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Elasticity Analyses, and Seed Bank Effects**

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DEMOGRAPHY OF AN AGE-STRUCTURED ANNUAL: RESAMPLED PROJECTION MATRICES, ELASTICITY ANALYSES, AND SEED BANK EFFECTS¹

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Abstract. The role of age-structured seed banks in influencing population dynamic parameters was investigated in a natural population of the winter annual *Collinsia verna*. Seed persistence was quantified by creating experimental seed banks in the field with seeds of known age. Survival and fecundities of adult plant stages were determined in quadrats of naturally occurring individuals in the field population. Bootstrapping was applied to the resulting data set to estimate means and 95% confidence intervals for population growth rate, stable age distributions, reproductive values, and elasticities. Analyses were performed to determine the extent of variation in these demographic parameters between two consecutive years and between three transects within each year. The results indicate that the presence of a seed bank, even of short duration, was critical to the demography of this population. The population was expanding rapidly in the 1st yr of the study (growth rate 1.80), but was declining during the 2nd yr (0.41). While the seed bank was demographically important in some transects during the good year (Year 1), the demographic effects of the seed bank were seen most significantly in the poor year (Year 2). The results of this study indicate the need for including age-structured seed banks in demographic analyses and the potential importance of seeds in age-structured seed banks in the shaping of plant life histories.

Key words: *bootstrapping; Collinsia verna; elasticity analysis; life history; population dynamics; projection matrices; seed bank; seed carry-over; seed persistence; spatiotemporal variation; stage/age structure.*

INTRODUCTION

The role of age structure in the ecological and evolutionary dynamics of populations continues to be a central issue in population biology. Changes in age structure and/or population size can significantly influence both the demography and the genetic equilibrium of a population (Charlesworth 1980). In annual plants, age structure can result from long-term persistence in the seed bank (seed survival without emergence), because emerging plants were produced in different generations (Schmidt and Lawlor 1983). To understand the potential effect of seed banks on annual plant demography, consider the impact of delayed reproduction. Seeds in a seed bank are analogous to an extended juvenile period in other organisms. Both result in delayed reproduction and significantly affect the intrinsic rate of increase of a population (Cole 1954). Harper and White (1974), Sarukhan and Gadgil (1974), Harper (1977), and Charlesworth (1980) discuss the

necessity and complexity of the inclusion of both the population of vegetative individuals and the populations of seeds of various ages in demographic models. Neglecting seed bank dynamics can lead to erroneous estimates of the intrinsic rate of increase of a population and the stable age distribution.

Many models have been developed to investigate the evolution of seed banks and the influence of seed banks on both the population dynamics and on the evolutionary process. Cohen (1966, 1967) explored the circumstances that would select for the evolution of a seed bank. His models predicted that the long-term growth rate of a population in a randomly varying environment would be optimized through the evolution of delayed germination. A predictable environment would select for nondormant seeds and a loss of the seed bank. MacDonald and Watkinson (1981) modeled the influence of seed banks on the return to equilibrium values after a disturbance. They found that seed banks can stabilize population numbers if the number of seeds produced fluctuates from year to year: recruitment from the seed bank augments the number of adult plants in years following low seed production. A seed bank can destabilize population dynamics and

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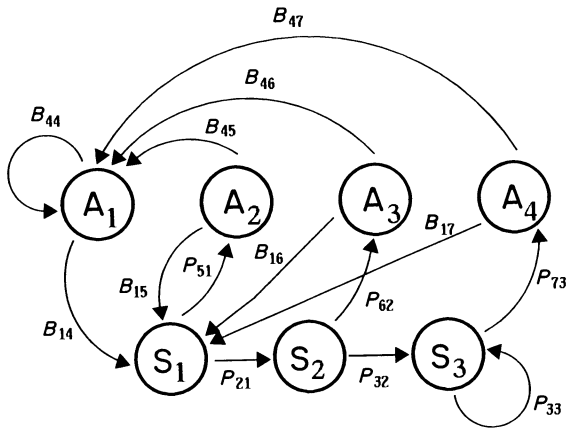


FIG. 1. Life cycle graph for the two-stage, four age-class life history of *Collinsia verna*, a winter annual. S_1 - S_3 represent seeds from 1 to 3 yr old, respectively. A_1 - A_4 represent adult plants from 1 to 4 yr old. Arrows connecting two circles (and the italic letters adjacent to them) indicate the probability of individuals at one stage passing into the next stage. The time scale for the transition between stages is 1 yr. The analysis performed in this study assumes that censuses are performed following germination of seeds in the fall.

lead to population extinction if more seeds enter the seed bank than germinate.

A number of models indicate the importance of the interaction between seed banks and the environment in influencing the evolution of plant life histories. Templeton and Levin (1979) modeled the role of seed banks in the evolution of adult plant characters, and demonstrated that seeds produced in "good" years for the adult plants come to numerically dominate the seed bank. When selection acts on adult plant characters, seed banks can retard the rate of change in adult gene frequencies by reintroducing genes and genotypes that were selectively favored in past environments. Horvitz and Schemske (1986), in a model of population dynamics for a perennial herb in a successional habitat, found that the strength of selection for seed dormancy was dependent upon the demographic sensitivity of the plant to the duration and dynamics of light gap formation. Dormancy was more important for shade-intolerant species than for shade-tolerant species. Other recent models have explored the complex relationships of seed banks to the evolution of adult traits (Ritland 1983), the joint evolution of correlated life history traits (including seed dormancy) to temporally varying environments (Brown and Venable 1986, Venable 1989), the joint optimization of dispersal and dormancy in relation to population dynamics (Levin et al. 1984, Klinkhamer et al. 1987) seasonal vs. generation dormancy (Silvertown 1988), density dependency (Leon 1985), density dependence and environmental variation (Ellner 1987), and single and multispecies models of annuals with a seed bank (Pacala 1986). Despite this strong theoretical framework, few empirical data address the dynamics of persistence in and emergence

from age-structured seed banks or measure how seed banks are related to fitness in natural populations.

