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Elevated CO_2 and tree fecundity: the role of tree size, interannual variability, and population heterogeneity

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Abstract

Long-term population effects of changes in atmospheric CO_2 will be largely determined by reproductive effort. Our research objectives were to quantify variability in seed production and rate of maturation among individual *Pinus taeda* L. (Pinaceae) trees growing in elevated CO_2 (ambient plus 200 $\mu L\,L^{-1}$) since 1996. Estimating tree fecundity in nature is frustrated by the difficulty of counting seeds from individual trees and the need for long-term data. We have used a hierarchical Bayes approach to model individual tree fecundity, accounting for the complexity of experimentation in a natural setting over multiple years. The study presented here demonstrates large variability in natural fecundity rates and contributes to our understanding of how both interannual variation and population heterogeneity influence elevated CO_2 effects. We found that trees growing under elevated CO_2 matured earlier and produced more seeds and cones per unit basal area than ambient grown trees. By 2004, trees grown in high CO_2 had produced an average 300 more seeds per tree than ambient grown trees. Although there was a trend toward decreasing mean CO_2 effect (difference in fecundity between elevated and ambient treatments) over time, the hierarchical analysis indicates that this decrease comes from the emergence of a few highly fecund ambient grown trees by 2002, rather than acclimation or downregulation among the fumigated trees. The most important effect of increased CO_2 in forest ecosystems may be the increase in fecundity reported here. Although biomass responses can sometimes be large, the increase in fecundity can have long-term impacts on forest dynamics that transcend the current generation.

Keywords: biodiversity, carbon dioxide, climate change, ecology, FACE, fecundity, forest, reproductive allocation, seed, *Pinus taeda*

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Introduction

Diversity of 21st century forests will depend on species-specific responses to rising atmospheric CO_2 concentrations. Seed production and timing of reproductive maturation are important determinants of tree population growth rates and species diversity (Ribbens *et al*., 1994; Hubbell *et al*., 1999; Loehle, 2000; Pachepsky *et al*., 2001; Clark *et al*., 2004, 2001, 1999, 1998). Although much research focuses on vegetative growth responses to elevated CO_2, the long-term population effects of global change will depend, in large part, on reproductive effort (Farnsworth & Bazzaz, 1995, Ward & Strain, 1997, Thurig *et al*., 2003). The direction and magnitude of changes in vegetative growth under elevated atmospheric CO_2 may not be predictive of reproductive response (Farnsworth & Bazzaz, 1995; Jablonski, 1997; Ward & Strain, 1997; Lewis *et al*., 2003). Research presented here evaluates 8 years of reproductive effort in pine trees grown at ambient and elevated atmospheric CO_2.

Seeds are inherently large carbon sinks (Wardlaw, 1990; Zamski, 1995), and plants growing in high atmospheric CO_2 may alter allocation to reproductive effort accordingly (Ward & Strain, 1997; Huxman *et al*., 1999; Jablonski *et al*., 2002). Research on herbaceous plants shows strong species-specific responses, with negative, positive, or no changes in seed number and mass

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(Jablonski *et al.*, 2002). Maturation rates and offspring quality also vary among species grown in an elevated CO_2 atmosphere (Jackson *et al.*, 1994; Farnsworth & Bazzaz, 1995; Farnsworth *et al.*, 1996; Huxman *et al.*, 1999; Jablonski *et al.*, 2002; Thurig *et al.*, 2003). Few studies have assessed reproductive effort in trees growing at elevated CO_2 (see Farnsworth *et al.*, 1996; LaDeau & Clark, 2001; Stiling *et al.*, 2004).

Rate of ontogeny, which determines age of reproduction, and fecundity, the amount of seed produced by mature plants, are both important for reproductive success and difficult to quantify in nature. Estimation requires long-term data sets that span interannual variation in seed production in natural settings and models that accommodate multiple types of error. Overlapping canopies of tall trees make it difficult to count seeds, and seed rain collected from seed traps can be difficult to assign to specific parent trees. Trees mature slowly and experience large variation in reproductive effort from 1 year to the next (Cain & Shelton, 2000, 2001; Kelly & Sork, 2002; Clark *et al.*, 2004; Koenig & Knops, 2005). Allocation responses to changing CO_2 may continue for several years, and responses may vary among years, depending on fluctuating resources and climate. Furthermore, models must accommodate changes in both population size and tree size that occur in natural systems over time and particularly with extreme weather events. Analysis of intact forest tree response is facilitated by the development of free-air CO_2 enrichment (FACE) technology (Hendrey *et al.*, 1999). FACE can be used to identify magnitudes and directions of forest response to the anthropogenic rise in atmospheric CO_2, while accommodating realistic interactions among interannual variability, population heterogeneity, and unpredictable events that are inherent to natural ecosystems.

Estimating CO_2 effects on fecundity requires consideration of complex processes and data (Clark *et al.*, 2004). First, the response variable, seeds on trees, cannot be directly observed and, thus, must be estimated based on indirect evidence. Second, fecundity is highly variable among years and within populations. Seed crops can experience order of magnitude fluctuations among years, and individuals of the same size can have vastly different reproductive capacities. Finally, the 'process' portion of the model must accommodate the complexity of the intervention design, including the intervention itself (change in CO_2 level over time), the time-series character of tree response, and random individual effects. Because data are indirect, yet available from several sources, the underlying (unobserved) fecundity process must be linked to observations with potentially complex data models.

We extend the hierarchical Bayes framework of Clark *et al.* (2004) to integrate two types of fecundity information: (1) cone counts on individual trees and (2) plot-level seed trap data. The Bayesian framework allows flexibility to incorporate data collected at multiple scales. We use this analysis to estimate individual variability in fecundity and ontogeny, interannual variability in fecundity, and the extent of CO_2 enhancement of reproductive effort over time.

Initial enhancements to reproductive allocation in *Pinus taeda* L. trees grown in high CO_2 at the Duke Forest FACE site were large in 1999 (LaDeau & Clark, 2001). The analysis of cone production for the data available at that time demonstrated that fumigated trees were twice as likely to be reproductively mature in 1999, and produced three times as many cones as ambient trees (LaDeau & Clark, 2001). Here, we present a longitudinal study of data extending from 1996 to 2004. Now, with sufficient time to allow analysis of long-term responses, we evaluate the persistence of CO_2 enrichment and potential long-term dynamics associated with changes in tree fecundity and forest demography.

