# Estimating seed vital rates

I describe how I estimate seed viability, survival, and germination from seed bag burial experiments. Because seeds are difficult if not impossible to follow in the same way as aboveground plants, following them has proven particularly challenging for plant ecologists. While many plants do not have seed banks, uncertainty about seed-related parameters can have big impacts on estimates of population growth rate and persistence. In particular, uncertainty about seed-related parameters can dominate overall uncertainty about population growth rate.

References: Lonsdale 1988, Kalisz 1991, Rees 1991, Kalisz and McPeek 1993, Rees and Long 1993, Doak et al. 2002, Evans et al. 2010, Elderd and Miller 2015, …

# Field experiment: seed bag burial

To estimate the survival and germination of seeds of different ages, we buried seeds for one, two, and three years. Seeds were collected in July and buried in October. Each buried bag contained 100 seeds. The bags were first revisited in January to count seedlings and remaining intact seeds in each bag. The bags were then buried again and unearthed in October when intact seeds were again counted.

We collected the following data from these trials:

* Number of intact, ungerminated seeds in January [p(s1)]
* Number of seedlings in January [p(g1)]
* Number of intact seeds in October [p(s2)]

# Lab experiment: two-stage trials

To estimate the viability of intact seeds, we conducted a two-stage trial in the lab. We used all or a subset of intact seeds from each bag for these trials. First, we conducted germination trials with these seeds. Seeds were placed on filter paper and followed for germination. Second, we took all or a subset of the seeds that did not germinate and tested them for viability by cutting them opening and staining them.

We collected the following data from these trials:

* Proportion of seeds germinating in the germination trials [nu\_g]
* Proportion of seeds viable in the viability trials [nu\_v]

# Inferred and derived quantities

I use the data from the seed burial and lab trials to infer the mean and variance of each set of data. Because the model I use is hierarchical, with population- and population-by-year groups, these estimates are ‘shrunk’ towards the group means. The amount of shrinkage in these estimates depends on the degree of within vs. between group variance. Sample size and sample variance both are correlated with the amount of shrinkage.

I check for model convergence and assess fit for these estimates. Fit can be assessed with posterior predictive checks and Bayesian p-values.

Many of the quantities that we are interested in for understanding seed bank dynamics are not directly observed in the experiments. Instead, these are derived quantities that are functions of the estimated parameters. We are interested in the following quantities:

* Viability in October: combines the two stages of the lab trials [nu]
* Probability of surviving to January: corrected for viability [p(v|s1)]
* Probability of germinating in January, given surviving: corrected for viability and estimate of survival [p(g1|s1,v)]
* Probability of surviving to October, given not germinating and surviving in January: corrected for viability and germination [p(s2|s1,v,g^c)]

In a Bayesian modeling workflow, all these quantities can be estimated simultaneously and uncertainty about one estimate can properly be transmitted to other estimates.

# Age structure

I estimated these rates for one-, two-, and three-year old seeds. Because of how I estimate germination and survival from October to January, these rates are estimated similarly as for one-year old seeds. However, survival from the start of the experiment to January covers different amounts of time. For one year old seeds, this is three months. For two year old seeds, this is 15 months. For three year old seeds, this is 27 months.

I will estimate viability for each age separately and plot estimates. If viability decreases over time it seems likely that the proportion of viable seeds decreases. If viability increases over time it seems likely that the proportion of intact seeds that are viable increases. This is possible if the seeds that are decaying are not viable. These patterns may also be associated with different probabilities of germination.

I will then estimate transitions from the start of the experiment to the current time (percent emerging and percent persisting cf. Kalisz 1991). I will estimate these for number of total seeds in January, seedlings in January, and intact seeds in October; each of these will also be corrected for the estimated viability of seeds. I will then estimate ­conditional probabilities of emergence and persistence (cf. Kalisz 1991), which will also be corrected for the estimated viability of seeds. This is relatively straightforward for age 1 probabilities but becomes more complicated for age 2 and 3 probabilities because these are the product of unobserved processes in the bag up to January of the year the bags are sampled.

# Combining experiments

This approach also gives us a way of combining different datasets. After the intensive seed bag experiments, Monica started a number of years of seed pot experiments. These experiments only include data on the number of initial seeds, and seedlings after one, two, and three years. These data are equivalent to the inferred parameter [p(g1)] in the first round, which is the product of viability and survival.

The structure of the data is such that for a single seed survivorship curve, we have multiple datasets. We can take the approach of fitting the data sequentially, estimating survival to the end of the first dataset and then adjusting subsequent rates. Alternatively, we can take the approach of fitting the data jointly, estimating the likelihood of all the data at once. Finally, we can ignore the structure of the data and simply fit a time-dependent function to the data.

# Age-dependent vital rates and decay functions

In the absence of data on the seed bank, previous studies (Evans et al. 2010 and Elderd/Miller 2016) have fit exponential decay functions to emergence data. Although seeds do not uniformly follow this pattern (Rees 1993) it seems like these functions are one way to incorporate the seed bank with limited information. With information about age-dependent survival and germination, we test how appropriate a decay function is.

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| Modeled quantities | | |
| nu\_g | Probability of germination | Lab trial, stage one |
| nu\_v | Probability of staining | Lab trial stage two |
| p\_1 | Probability of a seed being intact from October to January | Field experiment, January |
| p\_2 | Probability of a seedling emerging, conditional on seeds being intact | Field experiment, January |
| p\_3 | Probability of a seed being intact in October, conditional on being intact in January | Field experiment, October |
| p\_e | Probability of a seed being intact in October, conditional on being intact in January | Field experiment, October |
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| p\_5 | Probability of a seedling emerging year 2, conditional on seeds being intact in year 2 | Field experiment, January year 2 |
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| Derived quantities | | |
| nu\_1 | Probability of viability in year 1 | Composite of lab trial stages |
| s\_1 | Probability of a seed being intact and viable from October to January | Composite of viability, p\_1 and p\_2 |
| g\_1 | Probability of germination for a seed that is intact and viable in January | Composite of viability and p\_2 |
| s\_2 | Probability of a seed that is intact and viable in January being intact and viable in October | Composite of viability and p\_3 |
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| nu\_2 | Probability of viability in year 2 | Composite of lab trial stages |
| nu\_2c | Adjusted probability of viability in year 2 | Year 1 and year 2 viability composites if year 2 is less than year 1 viability, year 2 viability only if it is greater |
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