



## Research article

Current and future carbon stocks of a dominant forest plantation species, *Cryptomeria japonica*, throughout JapanRyo Nakahata<sup>a,b,\*</sup>, Tomohiro Egusa<sup>c</sup>, Tomo'omi Kumagai<sup>a,d</sup><sup>a</sup> Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan<sup>b</sup> Center for Tree Science, The Morton Arboretum, Illinois, United States<sup>c</sup> Faculty of Agriculture, Shizuoka University, Shizuoka, Japan<sup>d</sup> Water Resources Research Center, University of Hawaii'i at Mānoa, Honolulu, United States

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## ABSTRACT

Estimation of forest carbon stocks is essential in ecological and political contexts to understand material cycles and achieve a carbon-neutral society. Because old-growth forests are vital for determining forest growth capacity, and recent climate change has significantly influenced forests worldwide, integration of the most recent data sets covering a broad range of forest ages and geographical variation is needed to construct accurate growth models and to estimate current and future forest resources. Japan's National Forest Inventory (NFI) provides nationwide information regarding forest ecosystems, in which *Cryptomeria japonica* forests dominate and are indispensable for forest resources and the wood industry. This study aimed to establish accurate carbon-based growth models for *C. japonica* forests using NFI and other literature surveys and to reveal their geographical variation with a hierarchical model. We then used this model to predict future forest carbon stocks under several management scenarios. The model estimated that the maximum forest carbon density was 1.8 times higher than previously predicted based on outdated yield tables. However, the growth capacity varied across the country, likely due to environmental gradients and forestry practices. Our predictions indicate that *C. japonica* forests in Japan still have the capacity to accumulate substantial carbon resources consistently exceeding 750 TgC with sustainable wood supply under suggested management efforts to increase the reforestation rate. We conclude that updated forest growth models are required, especially for old-growth forests under ongoing climate change, and that appropriate forest management is necessary to maximize the potential for forest carbon accumulation.

## 1. Introduction

Forest ecosystems are major carbon sinks that significantly affect global biological and physical cycles (Keenan and Williams, 2018; Pan et al., 2011). Forests absorb carbon dioxide (CO<sub>2</sub>) from the atmosphere and store carbon resources mainly in soil organic matter and tree biomass for long periods. In global terrestrial ecosystems, forest ecosystems contribute up to 50 % of net primary production (NPP) and contain up to 45 % of carbon resources accumulated in their leaves, stems, and belowground parts (Bonan, 2008; Sha et al., 2022). Given that forest ecosystems comprise plant, animal, and microbial populations, forest carbon assimilation through biochemical reactions is driven by various biotic (e.g., species composition and symbiotic organisms) and abiotic (e.g., meteorological and edaphic conditions) factors (Barnett et al., 2023; Begović et al., 2023). Understanding and

predicting biomass growth patterns in various forest types with consideration of such biotic and abiotic factors are needed to understand carbon dynamics in forest ecosystems across a broad distribution worldwide.

Estimation of forest biomass resources is essential not only in the context of ecological aspects to understand material cycles (Keith et al., 2009; Pan et al., 2024) but also in the context of social issues such as providing a scientific consensus that guarantees carbon credits, with which governments and companies deal to optimize the global carbon balance (Fahey et al., 2010; Gren and Aklilu, 2016; van der Gaast et al., 2018). In order to promote social and environmental activities to achieve carbon neutrality, there is an urgent need to accurately evaluate the carbon accumulation capacity of forests. One role of researchers in forest science is to provide accurate estimations of annual carbon accumulation and sequestration in forest ecosystems and optimization of forest

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management to maintain forest resources in the future. This information assists governments to make decisions for building a sustainable society in relation to resource cycling and for mitigation of climate change caused by global warming (Stocker et al., 2014). For these policy issues, prediction of forest carbon stocks and their future changes is required, with consideration of the degree of uncertainty.

Several methods have been developed to estimate the carbon stock in forests. Generally, the forest carbon stock at a given time point can be estimated from direct measurements of individual tree sizes, such as diameter and height within a certain stand area, and converting the data to mass-based metrics (e.g., stem volume and biomass) with allometric equations (Chave et al., 2014; Vashum, 2012). Individual tree metrics can then be combined with measures of stem density to estimate total carbon densities. Forest carbon density then strongly depends on the stand age as individual tree size and stem densities both vary considerably with stand age, especially in even-aged forests. Forest biomass estimates must be defined as a function of stand age since plantation establishment or a catastrophic disturbance, such as a wildfire (Besnard et al., 2021), to calculate the future forest carbon stocks. However, the function and its accuracy in estimating forest biomass are generally species-specific and vulnerable to decreasing evenness of stand age. Given variability in growth rates and carbon densities among species, it is essential to establish species-specific relationships between forest carbon stock and stand age to evaluate the current carbon stock in forests and to predict temporal changes in the future. Forest measurement data covering a broad range of stand ages for a given species are therefore crucial to derive accurate relationships with consideration of uncertainty attributable to the potential contribution of old-growth forests (Gundersen et al., 2021; Luyssaert et al., 2008) and changes in forest management expected in each country and region.

Forest biomass accumulation with age has been evaluated worldwide. The accumulation capacity is generally lower in the boreal biome and higher in temperate and tropical regions (Pan et al., 2011; Pregitzer and Euskirchen, 2004). Within each biome, the accumulation patterns have been differentiated with forest type categories based on species composition, climate, and geography (Barnett et al., 2023; Repo et al., 2021). Notably, climate change may modify carbon accumulation patterns in various forest types at a continental scale (McMahon et al., 2010; Zhu et al., 2018). Thus, forest biomass depends not only on stand age but also on changes in growth environments, species composition, and stand structure. In Japan, forest stem volume and biomass are often estimated from stand age, usually based on yield tables representing the relationship between forest age and stem volume that were established several decades ago. However, the uncertainty of stem volume estimates based on yield tables has been noted as a result of severe changes in environmental conditions and social background (Egusa et al., 2020). Potential errors in yield table-derived estimates have been specifically attributed to the following factors: 1) the lack of data for old-aged forests, 2) improvement in forest growth environments owing to climatic changes in recent decades, and 3) lack of thinning due to a decline in timber demand and the resulting shift in forestry management practices. Considering these factors, there is a pressing need to improve outdated forest measurement data and to reconstruct equations to improve predictions of forest carbon stock changes with stand age considering older and more mature forests. Hereafter, we explicitly consider old-growth forests as forests in a biomass saturation stage beyond the maturation phase (e.g., stand ages with forest biomass more than 95 % of the maximum), while old-aged forests merely indicate forests in later stages of development (e.g., more than 50 years old for plantations) regardless of history in forestry practices.

It should be noted that direct measurement data in old-growth forests are limited compared with those for young and mature forests. Since the end of the Second World War, the use of forest resources has declined because of the increase in use of fossil fuels. Therefore, the average forest age in Japan and other countries has increased owing to reduced frequency of harvesting (Barnett et al., 2023; Egusa et al., 2024; Japan

Forestry Agency, 2023a). In such situations, it is essential to evaluate the biomass growth of old-aged forests in addition to understanding the influence of global warming (Zhu et al., 2018). Moreover, the growth potential of old-aged forests can be significantly affected by past disturbance and forestry practices, which causes substantial uncertainty when estimating carbon stock in these older forests (Begović et al., 2023; Gundersen et al., 2021). Previous studies conducted in diverse regions across the world suggest that a re-evaluation of the carbon assimilation rate in old-aged forests is needed (Barnett et al., 2023; Begović et al., 2023; Gundersen et al., 2021; Luyssaert et al., 2008), and that prediction of future forest resources with consideration of old-growth forests is a fundamental challenge.

Forests cover 68.4 % of the land area in Japan, which is one of the highest percentages of forest area among all countries (FAO, 2020) and constitutes a significant proportion of the total forest carbon stock in east Asia (Fang et al., 2005). Recent findings indicate that the forest carbon stock in Japan may have been significantly underestimated (Egusa et al., 2020), and therefore, its re-evaluation is needed. The most dominant and important forest types for nature landscape, forestry wood production, and carbon accumulation in Japan is *Cryptomeria japonica* D. Don forests (Fukuda et al., 2003; Japan Forestry Agency, 2023b). Surprisingly, the forests of this single species, *C. japonica*, cover 18 % of all forest areas and 44 % of total forest plantation areas in Japan (Japan Forestry Agency, 2023a). Most *C. japonica* forest stands are currently approximately 50 years old and transitioning to the old-aged phase, and regeneration of younger stands is not anticipated because of the low afforestation rate (Japan Forestry Agency, 2023a, 2023b). Thus, existing *C. japonica* forests in Japan will likely continue to age with minimal reforestation.

Meteorological and edaphic factors affect tree growth patterns, regeneration, and their geographical variation. *C. japonica* trees are well-known to grow taller and live longer than other tree species in Japan, but the maximum height, ages, and reproductive strategies also depend on the local habitats (Azuma et al., 2016; Nishizono et al., 2014; Suzuki and Tsukahara, 1987). Some *C. japonica* trees from specific provenances are shade tolerant, which enables their clonal regeneration and seedling recruitment under harsh environments in natural forests (Kimura et al., 2013; Ota et al., 2015; Tabuchi et al., 1981). Given that *C. japonica* forests are distributed throughout a broad latitudinal range from boreal to subtropical regions across Japanese archipelago (Fig. S1), meteorological and edaphic factors are likely to strongly influence tree aboveground growth characteristics and belowground nutrient acquisition strategies (Hirano et al., 2017; Nishizono et al., 2014; Tsumura et al., 2020; Wada et al., 2019). As a consequence of intergenerational adaptation, the dominant genotypes of *C. japonica* trees differ between west and east populations in Japanese archipelago. The western populations have a relatively high growth rate at an early stage of forest development, whereas the eastern populations grow to a higher maximum stand height. Importantly, these genotypic differences can lead to different stand characteristics, even when grown under the same environmental conditions (Azuma et al., 2023; Nakahata et al., 2024). Geographical variation in forest carbon accumulation attributable to environmental and genotypic factors should therefore be considered to understand and predict patterns of growth in *C. japonica* forests across Japan.

