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Modelling of stem biomass accumulation in *Pinus densiflora* seedlings exposed to aqueous-phase OH radicals generating mist

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Abstract

The present study aimed to evaluate the short-term biomass accumulation of forest trees exposed to wet acidic depositions. A hierarchical Bayesian model of tree growth was developed based on the data of a short-term experiment in which two-year old Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) seedlings were exposed to aqueous phase OH radicals generated by an iron-oxalate-H_2O_2 mist (a pseudo-polluted dew) over two growing periods. We conducted a statistical comparison of tree growth between the control and pollution treatment groups by using the growth model incorporated the random effects due to the unknown characteristics of each seedling. The variability among seedlings is expressed in this model by the posterior probabilistic distributions of unobserved dry weight of a stem cohort before exposure treatment. The analysis of the effects of pollution treatment on the stem growth revealed that this treatment decreases the biomass allocation in the current year stems. However, the effects on the relative growth rate of pre-existing stems were unclear. Based on these results is that, we can speculate that in a polluted environment, the short-term growth of the young stems in the seedlings inhibited by pollution treatment, thereby resulting in the slowdown of long-term biomass accumulation. This can explain the patterns observed in the declining Japanese red pine forests that are subjected to ·OH-generating dews in the polluted area of western Japan.

1 Introduction

Modelling and statistical analysis using inherent uncertainty and incomplete data have been widely conducted in the field of environmental science, for example, the dynamic vegetation model (Lexer and Höenninger, 2004) and the estimation of physiological parameters in lake ecosystems (Malve et al., 2005). A recent trend is the use of Bayesian methods for the statistical modelling of such situation (Clark et al., 2003; Ellison, 2004; Clark, 2005) in which we introduce the prior probabilistic distributions of unknown factors, such as the characteristics of unobservable/unobserved experimental materials, transitional changes during experimental period and fluctuations in environmental factors.

Controlling for unobserved factors is not completely solved in the modelling study of tree growth, whereas many detailed process-based and functional-structured models have been developed (Roux et al., 2001). The detailed tree simulators become more diverse, for example, physiological process-based models such as `TREGRO` (Weinstein and Yanai, 1994; Weinstein et al., 1998; Yun et al., 2001; Laurence et al., 2001); three-dimensional functional-structural tree models such as `LIGNUM` (Sievänen et al., 1997; Perttunen et al., 1998; Perttunen et al., 2001) and `PipeTree` (Kubo and Kohyama, 2005). These models that incorporate various physiological processes are

accepted because their usefulness and validity. Consequently, they share a common problem, i.e., model complexity, which can lead to failure, because these models require large number of parameters including those that are difficult to estimate (e.g. Mäkelä et al., 2000; Radtke and Robinson, 2006).

Bayesian inference provides two different approaches to deal with the problem of model complexity: tackling or avoiding. An example of the former approach, in the forest growth is the application of Bayesian modelling to generate the prior and posterior distributions of the parameters used for a complex process-based model on the basis of information from a reliable empirical growth model in lieu of field observations (Radtke and Robinson, 2006). In this case, Bayesian inference functions as a reliable generator of posterior distribution in a very high dimensional parameter space.

The other Bayesian policy, i.e., avoiding complexity, may be utilized if neither sufficient data nor reliable empirical models are available. Clark et al. (2003) emphasized the importance of modelling using the uncertainty/variability of parameters while maintaining the simplicity of the model process (in other words, not to increase the complexity of model by adding parameters) in situations where error structure is strongly affected by the differences in individual and site characteristics. Hierarchical Bayesian modelling can facilitate the detection of the manner in which

a focal factor changes the observed pattern in situations where insufficient information is available but considerable random effects exist in the data. This is because it expresses the uncertainty of unobserved measurements as the posterior distributions defined by the products of likelihood functions and hierarchical priors (Clark et al., 2003; Ellison, 2004; Clark, 2005).

The objective of the experiment in which the target data for the current study on the growth of Japanese red pine (*Pinus densiflora* Sieb. et Zucc., an evergreen coniferous tree) seedlings exposed to iron(Fe)-oxalate[$(COOH)_2$]-H_2O_2 mist, a pseudo polluted dew (Kobayashi et al., 2002), are as follows. This experiment was carried out to detect whether the chemicals present in the wet deposition in and around urban areas cause a decline of the pine forests in western Japan (refer to Kume et al., 2001; Chiwa et al., 2005). Hydrogen peroxide (H_2O_2) is well known as a reactive oxygen species that forms in plant cells and it affects biochemical processes such as photosynthetic pathways under environmental stresses, such as high light intensity and the presence of air pollutants (Asada, 1999; Halliwell and Gutteridge, 1999; Kondo, 2002). Although gaseous H_2O_2 had little effect on plant functions (Polle and Junkermann, 1994), Kume et al. (2001) and Kobayashi et al. (2002) showed that a mist containing iron-oxalate-H_2O_2 , which simulates polluted morning dew in the declining pine forests, changes some physiological traits, such as needle CO_2

assimilation rate of the Japanese red pine. Kume et al. (2005) suggested that these changes are induced by the system that generates the hydroxyl radical (·OH), the most aggressive oxidant, via a photochemical process in the polluted dew waters on the surface of pine needles.

If a "polluted" environment reduces the needle photosynthetic rate and then the accumulation rate of biomas in some form, it is likely to result in either less biomass accumulation at the plant level in the future, i.e., a decline in the growth of tree. This is consistent with field observations at Mt. Gokurakuji, western Japan (Kume et al., 2000a; Kume et al., 2000b; Kume et al., 2006) wherein the photochemical formation of ·OH in morning dew on the needle surfaces was considerably greater in a declining pine stand facing an urban area than in a healthy pine stand on the opposite side of the mountain (Nakatani et al., 2001).

