*,NS}$	nm
Geraniaceae:					
Geranium dissectum	182.68^{***}	168.61^{***}	143.05^{***}	173.64^{***}	
Geranium pusillum	6.08^{NS}	6.08^{NS}	6.09^{NS}	$20.22^{***,**}$	const^{NS}
Geranium robertianum	172.61^{***}	66.65^{***}	61.39^{***}	65.30^{***}	
Hypericaceae:					
Hypericum hirsutum	93.74^{***}	93.74^{***}	$.86^{NS}$	$6.39^{*,NS}$	+ive***
Hypericum perforatum	115.52^{***}	115.52^{***}	5.70^{NS}	24.87^{***}	+ive***
Labiatae:					
Ballota nigra	112.77^{***}	$11.46^{**,NS}$	$9.43^{**,NS}$	$9.60^{**,NS}$	−ive***
Lamium album	381.56^{***}	5.39^{NS}	$9.27^{**,NS}$	4.68^{NS}	−ive***
Lamium amplexicaule	$23.00^{***,**}$	$23.00^{***,**}$	$13.22^{**,NS}$	5.35^{NS}	nm
Lamium purpureum	52.71^{***}	52.71^{***}	1.32^{NS}	$19.66^{***,**}$	+ive***
Prunella vulgaris	52.03^{***}	52.03^{***}	2.10^{NS}	$13.28^{**,NS}$	+ive***
Stachys officinalis	59.52^{***}	5.92^{NS}	4.86^{NS}	$6.04^{*,NS}$	−ive***
Stachys sylvatica	176.06^{***}	50.17^{***}	51.32^{***}	49.61^{***}	
Leguminosae:					
Lathyrus pratensis	$17.94^{***,NS}$	$17.88^{***,*}$	$17.65^{***,*}$	$17.65^{***,*}$	const^{NS}
Lotus corniculatus	31.86^{***}	$9.06^{*,NS}$	5.45^{NS}	$12.50^{**,NS}$	−ive***
Medicago lupulina	132.05^{***}	132.05^{***}	51.74^{***}	2.71^{NS}	nm
Melilotus altissima	95.13^{***}	95.13^{***}	70.84^{***}	147.00^{***}	
Trifolium campestre	31.96^{***}	25.23^{***}	23.94^{***}	$13.98^{***,NS}$	−ive
Trifolium dubium	$16.69^{***,NS}$	$16.69^{***,*}$	$14.36^{***,NS}$	$8.41^{*,NS}$	nm
Trifolium repens	57.65^{***}	57.60^{***}	$18.13^{***,*}$	$.57^{NS}$	nm
Vicia cracca	178.41^{***}	178.41^{***}	94.16^{***}	$14.97^{***,NS}$	nm
Vicia hirsuta	327.01^{***}	327.01^{***}	25.45^{***}	3.64^{NS}	nm
Linaceae:					
Linum catharticum	338.94^{***}	339.99^{***}	36.21^{***}	81.10^{***}	

