
1 Ann Raiho

2 Homework 7

3 1 Introduction

4 An ecological threshold can be an important management tool when used to determine
5 whether or not an ecosystem is moving into an alternative stable state (Groffman et al.
6 2006). It is well known that large populations of mammalian herbivores can cause a severe
7 decline in riparian vegetation which may force a system beyond a threshold and into an
8 alternative state (Singer et al. 1994; Wolf et al. 2007). If willows (*Salix*) are inhibited from
9 recruitment or if they simply do not survive, their population can decrease substantially,
10 even beyond the point of reestablishment to their original stable state. Willows will not be
11 able to recruit new plants if either they have become too damaged to produce catkins or the
12 ground surrounding the seed producing willows is not fit for seedling establishment (Gage
13 and Cooper 2005). Willows become viable when they begin producing seeds; therefore, it is
14 useful to determine a threshold for seed production to know when soil for establishment can
15 also be a factor in new willow growth.

16 Willow reestablishment has become a forward issue on the Northern Range in Yellow-
17 stone National Park. Wolves (*Canis lupus*) were not present in Yellowstone from the early
18 1900s until their reintroduction in 1995. This allowed elk populations to grow exponentially
19 and nearly wipe out riparian willow communities. The reintroduction of wolves has signifi-
20 cantly reduced elk herbivory of riparian willows, but the keystone species, beaver, have not
21 recovered. Beaver and willow depend on each other for growth and recruitment. Beaver eat
22 willow and also use willow to build dams which raises the water table to an ideal level for
23 willow growth (Bilyeu et al. 2008). Eventually, the beaver dam will break, draining a water
24 pool and leaving exposed soil which is essential for willow seedling establishment (Gage and
25 Cooper 2005). Without beaver activity there is minimal soil for willow reestablishment along
26 the riparian corridors. Willows also play an important role in the structure of the stream

banks, which can become incised and further decrease the area of feasible willow habitat.

It has been shown that due to extirpation of wolves, heavy elk browsing, and a decreased beaver population a new stable state has arisen known as the elk grass state (Wolf et al. 2007). Tall willows that were ubiquitous in the early 1900s are now rare and lowered water tables have made it difficult for them to return to a tall willow community. This new stable state may have also prevented willows from reestablishing because there may be a lack of seed production. Data from our observational study suggests that most willow on Yellowstone's Northern Range are between 50cm and 200cm (Figure 1). This suggests that there is a missing older age class among willows that are still recovering from overabundant herbivore populations. Even if beaver populations were reintroduced to Yellowstone's Northern Range and began to thrive, willow reestablishment would still depend on seed production. It has been hypothesized that willows will not produce seeds until they reach a threshold height (Kay and Chadde 1991), but there has yet to be any objective basis for that claim. Here, we provide a model that uses data collected from 21 randomly selected riparian sites across Yellowstone's Northern Range to rigorously estimate the threshold height for willow reestablishment. Although the 200 cm threshold is based on appealing, rough-hewn logic and is widely cited in papers on ecosystem restoration in Yellowstone, no one has demonstrated a quantitative, functional basis for a ecological threshold based on willow height.

In this paper, we report investigations of the relationship between willow height and seed production on Yellowstone's northern range. We use this relationship to estimate a threshold at which seed production by willows increases above zero. We offer this threshold an indicator of necessary conditions for restoration of the riparian zone following reintroduction of wolves.

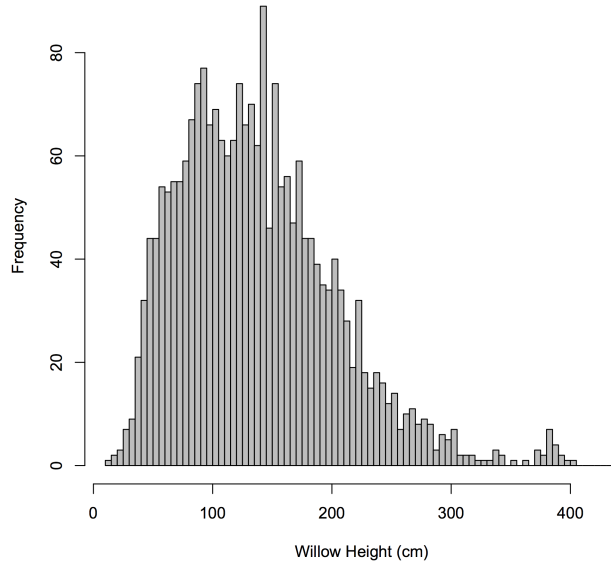


Figure 1: A histogram of the willow heights from over 2200 willows (*Salix*) randomly sampled across Yellowstone’s Northern Range. Here we see that most of the willows are between 50 cm and 200 cm suggesting that very little seed is being produced (Kay and Chadde 1991).