The National Forest Inventory (NFI) data collected by the Japan Forestry Agency are among the most comprehensive and reliable data sets for forests across Japan and have enabled improved estimates of national forest resources (Egusa et al., 2020, 2024). Several studies indicate that forest carbon density and its accumulation rate are larger, compared with that derived from the previous yield tables, in specific old-aged forests of *C. japonica*, evaluated by performing a rigorous ground-based tree census (Kunisaki and Yamazaki, 2021; Nishizono et al., 2005). To evaluate the carbon accumulation capacity of *C. japonica* forests at broader scales and understand how increases in the age of these stands impact their growth and total forest carbon stock, we

specifically address the following aims: 1) to estimate carbon accumulation patterns in *C. japonica* forests at the national level using stand-based data obtained from the latest NFI and a survey of the previous literature, 2) to clarify geographical variation in growth patterns by modeling growth functions at the regional, prefecture, and stand levels with hierarchical structures, and 3) to predict the future carbon stock in *C. japonica* forests using the novel growth models developed in this study and considering different forest management scenarios under the current levels of harvesting and reforestation rate.

## 2. Materials and methods

### 2.1. Data collection

We used the NFI data to estimate the carbon stock in *C. japonica* forests across Japan and then augmented this data set where data coverage was insufficient, most notably for old-aged forests. Therefore, we conducted an additional literature survey (LS) to compensate for the paucity of data covering a broad range of forest ages from early to old-growth stages. In addition to NFI data providing only a small number of time points for each stand, some LS data provided consecutive growth data over a long period from a specific forest, which enhanced the robustness of estimating forest growth trajectories.

Japan's NFI is implemented with the aim of obtaining objective forest information at 4 km grid points over the entire land area of Japan using a nationally standardized methodology; the information is necessary to set forestry policy for the promotion of sustainable forest management (Japan Forestry Agency, 2023a; <http://forestbio.jp/>). The survey for the 1st NFI was conducted from 1999 to 2003, and has been repeated at 5 year intervals since. In the survey, size metrics of tree individuals are measured in a consistent circular plot area of each grid point, and this was then repeated for the same plot area at each time interval unless the plots were inaccessible or catastrophically disturbed. The most recently collected data, forming the 4th NFI based on field surveys performed in 2014–2018, were released in February 2023. Importantly, among the four NFI surveys, the most recent two data sets (i.e., the 3rd and 4th NFI data) are the most reliable owing to methodological improvements such as the provision of technical training for investigators and supervision of data quality by experts. Therefore, we used the 3rd and 4th NFI data (hereafter, NFI3 and NFI4), obtained from the 2009–2013 and the 2014–2018 field surveys, respectively, for data analyses. First, we extracted data comprising forest stem volume ( $\text{m}^3 \text{ha}^{-1}$ ), stand age (yr), prefecture number, latitude, and longitude for forest plots dominated by *C. japonica* from NFI3 and NFI4. The number of forest plots dominated by *C. japonica* in NFI4 is 2645 (Table S1) out of a total ca. 15,000 plots, and 1996 plots within the *C. japonica* forest plots have the same plot identification as used in NFI3, thus those plots were consecutively surveyed from NFI3. The consecutive plots were mainly used for subsequent analyses so that we could evaluate growth functions for each forest stand with consideration of growth trends determined by two time point data between NFI3 and NFI4. Note that some plot data potentially have been influenced by forestry practices or meteorological disturbance because the NFI survey was performed regardless of the forest history.

In addition to the NFI data, published literature was reviewed to extract data on *C. japonica* forests across Japan. The literature survey was conducted through the online Google Scholar platform by searching academic journals and library sources using combinations of the following keywords: “Japanese cedar”, “*Cryptomeria japonica*”, “stem volume”, “biomass”, “carbon stock”, “stand age”, “growth function”, and “old-growth forest” in English and Japanese. Through the literature survey, data sets comprising location information, stand age (yr), and either stem volume ( $\text{m}^3 \text{ha}^{-1}$ ), biomass ( $\text{MgC ha}^{-1}$ ), or carbon density ( $\text{MgC ha}^{-1}$ ) at the stand level were compiled. If data were described only in figures without textual information, WebPlotDigitizer (Rohatgi, 2019) was used to extract values from the figure images. The data were

based on field studies that were mostly conducted in public forests where resource monitoring and management practices have been implemented for scientific objectives (e.g., Nishizono et al., 2008; Tange et al., 1994). Ultimately, 59 literature sources, including peer-reviewed research articles and bulletins from universities and research institutes, provided 1178 data points for forest carbon density and age from 426 forest stands distributed across 30 prefectures (Table S1). Many of the forest stands selected in the LS include consecutive time point data within each stand.

To compare a growth function (NFI-LS model) modeled with the NFI and LS data (hereafter, NFI-LS data) with that modeled using outdated forest data, we additionally compiled data sets for total stem volume ( $\text{m}^3$ ) and forest area (ha) of *C. japonica* forests for each stand age class based on the outdated yield tables (YT data) previously released by the Japan Forestry Agency (Japan Forestry Agency: Current status of forest resources). These data sets were established several decades ago by direct field measurements but likely underestimate the current forest carbon stocks (Egusa et al., 2020). Stand stem volume per area ( $\text{m}^3 \text{ha}^{-1}$ ) was calculated by dividing the total stem volume by forest area for each age class, and then converted into carbon biomass per unit area ( $\text{MgC ha}^{-1}$ ) (Fang et al., 2005) to derive an overall relationship between forest carbon density and stand age for *C. japonica* forests. This manipulation was conducted for four data sets released in 1981, 1986, 1991, and 1995, and these were then averaged and used for subsequent analysis of a growth model, i.e., the yield table model (YT model).

### 2.2. Estimation of forest carbon density from stem volume

Forest carbon density ( $C_d$ ;  $\text{MgC ha}^{-1}$ ) was calculated from forest stem volume per area ( $V_s$ ;  $\text{m}^3 \text{ha}^{-1}$ ) in the NFI-LS data as follows:

$$C_d = V_s \cdot CF \quad (1)$$

$$CF = WD \cdot BEF \cdot (1 + R) \cdot C \quad (2)$$

where  $CF$  ( $\text{MgC m}^{-3}$ ) is a conversion factor to convert forest stem volume to forest carbon density,  $WD$  is wood density ( $0.314 \text{ Mg m}^{-3}$ ),  $BEF$  is biomass expansion factor,  $R$  is the ratio of belowground biomass to aboveground biomass (0.25), and  $C$  is the carbon content in conifers ( $0.51 \text{ gC g}^{-1}$ ). The values for  $WD$ ,  $R$ , and  $C$  were obtained from the “National Greenhouse Gas Inventory Report of Japan 2022” (Ministry of the Environment, 2022).  $BEF$  is the ratio of aboveground biomass (leaves, branches, and stem) to stem biomass, and was modeled using  $BEF$  from the LS data (e.g., Tange, 2018) as a function of stand age ( $x$ ; yr) (Fig. S2) as follows (see “Statistical analysis”):

$$BEF(x) = x^b \cdot \exp(a) + 1 \quad (3)$$

where  $a$  and  $b$  are estimated parameters. In the LS data, if the literature provided  $BEF$  of itself or aboveground biomass data enabling us to calculate that, we used the provided  $BEF$  to estimate the  $C_d$ .

Regarding the NFI data, forest plots that seemed to have aberrant  $C_d$  values, likely due to data input error, were eliminated from the original data for subsequent model analyses (“Modeling of forest carbon density with age”), by using thresholds of 99 % intervals for probability distributions for the data (see “Supplementary Materials” and Fig. S3). After this manipulation, data from 1432 forest plots in both NFI3 and NFI4 were retained (Fig. S4). However, as an exception, data for one plot in Osaka prefecture from NFI4 were added, because this prefecture was the only one with no consecutive plots between NFI3 and NFI4. Ultimately, 2865 plot data for *C. japonica* forests (i.e., 1432 plots  $\times$  2 time points + 1 plot) were retained as the NFI data used for the following analyses.

### 2.3. Modeling of forest carbon density with age

Model estimation was conducted to evaluate carbon accumulation patterns with stand age up to and beyond the typical mature stage using

the NFI-LS data. The patterns were modeled based on the Chapman-Richards growth function (hereafter, the Richards function) as follows (Penaar and Turnbull, 1973; Richards, 1959):

$$c_d = G(x) = C_{d\_max}(1 - \exp(-k \cdot x))^{\frac{1}{1-m}} \quad (4)$$

where  $c_d$  is the mean forest carbon density ( $\text{MgC ha}^{-1}$ ) and is defined as a growth function  $G(x)$  of stand age  $x$ .  $C_{d\_max}$ ,  $k$ , and  $m$  are parameters of the growth function at the national level in Japan.  $C_{d\_max}$  is a scale parameter for carbon density and an asymptotic upper limit of  $c_d$ .  $k$  is a scale parameter for stand age and the rapidity of relative carbon accumulation to the maximum.  $m$  determines the shape of the growth curve and negatively affects the growth rate in the initial phase of forest growth (Fig. 1).

We further formulated the Richards functions for each region (Fig. 2) as

$$c_{d\_rgn} = G_{rgn}(x) = C_{d\_max\_rgn}[i](1 - \exp(-k_{rgn}[i] \cdot x))^{\frac{1}{1-m_{rgn}[i]}} \quad (5)$$

where,  $c_{d\_rgn}$  is mean forest carbon density ( $\text{MgC ha}^{-1}$ ) and is defined as a growth function  $G_{rgn}(x)$ .  $C_{d\_max\_rgn}[i]$ ,  $k_{rgn}[i]$ , and  $m_{rgn}[i]$  are the parameters at a regional level corresponding to  $C_{d\_max}$ ,  $k$ , and  $m$ , respectively.  $i$  is a vector  $i = \{1, 2, \dots, I\}$ , where  $I = 8$ , representing an index of the regions in Japan with native *C. japonica* forests (Fig. S1).