Malvaceae:					
Malva neglecta	161.95***	44.78***	36.90***	40.40***	
Malva sylvestris	243.80***	2.09$^{\mathrm{NS}}$	2.42$^{\mathrm{NS}}$	2.10$^{\mathrm{NS}}$	−ive***
Papaveraceae:					
Papaver argemone	72.30***	72.30***	14.03$^{***,\mathrm{NS}}$	2.08$^{\mathrm{NS}}$	nm
Papaver dubium	377.21***	377.21***	240.07***	260.01***	
Papaver lecoqii	397.38***	397.38***	6.36$^{*,\mathrm{NS}}$	49.26***	+ive***
Papaver rhoeas	7.95$^{*,\mathrm{NS}}$	7.82$^{*,\mathrm{NS}}$	7.92$^{*,\mathrm{NS}}$	1.33$^{\mathrm{NS}}$	nm
Plantaginaceae:					
Plantago lanceolata	875.68***	17.60***,*	18.90***,*	17.81***,*	−ive
Plantago major	4.68$^{\mathrm{NS}}$	3.51$^{\mathrm{NS}}$	3.55$^{\mathrm{NS}}$	5.02$^{\mathrm{NS}}$	const$^{\mathrm{NS}}$
Plantago media	.65$^{\mathrm{NS}}$	.65$^{\mathrm{NS}}$	.41$^{\mathrm{NS}}$	5.25$^{\mathrm{NS}}$	const$^{\mathrm{NS}}$
Polygonaceae:					
Fallopia convolvulus	4.57$^{\mathrm{NS}}$	4.57$^{\mathrm{NS}}$	4.41$^{\mathrm{NS}}$	5.48$^{\mathrm{NS}}$	const$^{\mathrm{NS}}$
Polygonum aviculare	191.67***	191.67***	165.04***	129.97***	
Polygonum lapathifolium	25.88***,**	15.90$^{***,\mathrm{NS}}$	10.64$^{**,\mathrm{NS}}$	31.82***	−ive***,**
Polygonum persicaria	125.73***	36.94***	25.40***	40.81***	
Rumex acetosa	92.91***	1.58$^{\mathrm{NS}}$	1.94$^{\mathrm{NS}}$	1.56$^{\mathrm{NS}}$	−ive***
Rumex acetosella	237.24***	237.24***	71.83***	33.90***	
Rumex crispus	18.38$^{***,\mathrm{NS}}$	18.39***,*	17.30***,*	48.36***	const$^{\mathrm{NS}}$
Rumex obtusifolius	194.84***	4.88$^{\mathrm{NS}}$	10.08$^{**,\mathrm{NS}}$	3.68$^{\mathrm{NS}}$	−ive***
Rumex sanguineus	90.85***	2.80$^{\mathrm{NS}}$	5.46$^{\mathrm{NS}}$	2.07$^{\mathrm{NS}}$	−ive***
Primulaceae:					
Anagallis arvensis	304.83***	304.83***	24.65***	4.48$^{\mathrm{NS}}$	nm
Ranunculaceae:					
Ranunculus acris	170.55***	.41$^{\mathrm{NS}}$	.39$^{\mathrm{NS}}$	.41$^{\mathrm{NS}}$	−ive***
Ranunculus repens	504.19***	504.19***	17.72***,*	6.58$^{*,\mathrm{NS}}$	nm
Ranunculus sceleratus	33.07***	33.07***	17.01***,*	12.59$^{**,\mathrm{NS}}$	nm
Resedaceae:					
Reseda luteola	42.67***	42.66***	40.04***	63.73***	
Rosaceae:					
Aphanes arvensis	344.98***	344.98***	67.78***	68.09***	
Geum urbanum		3.12$^{\mathrm{NS}}$	2.42$^{\mathrm{NS}}$	3.44$^{\mathrm{NS}}$	−ive***
Rubiaceae:					
Galium mollugo	201.63***	2.18$^{\mathrm{NS}}$	1.75$^{\mathrm{NS}}$	2.20$^{\mathrm{NS}}$	−ive***
Scrophulariaceae:					
Chaenorhinum minus	12.53$^{**,\mathrm{NS}}$	12.53$^{**,\mathrm{NS}}$	11.84$^{**,\mathrm{NS}}$	34.89***	const$^{\mathrm{NS}}$
Odontites verna	124.74***	124.74***	5.63$^{\mathrm{NS}}$	33.02***	+ive***
Rhinanthus minor	330.49***	330.49***	36.46***	3.08$^{\mathrm{NS}}$	nm

(continued)

TABLE B1 (*Continued*)

