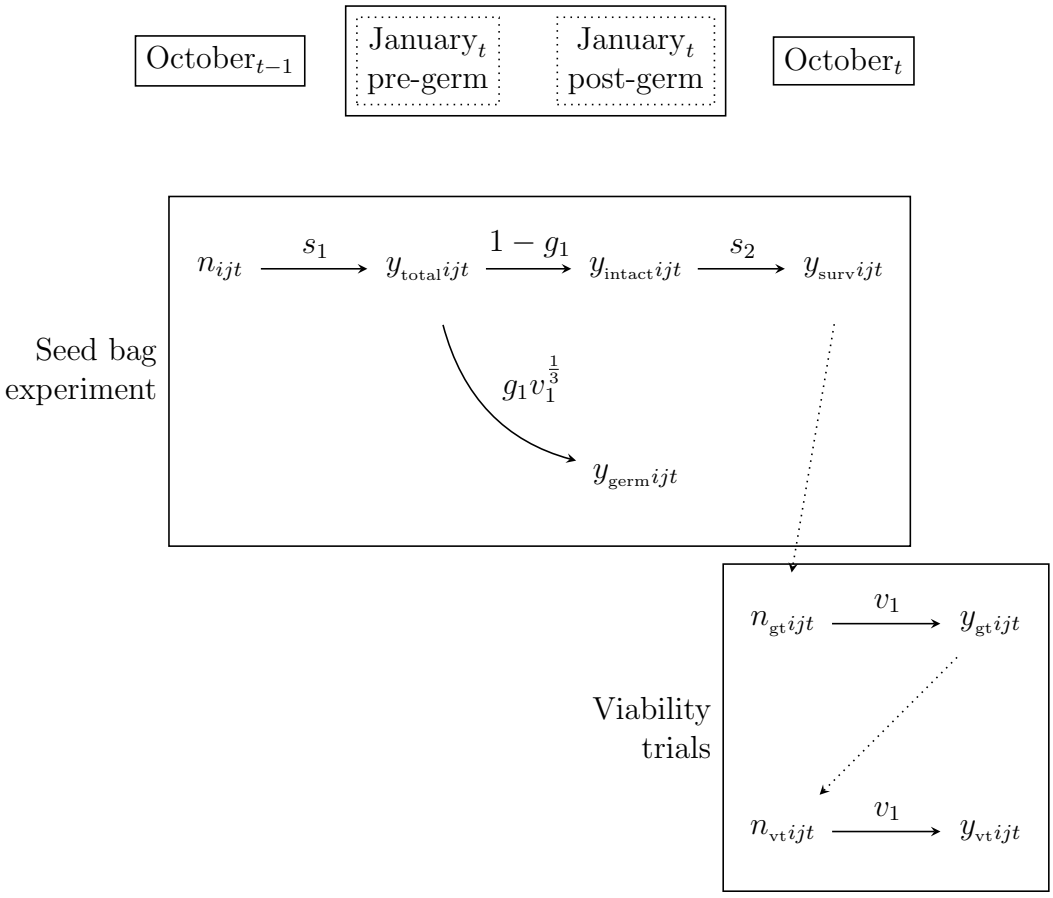
Parameter estimates for belowground transitions

The figure below illustrates the transitions in the first year the seed bags are buried. There are two boxes: one for the seed bag experiment and one for the viability trials. In the seed bag experiment, I split January into two steps, one for just before germination and one for just after. Solid arrows represent transitions and are labeled with corresponding vital rates. In the models, I have adopted $s_1 = \phi$, $g_1 = \gamma$, $s_2 = \rho$, and $v_1 = \upsilon$.



In the seed bag experiment, the parameter s_1 is the proportion of seeds from the start of the experiment that remain intact in January. In January, the remaining seeds are in one possible state: intact (this includes viable and non-viable seeds). We assume that there is no decay during germination (seed loss happens over extended periods of time, not instantaneously in January) so that the number of seeds before germination is equal to the number of seeds and seedlings after germination. At this point, the seeds have transitioned into one of four possible states. Intact and viable seeds may have (1) germinated or (2) not germinated and thus remain dormant. Because non-viable seeds could not have germinated (forbidden state 3), all other intact seeds would have been non-viable (4).