Growth characteristics of *C. japonica* forests are possibly differentiated with greater local and topographic variation within each region (Nishizono et al., 2014; Tsumura, 2023). Therefore, we established a hierarchical Bayesian model based on the Richards function in which model parameters at the national ( $C_{d\_max}$ ,  $k$ , and  $m$ ) and the regional ( $C_{d\_max\_rgn}$ ,  $k_{rgn}$ , and  $m_{rgn}$ ) levels were hierarchized into prefecture and forest stand levels (Fig. 2). Our model derived in this study is regarded as a Markov random field model, which considers the spatial structure of the parameters. To localize the model parameters, the Richards functions at the prefecture level were defined as

$$c_{d\_prf} = G_{prf}(x) = C_{d\_max\_prf}[j](1 - \exp(-k_{prf}[j] \cdot x))^{\frac{1}{1-m_{prf}[j]}} \quad (6)$$

where  $c_{d\_prf}$  is the mean forest carbon density ( $\text{MgC ha}^{-1}$ ) as in Eq. (5), and is defined as a growth function  $G_{prf}(x)$ .  $C_{d\_max\_prf}[j]$ ,  $k_{prf}[j]$ , and  $m_{prf}[j]$  are the parameters at the prefecture level corresponding to  $C_{d\_max}$ ,  $k$ , and  $m$ , respectively.  $j$  is a vector  $j = \{1, 2, \dots, J\}$ , where  $J = 46$ , representing an index of prefectures excluding Okinawa where native *C. japonica* forests are not included in the NFI (Fig. S1). The parameters at the national level,  $X = \{C_{d\_max}, k, m\}$ , and those at the regional level,  $X_{rgn}[i] = \{C_{d\_max\_rgn}[i], k_{rgn}[i], m_{rgn}[i]\}$ , were then calculated as area-weighted means of the parameters at the prefecture level,  $X_{prf}[j] = \{C_{d\_max\_prf}[j], k_{prf}[j], m_{prf}[j]\}$ , respectively. Accordingly,  $X$  and  $X_{rgn}[i]$  were defined by the following equations:

$$X = \frac{\sum_{j=1}^J A_{prf}[j] \cdot X_{prf}[j]}{\sum_{j=1}^J A_{prf}[j]} \quad (7)$$

$$X_{rgn}[i] = \frac{\sum_{j=j\_I[i]}^{J\_I[i]} A_{prf}[j] \cdot X_{prf}[j]}{\sum_{j=j\_I[i]}^{J\_I[i]} A_{prf}[j]} \quad (8)$$

where  $A_{prf}[j]$  (%) is the percentage of forest plot numbers among prefectures based on the NFI4 data (Table S1).  $j\_I[i]$  and  $J\_I[i]$  mean the first and last prefecture indexes for each region  $i$ , respectively. In addition, we assumed that each  $X_{prf}[j]$  is similar to that in adjoining prefectures. In

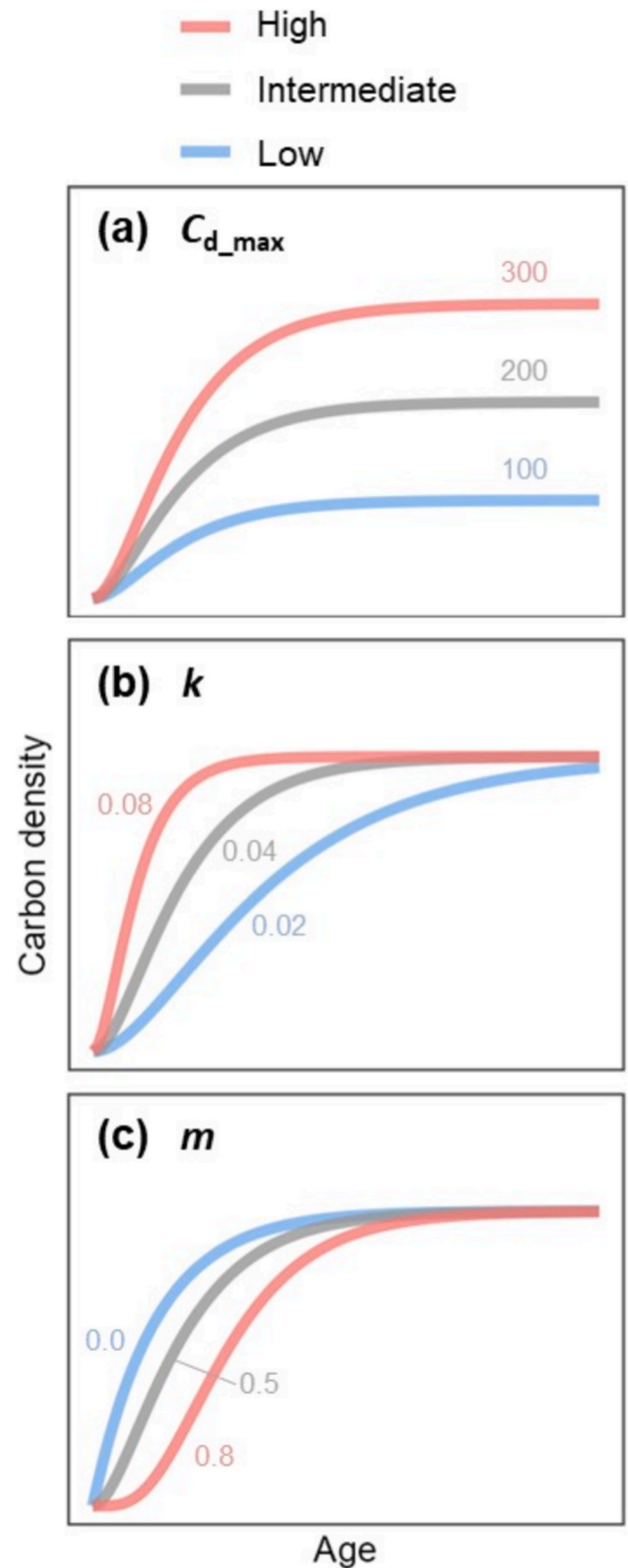
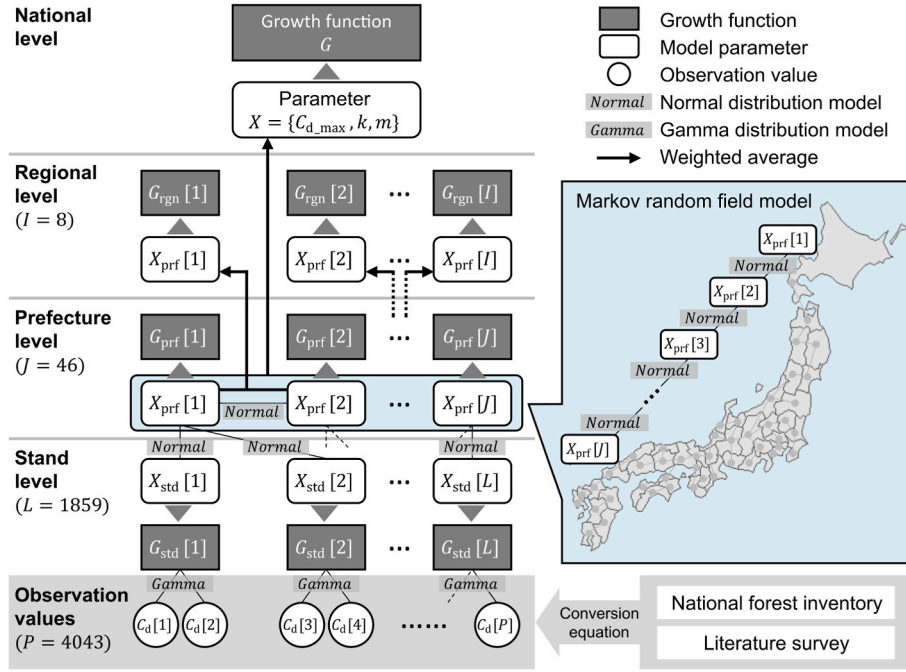


Fig. 1. Effects of changes in (a)  $C_{d\_max}$ , (b)  $k$ , and (c)  $m$  on the Chapman-Richards growth function (Eq. (4)).  $C_{d\_max}$  is a scale parameter for carbon density and an asymptotic upper limit.  $k$  is a scale parameter for stand age and the rapidity of relative carbon accumulation to the maximum.  $m$  determines the shape of the growth curve and negatively affects the growth rate in the initial phase of forest growth.





**Fig. 2.** Schematic illustration of the model structures. In this study, growth functions at the national, regional, prefecture, and stand levels were defined. The Markov random field model was applied to express the spatial structure of the model parameters at the prefecture level.

other words, the  $X_{prf}[j]$  between adjoining prefectures does not differ significantly from each other, which was applied by introducing a stochastic process based on the normal probability distribution as follows:

$$X_{prf}[To[n]] \sim Normal(X_{prf}[From[n]], \sigma_{X_{prf}}) \quad (9)$$

where  $\sigma_{X_{prf}} = \{\sigma_{C_{dm\_prf}}, \sigma_{k\_prf}, \sigma_{m\_prf}\}$  is the standard deviation of the normal distribution, either corresponding to  $X_{prf}[j] = \{C_{d\_max\_prf}[j], k_{prf}[j], m_{prf}[j]\}$ .  $To[n]$  and  $From[n]$  are indexes representing the adjacency relationship among prefectures, in which  $n = \{1, 2, \dots, N\}$  and  $N = 45$  (Table S2). This manipulation increases the likelihood in the model when the parameters assumed more similar values between adjoining prefectures.

