Comparison of Growth Responses to Climatic Conditions of Sugi (Cryptomeria japonica) and Hinoki (Chamaecyparis obtusa) Using a Carbon Balance-Based Growth Model

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Abstract: This paper aimed to reveal differences in growth response to climatic condition between sugi (Cryptomeria japonica) and hinoki (Chamaecyparis obtusa) by comparing parameters of a carbon balance-based growth model. Seven carbon balance-based growth model parameters related to the rate of photosynthesis, temperature and humidity controls were parameterized by a Bayesian calibration using growth data derived from permanent plots. A hierarchical Bayes model was applied to this parameterization, where the common parameter was estimated first and the species-specific parameters were derived from the common parameter thereafter. Simulated light-response curves using estimated parameters were similar and the photosynthetic rate of sugi was higher than that of hinoki. The patterns of response to temperature represented by estimated parameters were different between sugi and hinoki; sugi responded rapidly to changes in temperature while hinoki responded relatively slowly, resulting in a higher tolerance to low temperature than sugi. Estimated parameters indicated that the photosynthetic rate controlling function for humidity could not be implemented for either species in the model. The parameterization of a carbon balance-based growth model revealed differences in the potential photosynthetic ability and response to temperature of sugi and hinoki. However, we could not represent the control effect of humidity on the photosynthetic rate.

Keywords: process-based growth model, hierarchical Bayes model, Bayesian calibration, Markov Chain Monte Carlo

1. Introduction

Understanding the different growth traits of planting tree species is one of the most important issues for the sustainable management of planted forests. Knowledge of the autecology of planting tree species is essential when making decisions on the timing and intensity of thinning, timing of clear-cutting, and selecting tree species for replanting (e.g. Davis and Johnson, 1987; Klinka and Feller,1984). When selecting suitable species, site productivity is the most important information; it is affected by environmental factors, such as topography, geology (e.g. Kayahara et al.,1998; Mitsuda et al., 2007; Mitsuda and Ito, 2015; Wang and Klinka,1996). Climatic conditions are also a critical factor determining site productivity at the macro scale; therefore, the relationships between site productivity and climatic factors have been studied (e.g. Coops et al., 1998; Iverson et al., 1997; Mitsuda and Kitahara, 2015; Tickle et al., 2001).

Forest management decisions on selecting planting species after clear-cutting have become a critical issue in Japan. In Japan, sugi (Cryptomeria japonica) and hinoki (Chamaecyparis obtusa) are the dominant planting species, accounting for 44% and 25% of the planted forest area, respectively. A large part of these planted forests is mature enough for harvesting; thus timber production of both species has been increasing. As a consequence of harvesting by clear-cutting, management decisions on whether forest owners will replant or not are expected to arise. If forest owners decide to replant, the next decision will be selecting which planting species is better to replant, sugi or hinoki.

Climate change will affect the growth patterns of planted forests in the future (e.g. Coops and Waring, 2001; Pretzsch et al., 2014). Therefore, we need to elucidate the effects of climatic conditions on forest growth in order to predict the stand growth of sugi and hinoki planted forests. Process-based growth models consist of functions that describe the interactions between trees and their environment, as such, they can represent changes in growth patterns based on changes in the climatic condition (e.g. Kurz et al., 2009; Landsberg and Waring, 1997; Pretzsch, 2010). Several process-based growth models have been developed and are utilized for revealing good forest management practices (e.g. Battaglia and Stands, 1998; Mäkelä et al., 2012). Furthermore, some papers suggested
that better forest policies could be adopted to a future changing climate by using process-based models (e.g. Lemprière et al., 2013; Matsumoto et al., 2016; Mitsuda et al., 2013b; Seidl et al., 2007).

The objective of this study was to reveal differences in sugi and hinoki growth responses to climatic conditions by comparing carbon balance-based growth model parameters. The carbon balance-based growth model that we adopted is a kind of process-based growth model that focuses on the carbon cycle of a forest. In this study, the parameterized model for both sugi and hinoki planted forests were compared to interpret how the tree species respond to a climatic environment. The knowledge of sugi and hinoki species trait derived from this paper will help to predict their growth in planted forests under climate change, and allow managers to select better species for replanting at certain site.