I represent two transitions between pre-germination seeds in January and post-germination seeds and seedlings in January. The first is for seeds that are viable and germinate; these become seedlings. The second is for seeds that do not germinate; these remain seeds and include both viable and non-viable seeds (the sum of $(1-g_1)v_1^{\frac{1}{3}} and (1-g_1)(1-v_1^{\frac{1}{3}})$. For the purposes of parameter estimation, we only represent the number of seedlings —viability is estimated separately.

We want to incorporate the loss of viability into our model. We assume that the rate of loss of viability is constant, and that germination removes some number of seeds from the pool of viable seeds but does not change the rate of decay. Some fraction of the total seeds in January pre-germination is viable ($v_1^{\frac{1}{3}}$) and some of those viable seeds germinate. We include viability in our estimates of germination rate so as to not overestimate the true germination rate. The number of seeds that remain intact are those that do not germinate $(1-g_1)$, which includes both viable ($v_1^{\frac{1}{3}}$) and non-viable $(1-v_1^{\frac{1}{3}})$ seeds. Seeds that germinate must be viable.

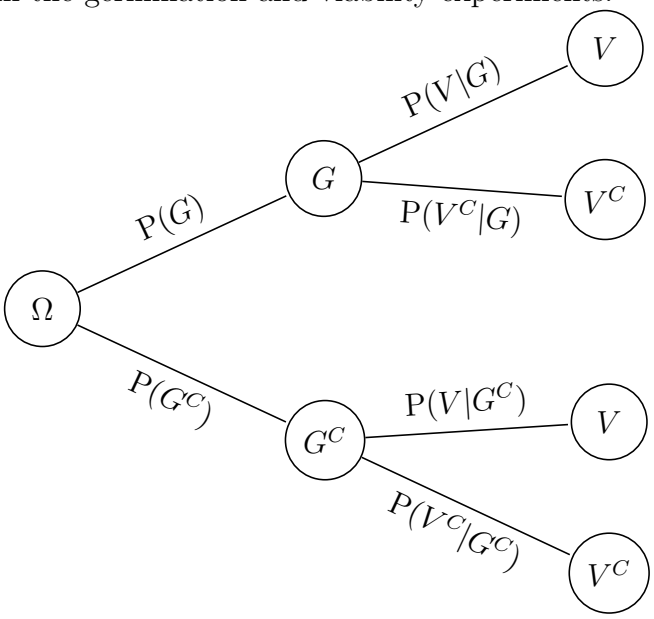
Here, we use viability in our germination estimates. For the full life cycle, this would model the rates of intact seeds and only incorporate viability in the germination transition.

Viability trials

In October (year $t+1$), we first removed the bags and counted the number of ungerminated, intact seeds. In the lab, we conducted germination trials and viability assays on subsets of the seeds from each bag to estimate the viability of the ungerminated, intact seeds. We collected the following data:

- $n_{\text{germ}ijt}$ = observed count of seeds at the start of the germination trial for the i^{th} bag, from the j^{th} site, in the t^{th} year, assumed to be measured perfectly
- $y_{\text{germ}ijt}$ = observed count of germinated seedlings in the i^{th} bag, from the j^{th} site, in the t^{th} year, assumed to be measured perfectly
- $n_{\text{viab}ijt}$ = observed count of seeds at the start of the viability trial for the i^{th} bag, from the j^{th} site, in the t^{th} year, assumed to be measured perfectly
- $y_{\text{viab}ijt}$ = observed count of viable seedlings in the i^{th} bag, from the j^{th} site, in the t^{th} year, assumed to be measured perfectly

We use a conditional probability tree to graphically represent how to compose the estimates from the germination and viability experiments.



We assume that (1) any seed that germinates is viable, P($V|G$)=1, and that (2) any seed that germinates can not be not viable, P($V^C|G$)=0. We used experiments to estimate the probability of germinating, P(G), and the probability of being viable conditional on not germinating, P($V|G^C$). We use these probabilities to calculate the total probability of being viable, P(V) = P(G) + P($V|G^C$)×(1-P(G^C)).

