Title: Statistical inference for seed mortality and germination with seed bank experiments

Running head: Statistical inference for seed banks

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Last updated: November 13, 2022

Open research statement: The R scripts, JAGS model code, and Maxima code to reproduce the simulations and analyses in this study have been archived on Zenodo: https://doi.org/10.5281/zenodo.7317528. The data collected as part of the literature synthesis in this study are available in the repository on Zenodo.

1 Abstract

Plant population ecologists regularly study soil seed banks with seed bag burial and seed addition experiments. These experiments contribute crucial data to demographic models, but we lack standard methods to analyze them. Here, we propose statistical models to estimate seed mortality and germination with observations from these experiments. We develop these models following principles of event history analysis, and analyze their identifiability and statistical properties by algebraic methods and simulation. We demonstrate that seed bag burial, but not seed addition experiments, can be used to make inferences about age-dependent mortality and germination. When mortality and germination do not change with seed age, both experiments produce unbiased estimates but seed bag burial experiments are more precise. However, seed mortality and germination estimates may be inaccurate when the statistical model that is fit makes incorrect assumptions about the age-dependence of mortality and germination. The statistical models and simulations that we present can be adopted and modified by plant population ecologists to strengthen inferences about seed mortality and germination in the soil seed bank.

Keywords: seed banks, demography, parameter estimation, identifiability, uncertainty

2 Introduction

Soil seed banks are a crucial part of plant life-history strategies that depend on long-lived stages to persist in variable environments. At the population level, a persistent soil seed bank can buffer populations from temporal variability in reproductive success (Evans et al., 2007), and produce age structure that increases generation time and affects the population growth rate (Kalisz and McPeek, 1992). However, it can be difficult to incorporate seed banks into empirical population models (Menges, 2000; Doak et al., 2002; Nguyen et al., 2019) because seed fates are partially or completely unobservable processes (Rees and Long, 1993). Individual seeds enter the seed bank from seed rain, and eventually leave through death or germination (Simpson et al., 1989). Seeds experience mortality by being consumed or destroyed by predators or pathogens, or through physiological death (Baker, 1989). In the field, seed mortality cannot be directly observed and, because seeds that germinate must have both survived and germinated, seed mortality complicates inferences about germination.

Population ecologists studying seed banks are often interested in understanding how seed mortality and germination influence population dynamics. Seed mortality and germination can be measured using experiments (e.g., Kalisz 1991) and natural variability in seed rain and seedling emergence (e.g., Evans et al. 2010). In particular, experiments are often used to study seed fates and estimate both seed mortality and germination for population models. Two kinds of experiments are most common. Briefly, seed bag burial experiments involve burying seeds in mesh bags and recovering them to count seeds that died or germinated. Seed addition experiments consist of adding seeds to plots and returning to census emerged seedlings. Ideally, these experiments would be used to obtain accurate estimates for age-dependent seed mortality and germination that are associated with quantified uncertainty (Doak et al., 2002). However, there is no standard statistical approach for estimating seed mortality and germination from field experiments, and even observations from the same kind of experiment are often analyzed in disparate ways. For instance, three recent studies that used seed bag burial experiments each analyzed the observations differently: by regressing seeds in year $t+1$ on seeds in year t (Kurkjian et al., 2017), fitting an exponential curve (Lommen et al., 2018), or estimating the proportion of surviving seeds (Tanner et al., 2021).

Decisions about how to estimate seed mortality and germination influence whether and how the seed bank is represented in structured population models. Because the seed bank cannot be directly observed, these choices are often made with limited information. Recent reviews indicate that over a third of published plant population matrix models exclude seed banks without justification (Doak et al., 2002; Nguyen et al., 2019). Omitting the seed bank or inaccurately estimating seed mortality or germination can bias estimates for population growth rate, particularly when aboveground rates exhibit high levels of temporal variability (Doak et al., 2002; Nguyen et al., 2019). Age-dependent seed mortality and germination contribute to population age structure, so the decision to represent the seed bank as unstructured or age-structured can also affect population growth rates (Kalisz, 1991; Rees and Long, 1993; Doak et al., 2002). In addition, the precision of vital rate estimates, including seed rates, influences uncertainty in estimates of population dynamics (e.g., Paniw et al.

2017; Nguyen et al. 2019). Seeds are hard to study and relatively little is often known about them, so authors may omit uncertainty in their estimates of seed related rates and in turn underestimate uncertainty in population growth rate and extinction probability.

Although existing studies address issues related to how seed banks are represented in structured population models, there is no work that examines statistical models for observations from the experiments that are commonly used to study seed banks. We identify three key unanswered questions about seed bag burial and seed addition experiments: (i) When can each experiment be used to obtain estimates for constant versus age-dependent seed mortality and germination? (ii) What is the accuracy and precision of estimates from each experiment? (iii) How are estimates affected by misrepresenting the age-dependence of seed mortality and germination in statistical models? We answer these questions by describing statistical models for observations from seed bag burial and seed addition experiments and addressing model *identifiability*, the *statistical properties* of estimates for seed mortality and germination, and the consequences of model *misspecification*.

In seed bag burial and seed addition experiments, observations of surviving seeds and seedlings reflect seed fates. We define likelihoods that link these observations to estimates of seed mortality and germination, and analyze the identifiability of the models under different assumptions about the age-dependence of mortality and germination. Informally, a statistical model is identifiable if it is possible to estimate the parameters in the model from a given set of data. For the models that we analyze, the crux of the issue is that the seed bank experiments produce different observations—seeds and seedlings for seed bag burial experiments, but only seedlings for seed addition experiments. To determine if each experiment generates observations that can be used to estimate seed mortality and germination, we analyze the identifiability of statistical models. Once we determine which statistical models are identifiable for particular experimental observations, we compare the accuracy and precision of seed mortality and germination estimates from seed bag burial and seed addition experiments. Finally, we 'stress-test' the models by assessing the consequences of fitting misspecified models. In current practice, studies may fit models that simplify the age-dependence of mortality or germination by assuming constant mortality or germination (e.g., Leimu and Lehtilä 2006; Burns et al. 2013). In this case, researchers may want to be parsimonious and reduce the number of parameters in a statistical model. Alternatively, studies may fit models with as many age-dependent parameters as observations permit (e.g. Eckhart et al. 2011; Bricker and Maron 2012). In this case, researchers may want to parameterize an age-structured seed bank for a population model, or may simply want to be cautious and avoid over-simplifying the age structure of the seed bank. These constraints are typically applied without evaluating alternative model structures, and we investigate how such assumptions influence the accuracy and precision of estimates of mortality and germination.

3 Developing the statistical models

In the following sections, we characterize seed bag burial and seed addition experiments, and the observations they produce, by way of idealized examples (Fig. 1). We apply the principles of event history analysis to develop a deterministic model for seed mortality and germination that describes seed fates in seed bank experiments. We then link the observations and deterministic processes with probability statements to define a statistical model for observations from each experiment. Throughout, we present general versions of the model to accommodate mortality and germination rates that depend on seed age. At select points, we use the specific case in which mortality and germination rates do not depend on seed age to interpret the general model.

We make several choices about how to develop the statistical models that are influenced by how population ecologists use seed bag burial and seed addition experiments. In a literature synthesis, we identified 57 studies conducted from 1991-present that used a total of 69 experiments to parameterize matrix or integral projection models (**Appendix: Literature synthesis**). We used these studies to inform how we constructed our idealized experiments, with the goal of representing the essential attributes of each kind of experiment. The majority of studies (94.7%) built population models with separate seed mortality and germination parameters, and we consider how to estimate both parameters as well. The majority of studies (84.2%) described discrete relationships between seed age and fate, which is also how we represent the relationship in the models we build.

3.1 Observations

We assume that we want to characterize seed mortality and germination for a plant species with a soil seed bank and discrete germination opportunities. For simplicity, we do not compare sites, treatments, or species. The seeds are too small to be followed individually, so we conduct experiments with unmarked cohorts of seeds. We consider two possibilities: seed bag burial experiments (Fig. 1A-B) and seed addition experiments (Fig. 1C-D). We work with idealized versions of these experiments because our study develops and analyzes statistical models.

In seed bag burial experiments, we add seeds and soil to mesh bags before burying them in the field (0 months in Fig. 1A). Researchers bury seeds in various enclosures (e.g., cages in Kalisz 1991, or mesh bags in Quintana-Ascencio et al. 1998) but to be concise we always refer to bags. Bags are recovered from the field after a certain time. Here, we collect bags after germination so that we count intact, ungerminated seeds and germinants (filled circles in Fig. 1A). Sampling tends to be destructive, particularly if intact seeds are tested for viability using a method such as tetrazolium staining. As a result, these studies typically retrieve different subsets of bags for seed and germinant counts at different times (Fig. 1A).