2. Materials and Methods

2.1. Target parameters of the carbon balance-based growth model

The carbon balance-based growth model used in this study was derived from the 3-PG (Physiological Processes Predicting Growth) model developed by Landsberg and Waring (1997). The model consists of the following six processes (Figure 1): (1) photosynthetically active radiation absorption; (2) photosynthetic production; (3) photosynthetic rate control by temperature and humidity; (4) respiration; (5) litterfall and turnover; and (6) growth partitioning. Details of the model were described in Figure 1 and our previous study (Mitsuda et al., 2011; 2013a).

To investigate the growth responses of sugi and hinoki to climatic conditions, we focused on the photosynthetic production and the photosynthetic rate control by temperature and humidity processes, because these two factors are major limiting factors of forest stand growth (e.g. Shidei and Kira, 1977).

In the photosynthetic production process, the gross primary production of the stand was estimated by the light-response curve of canopy photosynthesis (e.g. Hirose and Werger, 1987) using the following non-rectangular hyperbola equation:

\[ AG = \frac{aI + A_{max} - \sqrt{(aI + A_{max})^2 - 4aI\theta A_{max}}}{2\theta} \]

where \( AG \) is the gross photosynthetic rate per unit foliage weight, \( A_{max} \) is the light-saturated gross photosynthetic rate, \( a \) is the initial slope of the light-response curve, \( \theta \) is the convexity of the light-response curve, and \( I \) is the absorbed photosynthetically active radiation per unit foliage weight.

First, the gross photosynthetic rate without any environmental stress was calculated using Eq.[1], then the environmental stresses of lower temperature and drying air were considered as photosynthetic rate restriction factors. The temperature and humidity modifiers were introduced to represent restrictions of the climatic condition on the photosynthetic rate, which ranged from 0 to 1, where 0 means that photosynthesis stops under a severe climatic condition and 1 means that the climatic condition do not restrict the photosynthetic rate. In the photosynthetic rate control process by temperature, the temperature modifier was calculated as follows:

\[ M_T = \frac{1}{1 + \exp(-\beta_{T1}(T - \beta_{T2}))} \]

where \( M_T \) is the temperature modifier, \( \beta_{T1} \) and \( \beta_{T2} \) are coefficients representing the pattern of response of photosynthetic rate to temperature, and \( T \) is the monthly average temperature. Because temperature directly affects the biochemical reaction of photosynthesis, and photosynthetic activity falls drastically at lower temperatures (Hikosaka et al., 2006), the temperature modifier takes a lower value with a lower temperature.

In the photosynthetic rate control process by humidity, the humidity modifier was calculated as follows:

\[ M_H = \begin{cases} \exp(-\beta_{H1}(V - \beta_{H2})) & (V > \beta_{H2}) \\ 1 & \end{cases} \]
Eq. 1, 2, and 3 are given in text.

Eq. 4  \[ I = \frac{P \left(1 - \exp\left(-K_{sp} W_f\right)\right)}{W_f} \]

\( P \): solar radiation [MJ/ha/month]; \( W_f \): biomass [ton/ha] for each biomass pool (f: foliage, b: branch, s: stem, r: root); \( K_{sp} \): light-extinction coefficient for each species (sugi, hinoki)

Eq. 5  \[ R_f = \beta_{r1F} \exp(\beta_{r2F} T) \times W_f \quad R_{(b,s,r)} = \beta_{r1C} \exp(\beta_{r2C} T) \times W_{(b,s,r)}^{\frac{3}{4}} \]

\( R_f \): respiration [ton/ha/month] for each biomass pool (f: foliage, b: branch, s: stem, r: root); \( \beta_{r1F}, \beta_{r2F} \): coefficients of respiration rate-determining function (F: foliage, C: others)

Eq. 6  \[ L_{(f,b,fr,cr)} = l_{(f,b,fr,cr)} \times W_{(f,b,fr,cr)} \quad W_{fr} = 0.01 W_r \quad W_{cr} = 0.99 W_r \]

\( L_f \): turnover [ton/ha/month] for each biomass pool (f: foliage, b: branch, fr: fine root, cr: coarse root); \( l_f \): litterfall or turnover rate for each biomass pool.

Parameter values of \( K_{sp}, \beta_{r1F}, \beta_{r2F}, \) and \( l_f \) are given in Table 2.