We use the experiments to estimate:

- γ_i = the true, unobserved proportion of seeds that germinate in the October germination trials in the i^{th} bag
- υ_i = the true, unobserved proportion of intact seeds that are viable given that they did not germinate in the October germination trials in the i^{th} bag

The germination experiment and viability experiment can each be modeled as binomial trials.

$$[\boldsymbol{\gamma}|\boldsymbol{n}_{\mathbf{germ}}, \boldsymbol{y}_{\mathbf{germ}}] \propto \prod_{i=1}^{I} \text{binomial}(y_{\text{germ}i}|n_{\text{germ}i}, \gamma_i) \times \text{beta}(\gamma_i|1,1) \tag{1}$$

$$[\boldsymbol{\upsilon}|\boldsymbol{n}_{\mathbf{viab}}, \boldsymbol{y}_{\mathbf{viab}}] \propto \prod_{i=1}^{I} \text{binomial}(y_{\text{viab}i}|n_{\text{viab}i}, \upsilon_i) \times \text{beta}(\upsilon_i|1,1) \tag{2}$$

The binomial and beta distributions are conjugate distributions, so we can obtain a closed form for each posterior. These are given as beta distributions, $\text{beta}(\phi|\alpha_{posterior}, \beta_{posterior})$, where $\alpha_{posterior} = \alpha_{prior} + y$ and $\beta_{posterior} = \beta_{prior} + n - y$.

Eckhart et al. (2011) previously analyzed these data by obtaining point estimates for the proportion of seeds that germinate, P(G), and the proportion of seeds that do not germinate that are viable, P($V|G^C$). These estimates were then used to calculate the proportion of seeds that were viable, P(V) = P(G) + P($V|G^C$)×(1-P(G^C)).

The point estimates for germination and viability in Eckhart et al. (2011) are equivalent to the maximum a posteriori (MAP) of the posterior distribution for each experiment. The MAP is the mode of the posterior distribution. The mode of a beta distribution is given by:

...

Obtaining the point estimate for germination and viability probability by the method in Eckhart et al. (2011) and from the MAP of the beta posteriors gives identical results. Intuitively, this makes sense: the proportion of successes out of trials should be the same as the probability at which the distribution is maximized. So far so good. This establishes that the two approaches are equivalent. In both cases, we obtain point estimates for the probability that seeds in a bag are viable but this is estimate is not a parameter with a distribution but rather a point estimate.

This is a bit unsatisfying because it means that this term scales the binomial model for germination up or down, but only by a constant rather than a full probability distribution.

A possible approximation would be the following. The successes is the number of seeds that germinate plus the number of seeds that stain in viability trials. The number of trials is the

number of seeds that started the viability trial plus those that germinated in the germination trial. So the effect is to supplement the data from the viability trial with additional successes. This would be appropriate if all the ungerminated seeds were tested for viability (this wasn't usually met). We can get closer if we discard any of the data for which fewer than 50% of ungerminated seeds were tested.

The benefit of having viability be a parameter with a distribution is that it would be comparable to other parameters in the model. Our estimates of germination and dormancy from the seed bags are incorporate estimates of viability. If germination probability is a parameter with a distribution but viability is not, all the uncertainty in our estimate of germination is the result of uncertainty in germination rather than combined uncertainty in germination and viability. The same holds for dormancy.

I consider the following approximation. First, I discard the data for which fewer than 50% of ungerminated seeds were tested. This results in losing some data but means that we retain viability trials in which more than half the seeds that didn't germinate were tested for viability. [explain ...] The successes is the number of seeds that germinate plus the number of seeds that stain in viability trials. This is the total number of seeds that we identified as viable across both sets of experiments. The number of trials is the number of seeds that started the viability trial plus those that germinated in the germination trial. The effect is to supplement the data from the viability trials with additional successes and associated trials from the germination trials. Although this is a compromise between the two datasets, it would be appropriate if all the ungerminated seeds were tested for viability. Quantify this in some way...x% of seed bags had more than 50% of bags tested?

I also show that this is a reasonable approximation for this dataset by plotting the MAP of the posterior from the combined dataset against the viability probability obtained by point estimates. In Figure X, a 1:1 relationship between the two estimation methods suggests that the estimates are comparable. I show the relationship between the two estimates for all data, with only data ¿50% tested for viability (loss of x% of dataset), and with only data ¿75% tested for viability (loss of x% of dataset). The plots show the correlation and R2. Given that these estimates are relatively comparable, we proceed with the analysis using the combined dataset to estimate viability.