In the present study, the objective of the statistical analysis is to quantify the effects of ·OH-generating dew on the growth of seedlings based on the data of a pseudo polluted dew exposure experiment (Kobayashi et al., 2002). For this purpose, we focused on the biomass accumulation of stems because long-term tree growth is a consequence of the accumulation of short-term growth of stems (branches and trunks). Since this data appeared to be insufficient to develop a parameter-rich model for tree growth, such as `TREGRO`, we constructed an ecological model with a

simple process to analyze the growth of pine seedlings under pollution treatment conditions by using a hierarchical Bayesian model based on the structural data of the experimental seedlings.

2 Experimental methods

This section briefly describes the method of the tree growth experiment under pollution treatment (Kobayashi et al., 2002) and the data structure. Three-year old Japanese red pine seedlings were grown in O_3-reduced open-air system chambers placed at a sunny flat site on the Hiroshima University campus, western Japan from 10 August 1999 to 21 September 2000. The details of the pollution treatment and the procedure of the experiment are described previously (Kobayashi et al., 2002).

Four pine seedlings which were treated with iron-oxalate-H_2O_2 [1μM $FeCl_3$, 5μM $(COOH)_2$, and 100μM H_2O_2] and control mists were harvested the on 21 September 2000 (Fig. 1A). These seedlings were treated with the mists for approximately 14 months including two consecutive growing periods. From the first growing period, the needle CO_2 assimilation rate of these seedlings were significantly reduced by ·OH-generating iron-oxalate-H_2O_2 mist (Kobayashi et al., 2002). Prior to the harvesting of a seedling, its natural height was recorded, and then the above-ground parts were separated into flowers, buds, needles, and stem. The needles and stems were

subdivided according to their age (current-, one-, two- and three-year old). Stems of the same age are referred to as a cohort. More details such as the branching architecture and the connecting structure between the stems of the seedlings were not recorded. The cohort of stems that developed in 1997 is referred to as "cohort 1997" which was three years old in September 2000 (refer to Fig. 1A and B). The number of stems in each cohort was counted. The length and diameter of each stem were measured. All organs were dried at 70 °C and weighed.

3 Modelling

In order to detect the effects of the ·OH-generating mist exposure treatment (pollution treatment) on the growth of pine seedlings, we analyze the data of cohort 1999 (parts existing before exposure) and cohort 2000 (newly developed parts) under the treatment. First, a simple ecological model for the growth of a stem cohort of pine is defined as the frame of subsequent statistical modelling. In the next step, a statistical model to estimate parameters is constructed using the measurements of cohort 1999 and cohort 2000. The conceptual schema and notations for the growth model are shown in Fig. 2.

Our growth model of the stem cohort has the following two components: dry weight increment of cohort 1999 and biomass allocation between cohort 1999 and

cohort 2000 with a fixed ratio. Let i be the index for individual seedlings where $i \in \{\texttt{C\#1}, \cdots, \texttt{C\#4}\}$ for seedlings in control group exposed to the mists containing few ·OH, and $i \in \{\texttt{T\#1}, \cdots, \texttt{T\#4}\}$ for the treatment group exposed to ·OH-generating mists (pollution treatment). For a given seedling i, the expectation of the dry weight of cohort 1999 in September 2000 (Fig. 1, after exposure) y_i is proportional to its dry weight x_i in September 1999 (before exposure). We introduce a formula to express this relationship, $\mathrm{E}(y_i) = g_i x_i$, where g_i is the relative growth rate (RGR) of stem cohort 1999. The RGR g_i is affected by pollution treatment $g_i = \exp(\beta_0 + \beta_T T_i)$, where β_0 and β_T are the coefficients of constant term and treatment status T_i, respectively. The value of treatment status T_i is set to zero if seedling i is from control group, or to one if it is from the pollution treatment group. Since the dry weight x_i of cohort 1999 before the pollution treatment is not observed, we define x_i as a random variable sampled from a probabilistic distribution. Based on the definition of g_i, a negative β_T indicates that the stem RGR is decreased by the pollution treatment.

The expectation of the dry weight z_i of cohort 2000 in September 2000 is proportional to the growth of cohort 1999. The relationship is expressed as $\mathrm{E}(z_i) = a_i(y_i - x_i)$, where a_i is referred to as the allocation weight that also include a parameter of pollution treatment, $a_i = \exp(\alpha_0 + \alpha_T T_i)$, where α_0 is the baseline parameter

and α_T is the coefficient of pollution treatment. If a_i is smaller than one, biomass allocation is smaller in cohort 2000 (newly developed stems) than in cohort 1999 which was developing before the pollution treatment.

A hierarchical Bayesian statistical model is constructed based on the above ecological model of stem cohort growth. In Bayesian inference, all parameters (including missing data) are generated by prior distributions (e.g. Rivot et al., 2004; Agarwal et al., 2005; Clark, 2005). To obtain the values of parameters, Gibbs sampling methods driven by the Markov Chain Monte Carlo (MCMC) calculation generate sample sets from the joint posterior distribution of all parameters (Qian et al., 2003). All variables and parameters are listed in Table 1 with the means and variances of (prior) probabilistic distributions.