	Exponential	Compound Exponential	Weibull	Log Logistic	Hazard
Veronica arvensis	269.84^{***}	269.84^{***}	1.81^{NS}	39.15^{***}	+ive***
Veronica hederifolia	66.42^{***}	$11.24^{**,\mathrm{NS}}$	$20.54^{***,**}$	5.03^{NS}	−ive
Veronica persica	$23.90^{***,**}$	$17.21^{***,*}$	$20.40^{***,**}$	$13.77^{**,\mathrm{NS}}$	−ive
Veronica serpyllifolia	186.26^{***}	186.26^{***}	$18.36^{***,*}$	58.83^{***}	+ive
Solanaceae:					
Hyoscyamus niger	242.35^{***}	242.35^{***}	29.67^{***}	$12.17^{**,\mathrm{NS}}$	nm
Solanum dulcamara	108.41^{***}	$9.22^{*,\mathrm{NS}}$	$10.43^{**,\mathrm{NS}}$	$9.18^{*,\mathrm{NS}}$	−ive***
Solanum nigrum	183.45^{***}	$.71^{\mathrm{NS}}$	$.98^{\mathrm{NS}}$	$.73^{\mathrm{NS}}$	−ive***
Solanum sarrachoides	161.98^{***}	69.57^{***}	64.69^{***}	68.48^{***}	
Umbelliferae:					
Aethusa cynapium	282.30^{***}	282.30^{***}	$8.70^{*,\mathrm{NS}}$	23.08^{***}	+ive***
Angelica sylvestris	56.47^{***}	$.83^{\mathrm{NS}}$	2.91^{NS}	$.07^{\mathrm{NS}}$	−ive***
Anthriscus caucalis	$8.65^{*,\mathrm{NS}}$	$8.65^{*,\mathrm{NS}}$	$7.41^{*,\mathrm{NS}}$	16.61^{***}	const$^{*,\mathrm{NS}}$(−ive)
Anthriscus sylvestris	$.73^{\mathrm{NS}}$				const$^{*,\mathrm{NS}}$(−ive)
Chaerophyllum temulentum	$9.06^{**,\mathrm{NS}}$	1.88^{NS}		2.95^{NS}	−ive$^{*,\mathrm{NS}}$
Conium maculatum	7.03^{NS}	2.08^{NS}	2.73^{NS}	4.41^{NS}	const$^{*,\mathrm{NS}}$(−ive)
Daucus carota	33.45^{***}	33.45^{***}	$14.99^{***,\mathrm{NS}}$	5.30^{NS}	nm
Heracleum sphondylium	3.22^{NS}	$4.33^{*,\mathrm{NS}}$	$5.43^{*,\mathrm{NS}}$	3.56^{NS}	const, −ive
Sison amomum	$12.22^{**,\mathrm{NS}}$	$12.22^{**,\mathrm{NS}}$	4.05^{NS}	$9.61^{**,\mathrm{NS}}$	+ive$^{**,\mathrm{NS}}$
Torilis japonica	235.75^{***}	235.75^{***}	142.65^{***}	43.61^{***}	
Urticaceae:					
Urtica dioica	37.60^{***}	3.22^{NS}	$6.28^{*,\mathrm{NS}}$	$.62^{\mathrm{NS}}$	−ive***
Urtica urens	60.87^{***}	$8.31^{*,\mathrm{NS}}$	$9.06^{*,\mathrm{NS}}$	$10.31^{**,\mathrm{NS}}$	−ive***
Violaceae:					
Viola arvensis	5.17^{NS}	3.08^{NS}	1.94^{NS}	$9.22^{**,\mathrm{NS}}$	const$^{\mathrm{NS}}$

NOTE.—Parameters are χ^2. The first superscript of the χ^2 value gives the significance level for a single test, and the second is the significance level corrected for the number of times the distribution was fitted. For the hazard, *const* indicates a constant hazard, −*ive* indicates a decreasing hazard, +*ive* indicates an increasing hazard, and *nm* indicates a nonmonotonic hazard; the superscripts indicate the significance level based on a likelihood ratio test: the first figure is for a single test, and the second corrected for the number of likelihood ratio tests performed. Only one figure is given when the single test and corrected significance level are the same. When the likelihood ratio test indicated a constant or a nonconstant hazard depending on the significance level chosen, the nonconstant hazard is given in parentheses.