Materials and methods

The experiment was conducted in Duke Forest, in the Piedmont region of North Carolina (35°97′N 79°09′W). In August 1996, a FACE system was installed in a 13-year old loblolly pine (*P. taeda* L.) plantation (pines were planted as 3-year old seedlings) (Hendrey *et al.*, 1999). *P. taeda* trees are half-sibs, have a density of 1733 stems ha^{-1}, and accounted for 98% of the basal area in 1996 (Delucia *et al.*, 1999; Hendrey *et al.*, 1999). The stand is unmanaged and several deciduous species are present in the canopy at low densities (including *Liriodendron tulipifera*, *Liquidambar styraciflua* and *Acer rubrum*). Each of the six 30 m diameter FACE rings is surrounded by 32 vertical pipes that extend above the forest canopy. In the three fumigated rings, these pipes deliver CO_2 to maintain an atmosphere at ambient plus 200 $\mu L\,L^{-1}$ [CO_2]. The three ambient plots are identical to treatment rings without the addition of CO_2.

P. taeda seed cones develop over 2 years. Female primordia are initiated in late summer. Pollination occurs the following spring, but fertilization of the egg cell is not complete for over 12 months. Cone elongation and seed development occurs rapidly through the summer and early fall of the second year. Although some open grown saplings can produce cones at 3–5 years of age (Greenwood, 1980), substantial cone crops are not common before 25 years of age (Wahlenberg, 1960). Maturation age is prolonged and cone production is reduced in unmanaged, closed canopy stands. Interannual variation in cone crop is common, with good seed crops every 3–10 years (Schultz, 1997; Cain & Shelton, 2001).

Trees were not reproductively mature at the start of the experiment, so this study spans the onset of seed production. Seeds were collected monthly from 12 0.16 m^2 litter traps per ring. Because loblolly seed cones develop over two years, seeds counted before 1998 were considered pretreatment. [Cones casting seed in 1998 were initiated in summer 1996, before CO$_2$ fumigation.] September 1999 was the first year of significant cone production in the FACE forest stand. Cones on all *P. taeda* trees within the six rings were counted from above-canopy towers using binoculars in September 1999–2004. Cones produced in 1998 were estimated in 1999 (those having open scales and borne by previous year's growth). We estimated cone production in 1996 and 1997 from seeds in the litter fall collections at the FACE site during these years. Seeds were collected similarly from a nearby 80-year old mixed pine-hardwood stand (HW) beginning in 1999, in order to compare fecundity at the relatively young FACE site with a matured stand.

Data collected from the FACE site include annual cone counts (1998–2004), diameter (DBH) censuses (1998, 2002, 2004) for all individuals, and monthly seed trap estimates (1996–2004).

Data analysis

We use a hierarchical Bayes modeling framework to assess the combined effects of CO$_2$ fumigation, tree size, variation among years, and population heterogeneity. This framework accommodates changes in individual fecundity, a 2002 ice storm that severely damaged crowns and affected subsequent cone production, multiple data sets collected at different scales (i.e. plot vs. individuals), and changes in population size and reproductive state over time as trees reach maturity. The model is laid out graphically in Fig. 1. Our summary of the model includes two *process models* for maturation status and fecundity, as well as a third submodel for seed dispersal, *data models* for the four data types, and *parameter models* that accommodate population heterogeneity (Fig. 1).

Process model: Cone production for each tree is treated as a time series; this schedule is the underlying 'process' to be estimated. The time series for tree i starts when observations began in the stand it occupies t_i, and it extends until March 2005 (end of the '2004' seed year). For tree i, this last observation year is designated T_i. For all trees in the FACE site, $t_i = 1996$. Diameters are indicated by d_{it}, $t = t_i, \ldots, T_i$.

The process model includes (1) maturation status and (2) conditional fecundity. There are two reasons for adopting this approach. First, reproduction can fail for

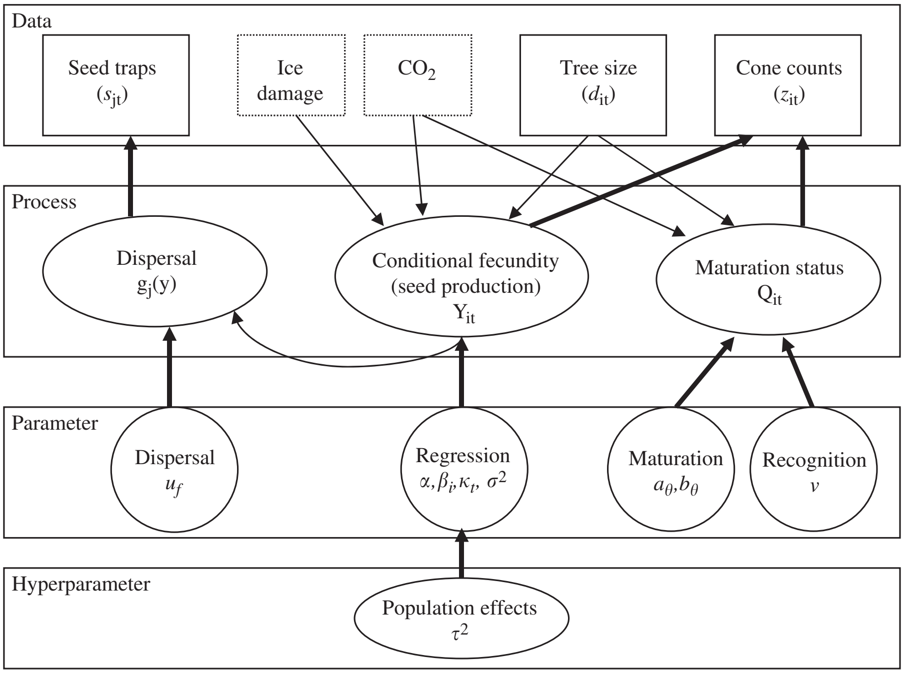

Fig. 1 Graphical model showing data, process, parameter and hyperparameter stages. Heavy arrows have stochastic components and involve estimates. Thin arrows are deterministic.

individual trees in specific years (i.e. 2001), and failure to produce seed by a mature individual should have a different effect on fecundity estimates than does lack of seed production by immature individuals (LaDeau & Clark, 2001). Second, the decomposition

$$\text{fecundity}|\text{maturation} \times \Pr\{\text{maturation}|\text{observation}\} \times \Pr\{\text{observation}\},$$

allows us to integrate observations of tree status (observed to have cones or not), which improves estimates of fecundity schedules.

We account for the fact that cones can be unobserved because (1) the tree is not yet reproductively mature, (2) it is mature, but seeds are not observed, or (3) the seed crop failed in a given year. We use the term 'partially hidden Markov model' (PHMM) to describe the submodel for maturation status Q_{it}. Maturation state is known for trees once cones have been observed. We wish to model the maturation status for individuals and years in which cones have not been observed based on the information that all other trees have to offer on the relationship between tree diameter and maturation status.

