American Journal of Botany 93(6): 891–902. 2006.

A STOCHASTIC POPULATION MODEL FOR *LEPIDIUM PAPILLIFERUM* (BRASSICACEAE), A RARE DESERT EPHEMERAL WITH A PERSISTENT SEED BANK[1]

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Population viability analysis (PVA) is a valuable tool for rare plant conservation, but PVA for plants with persistent seed banks is difficult without reliable information on seed bank processes. We modeled the population dynamics of the Snake River Plains ephemeral *Lepidium papilliferum* using data from an 11-yr artificial seed bank experiment to estimate age-specific vital rates for viability loss and germination. We related variation in postgermination demographic parameters to annual variation in precipitation patterns and used these relationships to construct a stochastic population model using precipitation driver variables. This enabled us to incorporate realistic levels of environmental variability into the model. A model incorporating best estimates for parameter values resulted in a mean trajectory for seed bank size that remained essentially stable through time, although there was a measurable risk of extinction over a 100-yr period for the study population under this scenario. Doubling the annual seed viability loss rate resulted in near-certain extinction, as did increasing first-year germination to 100%, showing the importance of the persistent seed bank. Interestingly, increasing environmental variance substantially decreased the risk of extinction, presumably because this plant relies on extremely good years to restock the persistent seed bank, while extremely bad years have little impact. If every year were average in this desert environment, the species could not persist. Simulated effects of livestock trampling resulted in greatly increased extinction risk, even over time frames as short as 15 years.

Key words: demography; endangered species; Jensen's inequality; population viability analysis; seed bank; simulation; slick spot peppergrass; stochastic model.

Conservation biologists and others concerned with management for preservation of rare species use many tools, but perhaps the most synthetic and powerful of these tools is population viability analysis (PVA; Beissinger and McCullough, 2002). In PVA, computer simulations are used to describe population demographic processes by incorporating ecological and life history information into a formal mathematical model. Such a quantitative model in effect represents a set of hypotheses about factors that influence the abundance of various life stages of the organism through time. PVA can theoretically be used to predict the fate of a population in absolute terms, but is better used to weigh the relative importance of different factors and management scenarios in determining the ability of a population to persist through time. As in any computer simulation procedure, the verisimilitude of PVA depends to a great extent on the quantity and quality of the ecological and life history information that goes into model construction.

Most currently existing PVAs have been constructed for animals, especially vertebrates (Beissinger and McCullough, 2002). A fundamental difference between quantitative population models for vertebrates and those for plants is the need to consider seed demographic rates. Because the seed bank is largely invisible and difficult to measure, plant population models that include explicit consideration of seed bank dynamics are relatively rare (Menges, 2000). This is particularly true for species with persistent seed banks, for which the field experiments needed to obtain age-specific vital rates for seed viability loss and seed germination must necessarily be long term (Doak et al., 2002). In addition, most studies that include quantitative analysis of seed demographic rates are for weedy species. Very few such studies have been carried out for nonweedy species, and almost none have been carried out for plants of conservation concern.

Doak et al. (2002) showed that, in the absence of good information on seed demographic rates, model predictions based on assumptions about a persistent seed bank can vary widely depending on the amount of variation in vital rates for the reproductive phases of the plant life cycle. This points to the need for realistic assessment of environmental variation and its impact at all life history stages.

Many plant population studies are presented as sets of deterministic models developed from data for specific years (e.g., Bierzychudek, 1982; Kalisz and McPeek, 1992). Efforts to introduce stochasticity into these models have often taken the form of choosing a sequence of matrices obtained for different years according to a random sampling scheme or a scheme designed to address theoretical questions (Bierzychudek, 1982; Kalisz and McPeek, 1993).

Alternatively, measured among-year variation in vital rates can be examined statistically to generate means, variances, and correlation structures that can be incorporated into the modeling procedure (Morris and Doak, 2002). This allows vital rates to vary randomly within the constraints of defined statistical distributions, resulting in greater realism than that obtained by selecting entire matrices randomly from an array of matrices.

A third approach for incorporating stochastic variation into a population model is to use documented long-term variation in environmental variables as drivers of among-year variation in demographic rates. This approach starts with regression of measured vital rates for a series of years on measured values

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[1] Manuscript received 12 April 2005; revision accepted 14 March 2006.

This research was supported in part by the Department of Defense Legacy Program. Members of the Orchard Training Area research technical staff provided valuable field assistance each season.

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TABLE 1. Precipitation data (mm) for key seasons from the OTA Range 2 weather station for the period 1991–2000, along with parallel long term precipitation data for Kuna, Idaho, a nearby NOAA reporting station with similar precipitation patterns (r = first-order temporal autocorrelation).

	Kuna long-term record (61 yr)					OTA Range 2 weather station: year of record									
Period	Mean	SD	Min	Max	r	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
Early winter (N–D–J)	55.4	23.4	17.8	106.2	+0.334	61	46	60	36	88	116	154	64	68	54
Late winter (F–M)	49.2	24.8	5.0	116.0	+0.230	28	35	93	27	49	44	0	56	43	95
Spring (A–M)	54.5	29.3	8.2	120.5	+0.082	72	20	44	46	52	58	50	115	30	39
Growing season (F–M–A–M)	103.7	38.4	31.0	193.5	+0.177	100	55	137	73	101	102	50	171	73	134
Summer (J–J–A)	33.0	21.7	2.0	102.0	+0.014	20	46	62	9	80	7	45	50	15	14
Water year (10/1–9/30)	249.9	65.5	76.5	391.5	—	192	169	279	138	288	243	282	312	161	214

for environmental driver variables for those years. These equations are then used to parameterize the model, so that the variance structure of the driver variables controls the variance structure of corresponding vital rates. This results in a correlation structure among vital rates that is mediated by their dependence upon common driver variables. This approach has the important advantage of incorporating realistic levels of environmental variation into the model and can be helpful in extrapolating demographic data collected over relatively short time spans (Fieberg and Ellner, 2001). It may be most appropriate in environments where abiotic factors such as precipitation are the main determinants of demographic performance.

Lepidium papilliferum (Henderson) Nelson and McBride (slick spot peppergrass, Brassicaceae) is an ideal species for study of both the dynamics of persistent seed banks and the role of environmental variation in mediating population dynamics. It is a primarily annual species that occurs in the semiarid, sagebrush steppe habitat of southwestern Idaho, an environment characterized by high year-to-year precipitation variation (Table 1). A short-lived plant species in such an unpredictable environment is likely to depend on a long-lived seed bank for population persistence (Brown and Venable, 1986). Our model examines the effect of stochastic environmental variation on population dynamics and more specifically on seed bank dynamics in this species, which was proposed for federal listing as endangered in 2002.

Lepidium papilliferum occupies a specific microhabitat within the matrix of sagebrush steppe vegetation, namely the "slick spots" that are small-scale sites of water accumulation (Meyer et al., 2005). The slick spots represent an environment where spring water availability is extended into summer, but where winter flooding can pose problems for survival. The species has a dual life history strategy. Seeds germinate in spring, and a fraction of the plants that establish function as summer annuals; these flower and fruit within a few months of emergence. The remainder of the cohort remains vegetative and has the potential to function as biennial. Those that survive over the summer and following winter flower and fruit along with the annual cohort of the following year. Biennials may have a much larger reproductive output than the annuals that fruit with them, but their survival to fruiting is greatly reduced, mainly because of mortality due to summer drought.