APPENDIX C

EFFECT OF UNOBSERVED VARIABILITY ON RECRUITMENT

Here we look at the effects of adding unobserved variability to populations in which the individual-level hazard is either constant or decreasing. We first establish some notation. Suppose recruitment times are distributed with cumulative distribution function $F(\underline{x}, t)$ and probability density function (PDF) $f(\underline{x}, t)$, where $\underline{x}$ is a vector of parameters. Then write

$$\begin{aligned} z(\underline{x}, t) &= 1 - F(\underline{x}, t), && \geq 0 \\ z'(\underline{x}, t) &= -f(\underline{x}, t), && < 0 \; \forall \, \underline{x}, t \\ z''(\underline{x}, t) &= -f'(\underline{x}, t). \end{aligned}$$

The conditional or individual-level hazard function is defined by

$$\begin{aligned} h(\underline{x}, t) &= \frac{f(\underline{x}, t)}{1 - F(\underline{x}, t)} \\ &= \frac{-z'(\underline{x}, t)}{z(\underline{x}, t)}, \end{aligned}$$

and its derivative is given by the following expression:

$$h'(\underline{x}, t) = \frac{1}{z(\underline{x}, t)^2}[z'(\underline{x}, t)^2 - z(\underline{x}, t)z''(\underline{x}, t)]. \tag{C1}$$

If $\underline{x}$ is distributed according to the PDF $q(\underline{x})$ then the unconditional distribution of recruitment times has PDF

$$\phi(t) = \int_{\underline{x} \in X} f(\underline{x}, t) q(\underline{x}) \, d\underline{x},$$

where X is the set of all possible parameters. The cumulative distribution function is

$$\begin{aligned} \Phi(t) &= \int_0^t \int_{\underline{x} \in X} f(\underline{x}, t) q(\underline{x}) \, d\underline{x} \, dt = \int_{\underline{x} \in X} \int_0^t f(\underline{x}, t) q(\underline{x}) \, dt \, d\underline{x} \\ &= \int_{\underline{x} \in X} F(\underline{x}, t) q(\underline{x}) \, d\underline{x}. \end{aligned}$$

The unconditional or population-level hazard, $H(t)$, is then given by

$$H(t) = \frac{-\int_{\underline{x} \in X} z'(\underline{x}, t) q(\underline{x}) \, d\underline{x}}{\int_{\underline{x} \in X} z(\underline{x}, t) q(\underline{x}) \, d\underline{x}}.$$

Function $H'(t)$ can be evaluated by differentiating through the integral providing $q(\underline{x})$ has finite variance (Weir 1973), giving

$$\begin{aligned} H'(t) = \frac{1}{\left[\int_{\underline{x} \in X} Z(\underline{x}, t) q(\underline{x}) \, d\underline{x}\right]^2} \Bigg\{ &\left[\int_{\underline{x} \in X} z'(\underline{x}, t) q(\underline{x}) \, d\underline{x}\right]^2 \\ &- \int_{\underline{x} \in X} z''(\underline{x}, t) q(\underline{x}) \, d\underline{x} \int_{\underline{x} \in X} z(\underline{x}, t) q(\underline{x}) \, d\underline{x} \Bigg\}. \end{aligned} \tag{C2}$$

THEOREM. If $h'(\underline{x}, t) = 0 \; \forall \; \underline{x} \in X$, t and $\underline{x}$ is distributed according to PDF $q(\underline{x})$ then the resulting unconditional or population level hazard is decreasing.

Proof. From equation (C1)

$$\begin{aligned} h'(\underline{x}, t) = 0 &\Rightarrow z(\underline{x}, t)z''(\underline{x}, t) = z'(\underline{x}, t)^2 \\ &\Rightarrow z''(\underline{x}, t) > 0 . \end{aligned}$$

Now by Cauchy-Schwartz inequality (Feller 1966) $E(XY)^2 \leq E(X^2)E(Y^2) \; \forall \; X, Y$ random variables. Therefore

$$\begin{aligned} E[z(\underline{x}, t)]E[z''(\underline{x}, t)] &\geq E[\sqrt{z(\underline{x}, t)z''(\underline{x}, t)}]^2 \\ &\geq E[|z'(\underline{x}, t)|]^2 \\ &\geq E[z'(\underline{x}, t)]^2 . \end{aligned}$$

Using this result in equation (C2) demonstrates that $H'(t) < 0$, indicating that the unconditional or population-level hazard is decreasing.

THEOREM. If $h'(\underline{x}, t) < 0 \; \forall \; \underline{x} \in X$, t and $\underline{x}$ is distributed according to PDF $q(\underline{x})$ then the resulting hazard is also decreasing.