The PHMM entails transition probabilities for change in status Q_{it} and for status conditioned on observations $Q_{it} \mid q_{it}$ (Clark *et al*., 2004). Maturation probability increases with diameter d_{it} as a gamma cdf,

$$\theta_{it} = CGam(d_{it};\, a_\theta,\, b_\theta), \quad i = 1, \ldots, n, \quad t = t_i, \ldots, T_i,$$

with distribution mean a_θ/b_θ. Transition probabilities derive from this maturation schedule: an immature tree remains so with probability $1-\theta_{it}$ and it enters the reproductive state with probability θ_{it}. If a tree changes status during the study, that year is designated f_i. Once mature, trees remain mature. Any subsequent reproductive failures are due to factors other than maturation status.

Our goals include estimation of the parameters describing maturation for both ambient ($a_{\theta a}$, b_θ) and elevated ($a_{\theta e}$, b_θ) CO_2 treatments. Note that the second parameter for this gamma cdf is taken to be the same for both treatments; thus the treatment effect is taken up in the first parameter. For the gamma distribution, the mean and variance are not represented by independent parameters, making this approach reasonable. Moreover, because maturation status is unknown before cones are first observed, we must also estimate the f_i's, which are implied by the estimated statuses. The conditional probabilities associated with hidden states Q_{it} based on observations q_{it} are determined using Bayes' theorem and given in Table 1. If $q_{it} = 1$ (cones observed), then the tree must be mature, and $Q_{it} = 1$. If cones are not observed, then $q_{it} = 0$, and the tree is mature with probability $\theta_{it}(1-v)$, the joint probability that a tree of diameter d_{it} is mature and failure to recognize maturity, $1-v$, divided by the total probability of not being observed in the mature state, $1-v\theta_{it}$. The probability of being immature is its complement.

The second submodel is the conditional fecundity process, which is a log-linear mixed model with (1) fixed effects for tree size (d_{it}), CO_2 intervention history (c_{it}), and ice damage (b_{it}), (2) fixed year effects (k_t), and (3) random individual effects (β_i) (a 'random intercept model'). The vector of fixed effects for tree i in year t, $\mathbf{x}_{it} = [1 \; \log(d_{it}) \; c_{it} \; b_{it}]$ has the corresponding parameter vector $\boldsymbol{\alpha} = [\alpha_0 \; \alpha_1 \; \alpha_2 \; \alpha_3]^T$. We scale CO_2 intervention (c_{it}) as log (365/365) for ambient plots and log (365/565) in elevated CO_2 plots after 1998. Thus, c_{it} is either 0 (ambient), or 0.192 (elevated). We use this convention, rather than a standard zero/one indicator for CO_2 effect, to allow for potential interpolation of our estimates to other CO_2 levels. We neither recommend such extensions, nor do we attempt them here. Nothing is lost by this scaling, and it appears to add some generality to results. The indicator variable for trees damaged in the ice storm (b_{it}) is 0 (undamaged trees and prestorm) or, after 2002, 1 for damaged trees. Here, we modeled fixed year effects in order to examine interannual variation that is shared among trees. For tree i in year t, seed production y_{it} is given as an allometric function of diameter with additional covariates,

$$Y_{it} \equiv \log(y_{it}) = \mathbf{x}_{it}\boldsymbol{\alpha} + \beta_i + \kappa_t + \varepsilon_{it},$$

$$i = 1, \ldots,\, n,\; t = f_i, \ldots,\, T_i, \quad t_i \le f_i,\, Q_{it} = 1,$$

$$\beta_i \sim N(0,\, \tau^2),$$

$$\varepsilon_{it} \sim N(0,\, \sigma^2),$$

β_i is the random effect for tree i and is normally distributed with mean 0 and variance τ^2. Estimates for τ^2 represent population heterogeneity. One of our primary modeling goals is to accommodate this variability

Table 1 Conditional probability of being in state Q given observation q, determined using Bayes' theorem

	$Q_{it} = 0 \mid q_{it}$	$Q_{it} = 1 \mid q_{it}$
$q_{it} = 0$	$p_{00} \equiv \Pr\{Q_{it} = 0 \| q_{it} = 0\} = \frac{1-\theta_{it}}{1-v\theta_{it}}$	$p_{10} \equiv \Pr\{Q_{it} = 1 \| q_{it} = 0\} = \frac{\theta_{it}(1v)}{1-v\theta_{it}}$
$q_{it} = 1$	$p_{01} \equiv \Pr\{Q_{it} = 0 \| q_{it} = 1\} = 0$	$p_{11} \equiv \Pr\{Q_{it} = 1 \| q_{it} = 1\} = 1$

among individuals within plots and between CO_2 treatments. The CO_2 treatment effect is $\boldsymbol{\alpha}_2$, which is estimated for trees in the elevated CO_2 plots beginning in 1998 (not in 1996, the start of fumigation, because seeds require two full years to develop).

Because the conditional fecundity model applies only to mature individuals, the indexing of time begins in the year of maturation f_i. For trees that are reproductive at the beginning of the study, $f_i = t_i$. For those that become reproductive during the study, $T_i \geq f_i > t_i$. For those that remain in the nonreproductive state throughout the study, the conditional fecundity model does not apply. The year effect κ_t, $t = 1996, \dots, 2004$, extends from the first to last observations of the entire study, such that trees having different sample durations reference the appropriate year effects. The time series for tree i is

$$\mathbf{Y}_i = \mathbf{X}_i\boldsymbol{\alpha} + \mathbf{1}_{T_i}\beta_i + \boldsymbol{\kappa}_i + \boldsymbol{\varepsilon}_i,$$

where

$$\mathbf{Y}_i = \left[\log(y_{f_i}), \dots, \log(y_{T_i})\right]^{\mathrm{T}},$$

is the sequence of log seed production once the tree is mature, $\mathbf{X}_i$ is the (T_i–f_i) by four design matrix, $\mathbf{1}_{Ti}$ is the length-(T_i–f_i) vector of ones, and $\boldsymbol{\kappa}_i = \left[\kappa_{f_i}, \dots, \kappa_{T_i}\right]^T$ indexes the year effects corresponding to the sampling history of individual i. The length-(T_i–f_i) vector of errors is $\boldsymbol{\varepsilon}_i$. An example design matrix for a tree that reached maturity in 1999 and was ice damaged in 2002 looks like this:

$$\mathbf{X}_i = \begin{bmatrix} 1 & \log(d_{i,1999}) & 0.192 & 0 \\ 1 & \log(d_{i,2000}) & 0.192 & 0 \\ 1 & \log(d_{i,2001}) & 0.192 & 0 \\ 1 & \log(d_{i,2002}) & 0.192 & 0 \\ 1 & \log(d_{i,2003}) & 0.192 & 1 \\ 1 & \log(d_{i,2004}) & 0.192 & 1 \end{bmatrix}.$$

If $\mathbf{X}_i$ described a tree in the ambient plots, the third column would be zeros. The design is imbalanced due to trees entering the regression in different years as they mature. There are $n_f = 557$ trees in the FACE plots. The process model potentially has a different duration for each tree.