2 Materials and Methods

2.1 Study Area

Observations of willow height and seed production were collected from 21 randomly selected riparian sites on the northern range of Yellowstone National Park during June and July of 2010. These 21 observational sites were chosen from a sampling frame of stream sections that were either historically known to have beaver or were hypothesized to be a potential habitat for beaver based on gradient and stream order (Marshall et al. 2013). Sites were selected from the frame using a spatially balanced random sampling algorithm (Theobald et al. 2007). Each observational site ran parallel to a stream for 100m and extended 25m away from the stream margin.

2.2 Observations

Willow seeds were collected using seed traps constructed from 30 cm² and 60 cm² plywood boards covered with a layer of adhesive (Tree Tanglefoot[®] Contech Inc.). Boards were staked into the ground using shelf brackets which were secured to the underside of each board. Two seed traps were placed 25 m from the margin of the 100 m river length transect line within 5 m of the river bank. These seed traps capture the ambient seed rain for the entire site. A third trap (measuring 30 cm²) was placed on an area within the transect determined optimal for seedling establishment. Willow seeds at each site were counted then removed from all traps each week during the willow seed production season. Every willow within each site was measured from the center of the root base to the highest branch in centimeters.

2.3 Analysis

We sought to estimate a threshold height for willow seed production (\tilde{h}). The number of plants exceeding this threshold should effect the number of seeds produced that exceeded the threshold height required for seed production to occur, so we represent the data with the following equation:

$$x_i = \sum_{j=1}^{J_i} I_{\{h_{ij} \geq \tilde{h}\}} \quad (1)$$

$$\tilde{h} \sim \text{Discrete Uniform}(0, 300) \quad (2)$$

where j indexes the individual plants, i indexes site, and $I_{\{h_{ij} \geq \tilde{h}\}}$ is an indicator variable = 1 when the condition within the $\{\}$ is true and 0 otherwise. Thus, x_i is a count of plants above the estimated threshold height (\tilde{h}) at each site.

We needed to account for two sources of zeros in counts of seeds: zeros that occurred because there was no seed production at a site and zeros that occurred as a result of sampling error when the true state of average seed production was > 0 . These considerations motivated us to use a zero inflated Poisson distribution to represent the relationship between seed

81 production and the number of willows in a stand exceeding the threshold height:

$$y_{ik} \sim \begin{cases} 0 & , x_i = 0 \\ \text{Poisson}(\lambda_i w_{ik}) & , x_i > 0 \end{cases} \quad (3)$$

82 where y_{ik} is the number of seeds per seed trap k in m^2 at a site i , and w_{ik} is an offset giving
 83 the area of each seed trap in m^2 . Equation 3 simply says that when there are no plants at
 84 the site are above the threshold height ($x_i = 0$), then we will observe 0 seeds with probability
 85 1. Otherwise, the number of seeds will be a Poisson distributed random variable with mean
 86 λ_i .

87 We estimated the mean seed production (i.e., λ_i , the intensity parameter of the Poisson)
 88 using

$$\log(\lambda_i) = \beta_0 + \beta_1 \log(x_i) + \gamma_i \quad (4)$$

$$\boldsymbol{\beta} \sim \text{Multivariate Normal}(\mathbf{0}, \sigma^2 \mathbf{I}) \quad (5)$$

$$\gamma_i \sim \text{Normal}(0, .000001) \quad (6)$$

89 where $\sigma^2 = 1$. An extra set of parameters γ_i were added to account for variation in seed
 90 detection between sites. Without these parameters, the posterior predictive p-value was
 91 equal to .005, and with these parameters, the dispersion is improved slightly (p-value =
 92 0.07).