Proof. From equation (C1)

$$\begin{aligned} h'(\underline{x}, t) < 0 &\Rightarrow z(\underline{x}, t)z''(\underline{x}, t) > z'(\underline{x}, t)^2 \\ &\Rightarrow z''(\underline{x}, t) > 0 . \end{aligned}$$

The individual hazards are all decreasing then $z(\underline{x}, t)$, $z''(\underline{x}, t) \geq 0$. Therefore applying the Cauchy-Schwartz inequality we obtain

$$\begin{aligned} E[z(\underline{x}, t)]E[z''(\underline{x}, t)] &\geq E[\sqrt{z(\underline{x}, t)z''(\underline{x}, t)}]^2 \\ &\geq E[|z'(\underline{x}, t)|]^2 \\ &\geq E[z'(\underline{x}, t)]^2 . \end{aligned}$$

Using this result in equation (C2) demonstrates that $H'(t) < 0$, indicating that the unconditional or population-level hazard is decreasing. Combining these two results shows that if the individual-level hazard is either constant or decreasing or any combination of constant and decreasing, then the population-level hazard is always decreasing.

LITERATURE CITED

Begon, M., and M. Mortimer. 1981. Population ecology: a unified approach of animals and plants. Blackwell, Oxford.

Bergelson, J., and R. Perry. 1989. Interspecific competition between seeds: relative planting date and density affect seedling emergence. Ecology 70:1639–1644.

Chepil, W. S. 1946. Germination of weed seeds. I. Longevity, periodicity of germination and vitality of seeds in cultivated soil. Scientific Agriculture 26:307–346.

Cook, R. 1980. The biology of seeds in the soil. Pages 107–129 *in* O. T. Solbrig, ed. Demography and evolution in plant populations. Blackwell, Oxford.

Cox, D. R. 1979. A note on the graphical analysis of survival data. Biometrika 66:188–190.

Cox, D. R., and D. V. Hinkley. 1968. A note on the efficiency of least-squares estimates. Journal of the Royal Statistical Society B 30:284–289.

Cox, D. R., and D. Oakes. 1984. Analysis of survival data. Chapman & Hall, London.

Edwards, A. W. F. 1972. Likelihood. Cambridge University Press, Cambridge.

Elandt-Johnson, R. C., and N. L. Johnson. 1980. Survival models and data analysis. Wiley, Chichester.

Feller, W. 1966. An introduction to probability theory and its applications. Vol. 2. Wiley, London.

Fenner, M. 1985. Seed ecology. Chapman & Hall, London.

Gorski, T. 1975. Germination of seeds in the shadow of plants. Physiologia Plantarum 34:342–346.

Graham, D. J., and M. J. Hutchings. 1988. A field investigation of germination from the seed bank of a chalk grassland ley on former arable land. Journal of Applied Ecology 25:253–264.

Harper, J. L. 1977. Population biology of plants. Academic Press, London.

Hoem, J. M. 1990. Identifiability in hazard models with unobserved heterogeneity: the compatibility of two apparently contradictory results. Theoretical Population Biology 37:124–128.

Hougaard, P. 1984. Life table methods for heterogeneous populations: distributions describing the heterogeneity. Biometrika 71:75–83.

Inouye, R. S. 1980. Density-dependent germination response by seeds of desert annuals. Oecologia (Berlin) 46:235–238.

King, T. J. 1975. Inhibition of seed germination under leaf canopies in *Arenaria serpyllifolia, Veronica arvensis* and *Cerastium holosteoides*. New Phytologist 75:87–90.

Linhart, Y. B. 1976. Density dependent seed germination strategies in colonising versus non-colonising plant species. Journal of Ecology 64:375–380.

Linhart, Y. B., and R. A. Pickett. 1973. Physiological factors associated with density dependent seed germination in *Boisdwallia glabella* (Onagracaea). Zeitschrift für Pflanzenphysiologie 70:367–370.

Lonsdale, W. M. 1989. Interpreting seed survivorship curves. Oikos 52:361–364.

Nelder, J. A., and R. Mead. 1965. A simplex method of function minimisation. Computer Journal 7:308–312.