This paper reports projection matrix analyses of variation in seed bank and plant dynamics and the role of spatial and temporal variation in age-structured seed bank formation for the winter annual *Collinsia verna* (Scrophulariaceae). Experimental seed banks in the field were used to directly measure the persistence in and emergence from the seed bank during a 3-yr period (Kalisz 1991). In separate quadrats, plant survivorship and fecundity were monitored over 2 yr. In this paper these demographic data (Kalisz 1991) were combined in age-structured projection matrices, and bootstrapping techniques were employed to obtain mean and variance estimates for population growth rate, stable stage/age distribution, reproductive values, and elasticities of different life history stages (de Kroon et al. 1986). Our analyses addressed three main questions: (1) Do natural spatial and temporal variation in seed bank and plant dynamics affect the estimates of population growth rate? (2) To what extent does the age structure due to seed dormancy influence estimates of population growth? (3) How important are different life history stages (e.g., seeds vs. adults) in determining fitness, as measured by population growth rate?

Our analyses indicated that the population had significantly different growth rates in different years and that the stages of the life history that were most important to determining overall population growth rate changed between years. In the first 1st yr population numbers were greatly increasing, and elasticity analysis indicated that adult survival and fecundity were the primary determinants of population growth rate. In the 2nd yr of the study, population numbers were greatly declining, and emergence from the seed bank was substantially more important to influencing overall population growth rate. In addition to this temporal variation, significant spatial variation in demographic parameters were also detected.

MATERIALS AND METHODS

Study species and life cycle graph

Collinsia verna ("blue-eyed Mary") is a winter annual of mesic eastern deciduous forests. Seeds are produced in the spring. Seeds have a high temperature afterripening requirement and lie dormant on or in the soil until autumnal temperature fluctuations cue germination (Baskin and Baskin 1983). The seeds germinate in the fall and overwinter as small plants. In the following spring plants grow rapidly, flower, fruit, and die. Details of the plant life history are given in Kalisz (1986, 1991). The research presented in this paper was conducted in a population of *C. verna* at the Raccoon Grove Forest Preserve, a virgin floodplain forest, in Will County, Illinois, USA, located ≈ 80 km south of Chicago (see Kalisz 1991 for a detailed site description).

Based on the data presented in Kalisz (1991) *C. verna* has a two-stage, age-structured life cycle (Fig. 1). Individuals are "born" when seeds are formed on the adults (not at germination). An individual in the (A) stage represents an adult plant in fruit, but prior to seed release. An individual in the (S) stage represents a seed in the seed bank. The letter A or S indicates the stage of the plant, while the numerical subscript indicates the age of the plant. For example, S_1 individuals are seeds that persisted in the seed bank for 1 yr while A_1 individuals are plants that germinated from seeds produced in the previous season. A_1 individuals are always derived from seeds produced in the previous spring. $A_2, A_3,$ and A_4 plants are derived from the seed bank from seeds produced two, three, or four springs ago, respectively. Movement from one stage/age to another along an arrow connecting two stages/ages (Fig. 1) takes place over 1 yr. The year is defined as beginning in the fall, immediately after seeds germinate. At this time only seeds in the seed bank (S) (1 yr old or older) and newly emerged seedlings (A) are in the population.

An individual in a seed stage (S) can follow one of three pathways: the seed can die, the seed can persist in the seed bank (grow older but remain a seed), or the seed can emerge and potentially become a fruiting adult. Seeds on the adult plant can have one of three fates within 1 yr. They can enter the seed bank (S_1 stage), or emerge and survive to become reproductive (A_1 stage), or die. The adult stage (A) encompasses all post-emergence developmental stages of the plant as well as reproduction. Once an individual has passed from the seed stage to the adult stage, it is constrained by its annual habit to reproduce and die. Therefore, the age of an individual, whether it is in a seed or adult stage, is determined by its duration in the seed bank. Seeds of *C. verna* can persist for at least 3 yr (Kalisz 1991). The life cycle graphs (Fig. 1) depicts the transition matrix (Table 1) used in the demographic analyses described below.

Demographic parameters

The model used in this analysis was the linear, time-invariant population projection matrix model (Caswell 1989) of the form:

$$\mathbf{x}(t + 1) = \mathbf{c}\mathbf{x}(t),$$

where $\mathbf{x}(t)$ is a vector of k stage/age classes, \mathbf{c} is a square matrix of dimension k . The elements of \mathbf{c} (i.e., c_{ij}) are transition probabilities and/or stage/age-specific fecundities that describe the generation of individuals in each class by individuals in all other classes from one projection interval to the next (i.e., 1 yr in this study). If \mathbf{c} is a constant matrix (which assumes no variation in its elements over time), iterative postmultiplication of \mathbf{c} by the population vector projects the future state of the population. The dominant eigenvalue of \mathbf{c} , λ , is the geometric growth rate of the population when the population reaches its stable distribution of stages/ages.

TABLE 1. Transition matrix for *Collinsia verna* with a 3-yr seed bank. The numerical subscript on row and column headings indicates the age of the seeds or plants in years. The matrix elements (transition probabilities) are divided into four functional groups. Transition probabilities in Group I describe the survival of seeds that remain in the seed bank. Group II transition probabilities describe emergence from the seed bank and survival of plants to fruiting. Matrix elements in Group III represent the fraction of seeds produced by adults at the end of one year that emerge and survive to flower at the end of the next year (i.e., individuals that do not enter the seed bank). Group IV matrix elements represent the fraction of seeds that enter the seed bank.

	SEED ₁	SEED ₂	SEED ₃	ADULT ₁	ADULT ₂	ADULT ₃	ADULT ₄
SEED ₁	0	0	0	B_{14}	B_{15}	B_{16}	B_{17}
SEED ₂	P_{21}	0	0	0	0	0	0
SEED ₃	0	P_{32}	P_{33}	0	0	0	0
ADULT ₁	0	0	0	B_{44}	B_{45}	B_{46}	B_{47}
ADULT ₂	P_{51}	0	0	0	0	0	0
ADULT ₃	0	P_{62}	0	0	0	0	0
ADULT ₄	0	0	P_{73}	0	0	0	0

The stable stage/age distribution (SAD) of the population is described by the right eigenvector of \mathbf{c} , \mathbf{w}_m :

$$\mathbf{c}\mathbf{w}_m = \lambda_m\mathbf{w}_m$$

and is the proportional representation of each stage/age class once the population has reached the equilibrium growth rate (Caswell 1989). The reproductive value (RV) of each stage/age class at this equilibrium growth rate is described by the left eigenvector \mathbf{v}_m :

$$\mathbf{v}_m\mathbf{c} = \mathbf{v}_m\lambda_m$$

and estimates the expected contribution of each stage/age class to population growth (Caswell 1989). Population growth rate, SAD, and RV are the primary descriptors of the future population dynamics of conditions remain constant.