Lepidium papilliferum is under consideration for listing as endangered for several reasons. The species has a small geographic range and very specific habitat requirements. Populations are small and fragmented, and the species is absent from most superficially suitable habitat, suggesting a history of past decline. And there are numerous threats to its continued survival. A frequently observed phenomenon is the apparent sudden decline of local populations following catastrophic livestock trampling disturbance (Meyer et al., 2005). Such a decline is evident as a near-complete absence of plants even in favorable years, when there are large populations on undisturbed sites.

Our population model for *L. papilliferum* is based on a demographic study carried out from 1992 through 2003 at the States study site on the Idaho Army National Guard Orchard Training Area (OTA) southwest of Boise, Idaho, USA (Meyer et al., 2005). The study included an 11-yr artificial seed bank investigation as well as quantification of in situ seed banks and a detailed demographic analysis based on survivorship and reproductive output data obtained from 1993–1996 (Table 2). These years included a wide range of annual variation in seasonal precipitation (Table 1), making it possible to develop predictive equations for vital rates from this 4-yr data set.

Our overall objective in developing the model was to examine the effect of stochastic variation in precipitation driver variables on population dynamics and risk of extinction for *L. papilliferum,* using predictive equations and parameter values based on our earlier demographic and seed bank studies (Meyer et al., 2005). More specifically, we planned to use the model to (1) determine sensitivity to variation in key transition probabilities, (2) examine the effect of manipulating variance of precipitation drivers, (3) ask questions about the life history of the species, and (4) examine putative effects of livestock trampling on population persistence.

MATERIALS AND METHODS

Development of life cycle diagram—The life cycle diagram for *L. papilliferum* is based on a 1-yr time step and assumes that sampling takes place just before seed dispersal in late June each year (Fig. 1). At that time, actively growing plants are present in one of three states, as fruiting annuals, fruiting biennials, or vegetative rosettes (biennial hopefuls). These stages are shown in square boxes in the life cycle diagram, while intermediate (within-year) steps are shown in rounded boxes.

The age-structured seed bank is also present at this time, in 12 stages representing seeds 1–12 years of age (Fig. 1). The seeds in the first seed bank stage (SB1) are those produced by plants the previous year. There is no germination of seeds produced in the current year; seeds require a full year to enter the seed bank from which germination takes place (Meyer et al., 2005). We observed in our artificial seed bank experiment that each year an approximately constant proportion of the original seeds germinated (0.058) or died without germinating (0.026), as determined by linear regression analysis. These values showed no large or systematic variation as a function of precipitation or other environmental variables over 11 years, and are considered constants (Table 2). The sum of these (0.084) represents absolute loss from each seed cohort each year. Seed bank attrition for a given seed cohort is therefore a linear function of time. The proportion of the remaining seeds in each cohort to germinate or die increases each year as the absolute number of seeds declines, resulting in increasing values for the germination fraction transitions G_1 through G_{12}, and decreasing values for the seed survival fraction

TABLE 2. Data sources for development of predictive equations in Fig. 2 and for other transition probabilities in Fig. 1. Data from Meyer et al. (2005) except where noted.

Transition probability	Symbol	Data source and explanation	Calcuation method
Probability of survival for seeds in SB1–SB11 (seeds 1–11 yr old)	S_1–S_{11}	Seed retrieval experiment (1992–2003); based on observed linear decrease in the absolute number of remaining viable seeds in a cohort through time (loss of viability 0.026/yr; germination 0.058/yr); survival probability therefore decreases with seed age.	Age-specific constant value based on linear decrease in viable seeds in a cohort each year. Examples: $S_1 = [1.00 - 0.026$ (loss of viability) $- 0.058$ (germination)$]/1.00 = 0.916 \div 1.00 = 0.916$; $S_2 = (0.916 - 0.026 - 0.058)/0.916 = 0.832 \div 0.916 = 0.908$; $S_3 = (0.832 - 0.026 - 0.058)/0.908 = 0.748 \div 0.908 = 0.894$.
Probability of germination for seeds in SB1–SB12 (seeds 1–12 yr old)	G_1–G_{12}	Seed retrieval experiment (1992–2003); based on observed linear decrease in the absolute number of remaining viable seeds in a cohort through time and the linear increase in the germinated seed fraction (germination 0.058 per year); germination probability therefore increases with seed age.	Age-specific constant based on constant fraction (0.058) of original cohort germinating each year. Examples: $G_1 = 0.058 \div 1.00 = 0.058$; $G_2 = 0.058 \div 0.916$ (surviving fraction) $= 0.063$; $G_3 = 0.058 \div 0.832 = 0.070$.
Probability of survival to census for germinated seeds.	GS	Size of recruited cohort in 1993, 1994, and 1995, coupled with mean germination fraction estimate from retrieval experiment and estimates of in situ viable seed density from comparable sites.	Calculated for each time step from late winter precipitation using the equation in Fig. 2A. Germinant survival is scaled to an estimated survival of 0.10 for the 1993 cohort as explained in the text.
Probability of survival from census as seedlings to annual fruiting time.	SS	Survival of censused seedlings to annual fruiting time in 1993, 1994, and 1995.	Calculated for each time step from spring precipitation using the equation in Fig. 2B.
Fraction to flower as annuals	AF	Fruiting time census in 1993, 1994, and 1995.	Calculated for each time step from growing season precipitation using the equation in Fig. 2C.
Fraction not flowering as annuals (potential biennials)	BF	Fruiting time census in 1993, 1994, and 1995.	Calculated as $(1 - \text{AF})$ for each time step.
Probability that potential biennials will survive the summer	OSS	End-of-summer census in 1993, 1994, and 1995.	Calculated for each time step from summer precipitation using the equation in Fig. 2E.
Probability that potential biennials that have survived summer will survive to fruiting.	OWS	Fruiting time census in 1994, 1995, and 1996.	Calculated for each time step from early winter precipitation based on the equation in Fig. 2F.
Seed output of an annual	ASO	Seed output measurements in 1993 and 1994.	Calculated for each time step from growing season precipitation based on the equation for annual plants in Fig. 2D.
Seed output of a biennial	BSO	Seed output measurements made in 1993 and 1994 on biennials of the 1992 and 1993 cohorts.	Calculated for each time step from growing season precipitation based on the equation for biennial plants in Fig. 2D.
Probability that a seed that enters the seed rain will survive to enter SB1	SRS	Set at 0.90, with a ceiling of 600 000 seeds/yr, based on literature on seed density/seed predation relationships (Crist and MacMahon 1992).	Set at constant value, with a constant seed rain ceiling.

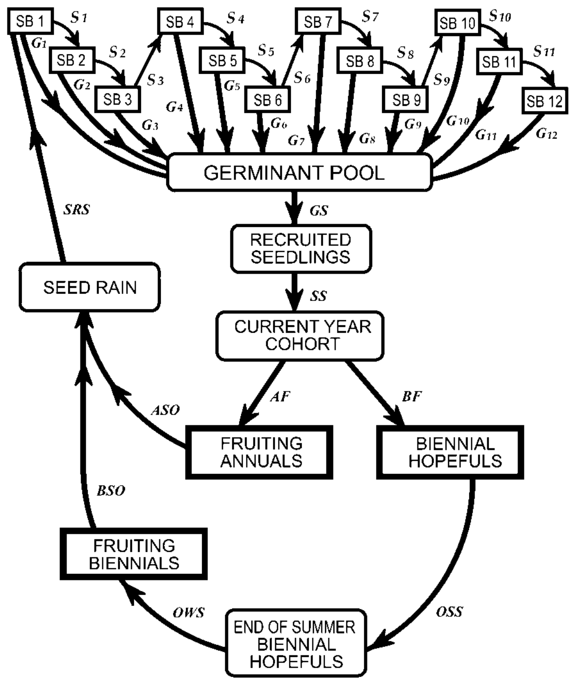

Fig. 1. Life cycle diagram for *Lepidium papilliferum*. Stages (square-cornered boxes) describe population status each year before seed dispersal at the end of June. The time step from one stage to the next is 1 yr. Intermediate variables (round cornered boxes) describe intermediate steps in the life cycle that take place during the year. The age-structured seed bank is represented by stages SB1–SB12. Transitions: S_1–S_{11} = seed bank survival from one year to the next, G_1–G_{12} = germinating fractions for seeds of each age, GS = fraction of germinants surviving to recruitment, SS = fraction of recruited seedlings surviving to June; AF = fraction of surviving cohort to flower and fruit as annuals; BF = fraction of surviving cohort to remain vegetative and potentially biennial, OSS = fraction of biennial hopefuls to survive the summer, OWS = fraction of biennial hopefuls to survive the winter and fruit the following year, ASO = seed output of an annual, BSO = seed output of a biennial, SRS = fraction of the seed rain that enters the seed bank.