Furthermore, the Richards functions for each forest stand,  $c_{d\_std} = G_{std}(x)$ , were modeled using data samples from each consecutive plot in the NFI-LS data as follows:

$$c_{d\_std} = G_{std}(x) = C_{d\_max\_std}[l](1 - \exp(-k_{std}[l] \cdot x))^{\frac{1}{1-m_{std}[l]}} \quad (10)$$

where  $c_{d\_std}$  is the mean forest carbon density ( $MgC\ ha^{-1}$ ) and is defined as a growth function  $G_{std}(x)$ .  $C_{d\_max\_std}[l]$ ,  $k_{std}[l]$ , and  $m_{std}[l]$  are the parameters at the stand level corresponding to  $C_{d\_max}$ ,  $k$ , and  $m$ , respectively.  $l$  is a vector  $l = \{1, 2, \dots, L\}$ , where  $L = 1859$ , representing an index of the stands included in the NFI-LS data. The parameters at the stand level, expressed as  $X_{std}[l] = \{C_{d\_max\_std}[l], k_{std}[l], m_{std}[l]\}$ , conform to the normal distribution with mean parameters of  $X_{prf}[j] = \{C_{d\_max\_prf}[j], k_{prf}[j], m_{prf}[j]\}$ , as follows:

$$X_{std}[l] \sim Normal(X_{prf}[Prf\_Std[l]], \sigma_{X_{std}}) \quad (11)$$

where  $\sigma_{X_{std}} = \{\sigma_{C_{dm\_std}}, \sigma_{k\_std}, \sigma_{m\_std}\}$  is the standard deviation of the normal distribution, either corresponding to  $X_{prf}[j] = \{C_{d\_max\_prf}[j], k_{prf}[j], m_{prf}[j]\}$ .  $Prf\_Std[l]$  is a vector with a length of 1859 and accords with the prefecture index for each stand.

Next, we describe the observation model, which describes the data

generation processes between the observation variables  $C_d[p]$  from the NFI-LS data and the latent variables  $c_{d\_std}$  defined with the aforementioned Richards functions. It was assumed that  $C_d[p]$  follows the gamma probability distribution where  $c_{d\_std}$  is the mean parameter defined as

$$C_d[p] \sim Gamma(\alpha_{std}[p], \beta_{std}[p]) \quad (12)$$

where  $\alpha_{std}[p]$  and  $\beta_{std}[p]$  are the shape and rate parameters of the gamma distribution, and  $p$  is an index of the observation variables ( $p = \{1, 2, \dots, P\}$  and  $P = 4043$ ).  $\alpha_{std}[p]$  is defined as  $\alpha_{std}[p] = \beta_{std}[p] \cdot c_{d\_std}[p]$  given that the mean parameter  $c_{d\_std}$  of the gamma distribution is determined by  $\alpha_{std}[p]/\beta_{std}[p]$ . As a characteristic of the gamma distribution, it forms the exponential distribution if  $\alpha_{std} \leq 1$ . However, as it is unlikely that forest biomass is distributed exponentially even in young forests, we defined  $\beta_{std}[p]$  as

$$\beta_{std}[p] = \theta \cdot c_{d\_std}[p]^\lambda + \frac{1}{c_{d\_std}[p]} \quad (13)$$

where  $\theta$  ( $0 < \theta$ ) and  $\lambda$  ( $-1 < \lambda$ ) are the estimated parameters for  $\beta_{std}$ . This forces  $\alpha_{std} > 1$  enabling the gamma distribution to be unimodal with any  $c_{d\_std}$  values. In this observation model,  $\theta$  and  $\lambda$  are the only estimated parameters, and  $\alpha_{std}$  and  $\beta_{std}$  are the transformed parameters.

The parameters in the present model were estimated using a Bayesian approach. Posterior distributions of the parameters were generated using the Hamiltonian Monte Carlo (HMC) method, a type of Markov chain Monte Carlo (MCMC) method (Carlin and Chib, 1995). Before the MCMC simulation, weakly informative prior distributions and conditions were given to parameters to enhance the sampling efficiency (Table S3). In the MCMC simulation, four parallel MCMC chains were run with 10,000 iterations that were retained, including an initial warmup of 2000 iterations. For each chain, the simulation samples were thinned to 20 % to obtain samples as posterior distributions (i.e., 6400 samples for each parameter estimate). The convergence of the MCMC sampling was assessed using the criterion  $\hat{R} < 1.1$  (Gelman et al., 1995). The MCMC method was performed using Stan (Carpenter et al., 2017), a probabilistic programming language, using the Rstan interface of the R statistical software (R Development Core Team, 2018).

## 2.4. Calculation of onset ages of forest development stages

To evaluate the onset ages of forest development stages quantitatively using the Richards functions at the national and regional levels, we defined the stages of early, young, mature, and old-growth forests according to the criteria used in the previous studies (Barnett et al., 2023; Salas-Eljatib et al., 2021). The early stage ranges from the beginning of the forest growth to the onset of the young stage, which is determined as the stand age when the carbon accumulation rate ( $dc_d/dx$ ; Eq. S(1)) reaches its maximum. The onset of the mature stage is the age when the carbon accumulation rate averaged over the stand age ( $c_d/x$ ; Eq. S(2)) reaches its maximum. The old-growth stage begins from the age when  $c_d$  reaches 95 % of the asymptotic upper limit in the Richards function ( $0.95 \cdot C_{d,max}$ ). In addition, these calculations of onset ages were conducted for carbon accumulation patterns of leaves and branches ( $c_{d,leaf}$ ), stems ( $c_{d,stem}$ ), and roots ( $c_{d,root}$ ), respectively. Equations for carbon density, carbon accumulation rate, and mean carbon accumulation rate over stand age for each living biomass are given according to the definitions of  $CF$  and  $BEF(x)$  (see “Supplementary Materials”).

## 2.5. Prediction of forest carbon stock in *C. japonica* forests in Japan

Predictions of future carbon stock in *C. japonica* forests were simulated from 2022 to 2112 using the Richards functions estimated either with the YT data (YT model) or the NFI-LS data (NFI-LS model). The total carbon stock in *C. japonica* forests across Japan can be estimated from the forest area for each stand age and the relationship between stand age and forest carbon density (i.e., the Richards function). Temporal changes in forest area for each stand age until 2112 were calculated with a first-order wave equation as follows:

$$\frac{\partial A(t, x)}{\partial t} = -\frac{\partial A(t, x)}{\partial x} - A_h(t, x) \quad (14)$$

where  $t$  is the A.D. year (yr), and  $A(t, x)$  and  $A_h(t, x)$  are the existing forest area and cutting forest area, respectively, for stand age  $x$  in year  $t$ .  $A_h(t, x)$  was expressed by multiplying  $A(t, x)$  by the harvest rate  $r_h(t, x)$  as follows:

$$A_h(t, x) = r_h(t, x) \cdot A(t, x) \quad (15)$$

However,  $r_h(t, x)$  changes with year and stand age were further defined as

$$r_h(t, x) = M_h(t, x)/M(t, x) \quad (16)$$

where  $M_h(t, x)$  and  $M(t, x)$  are the carbon stock in the cut forests and existing forests, respectively, for stand age  $x$  in year  $t$ .  $M_h(t, x)$  was further formulated as

$$M_h(t, x) = \frac{H_{CJ}}{\sum_x (M(t, x) \cdot CF(x)^{-1})} M(t, x) \quad (17)$$

where  $H_{CJ}$  ( $28.26 \text{ Mm}^3 \text{ yr}^{-1}$ ) is a constant for the annual cut stem volume in *C. japonica* forests across Japan, which was estimated as  $H_{CJ} = H_{total} \cdot P_{CJ}/P_{total}$  using  $H_{total}$ , the mean annual cut stem volume in all forest types, and the ratio of the mean annual stem volume yield of *C. japonica* to that of all forest types ( $P_{CJ}/P_{total}$ ) from 2017 to 2021, released by the Japan Forestry Agency (Japan Forestry Agency, 2023b). Note that  $H_{CJ}$  represents the cut stem volume consisting of that produced for the wood market ( $P_{CJ}$ ) and that cut but left in forests.  $CF(x)$  was defined by Eq. (2). In this study, under the assumption that forests more than 40 years of age are targets for harvest,  $r_h(t)$  was redefined with Eqs. (16) and (17) as

$$r_h(t) = \begin{cases} \frac{H_{CJ}}{\sum_{x \geq 40} (M(t, x) \cdot CF(x)^{-1})} & \text{if } x \geq 40 \\ 0 & \text{otherwise} \end{cases} \quad (18)$$

Forest area for age 1 in year  $t$  ( $A(t, 1)$ ) was calculated as the sum of the harvested forest area in the previous year ( $A_h(t-1, x)$ ) and reforestation rate ( $r_p$ ) as follows:

$$A(t, 1) = r_p \sum_x A_h(t-1, x) \quad (19)$$

where  $r_p$  is the constant 0.368, which is the mean ratio of reforestation area to harvested area from 2017 to 2021 in Japan (Japan Forestry Agency, 2023b).

The simulations of forest carbon stock and forest area based on the foregoing calculations were conducted from 2022 to 2112 by setting several assumptions for growth models and management parameters as follows (Table 1): scenarios based on the YT model and the NFI-LS model with no forest management (Cases 1.0 and 2.0, respectively); scenarios based on the YT model and the NFI-LS model with the current management conditions (i.e.,  $28.26 \text{ Mm}^3 \text{ yr}^{-1}$  for  $H_{CJ}$ , and 36.8 % for  $r_p$ ) (Cases 1.1 and 2.1, respectively); and scenarios based on the YT model and the NFI-LS model with active reforestation (i.e.,  $28.26 \text{ Mm}^3 \text{ yr}^{-1}$  for  $H_{CJ}$ , and 100 % for  $r_p$ ) (Cases 1.2 and 2.2, respectively).

## 2.6. Statistical analysis

To assess the YT model, a non-linear least-squares method was applied to examine three parameters ( $C_{d,max}$ ,  $k$ , and  $m$ ) of the Richards function (Eq. (4)).