The full posterior and joint distributions are given by

$$\begin{aligned} & \left[\boldsymbol{\gamma}, \boldsymbol{\beta}, \tilde{h} \mid \mathbf{y}, \mathbf{x} \right] \propto \prod_{i=1}^{21} \prod_{k=1}^3 \left(I_{\{y_i=0\}}^{I_{\{x_i=0\}}} \text{Poisson} \left(y_{ik} \mid \lambda_i w_{ik} \right)^{I_{\{x_i>0\}}} \right) \\ & \times \text{Multivariate Normal} \left(\boldsymbol{\beta} \mid \mathbf{0}, \sigma^2 \mathbf{I} \right) \text{Discrete Uniform} \left(\tilde{h} \mid 0, 300 \right) \text{Normal} \left(\gamma_i \mid 0, .000001 \right) \end{aligned} \quad (7)$$

2.3.1 Parameter Model

There are twenty-four unobserved quantities in this model, \tilde{h} , β_0 , β_1 , and γ_i . We chose priors based on simulated data that closely imitated the behavior of the observed data. The threshold height parameter has a discrete uniform prior because the willow heights were measured to the nearest centimeter resulting in a discrete height dataset.

2.3.2 Implementation

Marginal posterior distributions of states, parameters, and model predictions were estimated using Markov chain Monte Carlo (MCMC) methods in the R computing environment (RDevelopment 2011). Parameters were estimated using a random walk Metropolis-Hastings algorithm with discrete uniform and normal proposal distributions tuned to provide an acceptance rate of between 20% and 60% (See Appendix for full conditional distributions). Three chains were chosen for each estimated quantity. Convergence was assured by inspection of trace plots with varying initial conditions. All code and trace plots for this model can be found in the appendix.

3 Results

In Figure 2, we show the marginal posterior distributions of the model parameters, and in Table 1 we report the means and 95% credible intervals of each parameter. The parameters converged after 20,000 iterations of the MCMC Sampler as indicated by visual inspection of the trace plots for all parameters with a 4,000 iteration burn-in. It is also notable that the model has estimated the lower bound of the seed producing plots as the threshold for seed production (Figure 3).

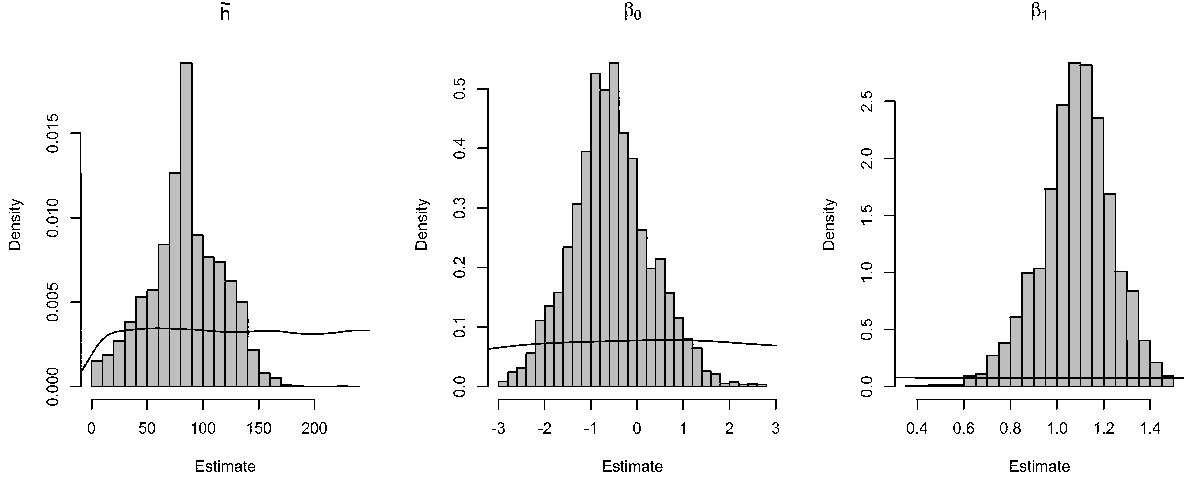


Figure 2: The marginal posterior distributions of the parameters of interest: threshold height parameter (\tilde{h}), the intercept β_0 , and the slope β_1 . The horizontal line is the prior distribution we defined for the parameter.

Parameter	Lower 95% Credible Interval	Mean	Upper 95% Credible Interval
\tilde{h}	27	85	145
β_0	-1.93	-0.60	1.22
β_1	.81	1.09	1.38

Table 1: The means and 95% credible intervals for each parameter estimated in the model.

