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-\(\text{H}_2\text{O}_2\) 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 \(\cdot\text{OH}\)-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 re-
quire 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) em-
phasized the importance of modelling using the uncertainty/variability of parame-
ters 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\([(\text{COOH})_2]\)-H$_2$O$_2$ 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$_2$O$_2$) 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$_2$O$_2$ 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$_2$O$_2$, 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 biomass 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 O₃-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-H₂O₂ [1μM FeCl₃, 5μM (COOH)₂, and 100μM H₂O₂] 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 CO₂ assimilation rate of these seedlings were significantly reduced by -OH-generating iron-oxalate-H₂O₂ 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 $i \in \{C#1, \cdots, C#4\}$ for seedlings in control group exposed to the mists containing few -OH, and $i \in \{T#1, \cdots, T#4\}$ 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, $E(y_i) = g_i x_i$, 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 $\beta_0$ and $\beta_T$ 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 $\beta_T$ 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 $E(z_i) = a_i (y_i - x_i)$, 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 $\alpha_0$ is the baseline parameter.
and $\alpha_T$ 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 $\rho_z$, 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
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 $w_i / \rho_x$. The individual specific mean $w_i$ is defined as a combination of measurements and the parameters of pollution effects, that is,

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

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 $\rho_x$ 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 (\( \alpha = \{\alpha_0, \alpha_T\} \) and \( \beta = \{\beta_0, \beta_T\} \)) 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 (\( \rho = \{\rho_z, \rho_y, \rho_x\} \)) 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,

\[
p(\{x_i\}, \alpha, \beta, \rho \mid \text{data}) \propto \prod_i p(z_i|y_i, x_i, \alpha_0, \rho_z) \, p(y_i|x_i, g_i, \rho_y) \, p(x_i|w_i, \rho_x) \\
\times p(\alpha_0) \, p(\alpha_T) \, p(\beta_0) \, p(\beta_T) \, p(\rho_z) \, p(\rho_y) \, p(\rho_x),
\]

where \{data\} is defined as \{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 soft-
ware, 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 $\alpha_T$ and $\beta_T$ 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 $\beta_T$, the effects of pollution treatment on RGR, includes $\beta_T = 0$ (Fig. 5D and Table 3). The 95\% credible interval of $\alpha_T$, 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 $\alpha_T$ (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 \(\alpha_T\), 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 
\[
a_i = \exp(0.27 - 0.48) \approx 0.81, \text{ i.e., biomass allocation ratio between cohort 1999 and cohort 2000 is approximately 1 : 0.81, while that for controls is } \exp(0.27) \approx 1.31 \text{ in which the allocation ratio is approximately 1 : 1.31. Thus, fraction of youngest stem is smaller in the seedlings exposed to the pollution treatment.}
\]

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 \(\beta_T\), 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 \(-\text{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 } -\text{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 \( \cdot \text{OH} \) -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 \( \cdot \text{OH} \) -generating mists on the leaf CO\(_2\) assimilation rate and the stem growth rate in the seedlings of Japanese apricot (\textit{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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References


to damage to forest tree? Environmental Science and Technology 28, 812–815.
Table 1 Variables and parameters of the growth model based on the stem biomass

<table>
<thead>
<tr>
<th>variable / parameter</th>
<th>distribution / prior distribution</th>
<th>mean</th>
<th>variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$x_i$ total weight of cohort 1999 in September 1999</td>
<td>Gamma</td>
<td>$w_i$</td>
<td>$w_i/\rho_x$</td>
</tr>
<tr>
<td>$y_i$ total weight of cohort 1999 in September 2000</td>
<td>Gamma</td>
<td>$g_i x_i$</td>
<td>$g_i x_i/\rho_g$</td>
</tr>
<tr>
<td>$z_i$ total weight of cohort 2000 in September 2000</td>
<td>Gamma</td>
<td>$a_i(y_i - x_i)$</td>
<td>$a_i(y_i - x_i)/\rho_z$</td>
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<tr>
<td>$\alpha_0$ allocation parameter (constant component)</td>
<td>Gaussian</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>$\alpha_T$ allocation parameter (treatment component)</td>
<td>Gaussian</td>
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<td>1</td>
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<td>$\beta_0$ growth rate parameter (constant component)</td>
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<tr>
<td>$\beta_T$ growth rate parameter (treatment component)</td>
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<td>1</td>
</tr>
<tr>
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<td>$10^3$</td>
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<tr>
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<td>Gamma</td>
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<td>$10^3$</td>
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<td>$10^3$</td>
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Table 2  Stem specifications of all the experimental Japanese red pine seedlings measured at the end of the exposure experiment in September 2000.