Since the c_{ij} 's are quantitative descriptors of the life history of an organism, identifying particular transitions between life cycle stages as demographically important (with respect to the action of natural selection and therefore fitness) can provide substantial insight into life history evolution (Caswell 1986). To identify important transition probabilities and stage/age-specific fecundities, we used elasticity analysis (Caswell et al. 1984, de Kroon et al. 1986, Crouse et al. 1987). The elasticity of each element, e_{ij} , is calculated as:

$$e_{ij} = \partial(\ln \lambda) / \partial(\ln c_{ij}) = (c_{ij} / \lambda) (\partial \lambda / \partial c_{ij}).$$

The e_{ij} 's quantify the relative contribution of each ma-

trix element to determining the population growth rate (de Kroon et al. 1986). Transition matrix elements with the greatest elasticity values have the greatest impact on determining population growth rate. Because the e_{ij} 's sum to one, elasticities calculated for different transition matrices that are based on the same life cycle graph can be compared to determine how changes in the magnitudes of matrix elements alter the importance of different life history stages/ages in determining population growth. We employed this feature of elasticity analyses to examine the importance of the seed bank in influencing population dynamics.

Variation in demographic parameters

Three factors influence the estimation of the mean and variance in the demographic parameters of a population. The first is the variation in survival probabilities and fecundities between individuals within a census period. All individuals in a population may not experience the same set of ecological conditions, and so may not express the same survival probabilities and fecundities, e.g., individual plants in a population may experience different microclimates that cause them to differ in survival probabilities or seed production. Also, demographic stochasticity (inherent variation in individual reproductive rates and times of death that are not due to differences in ecological conditions [Goodman 1987]) will introduce variation into the demographic parameters of a population for a given census period. Variation between census periods in the ecological conditions experienced by a population will also contribute to variation in the demographic parameters by altering the survival probabilities and fecundities from period to period (see Tuljapurkar 1989 for an extensive review of the theoretical machinery to deal with temporally varying vital rates). Finally, covariation between the elements of the transition matrix will influence the estimation of means and variances for demographic parameters. Within a census period, the survival probability and fecundity for a given stage/age may covary, and the survival probabilities and fecundities of different stages/ages may covary (e.g., if survival or fecundities of stages are dependent on the frequency or density of other stages). Also, the survival probabilities and fecundities of stages/ages could covary between census periods (Gani 1973).

Ideally, all of these potential influences on demographic parameters should be incorporated into the design of empirical studies of population demography. Variation among individuals within a census period can be incorporated by adequately sampling the population on the relevant scale of environmental variation. Variation between census periods can obviously be incorporated by sampling the population over many years (e.g., see Bierzychudek 1982). Maintaining the covariance between the survival probability and fecundity for a given stage/age class within a census period requires that both be estimated from the same set

of individuals. Maintaining the covariance between the survival probabilities and fecundities of different stages/ages within a census period requires that they be estimated from a set of individuals that are directly interacting to affect each other's vital rates. Finally, maintaining the covariance between different stages/ages across census periods requires that a cohort of individuals be followed throughout their lifetime (i.e., longitudinal censusing).

However, it is often impossible to incorporate all of these potential influences in a study, especially the maintenance of covariation structure between all survival probabilities and fecundities when studying species that have cryptic life history stages, are long lived, disperse over long distances, or are rare. Seeds in soil seed banks present especially difficult problems. Seeds that form seed banks are generally small and cryptic. Accounting for dispersal, survival, emergence, or death of individual seeds in soil seed banks has never been achieved: following the rates of individual seeds and the plants that emerge from them is impossible in the field without significantly disturbing the rest of the system and totally altering the demography of the population following such disturbance. Radiolabeling technology for locating individual seeds (sensu Winn 1989) is not applicable to long-term studies of seed banks.

Because of the presence of the seed bank, all survival probabilities and fecundities for *Collinsia verna* (Table 1) in this study could not be estimated from the same set of individuals. In this study we estimated survivorships and fecundities using data collected by stage: seed or adult plant. The data collection scheme was organized around three 75-m transects in the population (a more detailed description of the sampling methods is given in Kalisz 1991). The demography of adult plants was quantified along each transect in 25 permanently marked quadrats (40 × 40 cm). In each of two consecutive years (1982–1983 and 1983–1984) the fates of all seedlings emerging in roughly half of the quadrats along each transect were scored for their survival to fruit set and the number of seeds produced by surviving individuals. These data were used to quantify the probability of survival to fruit set (which we will designate as S), and the fecundity of surviving plants (F) during each of the two years of the study (hereafter referred to as Year 1 and Year 2). The number of quadrats sampled on Transects 1–3 for Year 1 (1982–1983) were 11, 10, and 12, respectively, and for Year 2 (1983–1984) were 12, 15, and 13, respectively, and sample sizes per quadrat are as follows (number of seedlings initially present per quadrat [mean ± 1 SD]: Year 1: Transect 1, 211.2 ± 106.4, Transect 2, 251.1 ± 112.7, Transect 3, 95.9 ± 59.1; Year 2: Transect 1, 165.1 ± 156.7, Transect 2, 170.5 ± 185.3, Transect 3, 111.8 ± 89.5. This sampling design allowed us to incorporate spatial and temporal variation in survival probabilities and fecundities into the demographic analyses of this population and maintains any covari-

ation between these two parameters by estimating both from the same set of individuals.

The survival, persistence, and emergence of seeds in the soil seed bank were estimated along these same three transects using experimentally constructed seed banks (see Kalisz 1991 for a detailed description). Experimental seed bank cages were constructed of fiberglass window screen (1 mm² mesh size), and contained autoclaved soil (to kill any existing seeds) from the field site and introduced *C. verna* seeds. Experimental seed banks were established in 1982 and set up again in 1983. In the fall of 1982, 12 experimental seed banks were embedded in the soil along each of the three transects (36 total cages), and 125 seeds were added to each cage. The number of seeds germinating during the first fall were quantified in each of these experimental seed banks to estimate the probability that seeds germinate without entering the seed bank (G1) for Year 1. Six of the experimental seed banks were destructively sampled from each transect in the spring of 1983 to determine the viability of the remaining seeds, and these data were used to estimate the probability of seeds entering the seed bank (D1) during Year 1. The remaining six experimental seed banks in each transect were used to quantify the number of seeds that germinate in the 3rd yr after their production (G3), and were destructively sampled in 1985 to estimate the probability of seeds remaining dormant from Age 2 to Age 3 (D3). Because replicate data were not obtained for each year of the study, these data (G3 and D3) were used in analyses described below for both years.