A generalized linear model (GLM) was applied to evaluate the relationship between  $BEF$  and stand age derived from the LS data. In the GLM,  $BEF - 1$  and stand age were used as the response and explanatory variables, respectively, assuming a gamma error distribution of response variables with the log link function (i.e., Eq. (3)).

Significant differences among the parameters in the Richards functions estimated with the Bayesian approach were examined based on whether the probability distribution of differences between the posterior MCMC samples overlapping 0 value is less than 5 %.

These statistical analyses were performed using the R statistical software (R Development Core Team, 2018).

## 3. Results

### 3.1. Carbon-based growth function for *C. japonica* forests

The present study examined the carbon accumulation patterns of *C. japonica* forests across Japan by applying a hierarchical Bayesian model. The medians of posterior distributions for the model parameters  $C_{d,max}$ ,  $k$ , and  $m$  at the national level in the NFI-LS model were 247.1

**Table 1**

Data source for the Richards function, yield of stem volume, and reforestation rate for different scenarios simulating the future carbon stock in *C. japonica* forests.

Scenario	Data for the Richards function	Yield of stem volume ( $\text{Mm}^3 \text{ yr}^{-1}$ )	Reforestation rate (%)
Case 1.0	YT <sup>a</sup>	0	0
Case 1.1	YT	28.26	36.8
Case 1.2	YT	28.26	100
Case 2.0	NFI <sup>b</sup> + LS <sup>c</sup>	0	0
Case 2.1	NFI + LS	28.26	36.8
Case 2.2	NFI + LS	28.26	100

<sup>a</sup> Yield table.

<sup>b</sup> National Forest Inventory.

<sup>c</sup> Literature survey.

MgC ha<sup>-1</sup>, 0.0321, and 0.469, respectively (Fig. 3a). In the NFI-LS model, the forest carbon accumulation rate reached a maximum at stand age of 20 yr, and the old-growth forest stage began at 113 yr (Table 2). In contrast,  $C_{d\_max}$ ,  $k$ , and  $m$  were 135.5 MgC ha<sup>-1</sup>, 0.0442, and 0.553 in the YT model. According to the YT model, the maximum carbon accumulation rate in *C. japonica* forests is reached at age 18 yr, and the old-growth stage begins at 86 yr. In comparison between the NFI-LS and YT models,  $C_{d\_max}$  in the NFI-LS model was significantly 1.82 times higher than that in the YT model, according to 95 % credible intervals (234.1 MgC ha<sup>-1</sup> to 260.5 MgC ha<sup>-1</sup>). Meanwhile,  $k$  and  $m$  in the NFI-LS model were significantly lower than those in the YT model.

Throughout forest development, the proportions of leaves and branches, stems, and roots in the carbon density and accumulation rate changed with time (Table 2 and Fig. 3). The carbon accumulation rate

( $dc_d/dx$ ) and mean carbon accumulation rate ( $c_d/x$ ) peaked in the order of leaves and branches, roots, and then stems. Leaves and branches are favored over other organs during early stages of growth, although the carbon accumulation rate became negative after 60 yr. The peak of the mean carbon accumulation rate in stems was at 45 yr, which was 9 yr later than that for whole-tree biomass. Notably, the carbon density in stems reached 95 % of the maximum at 366 yr, which is much later compared with that in whole trees.

### 3.2. Geographical variation in carbon density and growth functions for *C. japonica* forests in Japan

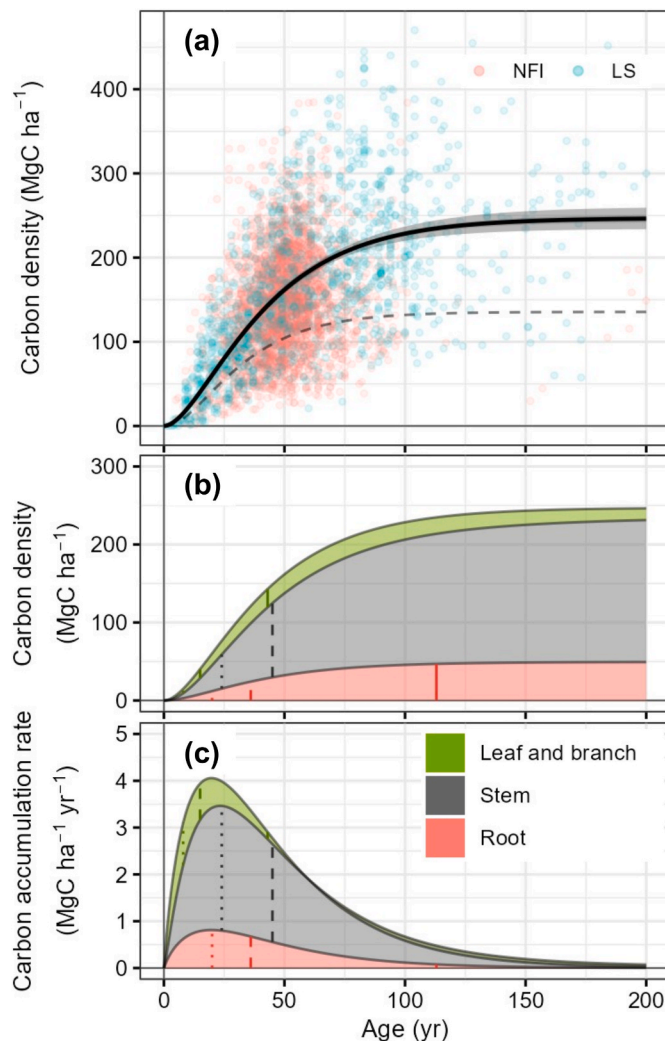
In the NFI4 data surveyed from 2014 to 2018, the median carbon density for each prefecture varied between 72.4 MgC ha<sup>-1</sup> and 196.7 MgC ha<sup>-1</sup>, while the median stand age ranged from 47 yr to 61 yr, except for Osaka which comprised data for a single plot (Figure S5 and Figure S6). Carbon density tended to be higher in plots on the Pacific Ocean side of Japan than on the Sea of Japan side, and stands in the Tohoku region were younger. However, no clear difference among regions was detected.

The hierarchical model that considers spatial structure enabled us to evaluate growth functions for each prefecture (Figure S7 and Figure S8) and further revealed the regional-level growth functions with the weighted means of the parameters (Fig. 4 and Table S4). The model estimates suggested that  $C_{d\_max\_rgn}$  in the Kanto region was significantly higher than that of all other regions, followed by that in the Tohoku region. In contrast, Chugoku and Kyushu (situated in the western part of Japan) had relatively low  $C_{d\_max\_rgn}$ . No significant difference in  $k_{rgn}$  was detected among the regions, and  $m_{rgn}$  was indicated to be lower in western Japan. Regarding the parameters at the prefecture level,  $C_{d\_max\_prf}$ ,  $k_{prf}$ , and  $m_{prf}$  varied between 198.3 MgC ha<sup>-1</sup> and 281.1 MgC ha<sup>-1</sup>, 0.0274 and 0.0369, and 0.401 and 0.572, respectively (Fig. 5, S7 and S8).

### 3.3. Prediction of carbon stock in *C. japonica* forests in Japan

Depending on six scenarios (Table 1), the predicted future carbon stock in *C. japonica* forests from 2022 to 2112 varied (Fig. 6). In the scenario based on the YT model that assumed the current cut stem volume and reforestation rate (Case 1.1), forest area decreased by 56 % from 4.41 Mha in 2022 to 1.92 Mha in 2100 (Fig. 6a). In contrast, in the case using the NFI-LS model and the same management parameters (Case 2.1), the forest area decreased by 34 % to 2.93 Mha in 2100.