transitions S_1 through S_{11}. After 12 years, all seeds in a cohort have either germinated or died.

Germinants from seeds of all ages enter a common germinant pool, a fraction of which (GS) survives to become the recruited cohort (Fig. 1). There is a further decrease in plant number during the period from recruitment to fruiting, determined by the spring survival fraction (SS). At fruiting time, a fraction of the surviving plants fruits as annuals (AF), while the remainder ($BF = 1 - AF$) remain vegetative and potentially biennial. The probability that a biennial-hopeful plant will survive the summer is OSS, while the probability that it will overwinter and fruit the following year is OWS. Annual and biennial plants have mean individual seed outputs (ASO and BSO, respectively). These become the seed rain. The probability SRS sets the fraction of the seed rain to enter SB1.

Development of predictive equations—We developed equations to predict the postgermination transition probabilities and reproductive outputs in the life cycle diagram from precipitation driver variables. Monthly rainfall data from a National-Guard-maintained weather station near the study site (OTA Range 2, 43°16′23.0″ N 116°09′0.4″ W, 1018 m a.s.l.) were available for the years 1991–2000 (Table 1). We used linear regression with independent variables derived from these data to generate the predictive equations for each vital rate. We tried different combinations of monthly totals to arrive at the combination that gave the equation with the highest coefficient of determination (R^2) for each vital rate. We defined five precipitation driver variables: early winter (November–December–January), late winter (February–March), spring (April–May), growing season (February–March–April–May), and summer (June–July–August).

We started with transitions for which measured values were available, namely all those involving transitions between censused plants of the 1993, 1994, and 1995 seedling cohorts (Table 2). These three cohorts were subjected to a wide range of scenarios in terms of seasonal precipitation patterns (Table 1), and these patterns were clearly reflected in the demographic data. Because plant size was not measured for the 1995 cohort, only 1993 and 1994 data could be used for the relationships predicting reproductive outputs.

A key transition probability in the model is germinant survival (i.e., survival from a germinated seed to a recruited seedling that could be censused). Because we could not directly measure the in situ seed bank at the States Study site due to the destructive nature of seed bank sampling, we used in situ seed bank estimates from nearby and similar populations (T Rex Hill, Meyer et al., 2005; Orchard Corner, Red Tie, and Quarry Butte, S. Meyer and D. Quinney unpublished data) to estimate germinant survival. We assumed that seed bank size was relatively constant across years, so that the size of the recruited cohort was a direct indicator of germinant survival. We estimated germinant survival for 1993, 1994, and 1995 as (number of seedlings in recruited cohort)/(total estimated seed bank × mean germination fraction). The total estimated seed bank (based on a mean seed density of 6.1 viable seeds per decimeter squared from the four populations listed above and a total area of 600 m^2 for the States study site where the demographic study was carried out) was 366 000 seeds. The mean germination fraction (0.109) is the weighted average of the germination fractions for SB1–SB12, based on the assumption that each seed cohort contributed equally to the seed bank. With a recruited cohort of 4000 seedlings, this gave a germinant survival probability of approximately 0.10 for 1993, the year with high late winter precipitation and the largest recruited cohort. We scaled survival probabilities for other cohorts relative to this value, referred to as the germinant survival scaling value, in deriving the equation to predict germinant survival.

The one transition probability for which we had no estimate was the survival of seeds in the seed rain. Rather than make the unreasonable assumption of no loss, we assigned some provisional values for this transition. First, we estimated that, in the absence of disturbance, perhaps 10% of the seed rain might be dispersed offsite prior to incorporation into the seed bank, might become buried too deeply, or might be consumed by seed predators. The probability of dispersal to unsuitable habitats is increased by the patchy nature of favorable habitat for this species. Second, we introduced an element of density dependence by assigning a ceiling to the quantity of seeds that could survive to enter the seed bank in any one year. This ceiling was based on the idea that local seed predators in this habitat are more likely to exploit high density seed patches (Crist and MacMahon, 1992). The ceiling value of 600 000 seeds per year corresponds to a density of 1 seed/10 cm^2. The model assumes that any recently dispersed seeds present in excess of this density will be subject to predation.

We did not introduce additional density dependence into the model, because plant densities that would be high enough for such processes to operate were rarely if ever encountered. Even at the relatively high densities observed in 1993, we encountered <7 plants/m^2 for a total cover value of $<3\%$. Processes in the life cycle apparently operate to keep densities below the threshold for negative intraspecific interactions (Watkinson et al., 1989).

Development of precipitation driver variables—The predictive equations in Fig. 2 permitted us to generate a set of transition probabilities and reproductive outputs for any yearly precipitation scenario. To use these equations to generate a model for *L. papilliferum* population dynamics in a stochastically varying environment, we needed a source of stochastically varying precipitation driver variables. We selected the NOAA long-range precipitation record from Kuna ID (43°29′27.2″ N 116°25′06.5″ W, 818 m a.s.l.) as this source. It was chosen because of the close agreement between the 61-yr Kuna record and the 10-yr record from the local rain gauge in terms of mean and extreme values for the seasonal precipitation periods of interest (Table 1). We calculated means and variances from the Kuna long-term data set and also calculated first order temporal autocorrelations. High positive autocorrelation indicates that runs of years with similar values are common, while autocorrelations near zero indicate that values each year are independent of each other. In the Kuna data set, the winter precipitation patterns had a much higher temporal autocorrelation than the summer pattern.