Data models: Seed trap data are represented as counts per trap per year, s_{jt} (monthly values are summed over seed year), for years $t_j, \dots, T_j$. Seed trap data span $t_j = 1996$ through $T_j = 2004$. The sampling distribution for seed trap data follows Clark *et al.* (2004). It is conditionally Poisson

$$s_{jt} \sim Pois(A_j g_j(\mathbf{y}_t)), \quad j = 1, \dots, m, \quad t = t_j, \dots, T_j,$$

where A_j is the area of trap j ($0.16\,\mathrm{m}^2$), and the density of seed rain at location j (in seeds per m^2) is

$$g_j(\mathbf{y}_t) = \sum_{i=1}^{n} y_{it} Q_{it} f(r_{ij};\, u), \quad j = 1, \dots, m.$$

Q_{it} is reproductive state, assuming a value of zero for trees not yet mature, and one for mature trees. Thus, $g_j(\mathbf{y}_t)$ is the summed contribution of seeds from all n trees to seed trap j. The dispersal kernel is a two-dimensional Student's t, a function of distance r_{ij} between tree i and trap j, with mean distance u in m^2 (see Clark *et al.*, 1999).

Cone counts come from the FACE stand, where surveys of these relatively small trees can be conducted from above the canopy (LaDeau & Clark, 2001). The cone count for the ith tree is z_{it}, $t = t_i, \dots, T_i$. The sampling distribution for cones is

$$z_{it} \sim Pois(\gamma Q_{it} y_{it}),$$

and only applies to mature trees ($Q_{it} = 1$). The Poisson parameter is given by the product of seeds per cone γ (mean $= 70$ seeds cone^{-1} in both CO_2 environments; authors' unpublished data) and seed production conditional on being in a reproductive state $Q_{it}\, y_{it}$. Because we are conditioning on the true state Q_{it}, which will often be estimated, rather than known, this likelihood differs from that of LaDeau & Clark (2001) only in that we previously marginalized over the unknown status. Here, the PHMM is used to explicitly follow status. The maturation status of a tree is scored as $q_{it} = 0$ if never previously observed to have cones, and $q_{it} = 1$, otherwise.

Parameter models: We use conjugate, noninformative priors for most parameters. Regression parameters have prior $N_4(\boldsymbol{\alpha}|\mathbf{a}_\alpha, \mathbf{V}_\alpha)$ with mean vector $\mathbf{a}_\alpha$ and prior covariance $\mathbf{V}_\alpha = \mathrm{Diag}[100,1,1,10]$. For year effects we use $\prod_{t=1996}^{2004} N(\kappa_t|0, v_\kappa)$ with prior variance $v_\kappa = 1000$. We place a sum-to-zero constraint on year effects. Random effects are normally distributed with prior $\prod_{i=1}^{n} N(\beta_i|0, \tau^2)$ and an inverse gamma hyperprior on the variance, $IG(\tau^2|0.1, 0.1)$. The error variance has prior $IG(\sigma^2|1, 0.1)$. We used a strong prior on recognition success v. Experience with repeated status observations indicate recognition success of $>95\%$ for the small FACE trees observed from towers.

Nonconjugate priors were used for parameters in the dispersal kernel $f(r_{ij}, u)$ and the maturation schedule θ_{it}. The dispersal kernel has a fitted parameter u, which is proportional to the mean squared dispersal distance (Clark *et al.*, 1999). We accounted for the fact that trees are relatively short in the FACE site and used the prior $Gam(u_f|5, 1)$. This has mean dispersal distance of 5 m, but is still rather vague. The full model is

$$p(\mathbf{y}, \boldsymbol{\theta}, \boldsymbol{\alpha}, \boldsymbol{\beta}, \sigma^2, \tau^2, \dots, \mathbf{X}, \mathbf{Z}) \propto,$$

$$\underbrace{\prod_{i=1}^{n_f}\prod_{t=t_i}^{T_i} Pois(z_{it}|\gamma Q_{it}y_{it})}^{\text{Cones}} \underbrace{\prod_{i=1}^{n_h}\prod_{t=t_i}^{T_i} Bernoulli(Q_{it}|\theta_{it})}^{\text{Maturationstate}} \underbrace{\prod_{j=1}^{m}\prod_{t=t_j}^{T_j} Pois(s_{jt}|A_j g_j(\mathbf{y}_t))}^{\text{Traps}} \,,$$

$$\prod_{i=1}^{n} N_{T_i}(Y_i|\mathbf{X}_i\boldsymbol{\alpha} + 1_{T_i}\beta_i + \kappa_i,\, \sigma^2\mathbf{I}_{T_i})N_4(\boldsymbol{\alpha}|\mathbf{a}_\alpha,\, \mathbf{V}_\alpha)\prod_{t=1}^{T} N(\kappa_t|a_{\kappa_t},\, v_\kappa)\prod_{i=1}^{n} N(\beta_i|0,\, \tau^2),$$

$$IG(\sigma^2|1,\, 0.1)IG(\tau^2|0.1,\, 0.1)Gam(a_\theta|4,\, 1)Gam(b_\theta|0.5,\, 1)Gam(u_f|5,\, 1).$$

Estimation is accomplished with a Gibbs sampler, which involves simulating the posterior density of parameters by alternately sampling from conditional posteriors and updating values. The conditional posteriors are given in the Appendix. Further details of this modeling approach are available in Clark & LaDeau (in press).

Results

Carbon dioxide enrichment affected mean cone production both through early maturation and increased fecundity. Trees at the FACE site were not reproductively mature before 1999 (Fig. 2), and low seed production occurred in 2001 and in 2004. Figure 2 includes seed rain data from a nearby mid-successional forest containing mature pine trees (HW) and demonstrates high synchronicity in seed production between the FACE plots and the nonexperimental mature forest. Elevated CO$_2$ atmosphere does not affect the synchronicity of pine seed production within this landscape.

Trees in the elevated CO$_2$ plots produced twice as many cones (4063 cones observed) between 1998 and 2004 as trees in the ambient plots (2070 cones) for 262 and 295 sample trees, respectively. Interannual variability ranged from 41 cones on 21 trees in 1998, to 1539 cones on 167 trees in 2000. The difference in mean cone number per tree between elevated and ambient CO$_2$ stands is shown for each year in Fig. 3. Trees grown in high CO$_2$ produced more cones during 5 of the 7 post-intervention years, with reduced or absent enrichment in years with correspondingly low regional seed production (i.e. 2001, 2004 in Fig. 2). The comparison of means in Fig. 3 demonstrates greater cone production in high CO$_2$ plots in 5 years, but disguises potentially important shifts in population demography. Figure 4 illustrates the extent of the variability in observed cone production among individuals. Figure 4a shows cone production in the 10 most fecund trees in each of the six plots.