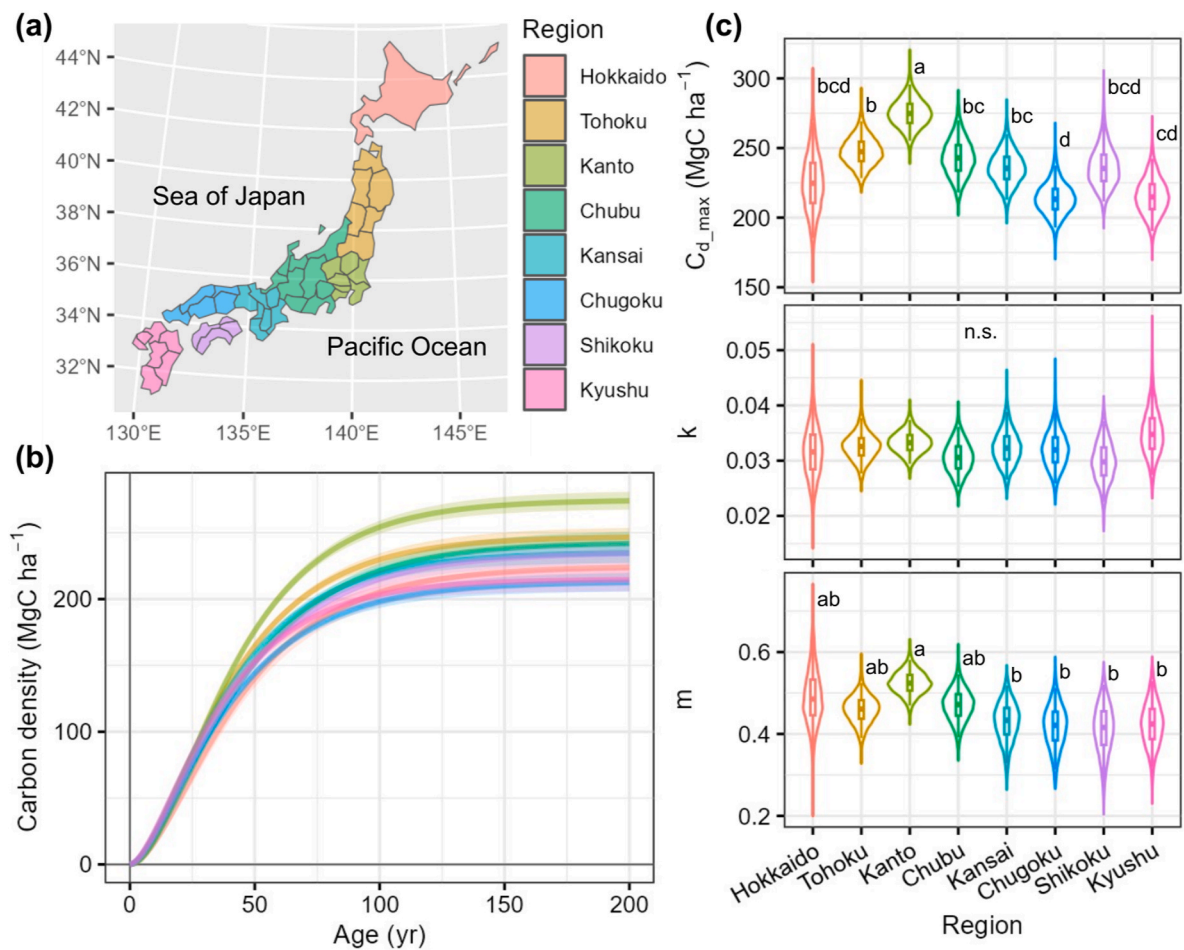
Under the scenario based on the YT model with no management (Case 1.0), the carbon stock increased by 26 % from 469.0 TgC in 2022 to 593.1 TgC in 2100 (Fig. 6b). With the current cut stem volume and reforestation rate (Case 1.1), the carbon stock decreased by 61 % compared with that in 2022 and was predicted to be 181.0 TgC in 2100, reflecting the change in forest area. In the scenario using a 100 % reforestation rate instead of the current rate of 36.8 % (Case 1.2), the carbon stock declined by 22 % and was calculated to be 367.5 TgC in 2100. In contrast, carbon stock in 2022 estimated with the NFI-LS model was predicted to be 756.6 TgC, which was 61 % higher than that based on the YT model. The NFI-LS model-based simulation with no management (Case 2.0) predicted that the carbon stock would increase by 39 % and reaches 1052.0 TgC in 2100, whereas the scenario with the current management parameters (Case 2.1) predicted that the carbon stock would increase to 769.0 TgC around 2032 and thereafter decrease but still store as much carbon as under Case 1.0 even in 2100. The growth models based on both the YT and NFI-LS data (i.e., YT vs. NFI-LS models) resulted in more than 3 times greater differences in carbon stock estimates in 2100. The scenario based on the NFI-LS model with a 100 % reforestation rate (Case 2.2) predicted a carbon stock of 788.6 TgC in 2100, which was slightly higher than that in 2022 and remained relatively stable throughout the simulation.



**Fig. 3.** (a) Relationship between forest carbon density and stand age at the national level, and (b) forest carbon density and (c) forest carbon accumulation rate divided by tree organs. (a) Red and blue points represent the NFI and the LS data, respectively. A solid line indicates the medians with a gray band showing 95 % credible intervals in the NFI-LS model. A dashed line is the regression curve for the YT model. (b) Carbon allocation to leaves and branches, stems, and roots was calculated using Eq. (1). The sum for each organ equals the solid line in the panel above (a). (c) Curves denote were derived by differentiating the Richards function (Eq. (4)) and the BEF model (Eq. (3)) with stand age. (c, d) Vertical dotted, dashed, and solid lines indicate stand ages at the onset of the young, mature, and old-growth stages for each organ, respectively. The age at the onset of the old-growth stage for stems is not shown because of an out-of-range value.

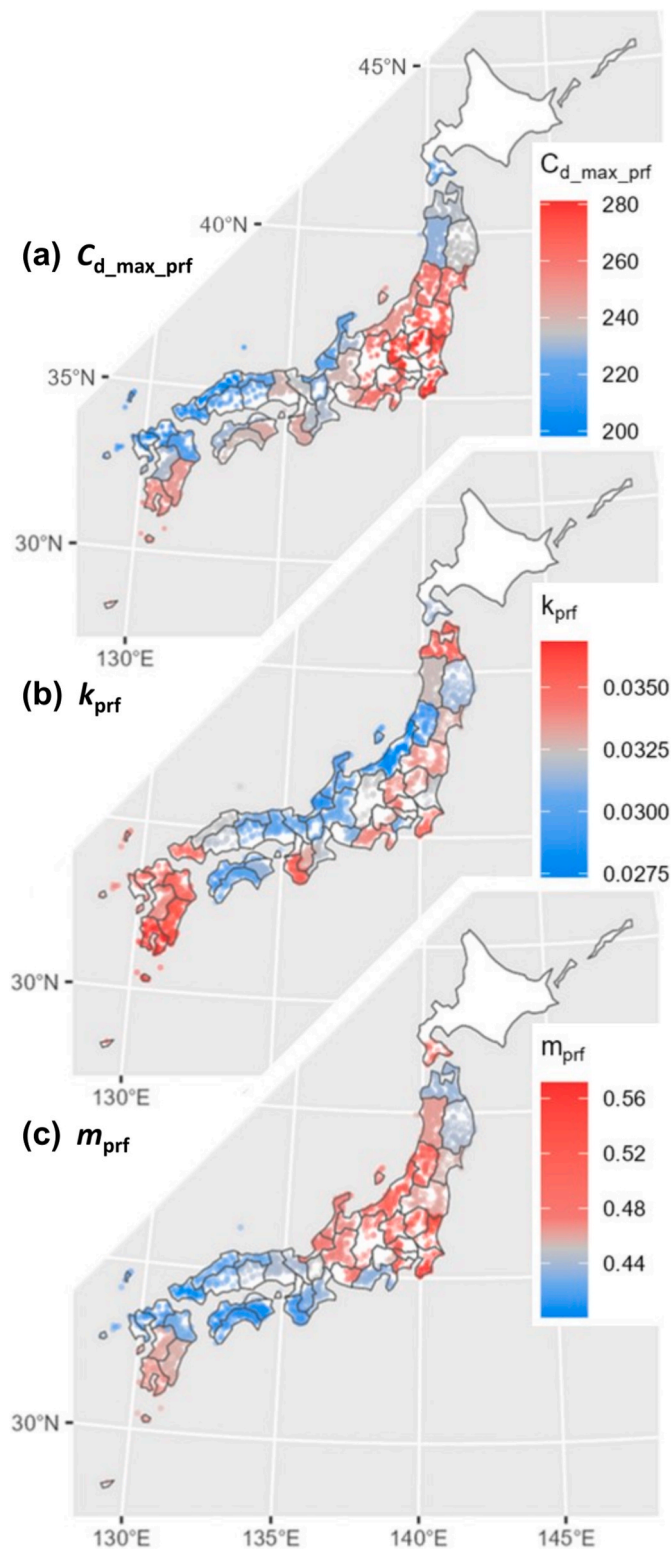
**Table 2**  
Estimated model parameters for the Richards functions based on either the YT data or the NFI-LS data, and stand age at the onset of each growth stage for the Richards functions and each organ of *C. japonica* tree.

Models	Spatial scales	Regions	Organs	Model parameters			Stand age at onset of growth stages		
				$C_{d\_max}$ (MgC ha <sup>-1</sup> )	$k$	$m$	Young (yr)	Mature (yr)	Old growth (yr)
YT model	National level			135.5	0.0442	0.553	18	33	86
NFI-LS model	National level			247.1	0.0321	0.469	20	36	113
			Leaf and branch				8	15	43
			Stem				24	45	366
			Root				20	36	113
	Regional level	Hokkaido		224.7	0.0316	0.485	21	40	119
		Tohoku		247.4	0.0326	0.461	19	35	112
		Kanto		274.8	0.0333	0.524	22	41	113
		Chubu		242.9	0.0306	0.472	21	38	120
		Kansai		235.4	0.0323	0.433	17	32	111
		Chugoku		213.3	0.0320	0.421	17	31	112
		Shikoku		235.3	0.0298	0.416	18	33	119
		Kyushu		214.9	0.0348	0.424	16	30	102

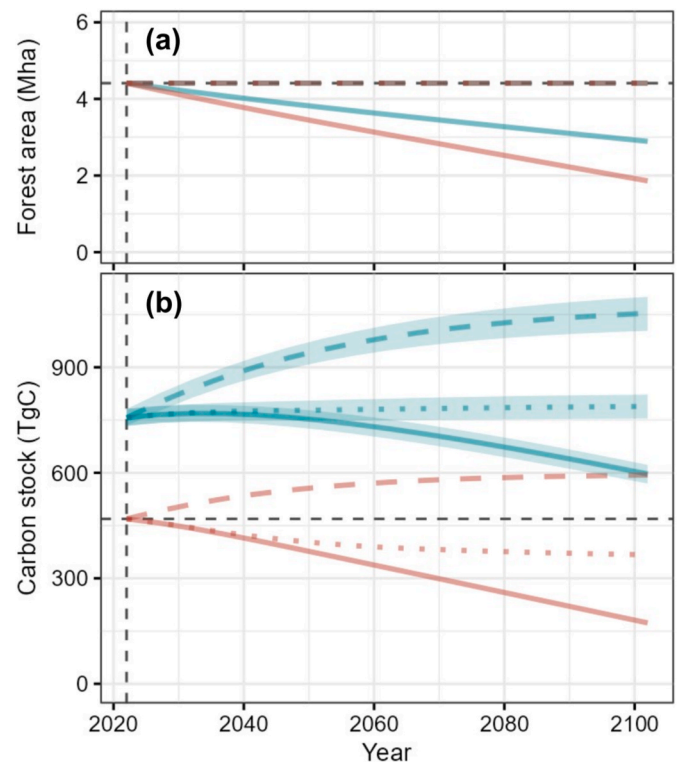


**Fig. 4.** (a) A Japan map showing regions, (b) the Richards functions estimated in the NFI-LS model, and (c) posterior distributions of the estimated parameters of the functions at the regional level. Regions are represented by the same color in all panels. (b) Solid lines mean the medians with bands showing 50 % credible intervals for each region. (c) Ranges of boxes and whiskers indicate 50 % and 95 % credible intervals, respectively, in the model. Different letters mean significant differences, and n.s. denotes no significant difference among the regions.