This would be a parameter in a joint posterior, and thus have an associated probability distribution. One problem: the two experiments are sequently and not truly independent. If a seed germinates in the first experiment, it isn't tested for viability. So when I considered modeling the germination and viability experiments with a shared viability parameter, but this didn't seem to make sense if germination and viability were nested responses. I considered obtaining a posterior from the first experiment in the form of a beta distribution, and then using this as a prior to analyze the second experiment. Again, this didn't really make sense because the responses were on the same seeds. I also thought about multiplying and

summing the beta posteriors. The product and sum of betas looks pretty ugly so I didn't go down this rabbit hole yet. But maybe this is the way to go? It seems messy and I guess I'm not sure what I get by pulling out this closed form. In particular, the closed form involves hypergeometric functions that are unlikely to be useful in writing up a mathematical expression for the joint posterior.

Next, I considered using a model with partial pooling for binary repeated trials. In the model above, the closed form neatly represents the per-bag viability. First, I wasn't sure how to use the per-bag viability in the joint posterior with the germination data. Should the germination model include the bag-level viability estimate or the site-level viability estimate? Germination itself was going to be a site-level estimate, but maybe it made sense to account for differences in viability among different bags. Thinking about this also had me wondering how I would calculate dormancy as a derived quantity. If dormancy involves the product of germination and viability, then these two terms must be calculated at the same level. The best way I could think of doing this involved rewriting the models with a log-odds parameterization. This makes it possible to estimate a mean for different levels (bag- and site-level means) with separate variances. I've coded the model to run for one population but need to get it up for multiple populations (issues with indexing). The other extension would be a non-centered parameterization.

I started with the following parameterization. I took one site k, and ignored bags j, so that I only modeled trials i as coming from a population of trials:

$$\begin{aligned}[\boldsymbol{\alpha}, \mu, \sigma, |\boldsymbol{n}, \boldsymbol{y}] \propto & \prod_{i=1}^{I} \text{binomial}(y_i|n_i, \text{logit}^{-1}(\alpha_i)) \\ & \times \text{normal}(\alpha_i|\mu, \sigma) \\ & \times \text{normal}(\mu|0, 100)\text{uniform}(\sigma|0, 100).\end{aligned} \tag{3}$$

I then tried to ignore site and give each bag at a single site k its own prior. I don't know if I coded this incorrectly but this model **did not fit well**. In any case this amounted to modeling trial i in bag j as:

$$\begin{aligned}[\boldsymbol{\alpha}, \boldsymbol{\mu}, \boldsymbol{\sigma}, |\boldsymbol{n}, \boldsymbol{y}] \propto & \prod_{j=1}^{J} \prod_{i=1}^{I} \text{binomial}(y_{ij}|n_{ij}, \text{logit}^{-1}(\alpha_{ij})) \\ & \times \text{normal}(\alpha_{ij}|\mu_j, \sigma_j) \\ & \times \text{normal}(\mu_j|0, 100)\text{uniform}(\sigma_j|0, 100).\end{aligned} \tag{4}$$

I then tried to change the data that I worked with. Rather than using individual trials, I summed all n attempts and y successes across all trial for a bag. This gave me one data

point per bag. I first modeled one site k with bags j (now equal to trials i):

$$\begin{aligned}[\boldsymbol{\alpha}, \mu, \sigma, |\boldsymbol{n}, \boldsymbol{y}] \propto & \prod_{j=1}^{J} \text{binomial}(y_j | n_j, \text{logit}^{-1}(\alpha_j)) \\ & \times \text{normal}(\alpha_j | \mu, \sigma) \\ & \times \text{normal}(\mu | 0, 100) \text{uniform}(\sigma | 0, 100).\end{aligned} \tag{5}$$