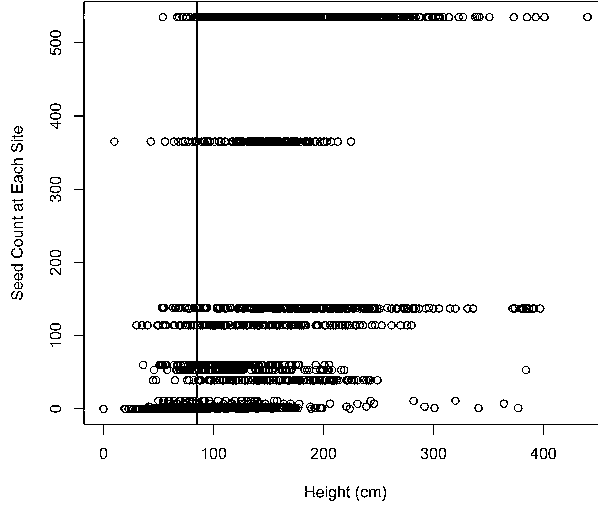


Figure 3: This plot shows the distribution of willow heights compared to the number of seeds counted at each plot. The vertical line represents the estimated mean of the threshold height for seed production parameter ($E(\tilde{h}) = 85$ cm).

114 4 Discussion

115 4.1 The Willow Height Threshold

116 Ecological thresholds have important implications for ecosystem management and ecological
117 theory. Yellowstone National Park has been a premier example of a major shift over a critical
118 threshold from one alternative stable state to another following the extirpation of a top
119 predator (Wolf et al. 2007). The reintroduction of the wolf reduced elk populations by 70%
120 supposedly paving the way for riparian willow recovery (Ripple and Beschta 2012). However,
121 alternative evidence suggests that wolves are not the only species needed to restore the
122 area's original willow populations. Beaver depend on willow for nourishment and protection,
123 so following the extreme decrease in the willow population beavers vacated Yellowstone.
124 Now without beaver, willows have been unable to reestablish because beaver dams raise
125 the water table which is essential for willow growth, and when the dams break, they also
126 create establishment soil for seedlings. This positive feedback has caused researchers to
127 conclude that Yellowstone has shifted to an elk grassland stable stage (Wolf et al. 2007). We
128 know that beavers are critical in the process of shifting Yellowstone's ecosystem back to its
129 historical stable state, but we do not know when willows will be able to produce seeds in
130 order to begin the reestablishment process. With this model and randomly collected data,
131 we estimate that the threshold height for willow seed production on Yellowstone's Northern
132 Range has an average of 85 cm.

133 The increase of riparian willow is the key to the restoration of Yellowstone, but it cannot
134 occur until more willows are producing seeds. In this study the heights of over 2200 willow
135 were measured and 77% of willow were above the threshold height of 85 cm (Figure 4). In
136 spite of this high percentage, only 14 of the 21 sites had more than 6 tall willows present.
137 All but one site had several up and coming willows between 25 - 50 cm. We suggest that
138 willows are beginning to produce seeds and that they will continue to grow because herbivore
139 populations have decreased, but that there do not yet seem to be enough tall plants to

allow the willow communities to expand to historic levels at all sites. A tall and large willow community that facilitates seedling recruitment will allow for willow recovery, but returning to this state may be impossible without more water and exposed soil for seedling establishment in the ri