In the spring of 1983, six additional experimental seed banks were embedded in the soil along each of the three transects (36 total cages), and 300 seeds were added to each cage. The number of seeds germinating during the first fall were quantified in each of these experimental seed banks to estimate the probability that seeds germinate without entering the seed bank (G1) for Year 2. Three of the experimental seed banks were destructively sampled from each transect in the spring of 1984 to determine the viability of the remaining seeds, and these data were used to estimate the probability of seeds entering the seed bank (D1) during Year 2. The remaining three experimental seed banks in each transect were used to quantify the number of seeds that germinate after being in the seed bank for 1 yr (G2), and were destructively sampled in 1985 to estimate the probability of seeds remaining dormant in the seed bank from Age 1 to Age 2 (D2). Because replicate data were not obtained for each year of the study, these data (G2 and D2) were used in analyses described below for both years. This sampling design for the seed bank allowed us to incorporate spatial and temporal variation in dormancy and germination probabilities into the demographic analyses of this population and maintains any covariation between the dormancy and germination probabilities for a given age of seeds. However, we were unable to maintain the

covariation among these probabilities between census periods, or to generate replicate estimates in each year for long-term persistence in or emergence from the seed bank. Interpretation of the following analyses therefore assumes that these are not critical components in determining the variation in the demographic parameters of this population.

These estimates of survival and dormancy probabilities for seeds and survival probabilities and fecundities for adults were used to construct transition matrices to describe the demography of the *C. verna* population during the 2 yr of this study (Table 1). The elements in the matrix were calculated as follows: P_{21} , P_{32} , and P_{33} are the probabilities of seeds persisting in the seed bank for another year given that the seed survived to that age (i.e., remaining in the seed stage but aging), where $P_{21} = D2$, $P_{32} = D3$, and $P_{33} = D3$. P_{33} represents a carry-over loop by which some seeds can remain in the seed bank for >3 yr. P_{51} , P_{62} , and P_{73} are the probabilities of germinating from the seed bank for seeds that have been in the seed bank for 1, 2, and 3 or more years, respectively, where $P_{51} = G2$, $P_{62} = G3$, and $P_{73} = G3$. The same data were used for both years to derive these matrix elements (P_{21} , P_{32} , P_{33} , P_{51} , P_{62} , P_{73}) in analyses described below. B_{14} , B_{15} , B_{16} , and B_{17} are the joint (probability of a plant surviving from a seedling to fruit set) \times (fecundities of adult plants that emerged from seeds 0 to 3 yr of age, respectively) \times (probability that a seed produced by that adult will enter the seed bank). In our analyses we assume that adult plants of different ages all have the same survival probabilities and expected fecundities, and seeds produced by plants of different ages have the same probability of entering the seed bank in a given year: i.e., $B_{14} = B_{15} = B_{16} = B_{17} = S \cdot F \cdot D1$. B_{44} , B_{45} , B_{46} , and B_{47} are the joint (probability of a plant surviving from a seedling to fruit set) \times (fecundities of adult plants that emerged from seeds 0 to 3 yr of age, respectively) \times (probability that a seed produced by that adult will germinate directly the following fall). In our analyses we also assume that seeds produced by plants of different ages have the same probability of directly germinating in a given year: i.e., $B_{44} = B_{45} = B_{46} = B_{47} = S \cdot F \cdot G1$. Means and ranges of these probabilities and fecundities are presented in Kalisz (1991: Tables 3–6).

We applied bootstrapping methods (Efron 1982, Lenski and Service 1982, Caswell 1989) to this data set to estimate means and confidence intervals for the demographic parameters of this population during the 2 yr of this study. Separate analyses were performed for each year. Data for the survival (S) and fecundity (F) of adults, and the fraction of the population germinating (G1) and remaining dormant (D1) for Age 1 seeds were available for each year. However, analyses for both years used the same data on the fraction of the population germinating (G2 and G3) and remaining dormant (D2 and D3) for Age 2 and 3 seeds. Anal-

TABLE 2. Population growth rate estimates from bootstrapped analyses of data for each year and for each of the three transects within years when the seed bank was included in the life cycle (A). Population growth rates for each year are also presented when the seed bank was deleted from the life cycle (B).

A) Seed bank included in life cycle			
		Population growth rates	
	Statistic	Year 1	Year 2
Overall	Mean	1.80	0.41
	95% CI	1.72-1.97	0.37-0.44
Transect 1	Mean	2.24	0.40
	95% CI	2.05-2.49	0.37-0.46
Transect 2	Mean	1.13	0.30
	95% CI	1.06-1.40	0.25-0.34
Transect 3	Mean	2.56	0.45
	95% CI	2.23-2.94	0.41-0.55

B) Seed bank deleted from the life cycle			
		Population growth rates	
	Statistic	Year 1	Year 2
Overall	Mean	1.72	0.32
	95% CI	1.63-1.89	0.28-0.35

yses using the data for all three transects were performed for each year to describe total population demography in each of the two years (Overall analysis), as well as separate analyses for each transect to examine the extent of spatial variation in demography within the population in each year (Transect analyses).