We identify each bag by an ID, index i, and the time that it was recovered, index j (columns 1-2 in Fig. 1B). We also record time as a variable, t_{ij} (column 3 in Fig. 1B). Each bag has three counts: the number of seeds added to the mesh bags at the start of the experiment, n_{ij}, the number of intact, ungerminated seeds, and the number of germinants, $y_{\mathrm{g},ij}$ (columns 4-6 in Fig. 1B). Here, we assume that all intact seeds are viable (but we discuss combining field experiments and lab viability assays in **Discussion: Extensions**). Finally, we calculate the number of seeds surviving to sampling as the sum of intact, ungerminated seeds and germinants – we assume this is both the number of survivors, y_{ij}, and the number of seeds surviving to just before germination, $n_{\mathrm{g},ij}$ (columns 7-8 in Fig. 1B).

In seed addition experiments, we lightly bury or sprinkle seeds on the soil surface (0 months in Fig. 1C). Seeds are buried in plots where we do not expect a substantial seed bank, or in pots or trays with seed-free soil. We might also include control plots without seed addition to account for natural seed rain. We survey the plots for seedlings after germination (filled circles in Fig. 1C). Typically, it is not possible to recover intact seeds from the soil but because seedling counts are non-destructive, we can resurvey plots (Fig. 1C).

We identify each plot by an ID, index i, and record the time it was surveyed, index j (columns 1-2 in Fig. 1D). We also record time as a variable, t_{ij} (column 3 in Fig. 1C). Each plot and survey time has two counts: the number of seeds added to the plot at the start of the experiment, n_{ij}, and the number of seedlings, $y_{\mathrm{g},ij}$ (columns 4 & 6 in Fig. 1C).

Studies that track natural variability in seed rain, n_{ij}, and seedling emergence, $y_{\mathrm{g},ij}$ over time can also produce similar data as seed addition experiments (e.g., Kauffman and Maron 2006; Elderd and Miller 2016). Seed rain is comparable to the number of seeds added to an experimental plot, and seedling surveys are similar to counting seedlings in an experiment. Natural variability can complement or provide an alternative to experimental manipulations, especially for species with limited dispersal or discrete recruitment pulses in which it is possible to link seed rain and seedling emergence. In this manuscript, we describe our statistical framework with reference to experimental observations, but it could also be used to estimate seed mortality and germination from field observations.

3.2 Deterministic model for seed fates

The fate of seeds in the seed bank can be characterized using methods from event history analysis (also called survival or failure time analysis; reviewed in Fox 2001; Landes et al. 2020). By focusing on a seed leaving the seed bank as the event of interest, we can characterize the distribution of times at which the event occurs using a set of key functions (Klein and Moeschberger, 2003). A survival function describes the probability that a seed remains in the seed bank until time t. The survival function is the term for the probability of the event occurring after time t; the term applies whether or not the event of interest is death. A probability density function describes the probability that the seed leaves the seed bank at time t. Finally, a hazard function describes the tendency that a seed remaining in the seed bank at time t leaves the seed bank at the next instant in time. The probability density function defines the unconditional probability of events, while the hazard function is associated with the conditional propensity for the event among individuals who have not yet experienced the event (Fox 2001, p. 245). We illustrate the relationship between these functions in **Appendix: Hazards determine the age-structure of the seed bank**.

We use these principles to describe how seed loss from the seed bank (the event of interest) depends on mortality and germination. We define hazard functions for each fate. The hazard function for mortality, h_m, is the risk that a seed remaining in the seed bank leaves the seed bank through mortality the next instant. The hazard function for germination, h_g, is the risk that a seed remaining in the seed bank leaves the seed bank through germination the next instant. The hazards thus summarize the "instantaneous risk" (Landes et al., 2020) of mortality or germination. In this paper, we assume that mortality precedes germination, but the principles we describe are flexible and specific equations should be reformulated to correspond to the biology of the study system.

We combine the mortality and germination hazards to describe a survival function for the expected probability that seeds remain in the seed bank up to a given time:

$$S(t) = \prod_{t_j \leq t} \left(1 - h_{\mathrm{m}}(t_j)\right) \times \left(1 - h_{\mathrm{g}}(t_j)\right). \tag{1}$$

Equation 1 is the product of discrete survival functions associated with mortality, $S_{\mathrm{m}}(t_j) = \prod_{t_j \leq t} 1 - h_{\mathrm{m}}(t_j)$, and germination, $S_{\mathrm{g}}(t_j) = \prod_{t_j \leq t} 1 - h_{\mathrm{g}}(t_j)$. If the hazards are on an annual timescale, S_{m} is the cumulative product of the complement of the mortality probability, up to the number of years t_j that seeds have been in the soil. Similarly, S_{g} is the cumulative product of the complement of the germination probability, up to the number of germination opportunities that seeds have experienced. In terms of the hazards, $h_m(1)$ is a seed's propensity for mortality in the first year and $h_{\mathrm{g}}(1)$ is the propensity for germination of a seed that does not die during the first year. The seeds that remain in the seed bank past one year do not die with propensity $1 - h_{\mathrm{m}}(1)$ and do not germinate with propensity $1 - h_{\mathrm{g}}(1)$.

To use the survival function (Equation 1) in a statistical model, we specify the hazards in terms of probabilities. The mortality hazard, $h_{\mathrm{m}}(t_j)$, is the probability of mortality during each time interval j, $p_{\mathrm{m},j}$. Specifically, it is the conditional probability of mortality for seeds that remain in the seed bank. We describe seeds remaining in the seed bank *after* the period in which they experience mortality, but *before* the germination opportunity. We assume that after this time interval, seeds have a discrete opportunity to germinate. The germination hazard, $h_{\mathrm{g}}(t_j)$, is the conditional probability of germination at each opportunity, $p_{\mathrm{g},j}$, for a seed that remains in the seed bank up to just before germination.

With these hazards, the mortality component is defined by $\prod_{j=1}^{J} 1 - p_{\mathrm{m},j}$. The germination component is defined by $\prod_{j=1}^{J}(1 - p_{\mathrm{g},j-1})^{I(j>1)}$, where $I(x)$ is an indicator function equal to 1 if the inequality is true, and 0 if it is not (Metcalf et al., 2009). We use the indicator function because at the first time j, seeds have not yet experienced a germination opportunity. After the first germination opportunity, the 'germination history' is defined by the product of past germination opportunities. The product of the mortality and germination components describe the probability that seeds remain in the seed bank after j time intervals (e.g., years) as

$$f(\boldsymbol{p}_{\mathrm{g}}, \boldsymbol{p}_{\mathrm{m}}) = \prod_{j=1}^{J} \overbrace{\left(1 - p_{\mathrm{m},j}\right)}^{\substack{\text{survival function} \\ \text{for mortality}}} \times \overbrace{\left(1 - p_{\mathrm{g},j-1}\right)^{I(j>1)}}^{\text{germination history}}. \tag{2}$$

The choice of how to represent mortality and germination makes explicit our assumptions about how those processes operate. The most simple version of the model in Equation 2 is one in which the hazards are constant; neither mortality nor germination probability change with seed age. In this case, $p_{\mathrm{m},1} = p_{\mathrm{m},2} = \cdots = p_{\mathrm{g},J}$ and $p_{\mathrm{g},1} = p_{\mathrm{g},2} = \cdots = p_{\mathrm{g},J}$. Mortality and germination are each described by a single parameter, p_{m} and p_{g}.

3.3 Likelihood functions for observations from seed bag burial and seed addition experiments

To estimate seed mortality and germination, we use probability statements to connect the observations from field experiments to the deterministic models. We describe likelihood functions for observations from seed bag burial (Fig. 1A-B) and seed addition (Fig. 1C-D) experiments. To illustrate our approach, we assume that mortality and germination do not depend on seed age. The general structure of the likelihood remains similar when we relax the assumption of constant hazards for mortality or germination (Table 1).