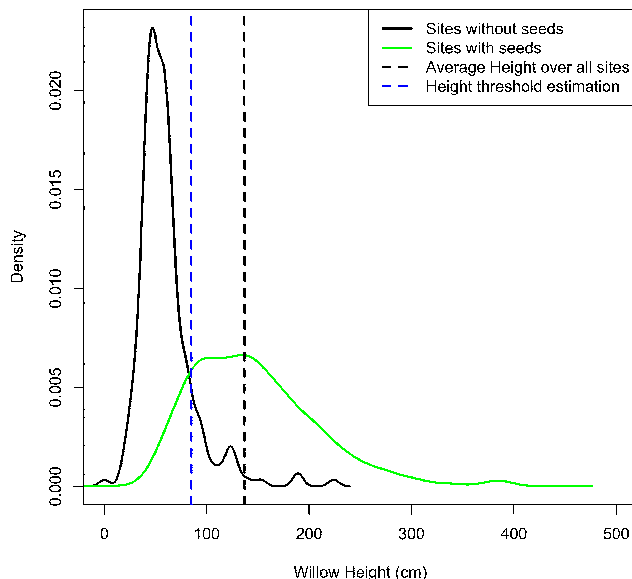


Figure 4: This is a plot of the frequency of the willow heights measured in this study. The black curve is the frequency of willow heights for sites that did not produce seeds. The green curve is the frequency of willow heights for the sites that did produce seeds. The black dotted line is the overall average willow height, and the blue dotted line is the estimated height threshold (\tilde{h}). Most willows (77%) are above the estimated threshold height for seed production (85 cm).

These types of models are becoming more critical as our world continues to change. Shifts in ecosystems are occurring rapidly. It will be important for managers to understand ecological thresholds and have a quantitative basis for estimating their values. Thresholds often form the basis for management action plans as well as interpreting the type of stable state an ecosystem is realizing. Mistakes in these estimations could lead to mismanagement which could lead to further ecological harm. In Yellowstone National Park, managers need to know these types of critical details for willow reestablishment in order to return the ecosystem to its historical stable state. They have taken courageous steps to reduce the herbivore population by reintroducing wolves, and now they seek to know more about what needs to happen to reconstruct their riparian corridors. Knowing an ecological threshold and

the inherent uncertainty is one step in a very complicated problem that can help managers and researchers further understand the transition from one stable state to another.

References

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Appendix

R Code for MCMC Algorithm

```
change.pt.pois.regMCMC.no.inflat1 <- function(n.mcmc,X,y.seed,opt.ht.
  strt,hshape1,hshape2,beta,beta.mns,beta.tune,beta.var,error.var,
  error.tune){
  ####
  #### Subroutines and Libraries
  ####
  library(mvtnorm)
  library(data.table)
  dunifdisc<-function(x, min=0, max=1) ifelse(x>=min & x<=max &
    round(x)==x, 1/(max-min+1), 0)
  runifdisc<-function(n, min=0, max=1) sample(min:max, n, replace
    =T)
  ####
  #### Storage
```

```

204     ###
205
206     opt.ht.save=rep(0,n.mcmc)
207     beta.save=matrix(0,n.mcmc,2)
208     error.save=matrix(0,21,n.mcmc)
209
210     mse.y=rep(0,n.mcmc)
211     mse.ypred=rep(0,n.mcmc)
212     msediffsave=rep(0,n.mcmc)
213     ypred=matrix(0,length(y.seed[,1])*3,n.mcmc)
214     msesave=rep(0,n.mcmc)
215
216
217     ###
218     ### Initial Conditions
219     ###
220
221     opt.ht = opt.ht.strt
222     error=rep(0,21)
223     error.mns=rep(0,21)
224     W = matrix(c(.5,.25,.25),1,3)
225     X1 = data.table(X)
226     x = cbind(1,log(X1[,list(A=sum(V3>opt.ht),B=V1),by=V1][,A]))
227
228     beta = beta
229
230     accept.opt.ht = 0
231     accept.beta = 0
232

```

```

233     ###
234     ### Begin MCMC
235     ###
236
237     for (k in 1:n.mcmc){
238 if (k%%1000==0) cat(k," ");flush.console()
239
240     ###
241     ### Sample Opt.ht
242     ###
243     if (TRUE){
244 opt.ht.star = runifdisc(1,opt.ht-100,opt.ht+100)
245
246 if (opt.ht.star>0 & opt.ht.star<=max(X[,3])){
247
248 x.star = cbind(1,log(X1[,list(A=sum(V3>opt.ht.star),B=V1),by=V1][,A
249     ]))
250
251     mh1.ht = sum(dpois(as.vector(y.seed[x.star[,2]>=0,]),as.
252     vector(exp(x.star[x.star[,2]>=0,]*%*%beta+error[x.star
253     [,2]>=0]))%*%W),log=TRUE)) + dunifdisc(opt.ht.star,hshape1,
254     hshape2) + dunifdisc(opt.ht,opt.ht.star-100,opt.ht.star
255     +100)
256
257     mh2.ht = sum(dpois(as.vector(y.seed[x.star[,2]>=0,]),as.
258     vector(exp(x[x.star[,2]>=0,]*%*%beta+error[x.star[,2]>=0])
259     %*%W),log=TRUE)) + dunifdisc(opt.ht,hshape1,hshape2) +
260     dunifdisc(opt.ht.star,opt.ht-100,opt.ht+100)
261     mh.ht = exp(mh1.ht - mh2.ht)