Figure 1. Flow diagram of the carbon balance-based growth model developed in this study. (Revised from Mitsuda et al. (2011)).
where $M_H$ is the humidity modifier, $\beta_{H1}$ and $\beta_{H2}$ are coefficients representing the pattern of response of photosynthetic rate to humidity, and $V$ is the monthly vapor pressure deficit (VPD) average, which represents the degree of air dryness related to water stress, and takes a higher value with a lower air humidity. As the VPD increases, stomata close and the photosynthetic rate decreases, therefore, the humidity modifier takes a lower value with a higher VPD and is regarded as an index of water stress.

Finally, the actual gross photosynthetic rate was calculated as $AG$ multiplied by $M_T$ and $M_H$, and then the gross primary production of canopy photosynthesis (GPP) is calculated as $AG$ multiplied by foliage biomass. The net primary production (NPP) was calculated as the surplus of GPP consumed by respiration, and then the biomass growth was estimated as the surplus NPP consumed by litterfall and turnover. The biomass growth was utilized to tree size growth.

2.2. Data

The growth data used in this study were derived from repeated measurement in established permanent plots of sugi and hinoki planted forests in the National Forest, which have been managed by the Forestry and Forest Products Research Institute (Iehara et al., 2001; Hosoda et al., 2014). A total of 13 and 12 permanent plots were selected for sugi and hinoki, respectively. The details of the permanent plots is shown in Table 1. In these permanent plots, all individual trees were identified and the diameter at breast height (1.2m) was measured. The total tree height was measured for selected trees or all standing trees.

### Table 1. Summary of permanent plots.

| No | Species | Number of observation | Age | Min | Max |
|----|---------|-----------------------|-----|-----|-----|
| 1  | sugi    | 4                     | 11  | 51  |
| 2  | sugi    | 4                     | 11  | 51  |
| 3  | sugi    | 2                     | 60  | 89  |
| 4  | sugi    | 2                     | 60  | 89  |
| 5  | sugi    | 3                     | 46  | 87  |
| 6  | sugi    | 2                     | 46  | 72  |
| 7  | sugi    | 2                     | 46  | 72  |
| 8  | sugi    | 4                     | 11  | 41  |
| 9  | sugi    | 4                     | 11  | 41  |
| 10 | sugi    | 3                     | 14  | 45  |
| 11 | sugi    | 3                     | 14  | 45  |
| 12 | sugi    | 3                     | 12  | 43  |
| 13 | sugi    | 3                     | 12  | 38  |
| 14 | hinoki  | 4                     | 46  | 82  |
| 15 | hinoki  | 4                     | 46  | 82  |
| 16 | hinoki  | 3                     | 51  | 91  |
| 17 | hinoki  | 3                     | 51  | 91  |
| 18 | hinoki  | 7                     | 16  | 51  |
| 19 | hinoki  | 7                     | 16  | 51  |
| 20 | hinoki  | 8                     | 18  | 58  |
| 21 | hinoki  | 8                     | 11  | 56  |
| 22 | hinoki  | 8                     | 10  | 50  |
| 23 | hinoki  | 7                     | 28  | 65  |
| 24 | hinoki  | 8                     | 23  | 66  |
| 25 | hinoki  | 6                     | 36  | 76  |

Time-series climatic values of the monthly amount of solar radiation, average mean temperature, and average VPD for the entire measurement period were estimated using 30-year average values at a 1-km resolution published by the Japan Meteorological Agency (2002) and the climatic data of the nearest meteorological stations for the plots.
2.3. Parameterization

Seven parameters, \( A_{\text{max}} \), \( a \), \( \theta \), \( \beta_{T1} \), \( \beta_{T2} \), \( \beta_{H1} \), and \( \beta_{H2} \) were selected as the target parameters that describe species trait in growth response to climatic conditions. For parameterization of the model, a Bayesian calibration by the Markov Chain Monte Carlo method (Van Oijen et al., 2005) was applied to obtain samples from the posterior distribution of parameters (conditioned parameter distribution for measured data). Periodic biomass growth of each period of each plot was estimated by using the carbon balance-based growth model with corresponding climatic values and then compared to the observed periodic biomass growth for calculating likelihood in the Bayesian calibration.