**Fig. 5.** Geographical distribution of *C. japonica* forests across Japan and medians of estimated parameters for (a)  $C_{d\_max\_prf}$ , (b)  $k_{prf}$ , and (c)  $m_{prf}$  at the prefecture level. Estimates are indicated with the same colors within each prefecture.



**Fig. 6.** Predictions of (a) area and (b) carbon stock for *C. japonica* forests in Japan. (a, b) Based on the six scenarios, numerical simulations were conducted for the period from 2022 to 2112. A vertical dashed line indicates 2022, and a horizontal dashed line denotes an estimate in 2022 based on the YT model. Red and blue lines represent estimates based on NFI-LS model (Cases 2.0, 2.1, and 2.2) and YT model (Cases 1.0, 1.1, and 1.2), respectively. Among them, dashed, solid, and dotted lines indicate scenarios with no forest management (Cases 1.0 and 2.0), the current management conditions (i.e.,  $28.26 \text{ Mm}^3 \text{ yr}^{-1}$  for  $H_{CJ}$ , and 36.8 % for  $r_p$ ) (Cases 1.1 and 2.1), and active reforestation (i.e.,  $28.26 \text{ Mm}^3 \text{ yr}^{-1}$  for  $H_{CJ}$ , and 100 % for  $r_p$ ) (Cases 1.2 and 2.2), respectively (see Table 1). Bands around lines show 95 % credible intervals.

#### 4. Discussion

##### 4.1. Significant updates on forest growth functions covering old-aged forests

Using the meta-analysis integrating NFI and LS data, we re-evaluated the growth characteristics of *C. japonica* forests across Japan. The new growth model (NFI-LS model) is significantly different from the old model (YT model) that was based on outdated national forest inventory data mainly surveyed in the 1960s. In particular, the asymptotic upper limit ( $C_{d\_max}$ ) in the NFI-LS model was 1.8 times higher than that in the YT model (Table 2 and Fig. 3), strongly supporting the possibility of underestimation in forest carbon stock previously noted by Egusa et al. (2020). Moreover, the NFI-LS model differed from the growth model for *C. japonica* forests based on the NFI3 data derived from forest surveys conducted in the period 2009–2013 (Egusa et al., 2024). Egusa et al. (2024) established a growth model based on the same Richards function using only the NFI3 data (hereafter, NFI3 model), but these authors did not hierarchize the model into the prefecture and stand levels. In contrast to the NFI3 model, the NFI-LS model estimated  $C_{d\_max}$  to be 1.5 times higher, and  $k$  and  $m$ , which are related to the length of the growth periods for each forest stage, also differed. As a result, the ages of peaks carbon accumulation rate differed among the YT, NFI3, and NFI-LS models (18 yr, 7 yr, and 20 yr, respectively), and the onsets of the old-growth stage also differed (86 yr, 68 yr, and 113 yr, respectively). This indicates that *C. japonica* forests can continue to accumulate

biomass longer than is currently predicted, and thus, forest management that incorporates longer periods is a possible option. Furthermore, although leaf and branch biomass tend to gradually decrease after the peak in the relatively early phase of forest development, as recognized in previous studies of *Picea abies* and *C. japonica* forests (Mund et al., 2002; Ogawa, 2018), the growth period for stem biomass accrual is much longer than those for whole-tree biomass (Table 2 and Fig. 3a and b). Importantly, from the perspective of wood production, the biomass accumulation pattern for the tree stems is a prime factor for determining logging plans to maximize forest stem volume per year (Nishizono, 2010; Nishizono et al., 2008), and logging practices with 45 yr intervals are the most rational at the national level, though in practice, local-specific rotation periods should be applied for each region according to the present results (Table 2).

The reasons why the NFI-LS model differs from the YT model are as follows: 1) the lack of data on old-aged forests in original YT data, 2) improvement in the forest growth environment in recent decades, and 3) a decline in timber demand in recent decades (Egusa et al., 2020). In the 1960s, when the forest survey was conducted to generate the yield tables, most *C. japonica* forests were young, and few old-aged forests existed. Accordingly, forest biomass in the old-growth forests was likely estimated by extrapolation, which introduced substantial uncertainty. There have also been suggested positive effects of environmental changes on forest growth in recent decades including the roughly 100 ppm increase in atmospheric CO<sub>2</sub> concentration since 1960 (IPCC, 2023) enhancing carbon assimilation in plants (McMahon et al., 2010; Ueyama et al., 2020), the rise in nitrogen deposition into forest ecosystems (Morino et al., 2011), and the lengthening of the growing season of plants within a year owing to global warming (Begović et al., 2023; Fang et al., 2014; McMahon et al., 2010). Furthermore, the declining utilization of forest resources and importing of wood has allowed forests to maintain woody biomass accrual with limited impact from forestry practices (Jørgensen et al., 2021; Lin et al., 2018; Nishizono, 2010).

The NFI3 model of Egusa et al. (2024) somewhat overcame the aforementioned three factors because it used the recently acquired NFI3 data representing forest metrics from 2009 to 2013. However, the present study indicates that even the NFI3 model may underestimate carbon density in comparison to the NFI-LS model. This model distinction is explicitly attributed to integration of the LS data, which includes well-developed mature forests. Notably, it implies that the NFI survey, conducted at 4 km grid points across the Japanese archipelago, does not effectively reflect elite old-aged forests with high growth capacity. To exploit the full potential of carbon accumulation in current *C. japonica* forests in the mature stage, we must take intensively managed forests into consideration through full stand maturity. Integration of data for such elite old-aged forests from the literature survey extended the range of stand age and reduced uncertainty caused by the extrapolation. The present meta-analysis demonstrates the importance of old-aged forest data for prediction of overall forest growth patterns in the future (Ciais et al., 2008; Luyssaert et al., 2008).

Another important addition to the NFI-LS model is the hierarchical structuring of spatial scales within the growth model to improve accuracy of the model estimation (Fig. 2 and Fig. S10). Some LS data provide consecutive plot data over several decades (e.g., Masaki et al., 2015), which enhances the robustness of fitting forest growth functions. Fitting the growth functions for each forest stand and adjusting error distributions based on the gamma distribution determines growth patterns more accurately than developing the model with defined functions only for large spatial scales (i.e., national and regional levels) (Barnett et al., 2023; Nishizono et al., 2014). This approach was achieved by using data from the consecutive plots present in both NFI3 and NFI4, which are of higher quality than the previous NFI data. Fitting models for each stand enabled us to avoid misinterpretation of growth patterns owing to variance among forest stands caused by unknown factors. Hierarchical models are useful for the meta-analysis of data with hierarchical structures, such as a broad range of spatial scales from individuals to regional

or national categories (Zhu et al., 2018). Notably, although hierarchical models using non-linear functions seem complex, a Bayesian approach is a powerful option to estimate their parameters, and thus, their widespread use is predicted to elucidate complex and comprehensive mechanisms of ecological systems.

We acknowledge that the NFI-LS model did not explicitly account for the effects of forestry practices because field surveys for NFI were implemented without consideration of the forest history. However, management factors will be important for further refinement of the growth models. For example, some forest plots have experienced forestry practices such as thinning, while others have not, potentially leading to large differences in growth and stand biomass accrual. Although it is unclear to what extent such practices affect growth models, there are several possibilities. The first one is that carbon density decreases temporarily after thinning, and the carbon accumulation rate is negative between the periods before and after thinning. In fact, some negative values in the accumulation rate were calculated by comparing the NFI3 and NFI4 data in the consecutive plots (Fig. S4). In contrast, immediately after thinning, the growth environment of the remaining trees improves and carbon assimilation increases (Kunisaki et al., 1999; Lin et al., 2018; Nishizono, 2010). Thinned forests deviate from the original course of the growth pattern and take time to recover carbon stock (Nishizono et al., 2008), or the maximum capacity for carbon density may decrease permanently (Jørgensen et al., 2021; Lin et al., 2018). Importantly, such situations can be caused directly by artificial phenomena, such as thinning, and by disturbance owing to the occurrence of abnormal weather events in recent years (Seidl et al., 2017). In natural and old-growth forests, survival capacities such as shade tolerance of seedlings and sub-canopy trees can be a key factor that maximizes the potential of carbon accumulation and recovery from gap occurrence. To predict forest development with consideration of tree mortality resulting from self-thinning and natural disturbance, an individual-based model assuming individual tree biomass and stand density would be useful. Growth functions at an individual tree level should be integrated into forest growth models to evaluate carbon dynamics flexibly in response to significant disturbance.

Climate change and human activities may also influence forest development patterns. Extreme climatic events are expected to intensify for the next several decades (Elsner et al., 2008; Hirabayashi et al., 2013), and wood demand on the international market may affect its supply from each country. To adjust to such issues, forest growth functions for *C. japonica* and other important forest types should be updated. The motivation to renew yield tables for biomass estimation has increased (Shimada, 2010). Repeating NFI-type surveys across many countries would provide valuable information to clarify and predict changes in forest resources (Barnett et al., 2023; Chen et al., 2022; Egusa et al., 2020; Molina-Valero et al., 2021; Ols et al., 2020; Repo et al., 2021; Zhu et al., 2018). Re-evaluation of forest resources and growth characteristics is feasible so long as NFI surveys are sustainably conducted in the future.