We also examined correlations among the five precipitation driver variables. There were no significant correlations ($P > 0.05$; df = 54) among early winter, late winter, spring, and summer precipitation variables, and R^2 values were never greater than 0.06. The composite variable growing-season precipitation

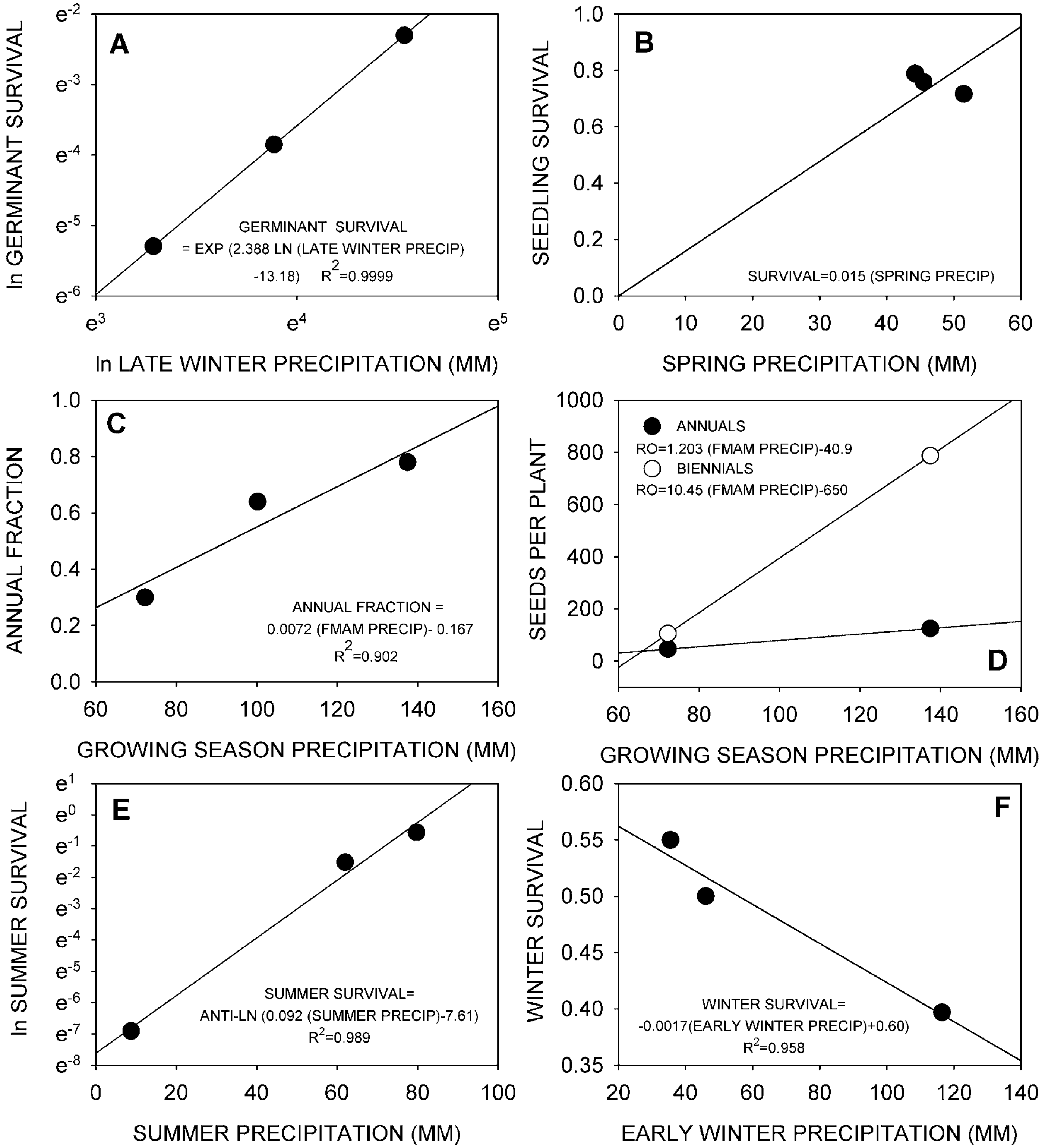

Fig. 2. Regression equations predicting variation in postgermination demographic rates from variation in seasonal precipitation (data from Meyer et al., 2005; see Table 2). Variables were transformed as necessary to obtain linear relationships. Demographic rates are (A) germinant survival, (B) spring seedling survival, (C) fraction to flower as annuals, (D) seed output of annuals and biennials, (E) oversummer survival of biennial hopefuls, (F) overwinter survival of biennial hopefuls.

was derived as the sum of late winter and spring precipitation, so it is not surprising that it was significantly positively correlated with each of them (R^2 of 0.602 for the relationship with spring precipitation and 0.437 for the relationship with late winter precipitation, $P < 0.0001$, df = 54).

The statistical distributions for early winter, late winter, spring, and summer precipitation driver variables were defined for use by the modeling program in terms of their means, variances, and temporal first order autocorrelations (Table 1).

Development of stochastic population models—We used Ramas Stage (Ferson, 1991) for the creation of stochastically varying population dynamics models. Our models incorporated only environmental stochasticity. We did not include any consideration of demographic stochasticity (i.e., the effect of fitness variance among individuals within a population; Lande, 1993). For each yearly time step, the program first chose values for the four primary precipitation driver variables according to their probability of occurrence based on the Kuna statistical distributions. The growing season precipitation driver variable was derived for each time step by summing selected values for late winter and spring precipitation.

The program then solved each transition and reproductive output equation (i.e., for vital rates that varied as a function of a precipitation driver variable; Fig. 2) in the matrix, based on these driver variable values. It used specified constant values for seed bank transitions, which did not vary as a function of precipitation (Table 2). This was repeated for each of the 100 time steps in an iteration, with each time step equivalent to solving a different population projection matrix. We performed at least three runs of 1000 iterations of a 100-yr time series for each of the models we examined. Model runs for each scenario were very similar. To verify this observation statistically, we performed 10 runs of 1000 iterations for the basic model and determined variance for the resulting risk statistics from this data set.

We focused on total seed bank size as an indicator of population status because actively growing plant numbers in this desert ephemeral species represent transient phenomena, oscillating widely among years and often going to zero. For the basic model, we started with a seed bank of 100 000, distributed among the 12 seed bank stages as if all years had identical inputs. All other stages had initial values of zero. We also ran numerous variants of the 100-yr model, to evaluate sensitivity to model parameter variation and to determine the effects of manipulating environmental driver variances, as well as to examine factors affecting the importance of the biennial life history strategy for this species.

We also performed a series of 15-yr and 50-yr simulations to address the issue of the putative impact of livestock trampling on short- and mid-term extinction probability in this species. We postulated two possible effects, burial of seeds at a depth that would effectively remove them from the active seed bank (i.e., a depth greater than 2.5 cm, S. Meyer and D. Quinney, unpublished data), and a decrease in germinant survival due to disruption of slick spot hydrology and/or silting over or weed invasion. To simulate a decrease in effective seed bank size, we reduced the initial seed bank by 90% and by 99% relative to the basic model. To simulate decreased germinant survival, we decreased the germinant survival scaling value from 0.10 to 0.05, 0.02, 0.01, 0.005, or 0.001.

RESULTS

Predictive equations—Five seasonal periods of precipitation were determined to be good predictors of one or more transition probabilities or fecundities. We found a positive relationship between late winter (February–March) precipitation and germinant survival (Fig. 2A). This relationship was strongly nonlinear and approximated a power function. Spring (April–May) precipitation was used as a predictor of survival from recruitment to flowering time. Because neither spring precipitation nor spring survival varied much during the 3 years of the study, this regression was constrained through the origin to get a more meaningful slope over a wider range of possible spring precipitation values (Fig. 2B). This was equivalent to making the assumption that spring survival would be zero if spring precipitation were zero.

Growing season precipitation (February–March–April–May) was a good predictor of the proportion of plants functioning as annuals, i.e., the higher the growing season precipitation, the larger the fraction of plants that flowered as annuals (Fig. 2C). There is apparently a size threshold for flowering, and in wetter springs more plants reach the threshold size in time to flower as annuals (Meyer et al., 2005). Growing season precipitation was also a good predictor of seed output for both annuals and biennials (Fig. 2D). The slope of the relationship was much steeper for biennials, reflecting their greater responsiveness to more favorable precipitation regimes.

The over-summer survival of potential biennials increased exponentially with increasing summer (June–July–August) precipitation (Fig. 2E). Overwinter survival was related to early winter (November–December–January) precipitation, but in this case the relationship was negative (Fig. 2F). This reflects the fact that the winter flooding of slick spots can negatively impact overwintering *L. papilliferum* plants (D. Quinney, personal observation).