For the seed bag burial experiment, we construct one likelihood for the observations of germinants and another likelihood for the observations of surviving seeds. First, we use the observations of germinants to describe a model for the probability of germination, p_g. We assume that the number of seeds that germinate, $y_{\mathrm{g},ij}$, is a binomial sample from the number of seeds surviving to just before germination, $n_{\mathrm{g},ij}$. Recall that the number of surviving seeds is the sum of germinants and ungerminated, intact seeds. We estimate the probability of germination, p_g, for a seed that survives up to just before germination. The likelihood is then $L(p_\mathrm{g}|\boldsymbol{y}_\mathrm{g}) = \prod_{i=1}^{I}\left[\prod_{j=1}^{J_i}\text{binomial}(y_{\mathrm{g},ij}|n_{\mathrm{g},ij},p_\mathrm{g})\right]$.

Next, we use the observations of surviving seeds to describe a survival function for the product of germination and mortality hazards. We assume that the number of seeds that survive to a given time is a binomial sample from the number of seeds that start the experiment in each bag: $\text{binomial}\big(y_{ij}|n_{ij},f(\ldots)\big)$. The number of surviving seeds is the sum of germinants and ungerminated, intact seeds. The deterministic model, $f(\ldots)$, is the product of the germination history and the survival function for mortality, and describes the probability of not germinating and not dying up to the time j. For the case in which mortality and germination do not depend on seed age, $f(p_\mathrm{m},p_\mathrm{g}) = \prod_{k=1}^{j}(1-p_\mathrm{m})(1-p_\mathrm{g})^{I(j>1)}$. The joint likelihood for observations of germinants and surviving seeds is

$$\begin{aligned} f(p_\mathrm{m},p_\mathrm{g}) &= \prod_{k=1}^{j}(1-p_\mathrm{m})\times(1-p_\mathrm{g})^{I(j>1)} \\ L(p_\mathrm{m},p_\mathrm{g}|\mathrm{y}_\mathrm{g},\mathrm{y}) &= \prod_{i=1}^{I}\left[\prod_{j=1}^{J_i}\left[\text{binomial}(y_{\mathrm{g},ij}|n_{\mathrm{g},ij},p_\mathrm{g})\text{binomial}\big(y_{ij}|n_{ij},f(p_\mathrm{m},p_\mathrm{g})\big)\right]\right]. \end{aligned} \tag{3}$$

In seed bag burial experiments, bags are destructively sampled so the indices for bag ID, i, and recovery time, j, are redundant (Fig. 1A). We write the likelihood function so that the index for the time the bag was recovered, j, is nested within the index for bag, i. We adopt this notation to avoid unobserved combinations of bag ID and recovery time (e.g., any bag i at a time j when the bag was not recovered). Using this notation also makes explicit the parallel with the likelihood for observations from seed addition experiments, for which there are multiple observation times j per bag i (Fig. 1B).

For the seed addition experiment, we construct a likelihood for the observations of seedlings.

We assume that the number of seedlings is a binomial sample from the number of seeds that start the experiment: $\text{binomial}\big(y_{\text{g},ij}|n_{ij}, f(\dots)\big)$. The number of seedlings is the product of mortality and germination. We describe the combination of those processes with a deterministic model, $f(\dots)$, that modifies Equation 2 to include germination. Each observation takes place at the time of germination, rather than after, so that $f(p_\text{m}, p_\text{g}) = p_\text{g} \times \prod_{k=1}^{j}(1-p_\text{m})(1-p_\text{g})^{I(j>1)}$. To account for germination, the function now includes the probability of germination, p_g, in addition to the survival function for mortality and the germination history. The likelihood for observations of seedlings is

$$\begin{aligned} f(p_\text{m}, p_\text{g}) &= p_\text{g} \times \prod_{k=1}^{j}(1-p_\text{m}) \times (1-p_\text{g})^{I(j>1)} \\ L(p_\text{m}, p_\text{g}|\text{y}_\text{g}) &= \prod_{i=1}^{I}\Big[\prod_{j=1}^{J_i}\big[\text{binomial}\big(y_{\text{g},ij}|n_{\text{g},ij}, f(p_\text{m}, p_\text{g})\big)\big]\Big]. \end{aligned} \tag{4}$$

4 Methods

We now conduct a comprehensive analysis of statistical models for seed bag burial and seed addition experiments. First, we determine whether the models can be used to estimate different combinations of constant (C) or age-dependent (A) seed mortality and germination. Population models that incorporate a seed bank typically parameterize seed mortality and germination with one of the following combinations of mortality/germination: C/C (e.g., Kurkjian et al. 2017), A/C (e.g., Yates and Ladd 2010), C/A (e.g., Elderd and Miller 2016), and A/A (e.g., Kalisz 1991). We thus analyze models for the following cases:

1. Constant mortality/constant germination (C/C): Mortality, p_m, and germination, p_g, hazards are the same for all seed ages.
2. Age-dependent mortality/constant germination (A/C): The mortality hazard is a function of seed age, $p_{\text{m},j}$, while the germination hazard is the same for all seed ages, p_g.
3. Constant mortality/age-dependent germination (C/A): The mortality hazard is the same for all seed ages, p_m, while the germination hazard is a function of seed age, $p_{\text{g},j}$.
4. Age-dependent mortality/age-dependent germination (A/A): Both mortality, $p_{\text{m},j}$, and germination, $p_{\text{g},j}$, hazards are functions of seed age.

For each of these four cases, we study the identifiability of models for seed bag burial and seed addition experiments to determine when each can be used to estimate seed mortality and germination. To directly compare the statistical properties of estimates for seed mortality and germination from seed bag burial and seed addition experiments, we fit a model with constant mortality and constant germination (C/C) to observations from a seed bank with constant mortality and constant germination (C/C). Finally, we study the consequences of model misspecification on parameter estimates. We stress-test the models with two cases in which the true age structure of the seed bank and the age-dependence of parameters in the statistical model are mismatched. First, we fit a model with age-dependent mortality and constant germination (A/C) to observations from a seed bank with constant mortality and germination (C/C). Second, we we fit a model with constant mortality and constant germination (C/C) to observations from a seed bank with age-dependent mortality and constant germination (A/C).

4.1 Identifiability analysis by the symbolic method

To determine when seed bag burial and seed addition experiments can be used to estimate constant or age-dependent seed mortality and germination, we analyze the identifiability of statistical models for the experiments. We study if parameters can be estimated in terms of the structure of the likelihood ('intrinsic identifiability') (Cole 2020). Intrinsic identifiability refers to cases where parameters in a model can be uniquely estimated. For example, models will not be identifiable if different combinations of mortality and germination have the same likelihood for a set of observations. If the model is not identifiable, there are no unique maximum likelihood estimates regardless of the quantity of data that is available.

To analyze the identifiability of statistical models for different combinations of experiment, hazard, and length of the experiment, we use an algebraic approach called the symbolic method (Catchpole and Morgan 1997; Cole et al. 2010; Cole 2020). With this method, we focus on general issues of experimental design and model structure rather than on specific datasets. We determine the intrinsic identifiability of statistical models for all combinations of experiment (seed bag burial vs. seed addition), hazards (C/C, A/C, C/A, A/A), and length of experiment (1, 2 or 3 years). All the likelihoods that we analyze are shown in Table 1. To apply the symbolic method, we summarize each model by a vector that completely determines the model (an 'exhaustive summary'). The exhaustive summary is simply the likelihood associated with each observation. The exhaustive summary is subsequently differentiated with respect to all of the constituent parameters to form a 'derivative matrix' (the transpose of the Jacobian). The model is identifiable if the rank of the derivative matrix is equal to the number of parameters in the model; the model is not identifiable if the rank of the derivative matrix is less than the number of parameters. We implement these steps using the computer algebra software Maxima (Maxima, 2014); for detailed methods and scripts, see **Appendix: Identifiability analysis**.

4.2 Simulation experiments

To compare the statistical properties of seed bag burial and seed addition experiments, and study the effect of model misspecification, we conduct numerical experiments in which we fit models to simulated data. To simulate data with the structure of seed bag burial and seed addition experiments (Fig. 1), we use the likelihoods corresponding to those observations (Table 1). In practice, we use mortality and germination hazards to calculate the expected probability of a seed remaining in the soil at the end of each year, and its subsequent probability of germinating. We use the expected probability of remaining in the soil to draw a binomial sample of seeds from the initial number of seeds in the bag. We use the probability of germination to draw a binomial sample of germinants from the seeds remaining in the bag. To simulate data with the structure of the seed addition experiment, we retain only the observations of seedlings.