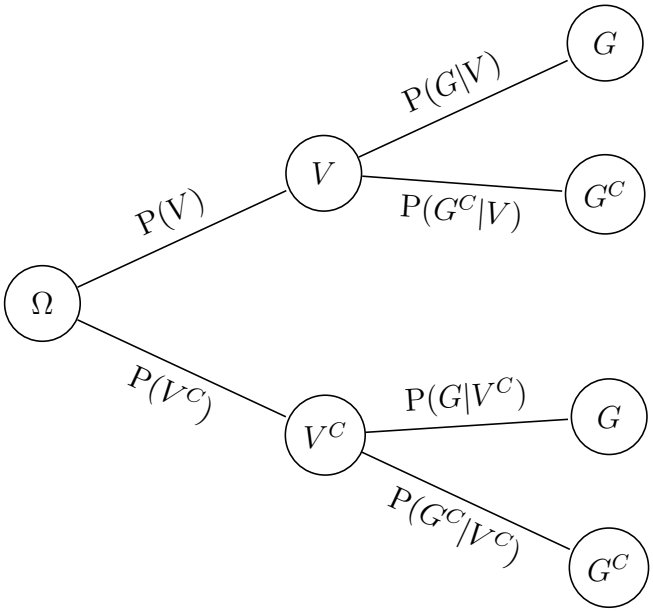
I then added multiple sites to the model. This meant giving each site its own prior distribution defined by μ_k and σ_k and is written as:

$$\begin{aligned}[\boldsymbol{\alpha}, \boldsymbol{\mu}, \boldsymbol{\sigma}, |\boldsymbol{n}, \boldsymbol{y}] \propto & \prod_{K=1}^{K} \prod_{j=1}^{J} \text{binomial}(y_{jk} | n_{jk}, \text{logit}^{-1}(\alpha_{jk})) \\ & \times \text{normal}(\alpha_{jk} | \mu_k, \sigma_k) \\ & \times \text{normal}(\mu_k | 0, 100) \text{uniform}(\sigma_k | 0, 100).\end{aligned} \tag{6}$$

Seed bag experiments

In October (year t), we buried 10 5 × 5-cm nylon mesh bags at each site, each containing 100 seeds collected at the site in June-July. In January (year $t + 1$), we removed these 10 bags and counted the number of germinated seedlings and the number of ungerminated, intact seeds in each bag. We then returned the ungerminated, intact seeds to the resealed bag and returned the bag to the field. In October (year $t + 1$), we removed these bags and counted the number of ungerminated, intact seeds. We collected the following data:

- n_{ijt} = observed count of seeds in the seed bags at the start of the experiment in October in the i^{th} bag, from the j^{th} site, in the t^{th} year, assumed to be measured perfectly
- $y_{\text{intact}ijt}$ = observed count of ungerminated, intact seeds in the seed bags in January in the i^{th} bag, from the j^{th} site, in the t^{th} year, assumed to be measured perfectly
- $y_{\text{germ}ijt}$ = observed count of germinated seedlings in the seed bags in January in the i^{th} bag, from the j^{th} site, in the t^{th} year, assumed to be measured perfectly
- $y_{\text{total}ijt}$= observed count of ungerminated, intact seeds plus germinated seedlings in the seed bags in January in the i^{th} bag, from the j^{th} site, in the t^{th} year, assumed to be measured perfectly
- $y_{\text{surv}ijt}$ = observed count of ungerminated, intact seeds in the seed bags in October in the i^{th} bag, from the j^{th} site, in the t^{th} year, assumed to be measured perfectly



The proportion of seeds that germinate is given by P($G|V$) × P(V). Probability of being viable is estimated separately (see section on viability trials) which means that the estimate

for γ is the probability of seeds that germinate given that they're viable. The seeds that are viable but do not germinate $\mathrm{P}(G^C|V) \times \mathrm{P}(V)$ are dormant, which is then the product of not germinating and being viable.

We modeled* seed survival and germination in the seed bags as:

$$\begin{aligned}[\boldsymbol{\phi}, \boldsymbol{\gamma}, \boldsymbol{\rho} | \boldsymbol{n}, \boldsymbol{y_{\text{total}}}, \boldsymbol{y_{\text{germ}}}, \boldsymbol{y_{\text{surv}}}] \propto & \prod_{t=1}^{T} \prod_{j=1}^{J} \prod_{i=1}^{I} \text{binomial}(y_{\text{total}ijt} | n_{ijt}, \phi_{jt}) \\ & \times \text{binomial}(y_{\text{germ}ijt} | y_{\text{total}ijt}, \gamma_{jt}) \\ & \times \text{binomial}(y_{\text{surv}ijt} | y_{\text{total}ijt} - y_{\text{germ}ijt}, \rho_{jt}) \\ & \times \text{beta}(\phi_{jt}|1,1)\text{beta}(\gamma_{jt}|1,1)\text{beta}(\rho_{jt}|1,1)\end{aligned} \tag{7}$$