Since the Gamma distribution is a distribution of non-negative values, we assume that the weights of the stem cohorts (z_i, y_i, and x_i) follow this distribution with a variance that is proportional to its mean. The distribution of z_i, the total weight of cohort 2000 in September 2000, has a mean $a_i(y_i - x_i)$ and variance that is equal to the mean scaled by the rate parameter ρ_z, i.e., $a_i(y_i - x_i)/\rho_z$. Here, we introduce a notation $p(z_i|y_i, x_i, a_i, \rho_z)$ that represents the conditional probability density (or likelihood) of z_i given by the Gamma distribution under $\{y_i, x_i, a_i, \rho_z\}$. As in cohort 2000, $p(y_i|x_i, g_i, \rho_y)$ represents the conditional probability density of the total weight

y_i of cohort 1999 in September 2000, given by the Gamma distribution of mean $g_i x_i$ and variance $g_i x_i / \rho_y$.

In this growth model, the total weight x_i of cohort 1999 in September 1999 (before exposure), is defined as a random variable following some appropriate prior distribution. The conditional probability density of x_i, $p(x_i|w_i, \rho_x)$, is given by the Gamma distribution as well as by the observed cohort weight y_i and z_i. The prior distribution of x_i has mean w_i and variance w_i/ρ_x. The individual specific mean w_i is defined as a combination of measurements and the parameters of pollution effects, that is,

$$\begin{aligned} w_i = & \text{(mean stem weight of cohort 2000 of } i) \\ & \times \text{(stem number of cohort 1999 of } i) \\ & \times \exp(-(\alpha_T + \beta_T)T_i), \end{aligned}$$

which includes the adjustment of the effects of pollution treatment by $\exp(-(\alpha_T + \beta_T)T_i)$ term. This is because the mean stem weight for x_i has to be revised when the current-year old stems in 2000 are smaller those in 1999 due to the effects of pollution treatment. This is the hierarchical structure in the Bayesian growth model, because the distribution of x_i is defined as a prior distribution that requires a hyper parameter ρ_x and its hyper prior distribution.

It should be noted that the uncertainty of x_i given by its posterior distribution

also acts as the random effects of seedling i on the growth of y_i and z_i. Crawley (2005) defines random effects in statistical models as they do not influence on the mean but only on the variance of the response variables. Therefore, it should be considered that the posterior distribution of x_i represents the mixed effects that influence both the mean and variance of the observed values y_i and z_i among the seedlings. This is important to detect the effects of pollution treatment under unknown heterogeneity among the experimental seedlings.

Since we do not prior knowledge regarding the parameters to be estimated, the distribution for each parameter of fixed effects ($\boldsymbol{\alpha} = \{\alpha_0, \alpha_T\}$ and $\boldsymbol{\beta} = \{\beta_0, \beta_T\}$) is assumed as a non-informative prior distribution. We adopt all the functional forms as the Gaussian distribution of mean zero and variance one. Prior distribution for each variance parameter ($\boldsymbol{\rho} = \{\rho_z, \rho_y, \rho_x\}$) is the non-informative Gamma distribution of mean one and variance 10^3.

The (joint) posterior distribution of parameters is proportional to the total products of likelihood functions, i.e., prior probabilistic densities,

$$\begin{aligned} p(\{x_i\}, \boldsymbol{\alpha}, \boldsymbol{\beta}, \boldsymbol{\rho} | \ \{\text{data}\}) \propto \prod_i & p(z_i|y_i, x_i, a_i, \rho_z) \ p(y_i|x_i, g_i, \rho_y) \ p(x_i|w_i, \rho_x) \\ & \times \ p(\alpha_0) \ p(\alpha_T) \ p(\beta_0) \ p(\beta_T) \ p(\rho_z) \ p(\rho_y) \ p(\rho_x), \end{aligned}$$

where $\{\text{data}\}$ is defined as $\{\text{data}\} \in \{\{y_i\}, \{z_i\}\}$. The MCMC sampling from the Gibbs distribution defined earlier was performed to infer the posterior distribu-

tions of parameters. The sampling was carried out using the Gibbs sampling software, JAGS-0.90 (developed by M. Plummer, http://www-fis.iarc.fr/~martyn/software/jags/). The size of sampling was 1000 with a 10 step interval after 40000 burn-in steps. The JAGS files for the growth model including the model definition in BUGS code and the data of red pines are available at http://hosho.ees.hokudai.ac.jp/~kubo/forest/redpine/v2006/.

4 Results and Discussion

Measurements of all the eight pine seedlings in September 2000 are shown in Table 2. Considerable variabilities were observed among the seedlings even within each treatment group. The relationship between the age of stem cohort and its total dry weight shows that with the exception of one seedling, almost all cohorts 2000 in the seedlings of the pollution treatment group are smaller than cohorts 1999. On the other hand, the biomass allocation between cohort 1999 and cohort 2000 is almost equivalent in the control group (Fig. 3). Since the variabilities among the seedlings shown in Table 2 and Fig. 3 cannot be negligible, we will focus on the results from the Bayesian analysis of the parameters for the relative growth rate of stems by incorporating the individual characteristics as random effects.

The means of posterior distributions of the stem dry weight x_i of cohort 1999

in September 1999 of seedling i is in range from approximately 2.66 to 6.61 dw g (Fig. 4 and Table 3). While the difference in the means of x_i between the treatment groups is unclear, the variance of posterior distributions in the pollution treatment group is considerably greater than that in the control group. This is because they are affected by the fluctuation in the parameters of treatment effects α_T and β_T during MCMC sampling.

The convergences of MCMC sampling are assessed by sampling transitions and the density plots of posterior distributions of parameters for the relative growth rate g_i and relative allocation factor w_i (Figs. 5 and 6). The 95% credible interval of β_T, the effects of pollution treatment on RGR, includes $\beta_T = 0$ (Fig. 5D and Table 3). The 95% credible interval of α_T, the effects of pollution treatment on biomass allocation, does not include $\alpha_T = 0$ (Fig. 6D and Table 3).