<table>
<thead>
<tr>
<th></th>
<th>T#1</th>
<th>T#2</th>
<th>T#3</th>
<th>T#4</th>
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<th>C#2</th>
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<th>C#4</th>
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<td>height of seedling (m)</td>
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<td>1.30</td>
<td>1.27</td>
<td>1.12</td>
<td>1.16</td>
<td>1.11</td>
<td>(NA)†</td>
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<tr>
<td>Total weight of stem (dw g)</td>
<td>107.4</td>
<td>94.1</td>
<td>130.8</td>
<td>135.9</td>
<td>150.9</td>
<td>135.0</td>
<td>147.2</td>
<td>131.4</td>
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<tr>
<td>needle (dw g)</td>
<td>135.1</td>
<td>157.7</td>
<td>107.8</td>
<td>135.5</td>
<td>127.2</td>
<td>110.6</td>
<td>113.2</td>
<td>136.2</td>
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<tr>
<td>flower &amp; vegetative bud (dw g)</td>
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<td>2.4</td>
<td>1.7</td>
<td>1.4</td>
<td>2.6</td>
<td>2.9</td>
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<td>0.7</td>
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<tr>
<td>root (dw g)</td>
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<td>169.6</td>
<td>191.5</td>
<td>108.1</td>
<td>93.6</td>
<td>211.2</td>
<td>168.1</td>
<td>137.1</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number of stem</td>
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<td>113</td>
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<td>113</td>
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<tr>
<td>mean stem weight (dw g)</td>
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<td>0.35</td>
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<td>65</td>
<td>106</td>
<td>64</td>
<td>109</td>
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<td>141</td>
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<tr>
<td>Cohort 1999</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number of stem</td>
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<td>8</td>
<td>17</td>
<td>15</td>
<td>14</td>
<td>15</td>
<td>11</td>
</tr>
<tr>
<td>mean stem weight (dw g)</td>
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<td>0.95</td>
<td>3.98</td>
<td>2.19</td>
<td>1.74</td>
<td>1.64</td>
<td>1.43</td>
<td>2.28</td>
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<tr>
<td>mean stem length (mm)</td>
<td>177</td>
<td>100</td>
<td>188</td>
<td>142</td>
<td>120</td>
<td>116</td>
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<td>121</td>
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<tr>
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<td></td>
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<tr>
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<td>1</td>
<td>1</td>
<td>3</td>
<td>8</td>
<td>5</td>
<td>4</td>
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<tr>
<td>mean stem weight (dw g)</td>
<td>30.54</td>
<td>4.92</td>
<td>44.10</td>
<td>37.60</td>
<td>15.60</td>
<td>4.78</td>
<td>7.62</td>
<td>7.58</td>
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<tr>
<td>mean stem length (mm)</td>
<td>334</td>
<td>233</td>
<td>395</td>
<td>428</td>
<td>342</td>
<td>177</td>
<td>235</td>
<td>204</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>number of stem</td>
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<td>1</td>
<td>1</td>
<td>1</td>
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<td>stem weight (dw g)</td>
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<td>33.00</td>
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<td>54.10</td>
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<td>62.90</td>
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<tr>
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<td>272</td>
<td>342</td>
<td>397</td>
<td>408</td>
<td>343</td>
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</table>

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

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<th>parameter</th>
<th>mean</th>
<th>[2.5%, 97.5%]</th>
<th>SD</th>
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<td>0.27</td>
<td>[0.05, 0.47]</td>
<td>0.11</td>
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<td>[-0.79, -0.15]</td>
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<td>[1.42, 1.99]</td>
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<tr>
<td>$\beta_T$</td>
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<td>[-0.98, 1.80]</td>
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<td>[0.55, 22.49]</td>
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<tr>
<td>$\rho_y$</td>
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<td>[0.24, 211.84]</td>
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<tr>
<td>$\rho_z$</td>
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<td>[0.23, 2.58]</td>
<td>0.60</td>
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<td>$x_{T#1}$</td>
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<td>[0.83, 11.78]</td>
<td>2.58</td>
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<tr>
<td>$x_{T#2}$</td>
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<td>[0.49, 6.44]</td>
<td>1.47</td>
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<tr>
<td>$x_{T#3}$</td>
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<td>[0.93, 13.53]</td>
<td>2.98</td>
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<td>$x_{T#4}$</td>
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<td>[1.18, 16.31]</td>
<td>3.69</td>
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<td>0.91</td>
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<tr>
<td>$x_{C#2}$</td>
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<td>[3.11, 6.02]</td>
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<td>[2.53, 5.15]</td>
<td>0.68</td>
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<tr>
<td>$x_{C#4}$</td>
<td>4.75</td>
<td>[3.41, 6.55]</td>
<td>0.83</td>
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</table>
**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$_2$O$_2$ 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
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 $\rho_x$ 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, $\beta_0$ and $\beta_T$. The 95% credible interval of the treatment effects, $\beta_T$, 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, $\alpha_0$ and $\alpha_T$. The 95% credible interval of the treatment effects, $\alpha_T$, includes $\alpha_T = 0$ (refer to Table 3).
Fig. 1

A

germination

harvest

exposure experiment


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
prior distribution of $x_i$

Gibbs sampling

$z_i$

stem cohort2000

biomass allocation

cohort1999

seedling $i$

$y_i$

Sep. 2000

$y_i$

growth

$y_i$

Sep. 1999

$x_i$

Sep. 1999

prior distribution of $x_i$

Gibbs sampling

$z_i$

stem cohort2000

biomass allocation

cohort1999

seedling $i$

$y_i$

Sep. 2000

$y_i$

growth

$y_i$

Sep. 1999

$x_i$
Fig. 5

(A) Plot of $\beta_0$ against step.

(B) Distribution of $\beta_0$.

(C) Plot of $\beta_T$ against step.

(D) Distribution of $\beta_T$. 

Fig. 6