Stochastic population models—When 100-yr simulations for the basic version of the stochastic model were run, they always predicted that, on average, total seed bank size would stabilize at or slightly above the starting value of 100 000 seeds. This means that, on average, the demographic processes defined in the model resulted in net replacement of seeds lost from the seed bank each year. There was always at least one run (in this and all subsequent models) that resulted in essentially monotonic decrease in the size of the seed bank to near zero, while maximum seed bank size ranged as high as three million. The standard deviations, which were very large once they leveled off during each set of 1000 runs, increased as a function of the mean, resulting in coefficients of variation that fell consistently between two and three. The large standard deviations were no doubt due to the large variances associated with the precipitation driver variables (Table 1). These standard deviations are a measure of the uncertainty characteristic of population processes in this dry and unpredictable climate.

The risk of seed bank quasi-extinction is another measure of environmental and demographic uncertainty. Ten independent runs of the basic model gave very similar results, resulting in low standard deviations for the resulting risk statistics. The risk of quasi-extinction at the 1000-seed threshold during a 100-yr simulation was 0.234 (SD 0.012), while the risk of quasi-extinction at the 100-seed threshold was 0.024 (SD 0.001).

Sensitivity to model parameters—Model behavior was not very sensitive to variation in initial seed bank size. When seed bank starting values were halved (50 000) or doubled (200 000), the average size of the total seed bank remained more or less constant through time, as in the basic model, and maximum and minimum values were similar. Extinction risk increased slightly when initial seed bank size was halved and decreased slightly when it was doubled (Fig. 3A).

The principal reason that maximum seed bank values in the preceding models did not exceed three million was the seed bank input ceiling of 600 000 seeds per year. When this constraint was removed, seed bank mean values gradually rose from 100 000 to over 300 000, while maximum values recorded in the simulation exceeded 27 million. When the seed rain ceiling was lowered to 100 000, mean seed bank values gradually dropped to 40 000, and the maximum observed value dropped to 700 000. Changes in the seed rain ceiling had little effect on risk of quasi-extinction (Fig. 3B).

Model predictions for total seed bank trajectories and

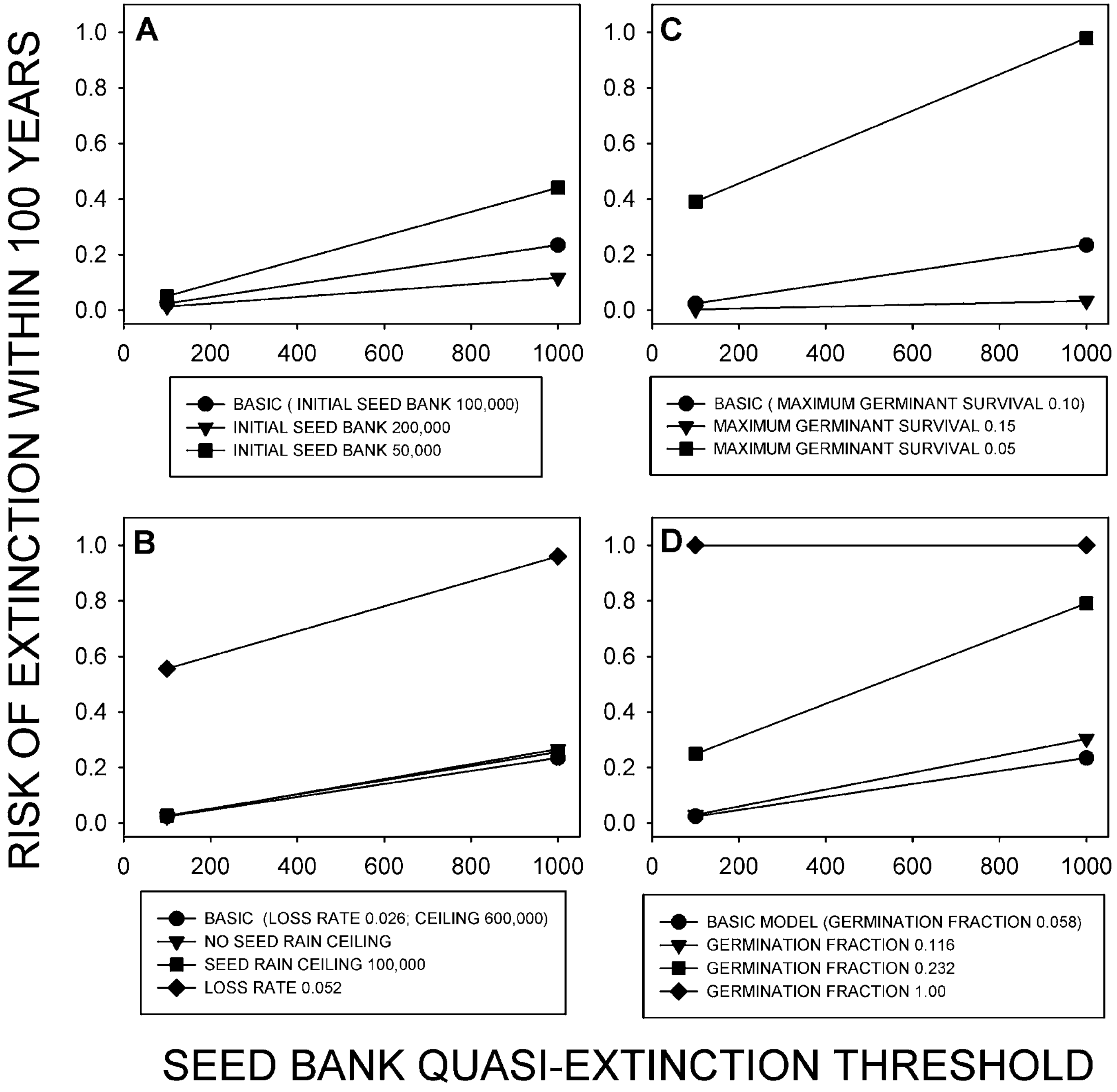

Fig. 3. Risk of seed bank quasi-extinction over a 100-yr time span at 100-seed and 1000-seed extinction thresholds, comparing the basic simulation model with (A) models with decreased and increased initial seed bank size, (B) models with increased and decreased seed rain ceilings and increased yearly seed bank loss rate, (C) models with decreased and increased maximum survival of germinants, and (D) models with increased and decreased yearly seed germination rates.

extinction risks were quite sensitive to the germinant survival scaling value (i.e., 0.10 in the basic model, the germinant survival for the 1993 cohort). Decreasing this value from 0.10 to 0.05 resulted in a monotonic mean decline toward zero in total seed bank size, with high risk of extinction within 100 years (Fig. 3C). In contrast, increasing this value to 0.15 resulted in a dramatic increase in mean seed bank size, which leveled off near one million. The risk of quasi-extinction dropped to very low levels in this second simulation.

The germinant survival scaling value is only provisionally estimated from our field seed bank, germination fraction, and seedling survival data, which were derived from several different populations and years. Use of a more accurate estimate for an individual population could have had consider-able impact on model predictions. Fortunately, our best estimate for germinant survival scaling value resulted in a model that predicted reasonably stable population behavior.