Bootstrap resampling methods were applied to each level of analysis in the following manner. First, the data on all relevant quadrats and experimental seed banks for that level of analysis were included in a base data set. We then resampled individuals from this base data set with replacement in an identical fashion to the original field sampling program to create a new bootstrapped data set. Specifically, a number of individuals equal to the total number of individuals present in the original data set for a quadrat was drawn with replacement from the original data for that quadrat, and these individuals constituted the bootstrapped sample of individuals for that quadrat. Because individuals are drawn with replacement, some individuals were drawn multiple times for the bootstrapped data set and others were not drawn. After a bootstrapped sample of individuals had been drawn from all relevant quadrats and experimental seed banks, adult survival probabilities and fecundities, dormancy and germination probabilities were calculated for the bootstrapped data set, a transition matrix was generated from these, and demographic parameters (lambda, stable stage/age distribution, reproductive values, and elasticities) were calculated for the transition matrix according to the methods of Caswell (1989). For each level of analysis, 1000 bootstrapped data sets were generated, and these data sets were used to estimate the means (after re-

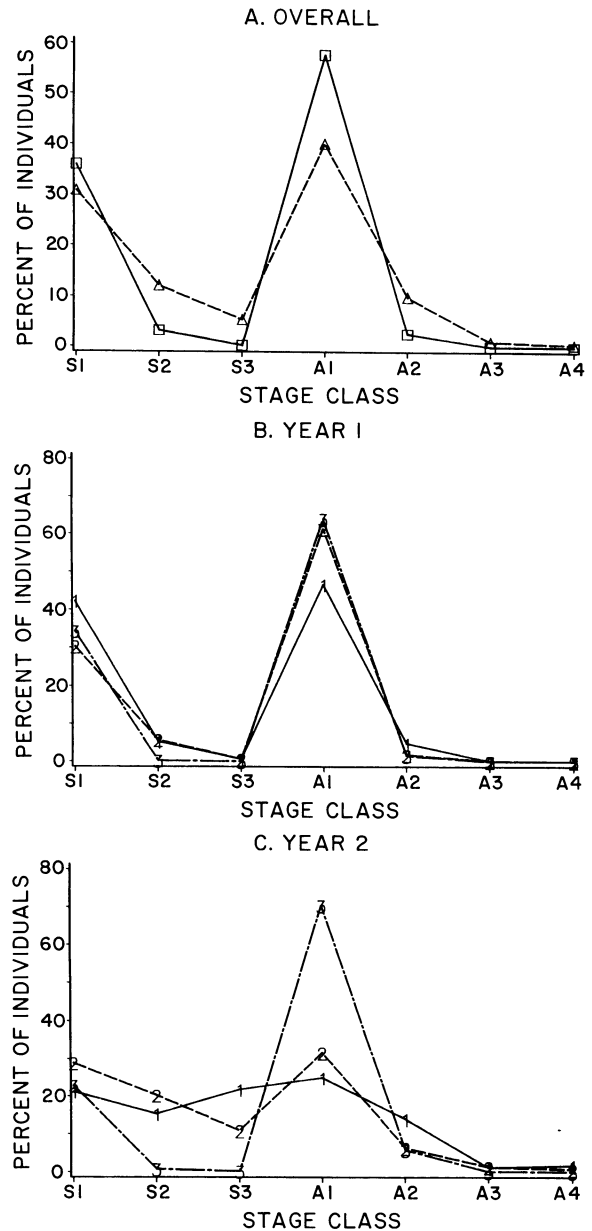


FIG. 2. Stable stage/age distributions of seed (S) and adult (A) classes for *Collinsia verna*. In (A), \square and — present the overall data for Year 1, and Δ and --- present the overall data for Year 2. In (A) the 95% CIs for every stage/age class in the 2 yr did not overlap. In (B) and (C) the transects are identified by numbers (Transect 1—1's and —, Transect 2—2's and --- lines, Transect 3—3's and ----). For Year 1 the 95% CIs indicated significant differences as follows: Transect 1 was significantly different from Transects 2 and 3, which were not significantly different, for S₁, A₁, A₂, A₃, and A₄; Transect 3 was significantly different from Transects 1 and 2, which were not significantly different, for S₂ and S₃. For Year 2 the 95% CIs indicated significant differences as follows: Transect 1 was significantly different from Transects 2 and 3, which were not significantly different, for A₂; Transect 3 was significantly different from Transects 1 and 2, which were not significantly different, for S₃, A₁, A₃, and A₄; All three transects were significantly different for S₂; All three transects were the same for S₁.

moving the inherent bias in bootstrapped mean estimates) and 95% confidence intervals for the demographic parameters. Confidence intervals were calculated by the percentile method (Efron and Tibshirani 1986, Caswell 1989). All statements concerning statistical significance are based on comparisons of these 95% confidence intervals.

RESULTS

Temporal variation

The estimates of the population growth rate, stable stage/age distribution, (SAD) and reproductive value (RV) from the bootstrapped projection matrix analysis for the total population differed dramatically between years. The growth rate for the total population indicated that the population was increasing during the 1st yr of the study but was declining during the 2nd yr of the study, and population growth rates in the 2 yr differed greatly (Table 2). Clearly, Year 1 was a good year and Year 2 was a poor year for the *C. verna* population.

When the seed bank was not included in the model (i.e., a true annual life cycle was assumed) the bootstrapped mean population growth rate for Year 1 was not different from the estimate derived when the seed bank is included, but the bootstrapped mean population growth rate for Year 2 was significantly lower than the estimate derived when the seed bank is included (Table 2).

The proportional representation of the stage/age classes in the bootstrapped stable stage/age distributions (SAD) differed significantly between the years as a result of between-year differences in persistence, emergence, survival, and fecundity (Fig. 2A). Overall in the SAD for Year 1, 39.5% of the population were in the S_1 - S_3 seed classes, and 57.8% were in the A_1 adult class. In Year 2, the poor year, the overall representation in the SAD for the seed bank increased: 48.3% of the population were in the S_1 - S_3 seed classes, while 40.2% of the population were in the A_1 adult class. The 95% confidence intervals for every stage/age class in the 2 yr did not overlap.

The RVs of the adult stage/age classes for the total population were significantly greater than the RVs of the seed classes in both years (Fig. 3A). The RV for the adult age classes differed significantly between the two years, but the seed classes did not. The RVs of the adult classes were higher in Year 1 than in Year 2.

Spatial variation

The three transects represented significantly different demographic environments for *Collinsia verna* within each year (Kalisz 1991), which resulted in large differences in the transect-level means of population growth, SAD, and RV. In both years, Transect 2 had a lower population growth rate than the other two transects, and Transects 1 and 3 were not different (Table 2).