```

```

262     if(mh.ht > runif(1)){
263         opt.ht=opt.ht.star
264         accept.opt.ht=accept.opt.ht+1
265         x=x.star
266     }
267 }
268 }
269
270
271
272 ####
273 #### Sample Betas
274 ####
275
276 if (TRUE){
277     beta.star = rnorm(2,beta,beta.tune)
278
279     mh1.beta = sum(dpois(as.vector(y.seed[x[,2]>=0,]),as.vector(
280         exp(x[x[,2]>=0,]*%*%beta.star+error[x[,2]>=0])%*%W),log=
281         TRUE))+dmvnorm(beta.star,beta.mns,beta.var*diag(2),log=
282         TRUE)
283
284     mh2.beta = sum(dpois(as.vector(y.seed[x[,2]>=0,]),as.vector(
285         exp(x[x[,2]>=0,]*%*%beta+error[x[,2]>=0])%*%W),log=TRUE))+
286         dmvnorm(beta,beta.mns,beta.var*diag(2),log=TRUE) #rep(beta
287         .var,2)*diag(2)#solve(t(x[x[,2]>0,])%*%x[x[,2]>0,])
288
289     mh.beta = exp(mh1.beta-mh2.beta)
290
291     if(mh.beta > runif(1)){
292         beta = beta.star

```

```

291         accept.beta = accept.beta+1
292
293     }
294 }
295
296 #####
297 ##### Sample Error
298 #####
299
300 if (TRUE){
301     error.star = rnorm(21,error,error.tune)
302
303     if (min(exp(x[x[,2]>=0,])%*%beta.star+error.star[x[,2]>=0])%*%
304         W)>=0){
305
306
307         mh1.error = dpois(y.seed[x[,2]>=0,],exp(x[x[,2]>=0,])%*%beta.
308             star+error.star[x[,2]>=0])%*%W,log=TRUE)+dnorm(error.star[
309             x[,2]>=0],error.mns[x[,2]>=0],error.var,log=TRUE)
310         mh2.error = dpois(y.seed[x[,2]>=0,],exp(x[x[,2]>=0,])%*%beta+
311             error[x[,2]>=0])%*%W,log=TRUE)+dnorm(error[x[,2]>=0],error
312             .mns[x[,2]>=0],error.var,log=TRUE) #rep(beta.var,2)*diag
313             (2)#solve(t(x[x[,2]>0,])%*%x[x[,2]>0,])
314         mh.error = exp(mh1.error-mh2.error)
315
316         mh.index=which(mh.error > runif(length(mh.error[,1])*length(
317             mh.error[,1]),arr.ind=TRUE)
318         error[unique(mh.index[,1])] = error.star[unique(mh.index[,1])
319             ]

```

```

320     }
321 }
322
323 #####
324 ##### Calculate Posterior Predictive Checks
325 #####
326
327
328     mn.nbinom=exp(x%%beta+error)%*%W
329     ypred[,k]=rpois(length(mn.nbinom),mn.nbinom)
330
331     mse.y[k]=mean((as.vector(y.seed)-mn.nbinom)^2)
332     mse.ypred[k]=mean((ypred-as.vector(mn.nbinom))^2)
333
334
335 #####
336 ##### Save Values
337 #####
338
339     opt.ht.save[k] = opt.ht
340     beta.save[k,] = beta
341     msediffsave[k]=mse.ypred[k]-mse.y[k]
342     error.save[,k]=error
343
344 }
345
346 #####
347 ##### Create Plots
348 #####

```

```

349     n.burn=round(.2*n.mcmc)
350     p.value=sum(mse.ypred[n.burn:n.mcmc] > mse.y[n.burn:n.mcmc]) /
351         (n.mcmc - n.burn)
352
353
354     layout(matrix(1:3,3,1))
355     plot(opt.ht.save[n.burn:n.mcmc], type="l", main="Threshold Height
356         ")
357     plot(beta.save[n.burn:n.mcmc,1], type="l", main=expression(paste(
358         beta[0])))
359     plot(beta.save[n.burn:n.mcmc,2], type="l", main=expression(paste(
360         beta[1])))
361
362
363
364     list(error.save=error.save, ypred=ypred, msediffsave=msediffsave, p.
365         value=p.value, opt.ht.save=opt.ht.save, beta.save=beta.save, accept
366         .beta=accept.beta, accept.opt.ht=accept.opt.ht)
367 }