Model predictions for seed bank size were also very sensitive to changes in parameters affecting seed bank persistence. When seed bank annual viability loss rates were doubled from 0.026 to 0.052 per year, the result was a monotonic mean decline and a greatly increased risk of extinction (Fig. 3B). The effect of increasing the annual germination fraction was more complex. When this value was doubled from 0.058 to 0.116, so that the seed bank persisted for 7 years, there was little effect on the risk of quasi-extinction (Fig. 3D). Increasing the annual germination fraction to 0.232, so that the seed bank persisted for only 4 years, raised the risk of quasi-extinction considerably more. Increasing the fraction germinating from SB1 to 100%, eliminating the persistent seed bank, resulted in certain extinction.

Effect of manipulating driver variances—When all precipitation driver variances were doubled in concert, extinction risk decreased (Fig. 4A). Conversely, when these variances were set at 0.25 of their original level, extinction risk increased. When the driver variances were set at zero in a time-invariant version of the simulation, the result was monotonic decline and certain extinction.

Changing only the variance associated with the early winter precipitation driver had little effect on extinction probability (Fig. 4B), while decreasing only the variance associated with the spring precipitation driver actually slightly decreased the probability of extinction (Fig. 4C). For both late winter and summer precipitation drivers, increasing driver variance decreased the probability of extinction, while decreasing late winter variance increased extinction probability (Fig 4D, E). The late winter driver variable apparently exerts a major impact on model behavior, as its effect alone is similar to the effect of manipulating variances for all drivers simultaneously.

The role of the biennial life history strategy—We also used the simulation model to investigate the role of the biennial life history strategy in the population biology of this species. In the basic model, the mean number of biennials is predicted to be very low (mean of less than three individuals) relative to the number of annuals (mean of 140 individuals), probably because of the high frequency of years with low summer precipitation (Fig. 5). Consequently the input of the seeds of biennials on average makes only a small contribution to the yearly seed rain (8% over the 100-yr simulation). The seed output of an annual over the 100-yr simulation averaged 114, while the average seed output of a biennial was 698, or six times that of an annual. In spite of this high output per plant, the contribution of biennials was relatively unimportant on a population level.

To establish the effect of limiting summer precipitation on the importance of the biennial life history strategy, we ran a simulation model that was identical to the basic model except that we doubled the mean summer precipitation from 33 to 66 mm. This had the expected result of increasing the mean number of biennials from less than three to around 75 individuals each year, and it increased their mean contribution to the yearly seed rain to 39% (Fig. 5). Perhaps more significantly, the large boost in the seed rain from these biennials had the effect of greatly increasing overall population size and seed rain from annuals as well as biennials. Mean yearly seed rain increased 276%, and mean seed bank size increased from the starting value of 100 000 to 850 000 under this scenario. The mean number of fruiting annuals increased substantially relative to the basic model, to 660. Risk of quasi-extinction dropped to low levels (Fig. 4F). Population success overall for this species is thus greatly limited by the dry summers, not just the success of biennials per se, even though the only direct effect of summer precipitation in the model is on biennial survival.

In contrast to the effect of doubling summer precipitation, a model run using half the mean summer precipitation had extinction probabilities similar to the basic model (Fig. 4F). Even though the contribution of biennials to the seed rain dropped from 8% to 2% under this scenario, this had little effect on seed rain overall.

Manipulating summer precipitation driver variance produced results parallel to those produced by manipulating mean summer precipitation (Fig. 4E, F). Increasing summer precipitation variance decreased extinction probability and increased yearly seed rain by 30%. Under this scenario, the mean contribution of biennials to the seed rain increased to 15% of the total. Thus increasing variance had the same effect as increasing mean summer precipitation, though not as large. Decreasing summer precipitation variance had little impact on seed rain or extinction probability, even though it too reduced the biennial seed contribution to 2% of the total, an effect very similar to decreasing mean summer precipitation.

Effect of physical disturbance—Extinction risk at the 100-seed level over 15 years for the basic version of the model (i.e., with the same parameter values used in the 100-yr simulations) was very close to zero (<0.001), making it very unlikely that a rapid population decline could be due to environmental stochasticity alone (Fig. 6). Reducing seed bank size by 99% increased 15-yr extinction risk only to 0.064 (Fig. 4). Similarly, reducing germinant survival to a very low level (0.001) increased extinction risk over 15 years, but only to 0.180. The only simulations that resulted in high 15-yr extinction risk (>0.80) were those that combined at least a 90% reduction in the effective seed bank with at least a 10-fold decrease in germinant survival.

Levels of disturbance that result in relatively low probability of extinction in the short run can still pose a threat to survival over the longer term. Quasi-extinction risk at the 100-seed level over 50 years was high (>0.80) for any level of disturbance that decreased maximum germinant survival to 0.02 or less, regardless of the level of seed bank destruction (Fig. 6). Decreasing the seed bank by 99% or reducing maximum germinant survival to 0.05 each resulted in substantial extinction risk over 50 years (>0.35 at the 100-seed level), while these scenarios posed a very low risk of quasi-extinction at the 100-seed level over the short term. This suggests that the negative effects of physical disturbance will manifest themselves in population declines over the long term, even if immediate declines are not evident. In those cases where decline is evident within 15 years, the level of disturbance must be extreme.

Complete destruction of the seed bank may not be necessary to result in apparent absence of actively growing plants. Even without disturbance, successful recruitment in a favorable year represents less than 1% of the seed bank. If disturbance results in sharply decreased survival of germinants, successful recruitment may become a very rare event even if seeds are still present.