Both maximum likelihood and Bayesian methods would be appropriate to fit the models associated with seed bag burial and seed addition experiments. We chose to fit Bayesian models to the simulated observations because we can readily estimate the parameters in the joint likelihood. All parameters in our models are probabilities with support $[0, 1]$ on which we place $\text{beta}(1, 1)$ priors; this is equivalent to a uniform prior. Fig. S4 shows the directed acyclic graphs corresponding to the joint and posterior distributions for the models. Parameters and details of simulations are given in the sections that follow. We wrote simulations and analyzed model output in R version 3.6.2 (R

Core Team, 2019). We wrote all models and sampled posterior distributions using JAGS 4.10 with **rjags** (Plummer et al., 2019). For each fit, we ran 3 chains with 3,000 iterations for adaptation, 5,000 for burn-in, and 5,000 for sampling. For computational efficiency, we thinned the chains and kept every 10^{th} iteration. We used the **MCMCvis** package to work with model output, check chains for convergence, and recover posterior distributions (Youngflesh et al., 2021).

4.2.1 Statistical properties of seed bag burial and seed addition experiments

To compare the statistical properties of estimates from identifiable models, we used a simulation experiment in which we fit a model with constant mortality and constant germination (C/C) to observations from a seed bank with constant mortality and constant germination (C/C). We generated data from a 3-year experiment with $n = (5, 10, 15, 20, 25, 30)$ bags or plots each year. Each bag or plot started the experiment with 100 seeds. For each number of bags or plots, we simulated 250 replicate datasets for four combinations of 'true' mortality and germination: low mortality/low germination $(0.1, 0.1)$, low mortality/high germination $(0.1, 0.5)$, high mortality/low germination $(0.5, 0.1)$, and high mortality/high germination $(0.5, 0.5)$. We fit each simulated dataset with two models; one for a seed bag burial experiment and one for a seed addition experiment.

To quantify the bias of estimates, we calculated the difference between the posterior modes and 'true' parameters for the probability of mortality or germination. Estimates are unbiased when the difference is 0. To quantify the uncertainty of parameter estimates, we calculated the width of the 95% credible interval. For each set of 'true' parameters and number of bags or plots, we estimated the mean difference and width, and quantified 95% confidence intervals for each with a t distribution (Pappalardo et al., 2020). To estimate the coverage of the 95% credible intervals, we calculated the proportion of credible intervals that contain the 'true' parameter value. Ideally, a 95% credible interval would contain the 'true' parameter value 95% of the time. We obtained confidence intervals for coverage with the Wilson method in the **binom** package (Pappalardo et al., 2020), and calculated root mean squared error as a measure of the combined effect of bias and uncertainty.

4.2.2 Consequences of model misspecification

To study the consequences of model misspecification, we studied two cases with a mismatch between the true age structure of the seed bank and the age-dependence of the statistical model. For these analyses, we were interested in the interaction between the data-generating process and the statistical model. We thus use simulations with a large number of bags or plots ($n = 30$).

First, we fit a model with age-dependent mortality and constant germination (A/C) to observations from a seed bank with constant mortality and constant germination (C/C). In this analysis, we examined the effect of fitting a model that has more parameters than the process that generated the observations (i.e., the model is overspecified). We used the observations that we simulated from a seed bank with constant mortality and germination in the previous section. We then fit a model with age-dependent mortality and constant germination, the A/C model, to these observations. The model has four parameters: one mortality parameter each for one-, two-, and three-year old seeds, $p_{\mathrm{m},1}$, $p_{\mathrm{m},2}$, and $p_{\mathrm{m},3}$, and one parameter for germination, p_{g}. For all parameters, we quantified bias, uncertainty, coverage, and root mean squared error.

Second, we fit a model with constant mortality and constant germination (C/C) to observations from a seed bank with age-dependent mortality and constant germination (A/C). In this analysis, we studied the effect of fitting a model that has fewer parameters than the process that generated the data (i.e., the model is underspecified). We generated data from a 3-year experiment with $n = 30$ bags or plots each year, and each bag or plot started the experiment with 100 seeds. The 'true' probability of mortality increased over time, so that $p_{\mathrm{m},1} = 0.1$, $p_{\mathrm{m},2} = 0.2$, and $p_{\mathrm{m},3} = 0.3$. The germination rate in all years was constant. To examine the influence of germination on statistical properties, we varied p_{g} from 0.1 to 0.5 across simulations. For each true germination probability, we simulated 250 replicate datasets. As before, we fit two models to each simulated dataset; one for a seed bag burial experiment and one for a seed addition experiment. Even though we only estimated one parameter for the probability of mortality, we compared properties of the estimate to the age-dependent probability of mortality in each of the three years. For all parameters, we quantified bias, uncertainty, coverage, and root mean squared error.

5 Results

5.1 Identifiability analysis by the symbolic method

All models for observations from seed bag burial experiments exhibit a deficiency of 0, indicating that the models are identifiable (Table 2). In all cases we consider, the models for seed bag burial experiments can be used to estimate parameters for seed mortality and germination. Models for observations from seed addition experiments only show a deficiency of 0 when mortality and germination rates are assumed to be constant, and when more than one year of observations is available (Table 2). In all other cases, models have a deficiency greater than 0, indicating that the models are not identifiable. Identifiability is directly related to the structure of a model's likelihood (Table 1). Models for a seed bag burial experiment contain the product of likelihoods for observations of intact seeds and germinants, each of which provides separate information on seed mortality and germination (Fig. S4A). However, models for a seed addition experiment only consist of a single likelihood for observations of seedlings, in which seed mortality and germination always appear as a product (Fig. S4B). In this case, the model is identifiable only when there are as many, or more, years of seedling observations as there are parameters in the model.

5.2 Statistical properties of seed bag burial and seed addition experiments

The C/C models fit to observations from the seed bag burial and seed addition experiments are identifiable when there is more than one year of data (Table 2); here, we analyze simulated data for 3-year experiments. Both experiments produce unbiased estimates of mortality (Fig. 2A-D) and germination (Fig. 2I-L) with large numbers of bags or plots. With small numbers of bags or plots, seed addition experiments are more likely to produce biased estimates for mortality (e.g., Fig. 2A, C). Estimates from seed addition experiments display greater uncertainty in all simulations (Fig. 2E-H, M-P). The difference in uncertainty of estimates between experiments depends on the true probability of mortality and germination. Seed mortality estimates show seven to nine times more uncertainty for seed addition experiments when germination is low, but roughly twice as much uncertainty when germination is high (Fig. 2E-H). Germination estimates from seed addition experiments displayed a similar pattern, though the overall difference in uncertainty was smaller.

Estimates from seed addition experiments are 2.3 times as uncertain when when mortality is low, and 1.8 times as uncertain when germination is high. Fig. 2M-P).

For both experiments, coverage is ∼95% (Fig. S8A-D, I-L), and root-mean squared error decreases with the number of bags or plots (Fig. S8E-H, M-P). For seed addition experiments, estimates of seed mortality show the greatest error when germination is low (Fig. S8E, G). The joint posterior distribution for mortality and germination is more positively correlated when germination is low; put another way, the model structure makes it challenging to determine whether small numbers of observed seedlings are due to low germination or high mortality.

5.3 Consequences of model misspecification

Fitting the A/C model to observations from a seed bank with constant morality and germination has a strong influence on parameter estimates for seed addition experiments. In particular, estimates of first year seed mortality from seed addition experiments are biased and associated with high uncertainty when the true probability of germination is low, and when both true probabilities of mortality and germination are high (Fig. S9A-H). In addition, parameter estimates for seed mortality in subsequent years also exhibit higher uncertainty (Fig. S9E-H). In contrast, parameter estimates for seed bag burial experiments are unbiased (Fig. S9A-D). However, uncertainty of second and third year mortality estimates is greater when the mismatched A/C model, rather than the correct C/C model, is fit to the data (compare filled points in Fig. 2E-H and Fig. S9E-H). Increased bias and uncertainty are especially pronounced in seed addition experiments because the likelihood produces strong positive correlations in the joint posterior distribution of first year seed mortality and germination (Fig. S6L). Especially for low germination rates, this correlation can introduce bias and uncertainty into parameter estimates. For seed bag burial experiments, correlations between second and third year seed mortality (Fig. S6I) similarly contribute to increased uncertainty in those estimates.