The most important result of the analysis of the experiment data of pine seedlings with and without ·OH-generating mist exposure (Kobayashi et al., 2002) is the detection of the negative effect of pollution treatment on the biomass allocation to the current year stems. This is shown by the posterior distribution of α_T (Fig˙ 6D and Table 3) generated by the hierarchical Bayesian model with the random effects caused by unobserved factors in each seedling that are expressed by the estimated posterior distribution of x_i (Fig. 4). In other words, the variability of x_i represents

all the uncertainty in the growth of seedling i.

By accepting the statistical significance of α_T, we can evaluate the geometric mean of biomass allocation weight by using the mean values listed in Table 3. The mean allocation weight of the seedlings in the pollution treatment group is $a_i = \exp(0.27 - 0.48) \approx 0.81$, i.e., biomass allocation ratio between cohort 1999 and cohort 2000 is approximately $1 : 0.81$, while that for controls is $\exp(0.27) \approx 1.31$ in which the allocation ratio is approximately $1 : 1.31$. Thus, fraction of youngest stem is smaller in the seedlings exposed to the pollution treatment.

On the other hand, we conclude that the analysis cannot detect any negative effects of pollution treatment on stem RGR of cohort 1999. This is because the 95% credible interval of β_T, the effects of pollution treatment on the RGR of two-year old stems before pollution treatment, includes $\alpha_T = 0$ (Fig. 5D and Table 3). A possible interpretation of the results is that ·OH-generating dews considerably reduce the growth rate of the youngest parts of pine seedlings that have developed after exposure than those of the stems existing before exposure. In agreement with this hypothesis, Kume et al. (2000a) reported that pine trees growing in the declining stands that are subjected to the ·OH-generating dew maintained radial growth of the trunk but had a smaller fraction of stem biomass in the current-year-old shoot than those in the non-declining stands.

If such the difference in the biomass allocation ratio of pine seedlings between the control and pollution treatment groups is due to the exposure treatment, it can be conjectured that that the ·OH-generating mist (aqueous-phase OH radicals) affects not only the short-term responses such as the decreasing in growth rate of the youngest parts at seedling phase but also the biomass accumulation over a longer period by less allocation of biomass to new stems in the life history of the pine tree. This may explain the patterns observed in the declining Japanese red pine forests (e.g. Kume et al., 2000a; Kume et al., 2000b). The wet acidic depositions that generate reactive oxygen species/free radicals from dissolved air pollutants are likely to suppress seedling growth weakly rather than do so rapidly and resulting in the radical death of seedlings. In support of this viewpoint, Yoon et al. (2006) also reported the negative effects of ·OH-generating mists on the leaf CO_2 assimilation rate and the stem growth rate in the seedlings of Japanese apricot (*Prunus mume*), a deciduous broad-leaved species.

In the present study, we also demonstrate a new application of Bayesian inference to estimate the tree growth rate from the static and structural data of seedlings (Fig. 3 and Table 2). Although the data set is characterized by missing measurements (the weight of stem cohort 1999 in September 1999) and variability due to unknown characteristics of each seedling, we can determine the effects of pollution treatment

on decreasing in biomass accumulation in the non-assimilation part of tree based on the observation with noise and uncertainty by using hierarchical Bayesian modelling that generates the posterior distribution of the unobserved size of the stem cohort. This could be an example of the concept described by Clark (2005), i.e., modern statistical computation facilitates the advancement of knowledge by using a basic structure that allows the application of simple models within a realistic context.

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Table 1 Variables and parameters of the growth model based on the stem biomass

	variable / parameter	distribution / prior distribution	mean	variance
x_i	total weight of cohort 1999 in September 1999	Gamma	w_i	w_i/ρ_x
y_i	total weight of cohort 1999 in September 2000	Gamma	$g_i x_i$	$g_i x_i/\rho_y$
z_i	total weight of cohort 2000 in September 2000	Gamma	$a_i(y_i - x_i)$	$a_i(y_i - x_i)/\rho_z$
α_0	allocation parameter (constant component)	Gaussian	0	1
α_T	allocation parameter (treatment component)	Gaussian	0	1
β_0	growth rate parameter (constant component)	Gaussian	0	1
β_T	growth rate parameter (treatment component)	Gaussian	0	1
ρ_x	variance parameter of x_i	Gamma	1	10^3
ρ_y	variance parameter of y_i	Gamma	1	10^3
ρ_z	variance parameter of z_i	Gamma	1	10^3

Table 2 Stem specifications of all the experimental Japanese red pine seedlings measured at the end of the exposure experiment in September 2000.

	Treated				Control			
	T#1	T#2	T#3	T#4	C#1	C#2	C#3	C#4
height of seedling (m)	1.08	0.94	1.30	1.27	1.12	1.16	1.11	(NA)†
Total weight of								
stem (dw g)	107.4	94.1	130.8	135.9	150.9	135.0	147.2	131.4
needle (dw g)	135.1	157.7	107.8	135.5	127.2	110.6	113.2	136.2
flower & vegetative bud (dw g)	1.9	2.4	1.7	1.4	2.6	2.9	3.6	0.7
root (dw g)	135.1	169.6	191.5	108.1	93.6	211.2	168.1	137.1
Cohort 2000								
number of stem	65	113	46	77	121	62	113	58
mean stem weight (dw g)	0.27	0.15	0.35	0.32	0.20	0.37	0.22	0.53
mean stem length (mm)	72	53	65	106	64	109	72	141
Cohort 1999								
number of stem	8	16	8	17	15	14	15	11
mean stem weight (dw g)	3.53	0.95	3.98	2.19	1.74	1.64	1.43	2.28
mean stem length (mm)	177	100	188	142	120	116	92	121
Cohort 1998								
number of stem	1	6	1	1	3	8	5	4
mean stem weight (dw g)	30.54	4.92	44.10	37.60	15.60	4.78	7.62	7.58
mean stem length (mm)	334	233	395	428	342	177	235	204
Cohort 1997								
number of stem	1	1	1	1	1	1	1	1
stem weight (dw g)	31.10	33.00	38.60	36.70	54.10	51.10	62.90	45.50
stem length (mm)	254	289	243	272	342	397	408	343

† unmeasured.