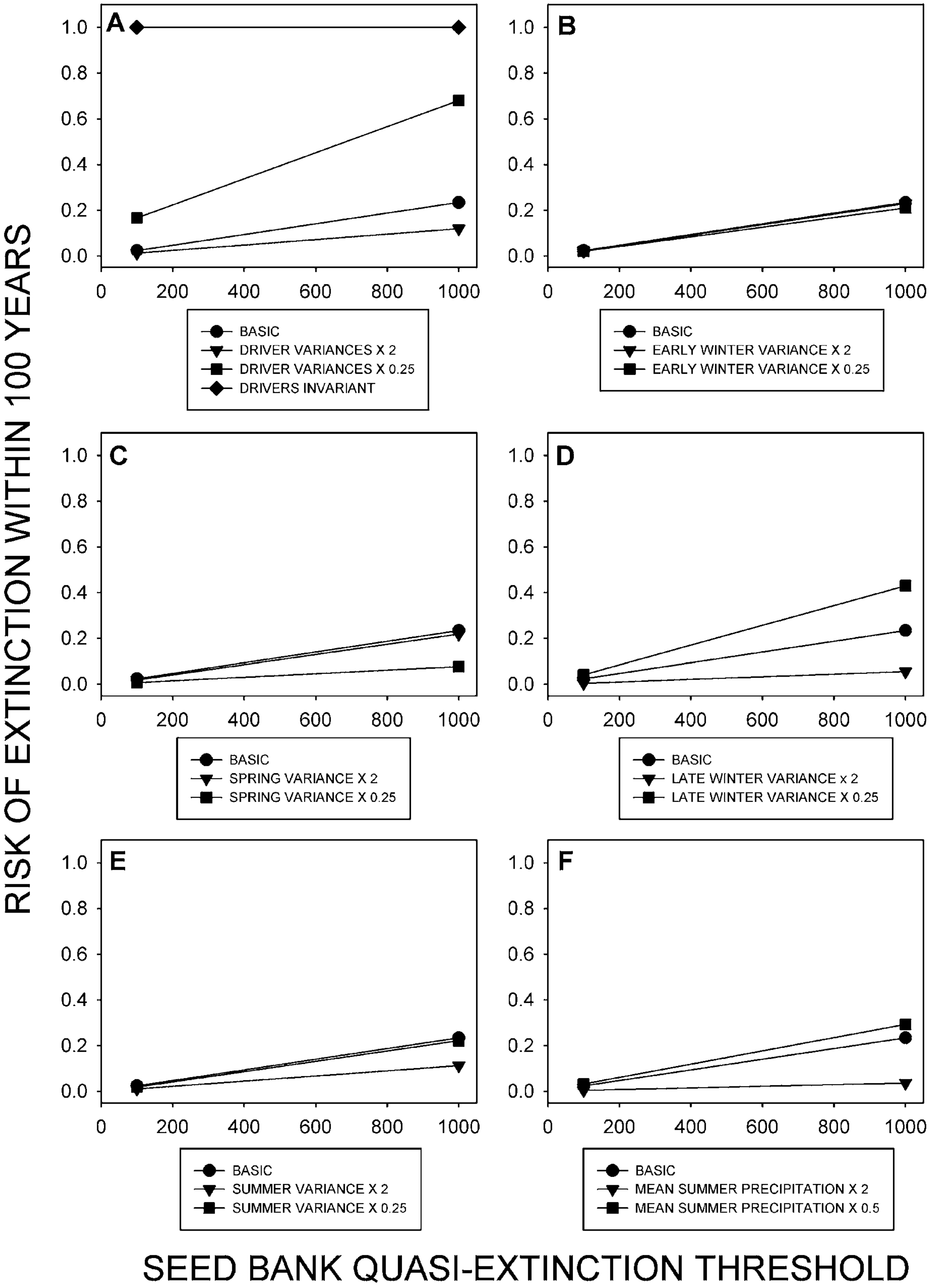

Fig. 4. Risk of seed bank quasi-extinction over a 100-yr time span at 100-seed and 1000-seed extinction thresholds, comparing the basic simulation model to models with increased and decreased variance of (A) all precipitation driver variables, (B) the early winter precipitation driver variable, (C) the spring precipitation driver variable, (D) the late winter precipitation driver variable, and (E) the summer precipitation driver variable, and to (F) models with increased and decreased mean summer precipitation.

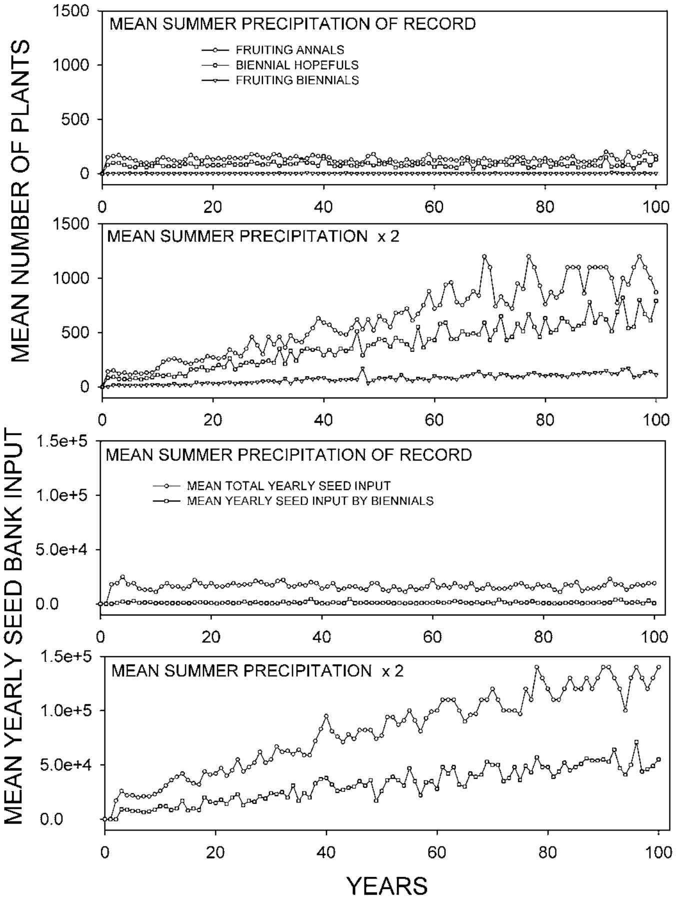

Fig. 5. Mean trajectories through 100 years of simulated time during 1000 simulations for mean number of *Lepidium papilliferum* fruiting annual, biennial hopeful, and fruiting biennial plants and mean yearly total seed bank input and seed bank input from biennials, under two modeling scenarios, the basic model using mean summer precipitation of record at Kuna ID as the mean for the driver variable summer precipitation, and a model identical to the basic model except for doubling the mean value of the summer precipitation driver variable.

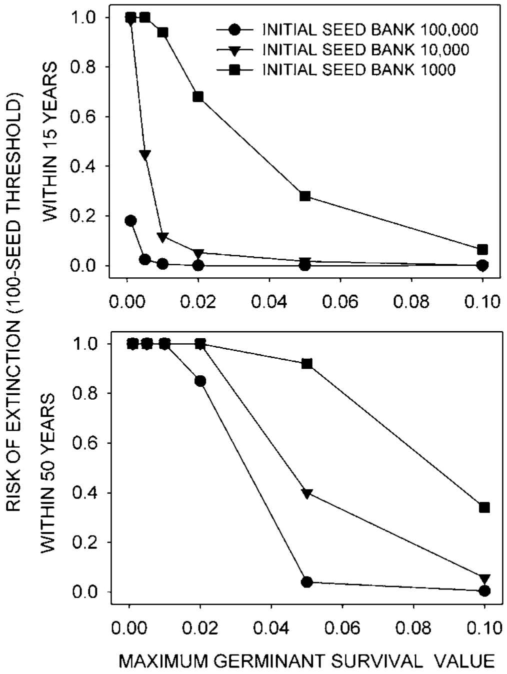

Fig. 6. Risk of seed bank quasi-extinction at the 100-seed level over 15-yr and 50-yr periods as a function of putative physical (livestock trampling) impacts on initial seed bank size and maximum germinant survival, based on 1000-iteration simulations using values from the basic model for the remaining parameters.

DISCUSSION

Our model clearly demonstrates the overriding importance of the seed bank in population persistence for *L. papilliferum*, and the sensitivity of the model to variation in age-dependent seed vital rates underscores the importance of obtaining accurate measures or at least reasonable estimates of these rates. In our 11-yr seed bank experiment, the fraction of the original cohort losing viability each year and the fraction germinating each year did not depend on environmental conditions, but were instead essentially constant, yielding a linear decrease in seed bank size through time for a particular cohort (Meyer et al., 2005). Rates of loss to seed death and to germination were thus age-dependent, each increasing with seed age. This is in contrast to the negative exponential decrease in seed bank size through time expected if seed vital rates are not age-dependent, and it is also different from the irregular rate of attrition that would result if loss rates through germination were strongly cued by the environment. The selective advantage to linear seed bank attrition may be that it spreads germination out uniformly across time, exposing more seeds to a wide sampling of environmental variation and increasing the chances of encountering the infrequent highly favorable year.

In our seed bank experiment, most of the viable seeds we retrieved at any point in time were dormant under a wide range of germination conditions. Innate dormancy that is lost gradually and that is relatively unresponsive to environmental cues seems to be characteristic of many native desert species with persistent seed banks (e.g., *Penstemon* spp., Meyer et al., 1995; *Atriplex confertifolia*, Meyer et al., 1998; Garvin and Meyer, 2003). These seeds usually have the ability to respond to cues that act to restrict their germination to the most favorable season, once they have become cue-responsive (e.g., *L. papilliferum* seeds always germinate in the spring under field conditions). This is quite different from the pattern for long-lived seeds of many weeds, which have cyclic dormancy and may germinate to high percentages if disturbance occurs at the right season (Baskin and Baskin, 1998). If the pattern of linear decrease in the size of a seed cohort through time that we observed for *L. papilliferum* holds true for other species, it might be possible to estimate long-term seed bank persistence using data from relatively short-term experiments that could give an indication of the slope of linear decrease through time.