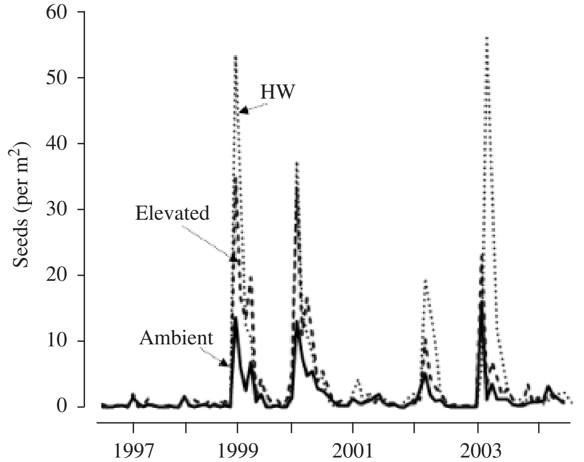

Fig. 2 Seed density collected from ambient (solid line) and elevated treatments (dashed line). Seed collections from a nearby mature, mixed hardwood-pine site began in 1999 (dotted line). All three plots experienced reduced seed production in 2001 and 2004.

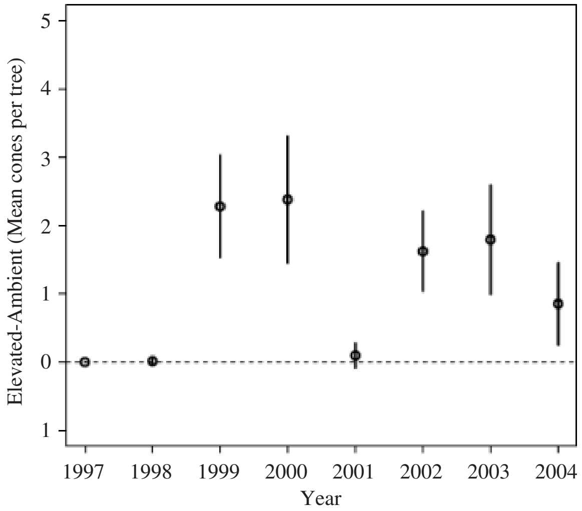

Fig. 3 The difference in mean number of cones per tree (observed) between high CO$_2$ and ambient plots. Error bars denote standard deviations.

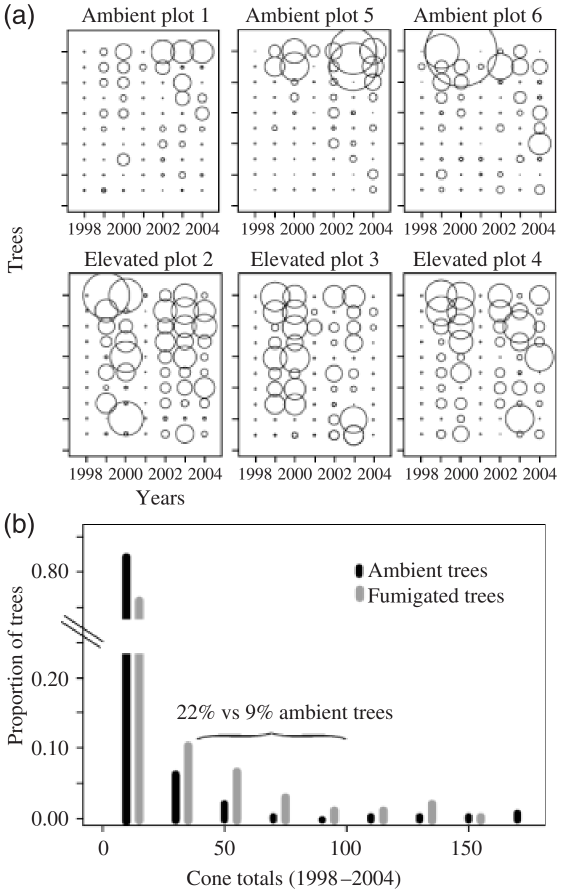

Fig. 4 (a) The 10 most fecund trees (1998–2004) are ordered along the *y*-axis for each of the six plots. Circles are scaled by the number of cones observed on a tree in each year. The same scaling factor is used for all plots. (b) Histogram of total cone production from 1998 to 2004 for all trees >15 cm DBH in ambient (dark bars) and elevated (light bars) CO_2 plots.

Fecundity was higher in the elevated plots compared with ambient plots in the early years and remained relatively consistent throughout the study (lower panel, Fig. 4a). Maturation of ambient trees occurred later and was more likely to increase over time (top panel, Fig. 4a). Twenty-two percent of the trees in high CO_2 produced between 40 and 100 cones during the study, compared with only 9% of ambient trees (Fig. 4b). Three of the four most fecund trees from 1998 to 2004 (>150 cones observed) grew in ambient plots.

Parameter estimates from the hierarchical regression model are shown in Table 2. The model estimated an overall CO_2 effect on mean seed production by mature trees ($\alpha_2 > 0$) and highlighted the importance of including the term for ice storm damage ($\alpha_3 < 0$). The ice storm in December 2002 affected variability among individuals and within individual time series. Up to 20% of the stems in each plot suffered canopy damage. The negative parameter estimate for ice storm effect quantifies the reduced fecundity potential of damaged trees and allows us to accommodate this large source of variability that occurs in the middle of our experiment. The diameter effect (α_1) was not a useful predictor of fecundity of mature trees in this model, largely due to the narrow range of diameters in the even-aged FACE plots and to the large variability in seed production among similar-sized individuals. Diameter is still an important component of the maturation submodel. As a rough index, the r^2 value for observed and predicted cones is 0.54.

Table 2 Estimates for regression parameters with posterior means, Bayesian standard errors (SE), and 95% credible intervals

Parameter	Posterior mean estimate	SE	25% CI	95% CI
Intercept α_0	1.494	0.091	1.317	1.674
Diameter α_1	−0.374	0.089	−0.550	−0.001
CO_2 α_2	0.743	0.375	0.003	1.477
Ice α_3	−1.04	0.191	−1.413	−0.666
σ^2	0.896	0.045	0.812	0.989
τ^2	0.215	0.027	0.166	0.272

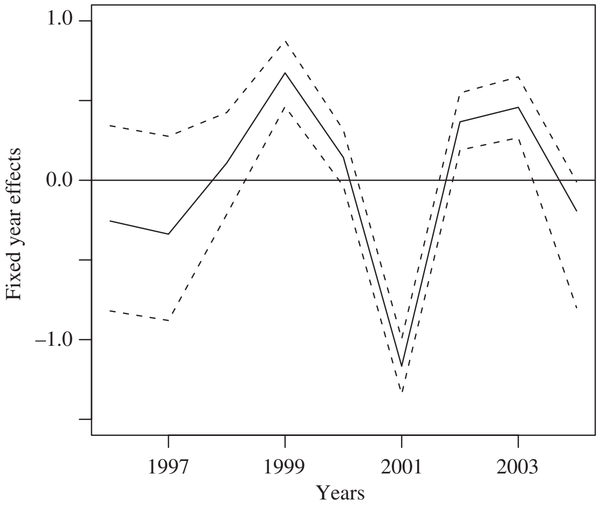

Fig. 5 Parameter estimates for year effects (κ in Fig. 1). Dashed lines indicate 95% credible intervals.