Pacala, S. W. 1986. Neighborhood models of plant population dynamics. IV. Single-species and multi-species models of annuals with dormant seeds. American Naturalist 128:859–878.

Palmblad, I. G. 1968. Competition in experimental populations of weeds with emphasis on the regulation of population size. Ecology 39:26–34.

Qadir, S. A., and M. Abbasi. 1971. Chemical interactions between seeds of common plants. Pakistan Journal of Scientific and Industrial Research 14:211–218.

Rees, M., and M. J. Long. 1992. Germination biology and the ecology of annual plants. American Naturalist 139:484–508.

Rice, K. J. 1985. Responses of Erodium to varying microsites: the role of germination cueing. Ecology 66:1651–1657.

Roberts, H. A. 1962. Studies on the weeds of vegetable crops. II. Effects of six years of cropping on the weed seeds in the soil. Journal of Ecology 50:803–813.

———. 1963. The problem of weed seeds in the soil. Pages 73–82 *in* E. K. Woodford, ed. Crop production in a weed-free environment. Blackwell, Oxford.

———. 1964. Emergence and longevity in cultivated soil of seeds of some annual weeds. Weed Research 4:296–307.

———. 1979. Periodicity of seedling emergence and seed survival in some Umbelliferae. Journal of Applied Ecology 16:195–201.

———. 1986. Seed persistence in the soil and seasonal emergence in plant species from different habitats. Journal of Applied Ecology 23:639–656.

Roberts, H. A., and J. E. Boddrell. 1983. Seed survival and periodicity of seedling emergence in eight species of Cruciferae. Annals of Applied Biology 103:301–309.

Roberts, H. A., and P. A. Dawkins. 1967. Effect of cultivation on the numbers of viable weed seeds in soil. Weed Research 7:290–301.

Roberts, H. A., and P. M. Feast. 1972. Fate of seeds of some annual weeds in different depth of cultivated and undisturbed soil. Weed Research 12:316–324.

———. 1973. Emergence and longevity of seeds of annual weeds in cultivation and undisturbed soil. Journal of Applied Ecology 10:133–143.

Roberts, H. A., and J. E. Neilson. 1980. Seed survival and periodicity of seedling emergence in some species of *Atriplex, Chenopodium, Polygonum* and *Rumex*. Annals of Applied Biology 94:111–120.

Sarukhan, J., and J. L. Harper. 1973. Studies on plant demography: *Ranunculus repens* L., *R.*

bulbosus L. and ***R.*** *acris* L. I. Population flux and survivorship. Journal of Ecology 61:675–716.

Silvertown, J. W. 1984. Phenotypic variety in seed germination behavior: the ontogeny and evolution of somatic polymorphism in seeds. American Naturalist 124:1–16.

———. 1987. Introduction to plant population ecology. Longman, London.

Southwood, T. R. E. 1978. Ecological methods with particular reference to the study of insect populations. Chapman & Hall, London.

Templeton, A. R., and D. A. Levin. 1979. Evolutionary consequences of seed pools. American Naturalist 114:232–249.

Vaupel, W. V. 1990. Relatives' risks: frailty models of life history data. Theoretical Population Biology 37:220–234.

Vaupel, W. V., and A. I. Yashin. 1983. The deviant dynamics of death in heterogeneous populations. RR-83-1, International Institute for Applied Systems Analysis. Laxenburg, Austria.

Vaupel, W. V., K. G. Manton, and E. Stallard. 1979. The impact of heterogeneity in individual frailty on the dynamics of mortality. Demography 16:439–454.

Venable, D. L. 1989. Modeling the evolutionary ecology of seed banks. Pages 67–87 *in* M. A. Leck, V. T. Parker, and R. L. Simpson, eds. Ecology of soil seed banks. Academic Press, London.

Watkinson, A. R. 1986. Plant population dynamics. Pages 137–184 *in* M. J. Crawley, ed. Plant ecology. Blackwell, Oxford.

Weir, A. J. 1973. Lebesgue integration and measure. Cambridge University Press, Cambridge.

Werner, P. A. 1975. A seed trap for determining patterns of seed deposition in terrestrial plants. Canadian Journal of Botany 53:810–813.

Associate Editor: Stephen W. Pacala