#### 4.2. Geographical variation in growth of *C. japonica* forests

Significant geographical variation in the growth characteristics of *C. japonica* forests (Figs. 4 and 5) may be attributed to the unique environmental diversity of the Japanese archipelago (Fig. S1). Environmental gradients caused by climates and geographical features range widely across Japan and regulate forest development in each region (Nakao et al., 2022; Nishizono et al., 2014). The Japanese archipelago is distributed over a 15° latitudinal range, leading to broad variation in temperatures. Additionally, the northeast monsoon and the warm ocean current influence the climate, and these factors result in two distinct climates represented by the Sea of Japan side and the Pacific Ocean side in Japan, where mountains dominate (Maejima, 1967; Uemura, 1989). Such strong contrast leads to significant relationships between growth characteristics and environmental factors (Nishizono et al., 2014). Using

data from the 1st national forest inventory (NFI1), Nishizono et al. (2014) showed that maximum stand height and age relationships differ depending on the regional climate. Specifically, in regions that experience low temperatures, heavy snowfall, low solar radiation, and low precipitation in summer, forests have a low growth rate in the initial growth phase but reach a higher maximum stand height. In contrast, in regions with the opposite climatic conditions, forests grow relatively rapidly in the initial phase but attain a low maximum height. The former belonging to the Sea of Japan area is called “Ura-sugi”, while the latter belonging to the Pacific Ocean area is called “Omote-sugi”. Assuming positive relationships between maximum stand height and forest carbon density, the present results might support these previous findings. In the NFI-LS model, the high maximum mean carbon density in the southern Tohoku and Kanto regions reflects the growth characteristics of Ura-sugi, whereas relatively rapid growth rates and earlier maturity in Kyushu and Wakayama reflects the characteristics of Omote-sugi (Nishizono et al., 2014). In Europe, it has been suggested that summer precipitation has positive effects on the radial growth trends of trees based on tree-ring measurements (Ols et al., 2020), and warmer temperature in winter positively influences tree growth of *P. abies* in southern parts of its natural distribution (Suvanto et al., 2016). Given that the effects of global warming on growth environments have been observed in Japan (Japan Meteorological Agency, 2024), understanding of the variation in carbon accumulation patterns among local regions with environmental factors is needed.

It is possible that both environmental and genotypic factors contribute to the geographical variation in growth characteristics of *C. japonica* forests. Although we did not design an analytic approach that combines growth characteristics with these factors, local environmental factors may affect forest growth. However, the factors that control the high maximum carbon density in the southern Tohoku and Kanto regions are unclear. As Nishizono et al. (2014) indicated, a multivariate analysis will be required to elucidate the controlling factors. Given that the NFI data include both natural and artificial forests, the influences of genotypic differentiation among natural forests (Tsumura et al., 2020) and of cultivars in plantation forests, as well as different planting techniques used in plantations cannot be ignored. In addition, even within the same mountain and watershed area, forest growth is affected by microtopography (Enoki et al., 2020; Nakao et al., 2022; Tange and Ge, 2020), which complicates the light, water, and nutrient conditions differentiating individual tree growth depending their shade and drought tolerance.

Differences in forest growth patterns with geographical variation suggest that region-specific optimization of harvest periods and forestry practices is desirable (Kunisaki et al., 1999; Nishizono, 2010; Nishizono et al., 2008). For example, forests that undergo rapid growth in the initial stage in Kyushu should be cut earlier than in other regions, whereas forests with a high maximum carbon density can be exploited for production of large-diameter trees. Improvement in wood production efficiency will be expected by consideration of the variation in forest growth characteristics among regions and optimization of forest management.

#### 4.3. Prediction of forest carbon stock of *C. japonica*

Capturing how forest biomass accrual changes with stand age is fundamental to prediction of future forest carbon stocks (Barnett et al., 2023; Zhu et al., 2018). The present study predicted the *C. japonica* forest area and carbon stock over the next 100 years based on different data sources and obtained distinct estimates with each data set (Fig. 6). To provide a constant supply of wood production every year under the current reforestation rate, the estimation based on the YT model (Case 1.1) concluded that a large percentage of the forest area will disappear by the end of this century (Fig. 6a). In contrast, the simulation with the NFI-LS model under the same management scenario (Case 2.1) indicates a reduction in forest area lost by half of that predicted with the YT

model. Thus, underestimation of forest carbon density (with the YT model) can overestimate the reduction in forest area and available carbon stock and further hinder appropriate forest management for wood supply.

The carbon stock in forests in 2022 based on the NFI-LS model was estimated to be 756.6 TgC, which is much higher than that (approximately 622 TgC in 2011) estimated based on the NFI3 model by Egusa et al. (2024). Surprisingly, in Case 2.0 assuming no management, the carbon stock of *C. japonica* forests across Japan will exceed 1000 TgC in 2100, which indicates that *C. japonica* forests have the capacity to accumulate approximately 300 TgC by 2100. Although, as Case 1.0 indicates, *C. japonica* forests have been considered to have little potential to accumulate carbon and to be of harvesting age, the management plan might require reconsideration. When using the current cut volume and reforestation rate (Case 2.1), the carbon stock was predicted to increase for several years but thereafter decrease until 2100. However, when assuming a reforestation rate of 100 % (Case 2.2), the carbon stock was predicted to remain stable or increase slightly for the entire period. This scenario enables continuation of the wood supply while maintaining forest carbon resources. The present results suggest that the *C. japonica* forests of Japan have strong potential to accumulate more carbon resources than previously predicted and that sustainable use of wood resources can be achieved by appropriate forest management.

The Japanese government has indicated that it aims to achieve a domestic supply of timber that accounts for more than 50 % of national needs which would necessitate increasing domestic timber supply from 31 Mm<sup>3</sup> in 2019 to 42 Mm<sup>3</sup> in 2030 (Japan Forestry Agency, 2011, 2021). In addition, the government has set a goal to become a carbon-neutral country, which offsets greenhouse gas emissions by their absorption within the country, by 2050 (Japan Forestry Agency, 2023a). Given that *C. japonica* is the most important species in the timber industry in Japan, the present findings provide positive scientific evidence regarding the feasibility of the current governmental plans. Assuming 28.3 Mm<sup>3</sup> yr<sup>-1</sup> as the annual cut stem volume in *C. japonica* forests, only two-thirds of the annual increment in stem volume is used currently. Therefore, *C. japonica* forests have sufficient growth capacity to supply additional wood to improve the timber self-sufficient rate. It is recommended that the government should base future decisions on these findings to promote sustainable forest supply and resource management.

Japan contains one of the largest forest carbon pools in east Asia owing to the high ratio of the forest to non-forest area (Fang et al., 2005). In particular, *C. japonica* forests have the largest carbon stock among all forest types (Egusa et al., 2020), and thus, predicting the carbon stocks in *C. japonica* forests largely influences the carbon stock estimate in Japan's total forests. According to the present results, *C. japonica* forests show a strong growth capacity to accumulate substantial carbon even in old-aged stands. Although we cannot draw a direct comparison because necromass was not included in the present estimates, the maximum carbon density seems to be higher than that of major broadleaved forests and some coniferous forests and is considered to be comparable to that of fir and spruce forests in the United States (Barnett et al., 2023). Further, the maximum carbon density may be approximately twice that of Norway spruce (Mund et al., 2002; Pretzsch et al., 2014) and boreal forests (Repo et al., 2021). Construction of carbon offset systems through carbon credits has been promoted worldwide (Badgley et al., 2022; Ellerman et al., 2016; Japan Forestry Agency, 2023a; Michaelowa et al., 2023). In Japan, annual CO<sub>2</sub> absorption in forests is estimated based on stand age classes as a simplified procedure. The present study implies that CO<sub>2</sub> absorption in each stand age class may be higher than expected so far and that re-evaluation of forest carbon density with age will accelerate carbon credit trading. To maximize the benefits from forest resources, optimization of forest management by reference to region-specific forest growth characteristics, including shade and drought tolerance of *C. japonica*, and improvement in the reforestation rate are essential factors in maintaining wood supply and forest carbon resources. In future studies,



additional forestry parameters, such as harvest period, yield stem volume, and reforestation rate, should be considered to determine the best forestry practices for optimal forest management. Prediction of carbon stock in forest ecosystems is fundamental for forest administrators and political decision-makers to achieve a carbon-neutral society.

## 5. Conclusions

The growth model for *C. japonica* forests based on the most recent NFI and LS data (NFI-LS model) differed significantly from the model based on outdated yield tables (YT model), suggesting that the maximum carbon density was 1.8 times higher and the stand age at the onset of the old-growth stage was 1.3 times older. Thus, the growth potential of *C. japonica* forests has been underestimated in recent decades owing to the lack of old-aged forest data and conflicts between previous and current growth environments. The growth model used for forest resource predictions and management should be updated with a suitable data set and appropriate model design because it may be affected by ongoing climate changes and human activities.

Geographical variation in the growth model parameters was revealed with the hierarchical Bayesian model framework. In particular, a parameter representing the maximum forest carbon density varied substantially among regions, suggesting general trends of higher and lower accumulation capacity in eastern and western Japan, respectively. The unique environmental diversity of Japanese archipelago results in geographical variation in the forest growth characteristics, and therefore, region-specific optimization of forestry practices is desirable to maximize forest carbon accumulation and wood production.

Simulations for current and future carbon stocks of *C. japonica* forests based on the present growth model (NFI-LS model) suggested positive results. *C. japonica* forests across Japan can accumulate more than 1000 TgC by 2100, assuming the scenario of no forest management (Case 2.0). Even if the current annual wood cut volume is maintained, carbon stocks in *C. japonica* forests would remain stable at more than 750 TgC throughout the present century under a consistent forest area (Case 2.2). In conclusion, *C. japonica* forests have strong potential to accumulate additional carbon resources, and sustainable use of wood resources can be achieved by appropriate forest management. The present findings provide supporting evidence to enhance the value of *C. japonica* forest resources across Japan and increase the feasibility of a carbon-neutral society in the country.

## CRedit authorship contribution statement

**Ryo Nakahata:** Writing – review & editing, Writing – original draft, Funding acquisition, Formal analysis, Data curation. **Tomohiro Egusa:** Writing – review & editing, Data curation. **Tomo'omi Kumagai:** Writing – review & editing, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2025.126981>.

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## Data availability

Data will be made available on request.

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