Year effect estimates from the longitudinal model describe interannual variability shared by all trees in the study (Fig. 5). Negative year estimates in 2001 correspond to reduced observations for both seed rain and pine cone production in that year among all trees from both CO_2 treatments (Figs 2 and 3). Accounting for interannual variability explicitly allows us to accommodate observations of low fecundity among trees with previous pine cone production in both high and ambient CO_2 plots.

Variability in ontogeny and fecundity among individuals was substantial. In 2004, 50% of the control trees and 25% of the CO_2 fumigated trees were still not reproductively mature, while other trees in these plots produced up to 80 cones a year. These demographic patterns were captured in our longitudinal analysis by the random intercept model and the maturation model. Including these demographic patterns of variability in the model enhances our ability to estimate CO_2 enrichment effects. Individual random effects ($\boldsymbol{\beta}$) were not grouped according to treatment or plot and ranged from −0.80 to 1.05, with mean 0. The standard deviation around the individual effects described a significant source of variability in fecundity among trees grown in both CO_2 treatments ($\tau^2 > 0$).

Trees grown in elevated CO_2 atmosphere made the transition to reproductive maturation at smaller diameters. Figure 6a illustrates a reduction in the diameter at which 50% of the trees are reproductive in the elevated CO_2 plots ($a_{\theta e}/b_\theta < a_{\theta a}/b_\theta$, see maturation submodel in Fig. 1). Maturation parameters were not sensitive to prior values, and means calculated from the posterior densities were clearly shifted from the prior (mean = 8 cm). Because this is an even-aged cohort, trees growing in high CO_2 not only reached reproductive maturation at smaller diameters, but also at younger ages. The onset of maturation in 1999 was most dramatic in the elevated CO_2 plots (Fig. 6b). Twice as many trees were reproductively mature in 1999 in the fumigated stands as compared with ambient stands, consistent with the previous analysis of the first years of data (LaDeau & Clark, 2001). The number of mature trees increased in both CO_2 treatments since 1999, so that by 2004 roughly 50% of ambient trees and 75% of fumigated trees have produced cones (Fig. 6b).

Figure 7a shows mean cone production calculated per tree basal area (m^2), conditional on being mature. The CO_2 enrichment effect (shaded in Fig. 7a) is greater in 1999 and 2000 than in subsequent years, thus appearing to have decreased with time. However, modest effects in 2002 and 2003 may reflect the emergence of a few highly reproductive ambient trees at this time rather than downregulation in the fumigated trees. Modeled cumulative seed production (Fig. 7b) is higher among trees in the CO_2 fumigated plots relative to ambient grown trees throughout the study period. By 2004, trees grown in high CO_2 have produced an average 300 more seeds per tree than the ambient grown cohort.

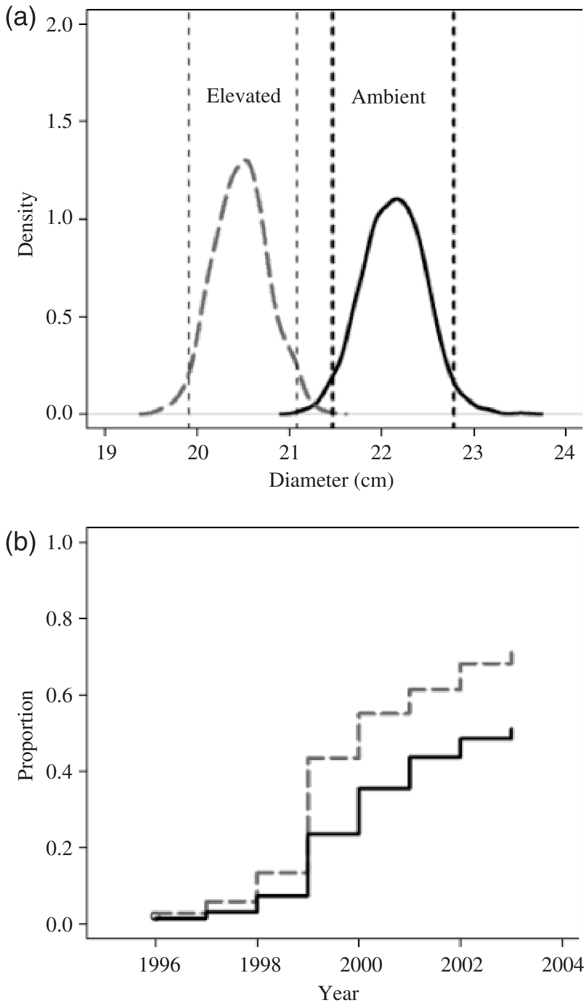

Fig. 6 (a) Density of parameter estimates for the diameter (DBH in cm) at which 50% of the trees become reproductive. Curves denote 95% credible intervals for the ambient (dark, solid lines) and elevated (light, dashed lines) plot estimates. (b) The estimated proportion of trees reproductively mature (Q_{it} equal to 1 in Fig. 1) in a given year for ambient (dark, solid line) and elevated (light, dashed line) plots.

Discussion

The possibility that elevated CO_2 may have persistent consequences for forest dynamics has long been questioned because there is experimental evidence to suggest the effects should be temporary (see Long *et al.*, 2004), and relevant data have been lacking. In this 8-year study that accounts for the broad range of contributions to tree fecundity, we find that previous short-term responses indeed persist. The fecundity response to high atmospheric CO_2 demonstrated in this study suggests long-term implications for both intraspecies demography and interspecific community dynamics. Our study suggests that long-term effects of CO_2 enrichment may be seen in reproductive biomass, though not necessarily at the magnitude suggested by early response. Although the magnitude of CO_2 enrichment varied among years and individuals, stands grown in