We fit the C/C model to observations from simulations in which the probability of seed mortality increases over time ($p_{\mathrm{m},1} = 0.1, p_{\mathrm{m},2} = 0.2, p_{\mathrm{m},3} = 0.3$), for a range of true germination probabilities. Note that when we analyze this case, we are comparing a single estimated parameter to three true mortality parameters. For both seed bag burial and seed addition experiments, seed age and the true probability of germination interact to determine the direction and magnitude of bias in mortality (Fig. 3A-C). Both experiments progress from overestimating to underestimating mortality. When the true probability of germination is low, mortality is overestimated more strongly (greater positive bias) for young than old seeds, but mortality is underestimated to a lesser extent (less negative bias) for old seeds. In the first year, seed bag burial experiments exhibit less bias than seed addition experiments; this pattern reverses by the third year. The relationship between true germination probability and parameter uncertainty is the same across all mortality parameters (Fig. 3E-G). Uncertainty decreases with germination rate for seed addition experiments, but increases slightly with germination rate for seed bag burial experiments. For most of the scenarios we considered, low accuracy of parameter estimates translates into low coverage (Fig. 3I-K). The single exception is that year two mortality exhibited nominal coverage (roughly 95%) at intermediate germination rates. The root-mean squared error (RMSE) for mortality is largely determined by the bias of estimates; estimates with a smaller absolute bias also show smaller RMSE (Fig. 3M-O).

The 'true' probability of germination does not depend on seed age in the simulation, but germination estimates are slightly biased for both seed bag burial and seed addition experiments (Fig. 3D). For both experiments, the bias of germination estimates also increases with the true probability of germination. Although the absolute magnitude of bias is smaller than for mortality estimates, germination is overestimated from 6-19% across all scenarios. The greater uncertainty of germination estimates from seed addition experiments (Fig. 3H) translates into higher coverage (Fig. 3L). However, coverage for both experiments is far below the desired level of 95%. As with mortality, RMSE is largely a function of the bias of parameter estimates (Fig. 3P).

6 Discussion

We develop and analyze statistical models for observations from field experiments commonly used to study the soil seed bank. We present the first systematic evaluation and comparison of inferences made with statistical models for seed bag burial and seed addition experiments. We show that seed bag burial experiments can separately estimate mortality and germination even if one, or both, are age-dependent. For seed addition experiments, we demonstrate that seed mortality and germination are only identifiable if both mortality and germination do not change with seed age and with more than one year of observations. In all other cases, it is impossible to separately estimate mortality and germination.

To compare the statistical properties of estimates from seed bag burial and seed addition experiments, we focus on identifiable models with constant mortality and constant germination. We place model identifiability upstream of the statistical properties of parameter estimates because the latter issues are contingent on having reliable statistical models. Estimates from both experiments are unbiased as the number of bags or plots increases. However, estimates from seed bag burial experiments are more precise for all parameter combinations that we consider.

In practice, researchers may fit models that describe seed mortality and germination with more or fewer parameters than necessary. We thus evaluate two scenarios in which we fit the wrong model to observations. In one case, we fit a model with age-dependent mortality and constant germination rates to observations produced by constant mortality and constant germination. Fitting the more complicated model makes the parameter estimates more sensitive to the structure of the model. The effect is strongest for seed addition experiments when germination rates are low, and introduces bias and uncertainty into estimates of mortality. In a second case, we fit a model with constant mortality and germination rates to observations produced by age-dependent mortality and constant germination. The bias of mortality estimates changes over time, and is exacerbated by increased precision at higher germination rates. Germination estimates are also biased, though to a lesser extent.

6.1 Recommendations for practitioners

We demonstrate how seed bag burial or seed addition experiments can be used to estimate seed mortality and germination. From a statistical perspective, seed bag burial experiments have several useful properties. When estimating constant mortality and germination, seed bag burial experiments will produce estimates that are more accurate and precise for a given number of bags or plots.

We suggest that the best way to adapt our general recommendations is to simulate data and fit models to those simulations. Practitioners likely know much about many of the key parts of a seed bank experiment. How many seeds could be collected and used for an experiment, how many replicates are logistically feasible, and for how long would the experiment run? With these pieces in hand, it is possible to use plausible values for seed mortality and germination rates to simulate observations. It will not be possible to know the 'true' values or their age-dependence, but simulations could explore likely scenarios (e.g., constant vs. increasing mortality). Fitting models to these simulations would make it possible to compare the statistical properties of estimates from seed bag burial versus seed addition experiments. To facilitate this process, we include the code for our study (https://doi.org/10.5281/zenodo.7317528); this includes R code to simulate observations, the JAGS code for the models, and the R code to fit the models to observations.

Our analysis can also help guide parameter estimation if observations have already been collected. Lack of identifiability creates issues for both frequentist and Bayesian statistical methods, which we illustrate in detail in **Appendix: Implications of identifiability for model fitting**. No amount of clever modeling can estimate parameters when they are intrinsically not identifiable. Observations from seed bag burial experiments give you the flexibility to fit models with constant or age-dependent mortality and germination. With observations from seed addition experiments, only models with constant mortality and germination are identifiable. Our analysis of model misspecification indicates that fitting a model with more age-dependence than necessary introduces noise into estimates from seed addition experiments but not seed bag burial experiments. In contrast, fitting a model with constant mortality or germination to observations from an age-structured seed bank produces biased estimates for both types of experiments.

Ultimately, the impact of bias or imprecision in estimates of seed mortality or germination on population growth rate depends on the sensitivity of population growth rate to those vital rates. The models and analyses we present will be most relevant to researchers working with plant populations in which aboveground vital rates exhibit high temporal variability because these populations are likely sensitive to transitions in the seed bank (Doak et al., 2002; Nguyen et al., 2019). Considering the broader context of the plant life history can help population ecologists determine which fieldwork and modeling approaches are sufficiently accurate and precise for their study system.

6.2 Extensions

Existing studies have used simulations and post-hoc comparisons to explore the consequences of age structure in the seed bank, emphasize how estimates of seed rates interact with temporal variability in aboveground success, and describe the effect of underestimating parameter uncertainty (Doak et al., 2002; Paniw et al., 2017; Nguyen et al., 2019). However, these methods do not provide an intuitive way to use observations to test assumptions about seed bank structure and associated parameter uncertainty. For example, the methods do not allow for model checks or model selection, both of which could be used to ask whether the fitted model is consistent with observations. Because accuracy and precision of estimates for seed mortality and germination interact with information about other components of the life cycle, it seems crucial to evaluate the model used to estimate seed mortality or germination separately from the population model.

Although estimates from seed addition experiments will be unbiased when mortality and germination do not change with seed age, researchers will generally not know whether this is the case before conducting an experiment. In our simulations, we can assess the accuracy of parameter estimates obtained with these models because we picked the values used to generate the data. While we lack this luxury for empirical datasets, it is possible that standard model checking (e.g., Conn et al. 2018) and model selection (e.g., Hooten and Hobbs 2015; Tredennick et al. 2021) methods could help determine whether the fitted model is consistent with the process that generated the data. For example, it may be possible to use model selection to determine whether a model with constant mortality and germination is a good fit to data from a seed addition experiment. However, further research is required to determine the effectiveness of such approaches.

The relationship between seed age and fate can also be described with continuous functions such as exponential models (e.g., Lommen et al. 2018). Population ecologists have not typically used this approach to analyze observations from seed bank experiments (**Appendix: Literature synthesis**; 12.3% fit models with continuous functions). However, continuous descriptions of seed fate could reduce the number of model parameters in cases where estimating the age-dependence of mortality or germination at many ages is of interest (Fox, 2001; Landes et al., 2020). Rees and Long (1993) studied seed bank dynamics by fitting continuous models for recruitment to observations of seedlings from a seed addition experiment. The authors used these models to demonstrate that recruitment is affected by the age-dependence of seed mortality and germination and that seed banks do not, as a rule, exhibit exponential decay (Rees and Long, 1993). However, they did not separately estimate seed mortality and germination, which are processes that population ecologists are often interested in obtaining separate information on (**Appendix: Literature synthesis**; 3.5% of studies built population models in which mortality and germination were combined).

Our study focuses on statistical issues associated with estimating seed mortality and germination from field experiments, and suggests that seed bag burial experiments present statistical advantages for jointly estimating seed mortality and germination. While we do not evaluate how experimental design affects observations from seed bag burial or seed addition experiments, it is crucial to collect observations that reflect natural levels of seed mortality and germination from the soil seed bank. For example, high seed densities in mesh bags may promote transmission of pathogenic fungi and increase seed mortality (Van Mourik et al., 2005), and seed burial depth can influence mortality and germination rates (Dille et al., 2017). However, researchers can aim to control how much burying seeds in bags alters natural biological processes. Fungal infection can be minimized by mixing seeds with sand or soil to reduce seed-to-seed contact and decrease seed densities (Van Mourik et al., 2005). Appropriate burial depths could be evaluated by conducting pilot experiments (Hernandez et al., 2020) or burying seeds at multiple depths (Philippi, 1993).