where

- ϕ_j = the true, unobserved proportion of seeds that remain intact in January (the probability of a seed remaining intact) at the j^{th} site, in the t^{th} year
- γ_{jt} = the true, unobserved proportion of seeds that germinate (the probability of an intact seed germinating) at the j^{th} site, in the t^{th} year
- ρ_{jt} = the true, unobserved proportion of seeds that remain intact in October (the probability of a seed remaining intact) at the j^{th} site, in the t^{th} year

We add the viability trials to the joint posterior in the following way, for bags i at a single site j:

$$\begin{aligned}[\phi, \gamma, \rho, \boldsymbol{\alpha} | \boldsymbol{n}, \boldsymbol{n_{\text{viab}}}, \boldsymbol{y_{\text{total}}}, \boldsymbol{y_{\text{germ}}}, \boldsymbol{y_{\text{surv}}}, \boldsymbol{y_{\text{viab}}}] \propto & \prod_{i=1}^{I} \text{binomial}(y_{\text{tot}i} | n_i, \phi) \\ & \times \text{binomial}(y_{\text{germ}i} | y_{\text{tot}i}, \text{f}(\gamma, \alpha)) \\ & \times \text{binomial}(y_{\text{surv}i} | y_{\text{tot}i} - y_{\text{germ}i}, \rho) \\ & \times \text{binomial}(y_{\text{viab}i} | n_{\text{viab}i}, \text{logit}^{-1}(\alpha_i)) \\ & \times \text{beta}(\phi|1,1)\text{beta}(\gamma|1,1)\text{beta}(\rho|1,1) \\ & \times \text{normal}(\alpha_i | \mu, \sigma) \\ & \times \text{normal}(\mu|0,100)\text{uniform}(\sigma|0,100).\end{aligned} \tag{8}$$

where $\text{f}(\gamma, \alpha) = \gamma \times (\text{logit}^{-1}(\alpha_i))^{\frac{1}{3}}$.

We fit this models with JAGS. In order to evaluate the effect of the prior, we obtained estimates for all parameters with a noninformative beta(1,1) prior and the informative prior on the logit transformed α parameter. In the derived quantities block, we calculated the

dormancy for each bag $(1-g)*v$. Question is how to get dormancy for the site because viability is bag level. We simulate data from this model and calculate test statistics.

Model runs for 2 sites with no missing data. Problems: how to deal with missing data (e.g. no viability trials), whether to take bag-level or site-level viability, which test statistics to use, how/whether to evaluate how much the posterior for viability changes after joint estimation.

Correlation

Venable (2007) estimated the fraction of seeds germinating $G = N/(N+S)$ as follows. The density of seeds germinating (N) was estimated by mapping germinants in 72 1 m^2 plots. The density of seeds not germinating (S) was determined from 180 23 cm^2 seed cores. Venable states that the soil cores sample **viable non-germinating seeds**, as they are collected each year after the germination season but before new seeds fall.

Venable (2007) estimated per capita reproductive success associated with germination using data on per capita survival from germination to reproduction and per capita fecundity of survivors. This meant multiplying the per capita probability of survival from germination to reproduction by the average per capita reproduction of survivors.

Venable (2007) estimated the risk associated with germination as the geometric standard deviation of per capita reproductive success (exp(SD[ln(per capita reproductive success)])), which he states is the standard deviation of proportional changes.

The first step would be to get site-level estimates for (1) dormancy or germination fraction and (2) per capita reproductive success. The straightforward thing to do would be to put everything in one model and get posteriors for individual parameters before multiplying them to get estimates with a distribution. We could then take the correlation of these distributions. Alternatively we could get the correlation in the MCMC sampling, calculating the correlation at each iteration in the sampler.