```

368 R Code for Script to Run MCMC Algorithm

```

369 rm(list=ls())
370 #####
371 ##### Load and Molt Data
372 #####
373
374 setwd("/Users/raiho/Documents/Willows")
375 library(reshape)

```

```

376 library(segmented)
377 raw_seeds=read.csv("raw_seeds.csv")
378 melt.raw.seeds=melt(raw_seeds)#,id=c("Site","Trap.Type","X..Seeds
379     "),na.rm=TRUE)
380 cast.raw.seeds=cast(melt.raw.seeds, Site ~ Trap.Type, sum)
381 #cast.raw.seeds1=cast(melt.raw.seeds, Site ~ Trap.Type, sum)
382 remove=c( 11, 12, 20) #,22 to remove WBT1
383 cast.raw.seeds.remove=cast.raw.seeds[,-remove,]
384
385 remove.cols=c(3,4,5,6,7,8)
386 seed.count.traps=cast.raw.seeds.remove[,-remove.cols]
387 as.numeric(seed.count.traps[,1])
388
389 y.seed=as.matrix(seed.count.traps[,2:4])
390
391 seed.count=rowSums(cast.raw.seeds.remove[,2:10])
392
393 ht.obs=(read.csv("sex_obs_sites.csv"))
394 seed1=(read.csv("seedrain1.csv"))
395 ht.obs$sex<-NULL
396 ht.obs$species<-NULL
397 head(ht.obs)
398 ht.obs=ht.obs[ht.obs[,1]!="Rose",] #Takes Rose out because it has
399     no heights
400 ht.obs[,1]=as.numeric(factor(ht.obs[,1])) #Giving index
401
402 ht.obs3=matrix(0,1,3)

```

```

403 ht.obs=matrix(rbind(as.matrix(ht.obs),ht.obs3),2229,3)
404
405 #####
406 ##### Run MCMC #####
407 #####
408
409 n.mcmc=20000
410 setwd("~/Documents/Willows")
411 source("change.pt.pois.regMCMC.no.inflat1.R")
412 output5 = change.pt.pois.regMCMC.no.inflat1(n.mcmc=n.mcmc,X=ht.obs
413       [1:2228,],y.seed=y.seed,opt.ht.strt=50,hshape1=0,hshape2=300,
414       beta=c(-1,1.5),beta.mns=c(0,0),beta.var=c(1,1),beta.tune=c
415       (.5,.1),error.var=.000001,error.tune=.01)

```

416 Trace Plots

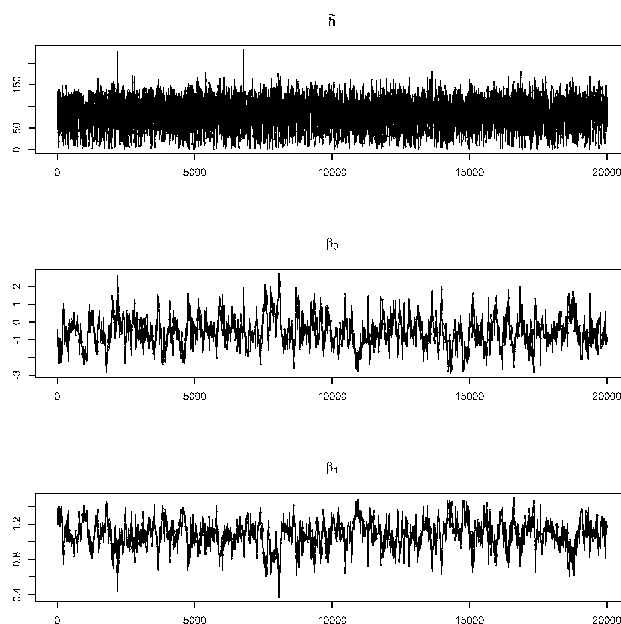


Figure 5: Trace plots for parameters for parameters of interest.