Table 3 Mean, 95% credible interval and standard deviation of the posterior distributions of parameters.

parameter	mean	[2.5%, 97.5%]	SD
α_0	0.27	[0.05, 0.47]	0.11
α_T	-0.48	[-0.79, -0.15]	0.16
β_0	1.71	[1.42, 1.99]	0.15
β_T	0.23	[-0.98, 1.80]	0.66
ρ_x	4.35	[0.55, 22.49]	6.03
ρ_y	35.84	[0.24, 211.84]	56.69
ρ_z	1.06	[0.23, 2.58]	0.60
$x_{\texttt{T\#1}}$	4.54	[0.83, 11.78]	2.58
$x_{\texttt{T\#2}}$	2.66	[0.49, 6.44]	1.47
$x_{\texttt{T\#3}}$	5.27	[0.93, 13.53]	2.98
$x_{\texttt{T\#4}}$	6.61	[1.18, 16.31]	3.69
$x_{\texttt{C\#1}}$	4.44	[2.70, 6.27]	0.91
$x_{\texttt{C\#2}}$	4.34	[3.11, 6.02]	0.78
$x_{\texttt{C\#3}}$	3.75	[2.53, 5.15]	0.68
$x_{\texttt{C\#4}}$	4.75	[3.41, 6.55]	0.83

Figure Legends

Fig. 1 (A) Schema of time course of the pseudo polluted mist exposure experiment. The range of the "exposure experiment" indicates the duration of exposure of the Japanese red pine were seedlings to ·OH-generating iron-oxalate-H_2O_2 and control mists in open-air system chambers. Downward solid arrow on September 2000 indicates the termination of treatment (seedlings were harvested). Seed germination has occurred in spring, 1997. The buds in the shoot tip have sprouted in spring and develop by the later part of each growing season. The elongation season of the stem cohort of year j is indicated as the durations "cohort j" along with "age" (defined in the text) in September 2000. (B) Schema of the relationship between shoot structure and stem cohort in a pine seedling.

Fig. 2. Schema of the growth model of a pine stem in the ·OH-generating mist exposure experiment. The shaded regions in cylinders indicate the growth in year 2000. In the growth process of seedling i, the observed total dry weight of cohort 1999 (y_i) in September 2000 depends on that in September 1999 (x_i) which is not observed. Biomass allocation process sets the total dry weight of cohort 2000 in September 2000 (z_i) that depends on the growth of cohort 1999, $y_i - x_i$. The prior distribution of x_i is a function of the stem population of the current-year, i.e., cohort

2000.

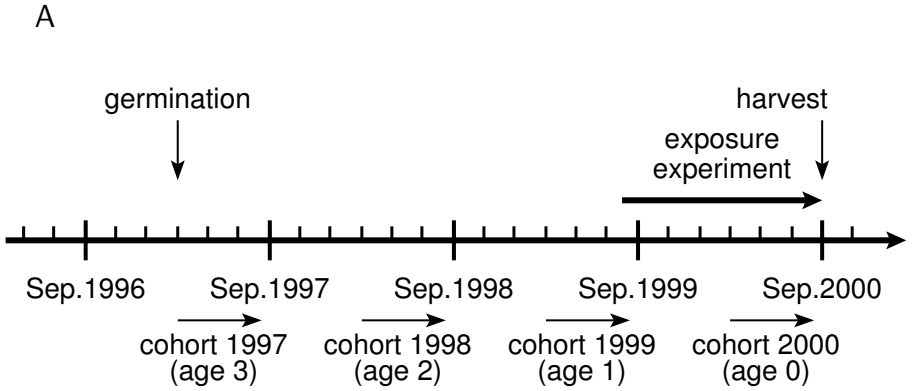
Fig. 3. Observed cohort structure of stem biomass in pine seedlings exposed to ·OH-generating and control mists at the end point of the exposure experiment (September 2000). The horizontal axis indicates the year of emergence of the stem cohort (group of stems of the same age), while the vertical axis indicates total dry weight of the stem cohort.

Fig. 4. Posterior distributions of total dry weight of stem cohort 1999 in September 1999 x_i. Since x_i is unobserved, the posterior distribution is generated from the prior distribution with an individual-specific mean and the variance parameter ρ_x shared among all seedlings (refer to Table 1).

Fig. 5. MCMC step traces (A and C) and posterior distributions (B and D) of the growth parameters, β_0 and β_T. The 95% credible interval of the treatment effects, β_T, includes $\beta_T = 0$ (refer to Table 3).

Fig. 6. MCMC step traces (A and C) and posterior distributions (B and D) of the biomass allocation parameters, α_0 and α_T. The 95% credible interval of the treatment effects, α_T, includes $\alpha_T = 0$ (refer to Table 3).