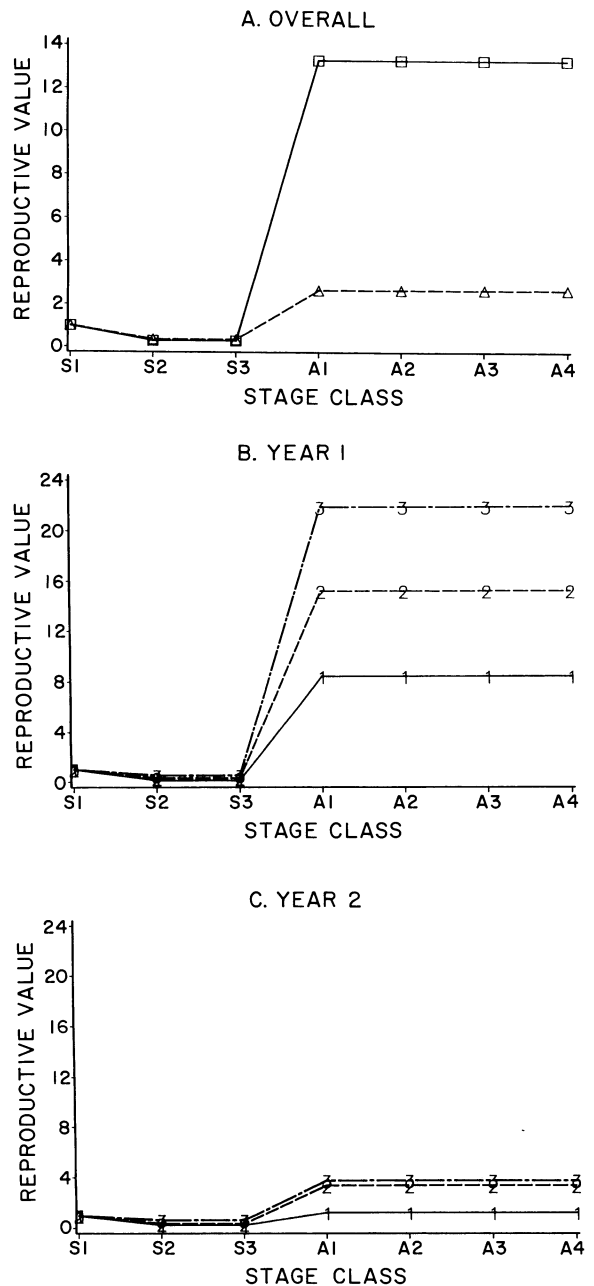


FIG. 3. Reproductive values for seed (S) and adult (A) classes for *Collinsia verna*. In (A), \square and — present the overall data for Year 1, and \triangle and --- present the overall data for Year 2. In (A) the 95% cis for the adult classes did not overlap, but the seed classes did not. In (B) and (C) the transects are identified by numbers (Transect 1—1's and —, Transect 2—2's and --- lines, Transect 3—3's and ----). In (B) and (C) the 95% cis indicated significant differences as follows: Transect 1 was significantly different from Transects 2 and 3, which were not significantly different, for the adult stage/age classes. The three transects did not differ for the seed classes.

TABLE 3. Summed elasticities for each stage/age class in each year. Data for the total population are presented with 95% confidence intervals in parentheses, with the range of values from the three transects given below each.

Stage/age class		Year 1		Year 2
S ₁	Overall	4.3%	(3.7–5.1%)	17.5% (16.1–19.5%)
	Transects		2–9%	7–26%
S ₂	Overall	0.1%	(0.07–0.1%)	2.4% (1.7–3.5%)
	Transects		0–0%	0–5%
S ₃	Overall	0.008%	(0.005–0.01%)	1.1% (0.7–1.8%)
	Transects		0–0%	0–2%
A ₁	Overall	91.3%	(89.7–92.4%)	61.5% (56.3–64.8%)
	Transects		82–95%	38–86%
A ₂	Overall	4.2%	(3.6–5.0%)	15.1% (13.7–17.0%)
	Transects		2–90%	7–21%
A ₃	Overall	0.1%	(0.07–0.2%)	1.7% (1.2–2.3%)
	Transects		0–0%	0–3%
A ₄	Overall	0.008%	(0.005–0.02%)	0.7% (0.5–1.2%)
	Transects		0–0%	0–3%

Transects also differed significantly in SAD (Fig. 2B–D). In Year 1, Transect 1 had the greatest cumulative percentage of the SAD in the seed bank (48.3%), Transect 2 was intermediate (36.7%), and Transect 3 had the lowest (34.5%). In Year 2, Transects 1 and 2 had similar cumulative percentages in the seed classes (Transect 1: 58.2%, Transect 2: 59.9%), and Transect 3 was lowest (23.7%). Although all age classes except A₃ and A₄ were significantly different, the SADs for the three transects for Year 1 were quite similar. However, the SADs differed dramatically for Year 2: compared to the first year, the relative frequencies of the S₂ and S₃ classes increased significantly while the A₁ class decreased for Transects 1 and 2, while the opposite was true for the relative frequencies on Transect 3.

The RVs for the transects (Fig. 3B–D) exhibited variation around the general pattern seen in the analysis of the total population. The magnitudes of the RVs of the adult ages were highest in Transect 3 for both years. The RVs for the S₂ and S₃ seed classes were not significantly different between the 2 yr, and were <1.0 for all transects in both years.

Elasticity analyses

The relative importance of the transitions between different stage/age classes in influencing the population growth rate is indicated by the magnitude of their elasticity values. As stated by de Kroon et al. (1986) "... the relative contribution of a single pathway to the population growth rate is always the same, regardless of the point in the life cycle where it is measured. Since any stage is only a junction of pathways, the total contribution of the inputs to a stage equals the total contribution of its outputs." Therefore, the row or column sums of the elasticity matrix can be used to examine the overall impact that each life history stage/age has on determining overall population growth rates. The column and the row sums for the elasticity matrices

were equal within rounding error. Summed elasticities associated with the stage/age classes ranged from <<1% to >90% (Table 3). Overall in Year 1, the A₁ class had the highest summed elasticity of any in the life cycle (Table 3); no other stage/age class accounted for >5% of the total. However, in Year 2 the summed elasticity associated with the A₁ class dropped substantially, and the summed elasticities for all other stage/age classes increased, especially those for the seed bank classes, which all increased by at least a factor of 4 (Table 3).

The role of the seed bank can be further understood by associating the e_{ij} values to their respective arrows in the life cycle graph (Fig. 4). In Year 1, besides the A₁ to A₁ loop only 1-yr-old seeds and 2-yr-old adults had associated elasticities, which are >1% in the total population (Fig. 4A). The life cycle in the good year nearly reduces to that of a true annual plant. In contrast, all stage/age classes contributed to determining population growth rate in the total population for Year 2 (Fig. 4B). Elasticities for survival and emergence for all seed ages increased, especially for long-term survival in the seed bank.