Using the stand condition at the start of the measurement period and climatic data as the input data, we parameterized seven parameters using the periodic biomass growth as an objective variable. We adopted a hierarchical parameter structure and estimated the species common parameter and species-specific parameter. Prior distributions of parameters for the Bayesian calibration were set for a certain parameter, \( X \), as follows:

\[
X_{\text{common}} \sim \text{Normal}(0,0.1)
\]
\[
X_{\text{sp}:i} \sim \text{Normal}(X_{\text{common}},\sigma_{sp}^2)
\]

where \( X_{\text{common}} \) is the common parameter, \( X_{\text{sp}:i} \) is the species-specific parameter for species \( i \) (\( i = 1 \) for sugi, 2 for hinoki), and \( \sigma_{sp} \) is the standard deviation for deriving a species level parameter and was set as a fixed value to reduce the number of parameters to be estimated.

Furthermore, a plot-specific parameter was introduced for only the light-saturated gross photosynthetic rate, \( A_{\text{max}} \), because of representative differences in site productivity between the plots.

\[
A_{\text{max:plot}:j} \sim \text{Normal}(A_{\text{max:sp}:i},\sigma_{\text{plot}}^2)
\]

\( A_{\text{max:plot}:j} \) is the plot-specific parameter for plot \( j \) and \( \sigma_{\text{plot}} \) is the standard deviation for deriving a plot level parameter and was set as the fixed value. If a planted species of plot \( j \) was sugi, \( A_{\text{max:sp}:1} \) was used in Eq.[6] for deriving a plot-specific parameter of plot \( j \). The prior distribution of the target seven parameters and the other parameters used in the model were set according to Mitsuda et al. (2011; 2013a) and their values are listed in Table 2.

| Parameter          | Prior distribution | Mean   | Standard deviation | Fixed value |
|-------------------|--------------------|--------|--------------------|-------------|
| \( A_{\text{max:common}} \) | 0.60               | 0.01   |                    |             |
| \( a \)           | 10.50              | 1.00   |                    |             |
| \( \theta \)      | 0.30               | 0.01   |                    |             |
| \( \beta_{T1} \)  | 0.32               | 0.05   |                    |             |
| \( \beta_{T2} \)  | 0.63               | 0.05   |                    |             |
| \( \beta_{H1} \)  | 0.38               | 0.05   |                    |             |
| \( \beta_{H2} \)  | 1.00               | 0.10   |                    |             |
| \( K_{\text{sugi}} \) | 0.21             |        |                    |             |
| \( K_{\text{hinoki}} \) | 0.40            |        |                    |             |
| \( \beta_{1F} \)  | 11.00              |        |                    |             |
| \( \beta_{2F} \)  | 2.50               |        |                    |             |
| \( \beta_{1C} \)  | 2.30               |        |                    |             |
| \( \beta_{2C} \)  | 1.00               |        |                    |             |
| \( l_f \)         | 0.22               |        |                    |             |
| \( l_b \)         | 0.08               |        |                    |             |
| \( l_{fr} \)      | 1.00               |        |                    |             |
| \( l_{cr} \)      | 0.01               |        |                    |             |

Table 2. Summary of the posterior distributions and fixed parameters values.
3. Results

The carbon balance-based growth model with estimated parameters could well explain the variations in the observed periodic biomass growth (Figure 2).

![Figure 2. Relationship between observed and estimated periodic biomass growth.](image)

The summary of samples from the posterior distribution of common and species-specific parameters derived from a Bayesian calibration is shown in Figure 3. Hereafter, the medians of each sample of parameters derived from a Bayesian calibration were regarded as the estimates of each parameter. The common parameter of the light-saturated gross photosynthetic rate, $A_{\text{max,common}}$, was 0.427 and the species-specific parameter was 0.424 for sugi and was 0.410 for hinoki. The plot-specific parameter, $A_{\text{max,plot}}$, ranged from 0.344 to 0.651 for sugi plots and from 0.337 to 0.591 for hinoki plots. The parameters of the initial slope of the light-response curve, $a$, were estimated as 14.49, 17.91, and 14.83 for common, sugi, and hinoki parameters, respectively. The common parameter of the convexity of the light-response curve was estimated as 0.303, and those for sugi and hinoki were estimated as 0.377 and 0.308, respectively. Simulated light-response curves for sugi and hinoki using the estimated species-specific parameters are shown in Figure 4. The common parameter of the coefficients of the temperature modifier function, $\beta_{T1}$ and $\beta_{T2}$, were 0.480 and 0.210, respectively. The species-specific parameter $\beta_{T1}$ was 0.913 for sugi and 0.246 for hinoki, and $\beta_{T2}$ was 0.248 for sugi and 0.176 for hinoki. Simulated curves of the temperature modifier function for sugi and hinoki using the estimated species-specific parameters are shown in Figure 5. The common parameter of the coefficients of the humidity modifier function, $\beta_{H1}$ and $\beta_{H2}$, were 3.910 and 1.036, respectively. The species-specific parameter of $\beta_{H1}$ was 1.902 for sugi and 7.410 for hinoki, and $\beta_{H2}$ was 2.222 for sugi and 1.576 for hinoki. Simulated curves of the humidity modifier function for sugi and hinoki using the estimated species-specific parameters are shown in Figure 6.