Ultimately, how researchers choose to study the seed bank will likely depend on multiple factors including issues related to experimental design, statistical properties of estimates, and the research question being addressed. A strategy for balancing these competing considerations may be to combine information from different types of experiments (e.g., Liu et al. 2005; Bricker and Maron 2012), or from experiments and field surveys (e.g., García 2003; Adams et al. 2005). Approaches that formally integrate data from multiple sources are an active area of research in ecology (Zipkin et al., 2021), and applying these ideas to seed bank studies could help researchers effectively use existing datasets and optimize the collection of future data.

6.3 Limitations

Event history analysis is developed for and appropriately applied to individual data (Zens and Peart, 2003; Landes et al., 2020), and the models we describe would be completely appropriate if applied to observations of individual seeds. Yet seeds of many plant species are too small for individuals to be tracked in the field. When examining aggregate data—from cohorts, or populations—heterogeneity between subpopulations and change in hazards over time can confound whether patterns are the result of changes to hazards or to population structure (Rees and Long, 1993; Zens and Peart, 2003). Our approach is not intended to assess changes to the hazards for individual seeds (unless individual-level data are available) but rather a framework for consistent inferences about seed mortality and germination.

To focus on the commonalities between seed bag burial and seed addition experiments, we describe stereotyped versions of each. Not all experiments in the literature exactly follow the schematic we describe; some seed bag burial experiments count intact seeds and estimate germination in another way (e.g., Lommen et al. 2018), or count only seeds at certain times, but both seeds and germinants at other times (e.g., Eckhart et al. 2011). Individual analyses will inevitably have to be tailored to specific data. We sought to explicitly describe the assumptions underlying our statistical models so that they could be readily modified. Investigators will naturally construct models that are appropriate to their system and aims.

6.4 Conclusion

Observations from seed bag burial and seed addition experiments are hard-won data, but statistical models for observations from these experiments have received little attention to-date. Studying these models can help plant population ecologists make the most of existing and future data by identifying potential models to fit, the statistical properties of parameter estimates, and potential bias introduced by making assumptions about age-dependence of mortality and germination. Our analysis contributes to efforts to make richer inferences from the trove of demographic data collected by plant population ecologists.

7 Acknowledgments

We thank W. F. Morris and T. E. X. Miller for discussions about seed bag experiments that helped prompt this research. We thank S. Ellner, J. Spaak, C Hernández, T. Lambert, A. Poulton, and two anonymous reviewers for comments that greatly strengthend the manuscript. G. Siegmund was supported by a Graduate Research Fellowship (DGE-1144153) from the U.S. National Science Foundation, and a Presidential Life Science Fellowship and Cornell Fellowship from Cornell University. M. A. Geber was supported by the U.S. National Science Foundation (LTREB 1256288 and 1754299).

8 Author contributions

GS and MAG conceived of the ideas in the study. GS developed the statistical model, analyzed identifiability & simulations, and wrote the manuscript with input from MAG.

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9 Tables

Table 1: Likelihoods of models for observations from seed bag burial and seed addition experiments.

Model		
Mortality	Germination	Likelihood
SEED BAG BURIAL EXPERIMENT		
C (p_{m})	C (p_{g})	$f(p_{\mathrm{m}}, p_{\mathrm{g}}) = \prod_{k=1}^{j}(1-p_{\mathrm{m}}) \times (1-p_{\mathrm{g}})^{I(j>1)}$ $L(p_{\mathrm{m}}, p_{\mathrm{g}} \mid \mathrm{y_g}, \mathrm{y}) = \prod_{i=1}^{I}\Big[\prod_{j=1}^{J_i}\big[\mathrm{binomial}(y_{\mathrm{g},ij} \mid n_{\mathrm{g},ij}, p_{\mathrm{g}})\mathrm{binomial}\big(y_{ij} \mid n_{ij}, f(p_{\mathrm{m}}, p_{\mathrm{g}})\big)\big]\Big]$
A ($p_{\mathrm{m},j}$)	C (p_{g})	$f(p_{\mathrm{m},j}, p_{\mathrm{g}}) = \prod_{k=1}^{j}(1-p_{\mathrm{m},j}) \times (1-p_{\mathrm{g}})^{I(j>1)}$ $L(\boldsymbol{p}_{\mathrm{m}}, p_{\mathrm{g}} \mid \mathrm{y_g}, \mathrm{y}) = \prod_{i=1}^{I}\Big[\prod_{j=1}^{J_i}\big[\mathrm{binomial}(y_{\mathrm{g},ij} \mid n_{\mathrm{g},ij}, p_{\mathrm{g}})\mathrm{binomial}\big(y_{ij} \mid n_{ij}, f(p_{\mathrm{m},j}, p_{\mathrm{g}})\big)\big]\Big]$
C (p_{m})	A ($p_{\mathrm{g},j}$)	$f(p_{\mathrm{m}}, p_{\mathrm{g},j}) = \prod_{k=1}^{j}(1-p_{\mathrm{m}}) \times (1-p_{\mathrm{g},j})^{I(j>1)}$ $L(p_{\mathrm{m}}, \boldsymbol{p}_{\mathrm{g}} \mid \mathrm{y_g}, \mathrm{y}) = \prod_{i=1}^{I}\Big[\prod_{j=1}^{J_i}\big[\mathrm{binomial}(y_{\mathrm{g},ij} \mid n_{\mathrm{g},ij}, p_{\mathrm{g},j})\mathrm{binomial}\big(y_{ij} \mid n_{ij}, f(p_{\mathrm{m}}, p_{\mathrm{g},j})\big)\big]\Big]$
A ($p_{\mathrm{m},j}$)	A ($p_{\mathrm{g},j}$)	$f(p_{\mathrm{m},j}, p_{\mathrm{g},j}) = \prod_{k=1}^{j}(1-p_{\mathrm{m},j}) \times (1-p_{\mathrm{g},j})^{I(j>1)}$ $L(\boldsymbol{p}_{\mathrm{m}}, \boldsymbol{p}_{\mathrm{g}} \mid \mathrm{y_g}, \mathrm{y}) = \prod_{i=1}^{I}\Big[\prod_{j=1}^{J_i}\big[\mathrm{binomial}(y_{\mathrm{g},ij} \mid n_{\mathrm{g},ij}, p_{\mathrm{g},j})\mathrm{binomial}\big(y_{ij} \mid n_{ij}, f(p_{\mathrm{m},j}, p_{\mathrm{g},j})\big)\big]\Big]$
SEED ADDITION EXPERIMENT		
C (p_{m})	C (p_{g})	$f(p_{\mathrm{m}}, p_{\mathrm{g}}) = p_{\mathrm{g}} \times \prod_{k=1}^{j}(1-p_{\mathrm{m}}) \times (1-p_{\mathrm{g}})^{I(j>1)}$ $L(p_{\mathrm{m}}, p_{\mathrm{g}} \mid \mathrm{y_g}) = \prod_{i=1}^{I}\Big[\prod_{j=1}^{J_i}\mathrm{binomial}\big(y_{\mathrm{g},ij} \mid n_{\mathrm{g},ij}, f(p_{\mathrm{m}}, p_{\mathrm{g}})\big)\Big]$
A ($p_{\mathrm{m},j}$)	C (p_{g})	$f(p_{\mathrm{m},j}, p_{\mathrm{g}}) = p_{\mathrm{g}} \times \prod_{k=1}^{j}(1-p_{\mathrm{m},j}) \times (1-p_{\mathrm{g}})^{I(j>1)}$ $L(\boldsymbol{p}_{\mathrm{m}}, p_{\mathrm{g}} \mid \mathrm{y_g}) = \prod_{i=1}^{I}\Big[\prod_{j=1}^{J_i}\mathrm{binomial}\big(y_{\mathrm{g},ij} \mid n_{\mathrm{g},ij}, f(p_{\mathrm{m},j}, p_{\mathrm{g}})\big)\Big]$
C (p_{m})	A ($p_{\mathrm{g},j}$)	$f(p_{\mathrm{m}}, p_{\mathrm{g},j}) = p_{\mathrm{g},j} \times \prod_{k=1}^{j}(1-p_{\mathrm{m}}) \times (1-p_{\mathrm{g},j})^{I(j>1)}$ $L(p_{\mathrm{m}}, \boldsymbol{p}_{\mathrm{g}} \mid \mathrm{y_g}) = \prod_{i=1}^{I}\Big[\prod_{j=1}^{J_i}\mathrm{binomial}\big(y_{\mathrm{g},ij} \mid n_{\mathrm{g},ij}, f(p_{\mathrm{m}}, p_{\mathrm{g},j})\big)\Big]$
A ($p_{\mathrm{m},j}$)	A ($p_{\mathrm{g},j}$)	$f(p_{\mathrm{m},j}, p_{\mathrm{g},j}) = p_{\mathrm{g},j} \times \prod_{k=1}^{j}(1-p_{\mathrm{m},j}) \times (1-p_{\mathrm{g},j})^{I(j>1)}$ $L(\boldsymbol{p}_{\mathrm{m}}, \boldsymbol{p}_{\mathrm{g}} \mid \mathrm{y_g}) = \prod_{i=1}^{I}\Big[\prod_{j=1}^{J_i}\mathrm{binomial}\big(y_{\mathrm{g},ij} \mid n_{\mathrm{g},ij}, f(p_{\mathrm{m},j}, p_{\mathrm{g},j})\big)\Big]$

[1] In columns 1 and 2, C is a constant hazard and A is an age-dependent hazard.