Monica and I discussed three potential measures for germination:

- g_1: the probability that a seed that is intact in January germinates
- $s_1 g_1$: effective emergence
- $s_1(1-g_1)s_2$: effective survival of seeds
- Venable's germination fraction $N/(N+S)$ would be the probability of a seed emerging in January. This would be equivalent to $g_1 v_1^{1/3}$
- true dormancy would be entering the seed bank, not germinating but being viable

We add the viability trials to the joint posterior in the following way, for bags i at a single site j:

$$\begin{aligned}[\phi, \gamma, \rho, \boldsymbol{\alpha} | \boldsymbol{n}, \boldsymbol{n_{\text{viab}}}, \boldsymbol{y_{\text{total}}}, \boldsymbol{y_{\text{germ}}}, \boldsymbol{y_{\text{surv}}}, \boldsymbol{y_{\text{viab}}}] \propto & \prod_{i=1}^{I} \text{binomial}(y_{\text{tot}i} | n_i, \phi) \\ & \times \text{binomial}(y_{\text{germ}i} | y_{\text{tot}i}, \text{f}(\gamma, \alpha)) \\ & \times \text{binomial}(y_{\text{surv}i} | y_{\text{tot}i} - y_{\text{germ}i}, \rho) \\ & \times \text{binomial}(y_{\text{viab}i} | n_{\text{viab}i}, \text{logit}^{-1}(\alpha_i)) \\ & \times \text{beta}(\phi | 1, 1) \text{beta}(\gamma | 1, 1) \text{beta}(\rho | 1, 1) \\ & \times \text{normal}(\alpha_i | \mu, \sigma) \\ & \times \text{normal}(\mu | 0, 100) \text{uniform}(\sigma | 0, 100).\end{aligned} \tag{9}$$

Our variance-covariance matrix C_1 includes the variances on the diagonal and covariances on the off-diagonal. Here, we include the variance of germination probabilities and the variance of interannual reproductive success. The value ρ gives the correlation between germination probability and interannual reproductive success. This gives the survival/germination estimate as a site-level estimate α_g plus a year-site effect α_t. We are interested in the correlation between the site-level estimate α_g and the variance ... I guess the goal would be to get estimates for seedling survival to fruiting, fruits per plant, and seed per fruit and multiply those. That could be a derived quantity in a 3 part model. The same model might include estimates for dormancy. Both could be calculated at the site level and the correlation of interest would be between the parameter for site-level germination probabilities. Both would be RVs and multiplying them obviates the need for bootstrapping.

$$y_{i,s} \sim \text{binomial}(\hat{y}_s) \tag{10}$$

$$\text{logit}(\hat{y}_{i,s}) = \alpha_g + \alpha_t \tag{11}$$

$$\alpha_s = \begin{bmatrix} \alpha_g \\ \alpha_r \end{bmatrix} \tag{12}$$

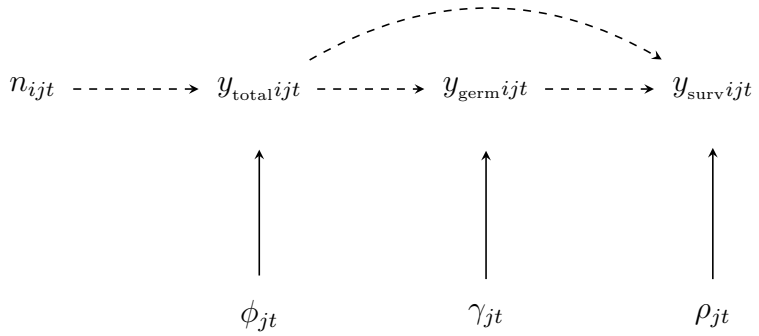
$$\alpha_s \sim \text{MVN}(\boldsymbol{\mu}, \boldsymbol{\Sigma}) \tag{13}$$

$$\alpha_s = \begin{bmatrix} \mu_g \\ \mu_r \end{bmatrix} \tag{14}$$

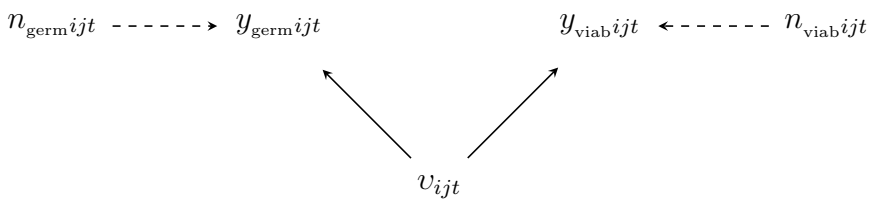
$$\boldsymbol{\Sigma} = \begin{bmatrix} \sigma_1\sigma_1 & \sigma_1\sigma_2\rho \\ \sigma_1\sigma_2\rho & \sigma_2\sigma_2 \end{bmatrix} \tag{15}$$