Fig.1


A
germination
harvest
exposure
experiment
Sep.1996
Sep.1997
Sep.1998
Sep.1999
Sep.2000
cohort 1997
(age 3)
cohort 1998
(age 2)
cohort 1999
(age 1)
cohort 2000
(age 0)

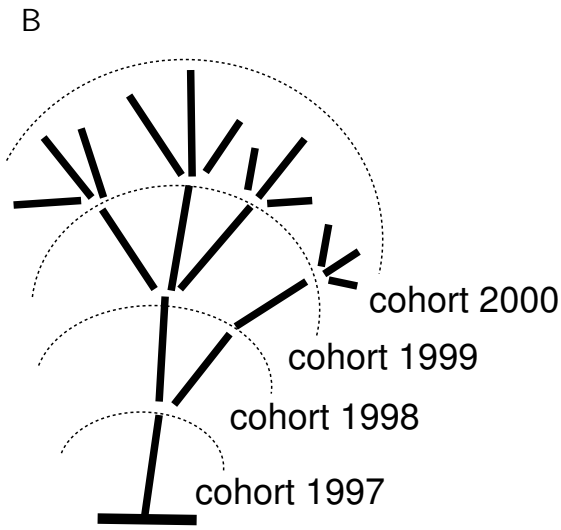

B
cohort 2000
cohort 1999
cohort 1998
cohort 1997

Fig.2

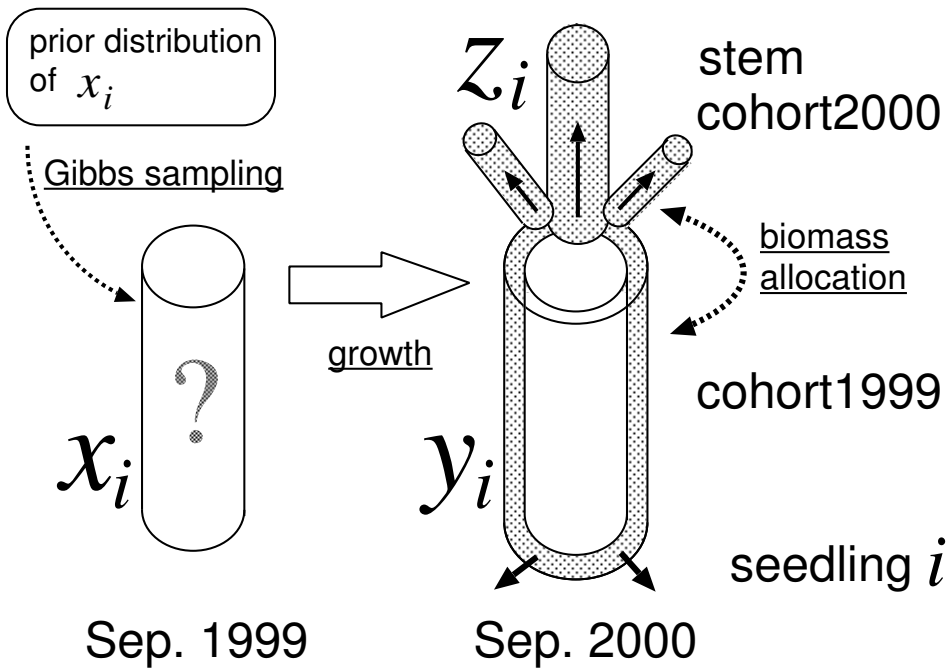

prior distribution of x_i
Gibbs sampling
x_i
?
growth
z_i
stem
cohort2000
biomass allocation
cohort1999
y_i
seedling i
Sep. 1999
Sep. 2000

Fig.3

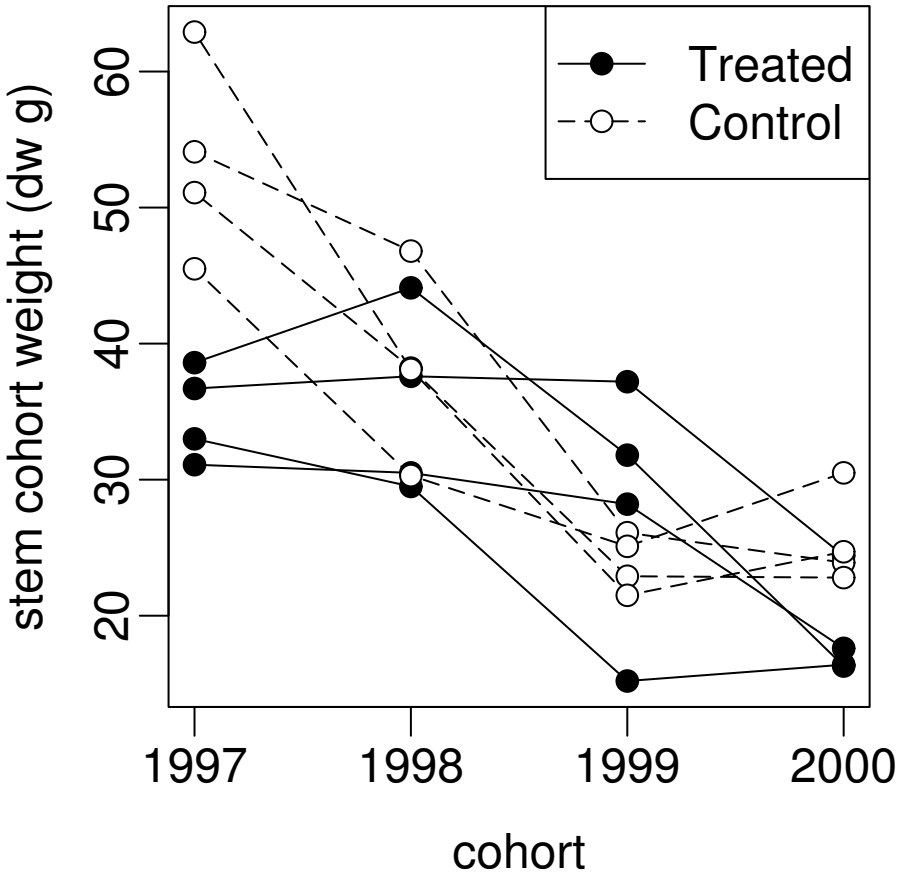

Treated
Control
stem cohort weight (dw g)
20
30
40
50
60
1997
1998
1999
2000
cohort