[2] In all likelihoods, $I(x)$ is an indicator function equal to 1 if the inequality is true, and 0 if it is not. As discussed in the main text, the indicator function identifies whether or not seeds have yet experienced a germination opportunity; at the first time point j, they have not.

Table 2: Analysis of intrinsic identifiability for models with different assumptions about whether germination and mortality are constant or age-dependent. Each row corresponds to a model in which the germination component is defined in column one and the mortality component is defined in column two. For each model, the columns show the results of the intrinsic identifiability analysis for 1, 2, or 3 years of observations. The analysis identifies the deficiency of the model for a given set of assumptions about the germination and mortality components. The deficiency is calculated as in Cole (2020): the number of parameters in the model minus the rank of the derivative matrix, the latter calculated by the symbolic method. Models with a deficiency of 0 are identifiable; models with a deficiency greater than 0 are not identifiable.

Model		Deficiency		
Mortality component	Germination component	1 year	2 years	3 years
SEED BAG BURIAL EXPERIMENT				
Constant (p_{m})	Constant (p_{g})	0	0	0
Age-dependent ($p_{\mathrm{m},j}$)	Constant (p_{g})	0	0	0
Constant (p_{m})	Age-dependent ($p_{\mathrm{g},j}$)	0	0	0
Age-dependent ($p_{\mathrm{m},j}$)	Age-dependent ($p_{\mathrm{g},j}$)	0	0	0
SEED ADDITION EXPERIMENT				
Constant (p_{m})	Constant (p_{g})	1	0	0
Age-dependent ($p_{\mathrm{m},j}$)	Constant (p_{g})	1	1	1
Constant (p_{m})	Age-dependent ($p_{\mathrm{g},j}$)	1	1	1
Age-dependent ($p_{\mathrm{m},j}$)	Age-dependent ($p_{\mathrm{g},j}$)	1	2	3

10 Figure captions

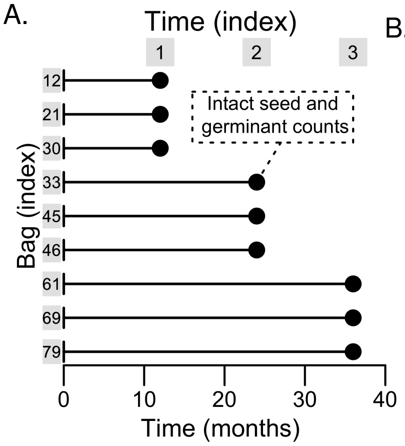
Figure 1. (A) Schematic of a seed bag burial experiment. Each bag in the experiment is represented by a single line from when the bag is buried at month 0 to when the bag is dug up for sampling (filled circles). The data are organized with indices for bag and sampling time. (B) Data from the seed bag burial experiment. Each row corresponds to a bag and sampling time. (C) Schematic of a seed addition experiment. Each plot in the experiment is represented by a single line from when seeds are added to the plot at month 0 to when plots are censused for seedlings (filled circles). The data are organized with indices for plot and time. (D) Data from the seed addition experiment. Each row corresponds to a plot and sampling time.

Figure 2. Results of simulation experiment in which we generated observations with constant mortality and germination, and fit a model with constant mortality and germination. (A-D) Bias for estimates of mortality, p_{m}, for different combinations of true mortality and germination probability. (E-H) Width of the 95% credible interval for p_{m}. (I-L) Bias for estimates of germination, p_{g}, for different combinations of true mortality and germination probability. (M-P) Width of the 95% credible interval for p_{g}. In all panels, error bars represent the 95% confidence interval based on a *t* distribution.

Figure 3. Results of simulation experiment in which we generated observations with age-dependent mortality and germination, and fit a model with constant mortality and germination. The true probability of mortality increases over time: $p_{\mathrm{m},1} = 0.1,\ p_{\mathrm{m},2} = 0.2$, and $p_{\mathrm{m},3} = 0.3$. From left to right, columns are analyses of mortality for ages 1, 2, and 3, and germination. Each panel shows the statistical properties for parameters from simulations with true probabilities of germination from 0.1 to 0.5. The number of bags or plots is always $n = 30$. (A-D) Bias for estimates of mortality and germination. Error bars represent the 95% confidence interval based on a *t* distribution. (E-H) Width of the 95% credible interval for mortality and germination. Error bars represent the 95% confidence interval based on a *t* distribution. (I-L) Coverage for mortality and germination. Error bars represent the 95% confidence interval calculated using the Wilson method for binomial proportions. (M-P) Root mean squared error for mortality and germination.

11 Figures

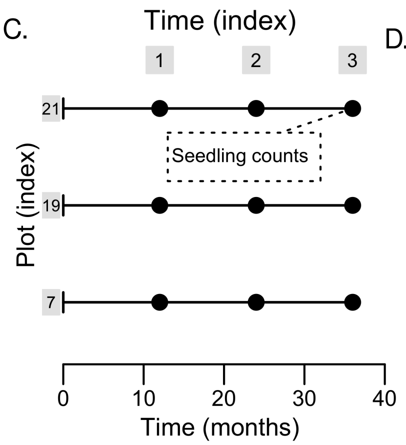
A.



B.

Indices		Variable	Data (counts)			Calculated (counts)	
Bag	Time	Time (months)	Starting seeds	Intact seeds	Germinants	Survivors	Surviving seeds
i	j	t_{ij}	n_{ij}	—	$y_{g,ij}$	y_{ij}	$n_{g,ij}$
12	1	12	100	27	27	54	54
21	1	12	100	25	29	54	54
30	1	12	100	21	22	43	43
33	2	24	100	2	4	6	6
45	2	24	100	8	9	17	17
46	2	24	100	1	4	5	5
61	3	36	100	0	1	1	1
69	3	36	100	1	2	3	3
79	3	36	100	2	2	4	4

C.



D.

Indices		Variable	Data (counts)	
Plot	Time	Time (months)	Added seeds	Seedlings
i	j	t_{ij}	n_{ij}	$y_{g,ij}$
7	1	12	100	22
19	1	12	100	26
21	1	12	100	29
7	2	24	100	7
19	2	24	100	8
21	2	24	100	4
7	3	36	100	3
19	3	36	100	1
21	3	36	100	1

Figure 1: (A) Schematic of a seed bag burial experiment. Each bag in the experiment is represented by a single line from when the bag is buried at month 0 to when the bag is dug up for sampling (filled circles). The data are organized with indices for bag and sampling time. (B) Data from the seed bag burial experiment. Each row corresponds to a bag and sampling time. (C) Schematic of a seed addition experiment. Each plot in the experiment is represented by a single line from when seeds are added to the plot at month 0 to when plots are censused for seedlings (filled circles). The data are organized with indices for plot and time. (D) Data from the seed addition experiment. Each row corresponds to a plot and sampling time.