Extra material

The factored joint distribution is represented visually by the corresponding directed acyclic diagrams:



and



*Equivalent notation would be:

$$
\begin{aligned}
[\boldsymbol{\phi}, \boldsymbol{\gamma}, \boldsymbol{\rho} | \boldsymbol{n}, \boldsymbol{y_{\text{total}}}, \boldsymbol{y_{\text{germ}}}, \boldsymbol{y_{\text{surv}}}] \propto & \prod_{t=1}^{T} \prod_{j=1}^{J} \prod_{i=1}^{I} [y_{\text{total}ijt} | n_{ijt}, \phi_{jt}] \\
& \times [y_{\text{germ}ijt} | y_{\text{total}ijt}, \gamma_{jt}] \\
& \times [y_{\text{surv}ijt} | y_{\text{total}ijt} - y_{\text{germ}ijt}, \rho_{jt}] \\
& \times [\phi_{jt}][\gamma_{jt}][\rho_{jt}]
\end{aligned}
$$

where

$$
\begin{aligned}
y_{\text{total}ijt} &\sim \text{binomial}(n_{ijt}, \phi_{jt}) \\
y_{\text{germ}ijt} &\sim \text{binomial}(y_{\text{total}ijt}, \gamma_{jt}) \\
y_{\text{surv}ijt} &\sim \text{binomial}(y_{\text{total}ijt} - y_{\text{germ}ijt}, \rho_{jt}) \\
\phi_{jt} &\sim \text{beta}(1, 1) \\
\gamma_{jt} &\sim \text{beta}(1, 1) \\
\rho_{jt} &\sim \text{beta}(1, 1).
\end{aligned}
$$

Code

I implemented the model to estimate seed survival and germination in R with the following JAGS code block:

```
    model {

    # priors
    for(j in 1:nsites){
      for(i in 1:nyears){
         ps[j,i] ~ dbeta(1, 1)
         pg[j,i] ~ dbeta(1, 1)
         pr[j,i] ~ dbeta(1, 1)
      }
   }

    # likelihood
    for (i in 1:N){
      yt[i] ~ dbin(ps[site[i],year[i]], n[i])
      yg[i] ~ dbin(pg[site[i],year[i]], yt[i])
      yo[i] ~ dbin(pr[site[i],year[i]], yt[i]-yg[i])
    }
}
```

I implemented the model to estimate viability in R with the following JAGS code block:

```
    model {

    # priors
    for(j in 1:nsites){
      for(i in 1:nyears){
         for(k in 1:nbags)}
            v[j,i,k] ~ dbeta(1, 1)
            }
      }
   }

    # likelihood
    for (i in 1:N){
      yg[i] ~ dbin(v[site[i],year[i],bag[i]], ng[i])
      yv[i] ~ dbin(v[site[i],year[i],bag[i]], nv[i])
    }
}
```

I implemented the model to estimate seed survival and germination in R with the following JAGS code block:

```
    model {

    # priors
    for(j in 1:nsites){
      for(i in 1:nyears){
         ps[j,i] ~ dbeta(1, 1)
         pg[j,i] ~ dbeta(1, 1)
         pr[j,i] ~ dbeta(1, 1)
       }
   }

   for(i in 1:N){
   v[i] ~ dbeta(1 + yv[i], 1+ nv[i] -yv[i])
   }

    # likelihood
    for (i in 1:N){
      yt[i] ~ dbin(ps[site[i],year[i]], n[i])
      yg[i] ~ dbin(pg[site[i],year[i]]*(v[i])^(1/3), yt[i])
      yo[i] ~ dbin(pr[site[i],year[i]], yt[i]-yg[i])
    }
}
```