A notable feature of our modeling approach is incorporation of stochasticity that is based on documented temporal variation in environmental variables. We were admittedly fortunate to sample such a wide range of variation in the relevant environmental variables in our 4-yr demographic study. But we were able to generalize our sample to an even wider array of conditions by relating among-year variation in demographic measures to among-year variation in environmental variables. This enabled us to use stochastic driver variables based on measured long-term environmental variation, thereby incorporating more realistic levels and patterns of variation in demographic rates.

An interesting result of the interplay between seed bank dynamics and stochastic environmental variation in our model was the fact that population persistence for *L. papilliferum* was favored by higher levels of environmental variability. Theoretical treatments generally predict that increased environmental stochasticity will increase the probability of extinction (Lande 1993). But in an environment that is marginal, as the sagebrush steppe of southern Idaho appears to be for *L. papilliferum*, increasing environmental stochasticity increases the chances of exceptionally good years that allow restocking of the seed bank, while the effect of poor years with little or no reproduction is buffered by the presence of the seed bank. The model demonstrated clearly that, if every year were average, *L. papilliferum* could not persist.

The mechanistic explanation of reduced extinction risk with increased environmental variance for *L. papilliferum* in our model is most likely to lie in the shape of the relationships between vital rates and their underlying driver variables. Most of these relationships were modeled as linear, but two of the key survival probabilities in the model were modeled as nonlinear, accelerating functions, (i.e., y increases at an increasing rate as a function of x). These nonlinear equations are for germinant survival and oversummer survival of biennial hopefuls (Fig. 2A, E). These are also the two transitions whose precipitation drivers had the strongest positive effect of increased variance (Fig. 4D, E). A property of nonlinear systems known as Jensen's inequality is that, for accelerating functions, increasing variance increases the mean effect of the independent variable upon the dependent variable (Ruel and Ayres 1999). The converse is true of decelerating functions, but none of the equations in the model have this form. Pazstor et al. (2000) briefly discuss how Jensen's inequality can be applied to the study of optimal life history strategies in stochastic environments. They use the term "promising uncertainty" to describe the effect of increased variance on processes characterized by accelerating functions and refer to the effect of increased variance on processes characterized by decelerating functions as "threatening uncertainty." For *L. papilliferum*, increased variance results in "promising uncertainty." We demonstrated that increasing either the mean or the variance for the summer precipitation driver had positive effects on biennial contribution, providing clear evidence of the impact of the nonlinear relationship between summer precipitation and biennial oversummer survival.

Another possible explanation for reduced extinction risk in the face of increased environmental stochasticity is the idea that exceptionally favorable years can more than compensate for unfavorable years for plant species whose life histories include storage of reproductive potential across years, for example, as seeds in a persistent seed bank (the "storage effect"; Chesson and Huntly 1989; Higgins et al., 2000). This explanation is supported by the fact that the long-lived seed bank was essential to population persistence in a stochastically varying environment, but even seed bank persistence could not prevent extinction under the scenario of no year-to-year variation.

A third possible explanation for the positive effect of increased environmental variance on *L. papilliferum* extinction risk could lie in correlations among vital rates and their underlying drivers. Doak et al. (2005) point out that negative correlations among vital rates can override the general result of negative sensitivities of fitness or population growth to increased variance in an individual vital rate, sometimes resulting in a positive effect of increased variance. This is not a likely explanation for the positive effects of increased variance in our model, because the vital rates are either constants (seed bank transitions), uncorrelated with other vital rates (because their values are controlled by unique driver variables that are uncorrelated with any other driver variable), or positively correlated with other vital rates through dependence on common driver variables. For example, growing season precipitation and its two components late winter and spring precipitation have positive effects on germinant and spring survival as well as on seed outputs of both annuals and biennials, so that all of these vital rates are positively correlated. According to Doak et al. (2005), these positive correlations should tend to result in lower cumulative growth rate and increased extinction risk in the presence of increased variance. Presumably the "storage effect" in concert with the effects of "promising uncertainty" overcame any negative effects of positive correlations among vital rates in our model.

We used a risk analysis approach in interpreting the results of our simulations (Burgman et al., 1992). Thus, while a deterministic model may say that the population will increase and a stochastic model may say that it will probably increase, there is still a measurable probability that the population will fall to some unacceptably small level. Risk analysis provides a means of estimating this probability. Risk assessment also involves an element of time; our risk statistics give the probabilities of dropping below threshold values within 100 years (or 15 and 50 years in the case of the short and mid-term term simulations). As part of a graphical scheme relating risk assessment to endangerment categories, Akcakaya (1992) provisionally regarded risks of <10% for dropping below a threshold level within a hundred year period as "safe", while a risk of >80% in the same time period represented "critical endangerment". Examining the results of our simulations in this light suggests that the population we studied has a small but measurable risk of extinction during a 100-yr period due to the effects of natural stochastic environmental variation alone. It is therefore possible that local populations of *L. papilliferum* can become extinct solely as a consequence of stochastic processes. But negative impacts of human activities are undoubtedly accelerating the rate of local extinction.

We examined the postulated short-term effects of livestock trampling on *L. papilliferum* population dynamics and concluded that abrupt declines following catastrophic trampling events are likely to result from a combination of deep burial of seeds and increased germinant mortality. And even when abrupt declines are not observed, the model showed that trampling disturbance at lower levels of impact can still set in motion a long-term trajectory of decline. It seems likely that one reason that so much potential *L. papilliferum* habitat is currently unoccupied is related to a 150-yr history of continuous livestock grazing in the area. Whether any of this unoccupied habitat is still capable of supporting the species is not known. The "slick spot" sometimes resumes the appearance of normalcy within a few years following a catastrophic trampling event, but our preliminary data suggest that the underlying soil structure essential for *L. papilliferum* recruitment may be permanently destroyed (S. Meyer and D. Quinney, unpublished data).

Using seed bank size as a measure of population status, as we have in this study, is logical given the ephemeral nature of actively growing plants of this species. But it presents some logistical difficulties in terms of application to management for conservation. Fortunately, it is possible to use this model to address conservation issues even without detailed seed bank data. If a population known to have produced seeds in past years fails to recruit plants in years predicted by the model to be good years for *L. papilliferum* recruitment and seed production, there is reason to suspect that human-caused disturbance could be responsible for the decline. Anthropogenic disturbances known to negatively impact *L. papilliferum* populations include off-road vehicle traffic, wildfire, weed invasion, and postfire rehabilitation practices such as the use of pre-emergent herbicides, the seeding of invasive species such as *Kochia prostrata* (forage kochia), and drill-seeding, in addition to livestock trampling (Meyer et al., 2005). A careful evaluation of the effects of these impacts, possibly using existing long-term monitoring data in combination with the modeling approach we describe, could be very valuable in managing for *L. papilliferum* species persistence.

Plant population viability analysis is still in the early stages of development, but this approach shows great promise. It is useful not only as a tool for rare plant conservation, but also as a formal method for examining the causes and consequences of life history variation among and within more widely distributed plant species as they interact with stochastically varying environments (Brigham and Schwartz 2003). Hopefully the modeling procedure reported here provides both new methodology and a clear example to guide future studies, especially for plants with persistent seed banks.

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