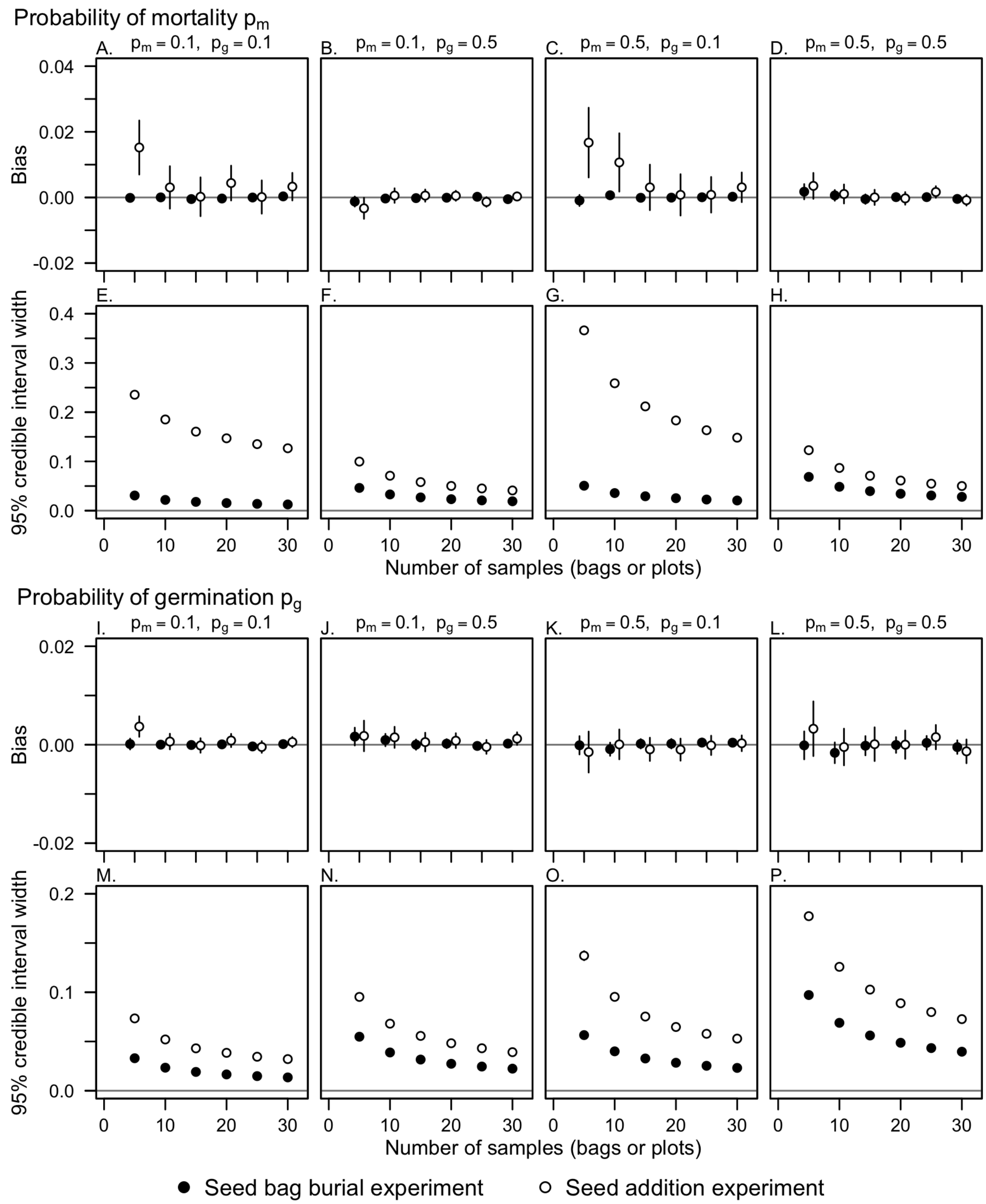


Figure 2: Results of simulation experiment in which we generated observations with constant mortality and germination, and fit a model with constant mortality and constant germination parameters. (A-D) Bias for estimates of mortality probability, p_{m}, for different combinations of true mortality and germination probability. (E-H) Width of the 95% credible interval for p_{m}. (I-L) Bias for estimates of germination probability, p_{g}, for different combinations of true mortality and germination probability. (M-P) Width of the 95% credible interval for p_{g}. In all panels, error bars represent the 95% confidence interval based on a t distribution.

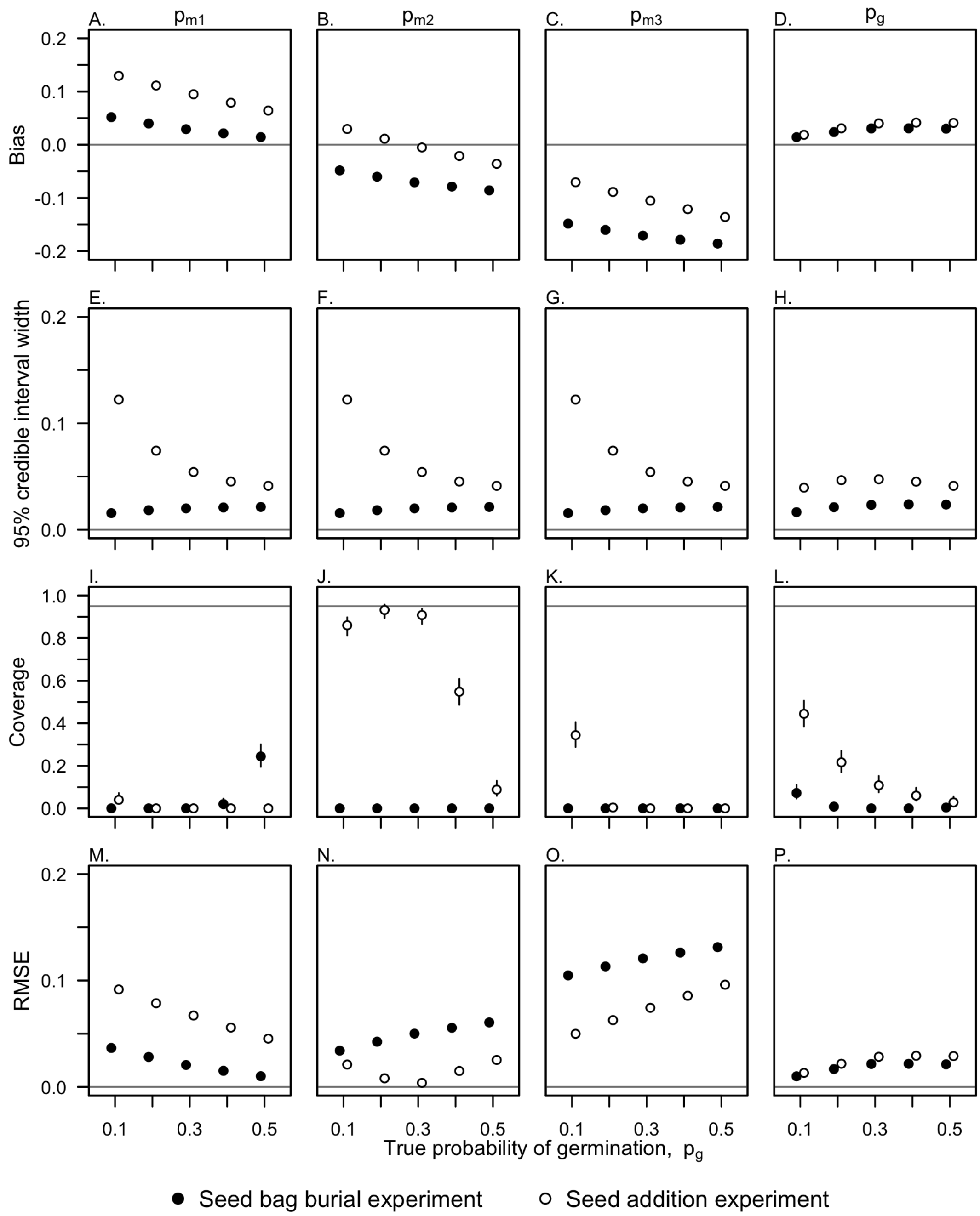


Figure 3: Results of simulation experiment in which we generated observations with age-dependent mortality and germination, and fit a model with constant mortality and germination. The true probability of mortality increases over time: $p_{m,1} = 0.1$, $p_{m,2} = 0.2$, and $p_{m,3} = 0.3$. From left to right, columns are analyses of mortality for ages 1, 2, and 3, and germination. Each panel shows the statistical properties for parameters from simulations with true probabilities of germination from 0.1 to 0.5. The number of bags or plots is always $n = 30$. (A-D) Bias for estimates of mortality and germination. Error bars represent the 95% confidence interval based on a t distribution. (E-H) Width of the 95% credible interval for mortality and germination. Error bars represent the 95% confidence interval based on a t distribution. (I-L) Coverage for mortality and germination. Error bars represent the 95% confidence interval calculated using the Wilson method for binomial proportions. (M-P) Root mean squared error for mortality and germination.