The transects also differed in the relative importance of the life history classes to determining population growth rates (Fig. 4C–H). Transect 1 (Fig. 4C, D) had the greatest elasticity values for input into and emergence out of the seed bank and the lowest elasticities associated with the A₁ class compared to the other transects. The A₁ to A₁ transition had the highest elasticity in both years in Transect 3 (Fig. 4G–H) with only a small fraction of the total elasticity distributed over the remaining transitions. The elasticities in Transect 2 (Fig. 4E, F) were intermediate relative to Transects 1 and 3 in both years.

To further understand the demographic importance of seeds in seed banks and the contribution of the seed bank relative to adult stages/ages, the matrix of elasticity values for the total population was partitioned

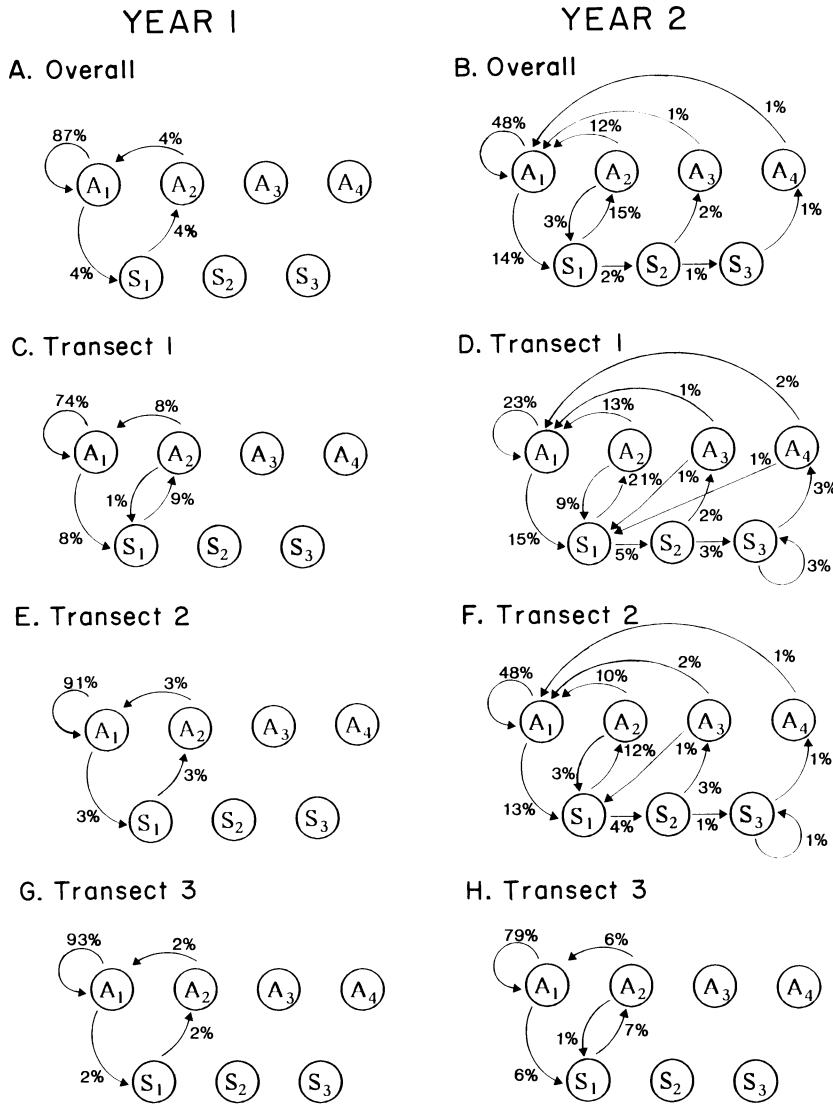


FIG. 4. Life cycle graphs with elasticity values >1% indicating transitions that have relatively large effects of population growth rates.

into four functional groups (Table 1). The elasticities in Group I reflect the transitions within the seed bank and denote the importance of changes in survival in the seed bank. Group II reflects the importance of changes in emergence from the seed bank. Group III represents changes in the fraction of seedlings that survive to fruit, the fecundity of surviving plants, and the direct development of seeds into seedlings the following year. This pathway (Group III) represents the “true annual” pathway in the life cycle of *C. verna*. Group IV represents the importance of movement of newly produced seeds into the dormant seed bank. By definition, the elasticities of groups I + II + III + IV = 100%. Table 4 summarizes these group elasticities. In the good year (Year 1), the summed elasticities for the dormant fraction of the seed bank (I) was ≈0%, the

elasticities associated with emerging from the dormant seed bank (II) and with entering the seed bank (IV) were low, and changes in survival and fecundity of plants and direct development of seeds (III) had by far the greatest summed elasticity (Table 4). In the poor year (Year 2), the importance of the seed bank pathways increased dramatically. Summed elasticities for emergence from the seed bank (II) and elasticities for entering the seed bank (IV) were over 4 times as great in Year 2 as in Year 1. Conversely, the summed elasticities for plants obtained from newly derived seeds (III) decreased by almost one-third.

DISCUSSION

The addition of seed bank age structure increases generation time, in that seed dormancy delays repro-

TABLE 4. Summed elasticities for the four functional groups defined in Table 1, for the 2 yr. Data for the total population are presented with 95% confidence intervals in parentheses, with the range of values from the three transects given below each. See Table 1 for more complete explanation of the functional groups.

Functional group		Year 1	Year 2
I	Seeds remaining in the seed bank	Overall Transects	Overall Transects
		0.1% (0.08–0.2%) 0–0%	3.5% (2.4–5.3%) 0–11%
II	Emergence from the dormant seed bank	Overall Transects	Overall Transects
		4.3% (3.7–5.1%) 2–9%	17.5% (16.1–19.5%) 7–26%
III	Survival and fecundity of seedlings, and seeds development directly (true annuals)	Overall Transects	Overall Transects
		91.3% (89.7–92.4%) 82–96%	61.5% (56.3–64.8%) 38–86%
IV	Survival and fecundity of seedlings, and seeds enter seed bank	Overall Transects	Overall Transects
		4.3% (3.7–5.1%) 2–9%	17.5% (16.1–19.5%) 7–26%

duction for one or more years in some individuals. Theory predicts that increased generation time slows both the rate of population increase when the population is growing and the rate of population decrease when a population is in decline (Lewontin 1965, Mertz 1971). Population growth rates for *C. verna* estimated with and without the age-structured seed bank only partially supported this prediction. The estimated growth rates for the total population when the seed bank was included in the life cycle and when a true annual life cycle was assumed only differed for the year in which the population was declining (the estimate without the seed bank was significantly lower than the estimate with the seed bank included for Year 2). These results indicate the importance of quantifying seed bank age structure in demographic analyses of plant populations, especially in declining populations. For plant species that have greater seed longevity than measured in this study, even greater effects of seed age structure on population dynamics should be expected.