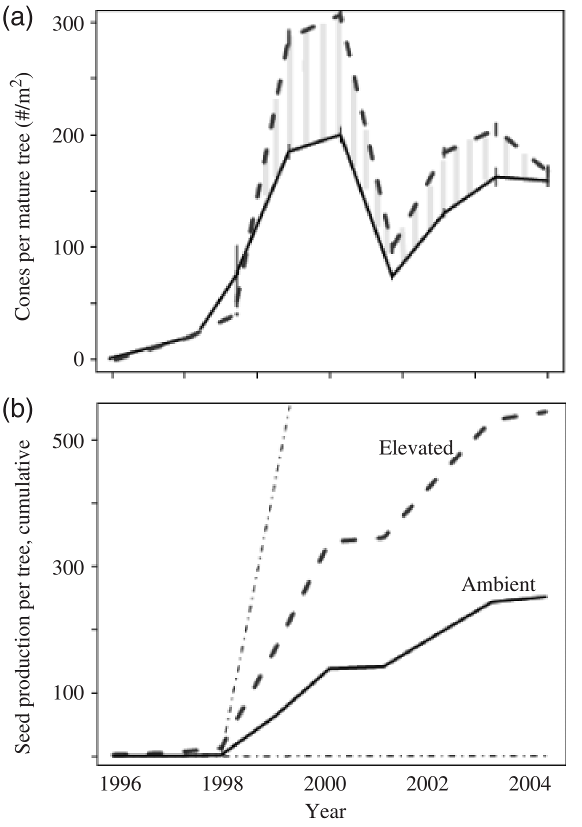

Fig. 7 (a) Estimated cone production (Y_{it} in Fig. 1, divided by 70 seeds cone^{-1}) per woody basal area (m^2) of mature trees, from 1996 to 2004. The dashed line shows the mean estimate for high CO$_2$ trees. The shaded area is the estimated mean CO$_2$ enrichment. (b) Modeled cumulative seed production averaged over all ambient (solid line) and elevated (dashed line) CO$_2$ grown trees. The 95% credible interval around the ambient mean incorporates both the random individual effects, which constitute the largest source of variation, as well as estimation error.

elevated atmospheric CO$_2$ since August 1996 produced nearly twice as many seeds per tree as ambient stands (Fig. 6b). The mean enrichment response appears to have declined during our study (Fig. 6a), though we suggest that this is due to the emergence of a few highly productive ambient grown trees, some of which were prolific seed producers (Fig. 4), and not to downregulation in the CO$_2$ fumigated stands.

Once trees in the FACE site reached maturity, seed production by both ambient and fumigated trees was synchronized with surrounding, mature pine trees (Fig. 2). Poor cone crops (i.e. observed in 2001 and 2004) have been related to spring drought, pollen limitation, and predation (Wenger, 1957; Schultz, 1997; Cain & Shelton, 2000). Our estimates of negative year effects (Fig. 5) and observed low regional seed production (Fig. 2) correspond to seed dispersal from cones initiated during growing seasons with notably low precipitation. During the growing seasons of 1999 and 2002, precipitation totaled only 66% and 81% of the long-term average (data from www.erh.noaa.gov, collected at the Raleigh–Durham International Airport). Cones initiated in 1999 and 2002 would have been censused in 2001 and 2004, respectively. Thus, regional drought during the spring and early summer of 1999 and 2002 may have led to reduced reproductive bud set. Although few years limit our ability to determine the cause of low cone production in 2001 and 2004, we can conclude that excess photosynthate in the fumigated plots did not compensate for regional drought. More years of data are needed to effectively address these time-series dynamics.

Model results demonstrate the need to accommodate changes in population variance because of extreme weather. The ice storm that occurred during this study destroyed the canopies of many trees in this study, not killing them but effectively reducing their fecundity potential. The relative decrease in fecundity due to the ice storm was greater than any increase due to CO$_2$ enrichment (Table 2). Rather than removing all storm damaged trees from the study (or somehow deciding which trees were damaged to an extent requiring removal) the hierarchical modeling structure employed allows us to accommodate this unexpected change in the system. Including multiple sources of variability was especially important given that diameter was not a useful predictor of fecundity once trees matured (Table 2).

Quantifying CO$_2$ effects on tree ontogeny was a key goal of this study. Including observations of reproductive maturation and explicitly modeling the observation error was critical to achieving this goal. Observations of zero cones on individuals could have resulted from failure to observe cones present, observation during a poor cone production year (such as 2001 counts), or because a tree was actually immature. CO$_2$ enrichment increased ontogeny of *P. taeda* in our study (Fig. 6). Maturation rates are key determinants of colonization ability. Species that grow faster and reproduce more will be favored in highly disturbed landscapes. However, development rate is inversely correlated with life span across tree species (Govindaraju, 1984; Enquist *et al.*, 1999; Loehle, 2000, 1988; in conifers). If the responses obtained in this study result in allocation tradeoffs, and these trees reproduce early and die young, then CO$_2$ enrichment may increase population turnover rates rather than stand biomass.

A large proportion of trees in both treatments remained in the juvenile stage throughout our study (Fig. 6b). Failure to mature may result from light limitation and many of these juvenile trees will likely succumb to natural stand thinning in the near future. Differences in ontogeny suggest that the effects of competition on reproductive activity may be reduced in the high CO_2 plots. Fewer ambient grown trees reached maturity (i.e. Fig. 4a). By comparison, more trees growing in elevated CO_2 contributed to the seed pool than ambient grown trees, and they began to do so while smaller and younger. If it persists, the apparent shift from a few large producers in the ambient plots to many, more equitable producers in the high CO_2 plots may have implications for population genetics and stand fitness. *P. taeda* trees that produce large seed crops early in their life span tend to continue to be prolific producers (Schutlz, 1997), suggesting that individual responses seen in this young forest may be sustained over their life span. Although beyond the scope of this paper, further research demonstrates no change in seed viability between seeds grown in ambient and elevated plots at this site (LaDeau, 2005; but see Hussain *et al*., 2001). Still, future changes in climate may be less conducive to seed germination or seedling survival, effectively diminishing the CO_2-enrichment response reported here.

Forecasting ecological response to climate change involves understanding complex dynamics in space and time. Neither species, nor individuals all behave identically. Nor is the response constant over time. Estimating CO_2 effect on tree fecundity in this study was challenging due to the natural processes of weather and tree maturation, and considerable heterogeneity among individuals. Explicitly accommodating these variables in our model strengthens our longitudinal estimate of the CO_2 enrichment. Our study demonstrates the importance of considering both ontogeny and fecundity of multiple individuals over several years when evaluating reproductive effort and CO_2 enrichment response.

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Appendix

Gibbs samplers have been described for a number of ecological settings by Clark (2003) and Clark *et al*. (2003, 2004). Here, we summarize sampling for PHMM and provide conditional posteriors for other parameters.

Conditional posteriors

y_{it} : Seed production must be estimated for each mature tree and year. It is conditionally dependent on cone counts and seed trap data.

$$p(y_{it}|\ldots) \propto Pois(z_{it}|\gamma Q_{it} y_{it}) \prod_{j=1}^{m} Pois(s_{jt}|A_j g_j(\mathbf{y}_t)) N(Y_{it}|\mathbf{x}_{it}\boldsymbol{\alpha} + \beta_i + \kappa_{it}, \sigma^2).$$

This was sampled with a Metropolis step using a Gaussian proposal density. We used an adaptive step size to generate proposals for $\log y_{it}$,

$$p\left(Y^*\middle|Y_{it}^{(g)}\right) = N\left(Y^*\middle|Y_{it}^{(g)}, \left(Y_{it}^{(g)}/50\right)^2\right),$$

and then fixed the step sizes based on the imputed values of that iteration.