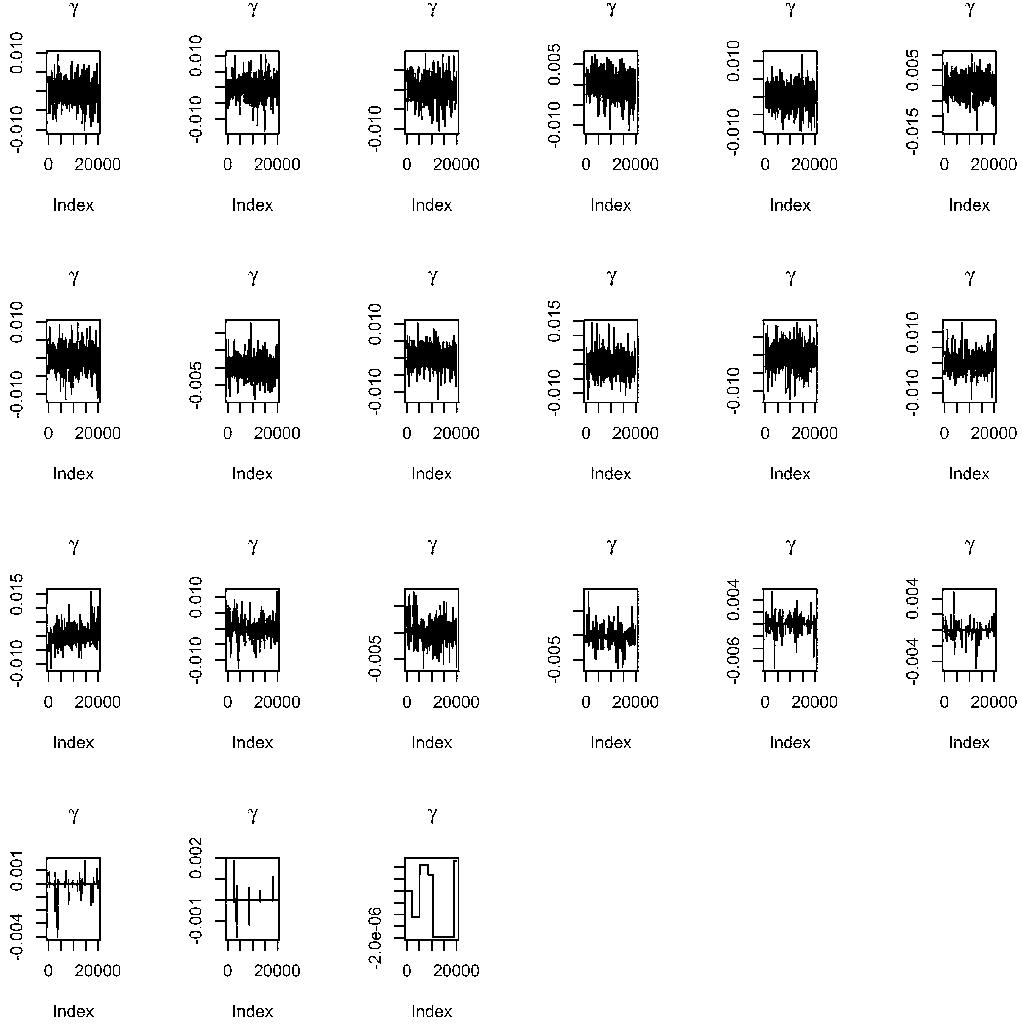


Figure 6: Trace plots of the error parameters for each site (γ_i).

417 Full Conditionals

$$\begin{aligned}
 [\tilde{h}|\cdot] &\propto \prod_{i=1}^n \prod_{k=1}^3 (1_{\{y_i=0\}} 1_{\{x_i=0\}} + 1_{\{x_i>0\}} \text{Poisson}(y_{ik}|\lambda_i w_k)) \text{Discrete Uniform}(\tilde{h}|0, 400) \\
 [\beta|\cdot] &\propto \prod_{x_i>0} \prod_{k=1}^3 \text{Poisson}(y_{ik}|\lambda_i w_k) \text{N}(\beta|\mathbf{0}, \sigma_\beta^2 I) \\
 [\gamma|\cdot] &\propto \prod_{x_i>0} \prod_{k=1}^3 \text{Poisson}(y_{ik}|\lambda_i w_k) \text{N}(\gamma|\mathbf{0}, \sigma_\gamma^2 I)
 \end{aligned}$$