Variation in seed bank formation

The heterogeneity in the existence of seed bank age structure quantified in this study is the result of both temporal and spatial variation that is prevalent in natural systems. The largest differences in this study among estimates of population growth rates, RVs and SADs were between years, rather than within years. All transects had growth rates >1 in Year 1 and $\ll 1$ in Year 2. Clearly, the annual variation in adult survival and fecundity, coupled with differences in persistence and emergence (Kalisz 1991), have greater effects on estimates of population dynamics than does spatial variation. However, spatial variation in demographic parameters was prevalent in both years.

Seed banks are expected to evolve when populations experience temporal variation in the quality of the environment. Seed banks are expected to increase population growth rate when the quality of the environment improves after a period of poor environmental quality (Cohen 1966). Thus, the long-term ecological benefit of a seed bank will be to increase the persistence of a population. This occurs because individuals

emerging from the seed bank can substantially increase the growth rate of the population in years following poor survival or reproduction of adults. The frequency of good and poor years will determine the restorative power and ultimate importance of the seed bank. The duration of *C. verna* seeds in the study population was relatively short (≈ 4 yr) and fits the Type III (short-lived) seed bank description of Thompson and Grime (1979). Grime (1989) categorized the environmental conditions in which Type III and Type IV (very long-lived) seed banks are found as those "habitats subjected to temporally unpredictable disturbance." This suggests that the frequency of poor years has likely been low for this population.

A mosaic seed bank exists in this population with areas of high and low seed persistence, seed mortality, and/or emergence. Soil cores ($n = 150$, total area sampled 4.98 m²) taken in the field site in the spring prior to seed release (S. Kalisz, unpublished data) indicated that dormant seeds were very patchy in their distribution, ranging from 0 to 23 seeds per core. Forty-nine percent of the cores had no seeds. Our demographic analyses also suggest that spatial variation in seed bank age structure significantly affected the estimates of population dynamics and age structure that should develop along the three transects (Fig. 2). Transect 3 had very little seed bank formation and the largest estimated growth rate in both years. In Transect 1, where high levels of persistence were common, seed age classes contributed significantly to local population dynamics. These results emphasize that widely different demographic results can be generated, which depend on the spatial scale of the investigation and the degree of seed bank development.

The within-year variation in transitions within the experimental seed banks (Kalisz 1991) is the result of environmental heterogeneity rather than genetic differences among the seeds. Seeds used in the experimental seed banks were a random draw from a mixture sampled from the three transects. Therefore, variation among the experimental seed banks along the three transects was not due to genetic variation associated with local selection or adaptation to the environments

of the transects. Seed bank formation was probably due to differences in microtopography, canopy cover, depth of the leaf litter layer, and the number of herbaceous plants surrounding the experimental seed banks. These aspects of the physical and biological environment influence light and moisture availability. They also may have altered the autumn diurnal temperature fluctuations at and below the soil surface that cue germination in this species (Baskin and Baskin 1983).

Elasticity analyses and life history consequences

As in most demographic analyses, the perceived effect of a stage or age on population growth rate is a composite of several transition probabilities. Predictions about the importance of the seed bank relative to adult survival and fecundity have been made by Schmidt and Lawlor (1983). They described two models for calculating population growth rates for an annual with a short-lived seed bank. Results from their analytical model (with a fixed seed decay rate) indicated that population growth rate was more sensitive to changes in the percent germinating from the seed bank than to changes in adult fecundity. In their Leslie matrix model, population growth rate was more sensitive to changes in adult fecundity than in germination from the seed bank.

The results of the present study indicate that the importance of survivorship in and germination from the age-structured seed bank relative to adult fecundity in determining population growth rate changes as a function of both temporal and spatial variation in the habitat. In both years the major determinants of population growth rate were the survival and reproduction of adults and the fraction of seeds not entering the seed bank (Group III, Table 4), which describe the "true annual" pathway of the life cycle. In the good year, this "true annual" pathway accounted for >90% of the elasticity in population growth rate. However, in the poor year the importance of the "true annual" pathway decreased, and the summed elasticity values for the other three pathways associated with aspects of the seed bank all increased by more than fourfold (Table 4). Substantial variation between transects also existed in the summed elasticities with each year.

The models of Schmidt and Lawlor (1983) also assume that the survivorship and fecundities of the different-aged plants do not differ. As reported in Kalisz (1991) plants derived from the older seed cohort had significantly later emergence dates than did those derived from the natural seed cohort. In a field study in the same population (Kalisz 1986) emergence date was negatively correlated with both adult survival and fecundity. The presumed fitness advantage of seed-bank-derived seedlings emerging into less competitive or generally better environments may not always be true.

The influence of traits that are expressed early in the life cycle of plants (e.g., seed dormancy, seed size, or

emergence date) on life history evolution may be great. Evidence for the role of such characters in the evolution of plant life histories can be found in the study of the fitness effects of emergence date, mating system, and/or seed mass (e.g., Gross 1984, Stanton 1985, Kalisz 1986, Roach 1986, Miller 1987, Kalisz 1989, Gross and Smith 1991), and similar life history characters in organisms with egg banks (e.g., Hairston and de Stasio 1988). The action of natural selection will determine the evolution of phenotypically correlated traits that balance dormancy and survival in the seed bank with emergence and survival of juveniles. Persistence of seeds in the seed bank is an important life history trait in that it directly affects fitness (population growth rate). The fitness effects of seed or egg banks can be expected at the individual, population, and community levels. The fraction of seeds or eggs that enter the dormant bank and the genetic composition of those seeds will affect the genetic demography of a population. How natural selection acts within the life history to produce and maintain soil seed banks and the ability of species to genetically respond to natural selection remain important empirical questions.

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