Fig.4

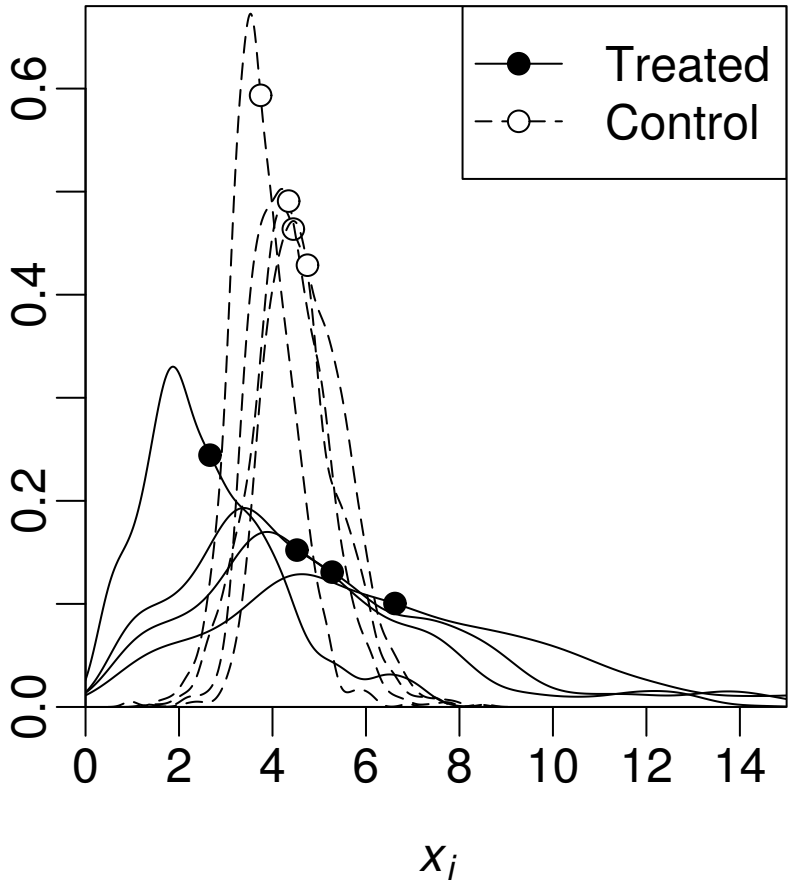


Fig.5

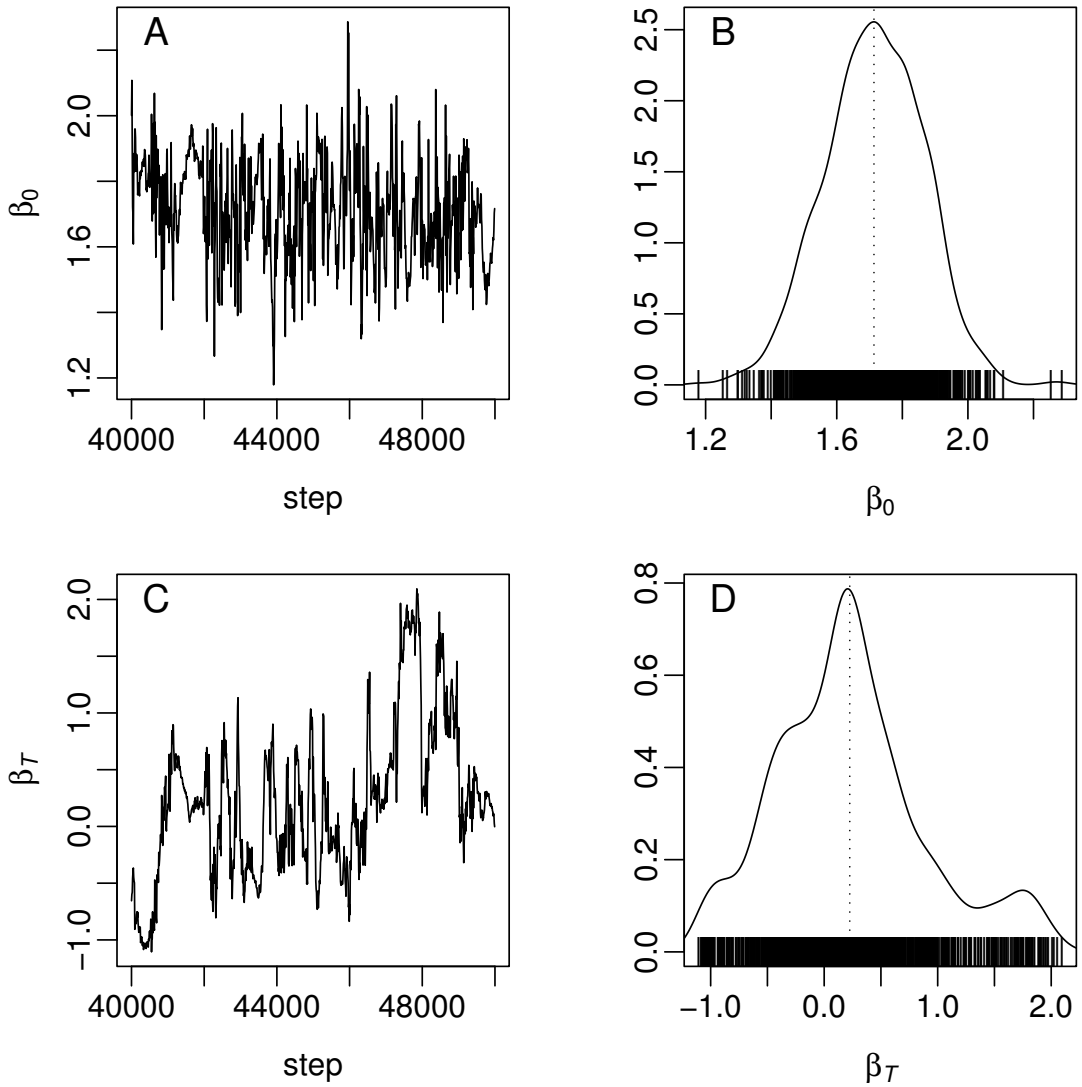
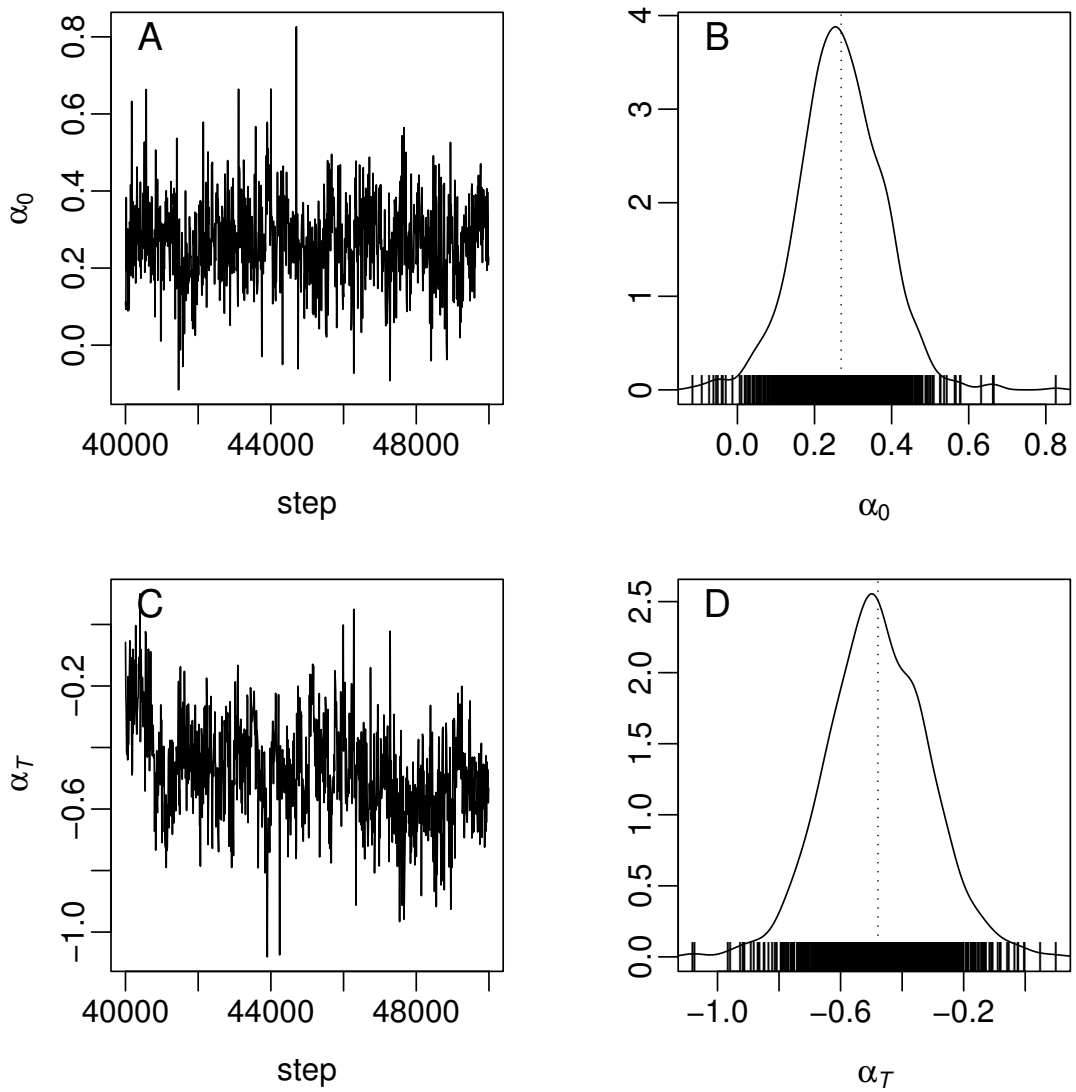

A
B
C
D
β_0
β_T
step
1.2
1.6
2.0
40000
44000
48000
0.0
0.5
1.0
1.5
2.5
−1.0
0.2
0.4
0.6
0.8

Fig.6


A
B
C
D
α_0
α_T
step
0.0
0.2
0.4
0.6
0.8
40000
44000
48000
0
1
2
3
4
−1.0
−0.6
−0.2
0.5
1.0
1.5
2.0
2.5