4. Discussion

As shown in Figure 4, the shapes of the light-response curves were similar for both species, while the gross photosynthetic rate ($AG$) of sugi was superior to that of hinoki under any absorbed photosynthetically active radiation condition. In other words, the photosynthetic rate of sugi without any environmental stress was superior to that of hinoki under any light condition. This result means that the potential photosynthetic ability and resulting stand growth is higher in sugi than in hinoki. Our results were consistent with the standard age growth functions developed for reporting
Figure 3. Summary of samples from a posterior distribution of parameters. (The bold horizontal line represents the median, boxes represent 50% range, and vertical lines represent 95% range.)
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Figure 4. Simulated light-response curves for sugi and hinoki.

Figure 5. Simulated curves of the temperature modifier function for sugi and hinoki.
national carbon stocks to the Kyoto Protocol that showed that sugi grow faster than hinoki (e.g. Greenhouse Gas Inventory Office of Japan et al., 2016). Figure 5 shows a quite different pattern for the temperature modifier between sugi and hinoki. The simulated curve of the temperature modifier function of sugi is depicted as two horizontal lines that switch at a threshold temperature, which was approximately 0 °C in monthly mean temperature. This means that photosynthesis will stop under the threshold temperature and that temperature will not be a photosynthetic controlling factor at temperatures higher than the threshold temperature. On the other hand, hinoki responded to changes in temperature more slowly than sugi. The simulated temperature modifier did not reach to 1.0 with temperature ranged between 0 to 20 °C, while that did not reach to 0.0 with temperature ranged between -10 to 0 °C. For hinoki, temperature works as the photosynthetic rate controlling factor over a wider range than sugi, however, it does not work as the photosynthetic rate stopping factor even at -10 °C. Comparing the simulated temperature modifier function shows that hinoki has a superior tolerance to low temperature than sugi.

Estimated parameters of the humidity modifier function suggested that the humidity modifier did not work well in the carbon balance-based growth model. The coefficient $H_2$ represented the lowest VPD value that affected the photosynthetic rate as an environmental stress, and the photosynthetic rate was reduced by water stress derived from air dryness with a higher VPD than $H_2$. Simulated curves of the humidity modifier function shown in Fig.6 indicated that air dryness did not affect the photosynthetic rate with a lower VPD ($< 1.5$ kPa) for both species, while at a higher VPD, hinoki was more vulnerable to water stress than sugi. However VPD did not usually get any higher than 1.5 kPa, in fact 95% of the VPD values of the climatic data used in this study were lower than 1.5 kPa. Furthermore, past studies noted that sugi was sensitive to water stress (e.g. Matsumoto et al., 1992). Thus, we concluded that the parameterization for the humidity modifier function did not succeed in this study. VPD was assumed as a growth limiting factor in summer dry season, on the other hand respiration rate increased with increase of temperature in summer, and then reduced biomass growth. Because higher temperature acted as a growth limiting factor in summer, the effect of air dryness indicated by VPD might not be represented well.

The estimated parameters in this study revealed that the potential photosynthetic ability of sugi was better than that of hinoki, and hinoki had a better tolerance to low temperature than sugi. On the other hand, air dryness did not behave well as a photosynthetic rate controlling factor in the carbon balance-based growth model developed in this study. Thus, differences in growth responses to climatic conditions between sugi and hinoki were not revealed well in this study, because water stress is a critical factor in sugi planted forests. We need to modify the model structure to reflect the effect of water stress caused by dry air on photosynthesis and stand growth.
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