Regression parameters: Direct sampling was used for regression parameters. For fixed effects we have

$$\begin{aligned} &p(\boldsymbol{\alpha}|\mathbf{y}, \mathbf{X}, \boldsymbol{\beta}, \kappa, \sigma^2, \tau^2, \ldots) \\ &\quad \propto \prod_{i=1}^{n} N_{S_i}(Y_i|\mathbf{X}_i\boldsymbol{\alpha} + \mathbf{1}_{S_i}\beta_i + \boldsymbol{\kappa}_i, \sigma^2\mathbf{I}_{S_i}) N_4(\boldsymbol{\alpha}|\mathbf{a}_\alpha, \mathbf{V}_\alpha) \\ &\quad = N(\boldsymbol{\alpha}|\mathbf{V}\mathbf{v}, \mathbf{V}), \end{aligned}$$

$$\mathbf{V}^{-1} = \frac{1}{\sigma^2}\sum_{i=1}^{n} \mathbf{X}_i^T \mathbf{X}_i + \mathbf{V}_\alpha^{-1},$$

$$\mathbf{v} = \frac{1}{\sigma^2}\sum_{i=1}^{n} \mathbf{X}_i^T(\mathbf{Y}_i - \mathbf{1}_{S_i}\beta_i - \kappa_i) + \mathbf{V}_\alpha^{-1} a_\alpha.$$

where $S_i = T_i - f_i$. marginalized over random effects, these become

$$\mathbf{V}^{-1} = \sum_{i=1}^{n} \mathbf{X}_i^T \mathbf{D}^{-1} \mathbf{X}_i + \mathbf{V}_\alpha^{-1},$$

$$\mathbf{v} = \sum_{i=1}^{n} \mathbf{X}_i^T \mathbf{D}^{-1}(\ln \mathbf{y}_i - \kappa_i) + \mathbf{V}_\alpha^{-1} a_\alpha,$$

where

$$\mathbf{D} = \sigma^2 \mathbf{I}_{S_i} + \tau^2 \mathbf{1}_{S_i \times S_i}.$$

Individual tree effects are given by

$$\begin{aligned} &p(\beta_i|\mathbf{y}, \mathbf{X}, \boldsymbol{\alpha}, \boldsymbol{\kappa}, \sigma^2, \tau^2 \ldots) \\ &\quad \propto N_{S_i}(Y_i|\mathbf{X}_i\boldsymbol{\alpha} + \mathbf{1}_{S_i}\beta_i + \boldsymbol{\kappa}_i, \sigma^2\mathbf{I}_{S_i}) N(\beta_i|0, \tau^2) \\ &\quad = N(\beta_i|V_i v_i, V_i), \end{aligned}$$

where

$$V_i^{-1} = \frac{S_i}{\sigma^2} + \frac{1}{\tau^2},$$

$$v_i = \frac{1}{\sigma^2}\mathbf{1}_{S_i}^T(\mathbf{Y}_i - \mathbf{X}_i\boldsymbol{\alpha} - \boldsymbol{\kappa}_i) = \frac{1}{\sigma^2}\sum_{t=f_i}^{T_i}(Y_{it} - \mathbf{x}_{it}\boldsymbol{\alpha} - \kappa_{it}).$$

Year effects are given by

$$\begin{aligned} p(\kappa_t|\mathbf{y}, \mathbf{X}, \boldsymbol{\alpha}, \boldsymbol{\beta}, \sigma^2, \tau^2 \ldots) &\propto \prod_{i\in\{t\}} N(Y_{it}|\mathbf{x}_{it}\boldsymbol{\alpha} + \beta_i + \kappa_t, \sigma^2)N(\kappa_t|a_{\kappa t}, v_\kappa) \\ &= N(\kappa_t|V_t v_t, V_t), \end{aligned}$$

where $\{t\}$ is set of all trees for which observations are available in year t, and

$$V_t^{-1} = \frac{n_t}{\sigma^2} + \frac{1}{v_\kappa},$$

$$v_t = \frac{1}{\sigma^2}\sum_{i\in\{t\}}(Y_{it} - \mathbf{x}_{it}\boldsymbol{\alpha} - \beta_i).$$

The variance for residual error is sampled from

$$\begin{aligned} p(\sigma^2|\beta, \ldots) &\propto \prod_{i=1}^{n} N_{S_i}(\mathbf{Y}_i|\mathbf{X}_i\boldsymbol{\alpha} + \mathbf{1}_{S_i}\beta_i + \boldsymbol{\kappa}_i, \sigma^2\mathbf{I}_{S_i})IG(\sigma^2|0.1, 0.1) \\ &= IG\left(\sigma^2 \middle| 0.1 + \frac{1}{2}\sum_{i=1}^{n} S_i, 0.1 + \frac{1}{2}\sum_{i=1}^{n}\sum_{t=f_i}^{T_i}(Y_{it} - \mathbf{x}_i\boldsymbol{\alpha} - \beta_i - \boldsymbol{\kappa}_{it})^2\right). \end{aligned}$$

The variance for random individual effects is

$$\begin{aligned} p(\tau^2|\beta, \ldots) &\propto \prod_{i=1}^{n} N(\beta_i|0, \tau^2)IG(\tau^2|0.1, 0.1) \\ &= IG\left(\tau^2 \middle| 0.1 + \frac{n}{2}, 0.1 + \frac{1}{2}\sum_{i=1}^{n}\beta_i^2\right). \end{aligned}$$

Maturation schedule: Parameters for the maturation schedule cannot be sampled directly. A Metropolis step was used. Conditionals are:

$$p(a_\theta|\ldots) \propto \prod_{i=1}^{n_h}\prod_{t=t_i}^{T_i} Bernoulli(Q_{it}|\theta_{it})Gam(a_\theta|\mathbf{4}, 1),$$

$$p(b_\theta|\ldots) \propto \prod_{i=1}^{n_h}\prod_{t=t_i}^{T_i} Bernoulli(Q_{it}|\theta_{it})Gam(b_\theta|0.5, 1).$$

A proposal was generated from a uniform distribution centered on the currently imputed value and width 0.4 times as that value. The same scheme was used for both parameters. There is a pair of parameters for both the ambient and elevated CO$_2$ treatments.

Dispersal parameters: The dispersal parameter u_f was sampled from the conditional posterior

$$p(u_f|\ldots) \propto \prod_{j=1}^{m}\prod_{t=t_j}^{T_j} Pois(s_{jt}|A_j g_j(\mathbf{y}_t))Gam(u_f|a_f, b_f),$$

using a Metropolis step using the same approach as for maturation parameters.