

Effects of stand factors on tree growth of Chinese fir in the subtropics of China depends on climate conditions from predictions of a deep learning algorithm: A long-term spacing trial

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ABSTRACT

Stand and climate related variables are the main driving forces controlling individual tree growth. Two machine learning algorithms called deep learning and random forest were used to explore how annual diameter growth varied with stand and climatic variables. Data was obtained from a long-term spacing trial of Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.) plantations in four provinces of southern China. Results from model comparisons showed the deep learning model with 8 hidden layers and 90 neurons in each hidden layer achieved the best performance, and the RF model ranked 4th among 9 selected models. In addition, sensitivity analysis showed that individual tree growth increased with an increase in Gini coefficient, while growth decreased with an increase in stand age (A) and the basal area of larger trees (BAL). The relationships between diameter growth and summer mean maximum temperature (SMMT), as well as winter mean minimum temperature (WMMT) and annual precipitation (AP) were not constant, which depended on the range of values of each climate factor. BAL had the greatest influence on diameter growth among all the variables. From an interaction analysis, we found that climate factors exacerbated the negative effects of competition on growth. Climate change promoted the growth of younger trees but restrained the growth of older trees. With climate variables considered, tree growth under high and middle stand structural heterogeneity were similar, and observably higher than that with low stand structural heterogeneity. Positive influences of climate tended to promote tree growth under lower competition and older individuals were more vulnerable to WMMT changes. Our findings enhance our understanding of the mechanisms driving individual Chinese fir growth in southern China in the face of future climate uncertainty.

1. Introduction

Forests act as the largest component of the terrestrial carbon pool, serving a key role in the process of the global carbon cycle and mitigation of global climate change (Zhang et al., 2019). Tree growth plays an important role in determining forest structure and dynamics (Wyckoff and Clark, 2002). Stand and climatic factors have long been recognized as main driving factors to determine spatiotemporal variation patterns in tree growth (Copenhaver-Parry and Cannon, 2016; Devi et al., 2020). However, given the complexity of the interactions and the spatial and temporal scales involved in dealing with trees, it is meaningful to predict

tree growth accurately and explore the growth mechanism.

Among the stand factors, competition is generally considered the most important factor affecting tree growth, and is defined as the process by which two or more individuals obtain resources from a common resource that may be limited in supply (Kunstler et al., 2011; Ford et al., 2017). This includes aboveground competition for available photosynthetic radiation and belowground competition for water or nutrients (Prior and Bowman, 2014). Most research has found the negative effect between forest growth and competition (Mainwaring and Maguire, 2004; Ford et al., 2017; Navarro-Cerrillo et al., 2020). Meanwhile, Calama et al. (2019) holds the opinion that competition plays a dual

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role: (i) competition determines the availability of a subject tree to limited resources due to the neighboring effect, which further defines resource uptake patterns and spatial variations during forest succession; and (ii) competition regulates the response of tree growth to climatic or other site variables during forest succession. As an example, for the latter one, Jiang et al. (2018) concluded that negative plant-plant interactions such as competitive effects would be intensified in stressed environments. In contrast, a widely cited stress gradient hypothesis (Callaway and Walker, 1997) postulated that the association of neighbors among stand could be transformed from negative to positive relations under more unfavorable conditions. Calama et al. (2019) explained that the contradiction about these opinions can be understood, for the effect of high competition on tree growth could be shifted from negative to positive in a short-term if we assume that competition is responsible for long-term growth trends along resource availability gradients.

Stand structure is another important factor driving tree growth, but many previous studies had overlooked its effect (Forrester and Bauhus, 2016; Kweon and Comeau, 2019). Stand structure can influence forest growth by causing discrepancies in competition intensity and resource utilization among individuals from the same forest (Luo and Chen, 2011). Morin (2015) and Forrester et al. (2018) found that a heterogeneous stand structure might promote forest growth by enhancing light capture. Stand structure index was often defined as a measurement of stem diameter distribution (McElhinny et al., 2005) or spatial heterogeneity (McRoberts et al., 2008). There are many indicators to describe the size inequality including the Shannon, Simpson indices (Sterba and Ledermann, 2006), and size variation coefficient (Staudhammer and Lemay, 2001). However, recent studies have emphasized the strength of another index: the Gini coefficient for measuring the structural diversity (Zhang et al., 2020a; Wang et al., 2021). During forest succession, stand structure is considered as an important factor for predicting forest dynamics (i.e., mortality, productivity, and growth) since it gives rise to a size hierarchy and can affect competition dynamics between individuals in a stand (Flake and Weisberg, 2019; Forrester, 2019). Besides, previous studies suggested that age and site condition also have fundamental influences on forest dynamics (Guo and Ren, 2014; Zhang et al., 2019).

While prior research has commonly assessed the effect of competition intensity and other stand variables on forest growth and biomass (Huang et al., 2013; Curto et al., 2021), the potential impact of climatic variables has not received the same considerations. When climate is not accounted in exploring drivers of tree growth, an implicit assumption is that the climatic situation is stable (Crookston et al., 2008). Despite short-term variability, there exist no changes in long-term trends and inter-annual variability in environmental drivers will be compensated in future years. Without doubt, under the background of climate change uncertainty, these assumptions can hardly hold true (Calama et al., 2019). Several cases of climate influencing forest dynamics have been extensively explored (Ford et al., 2017; Liang et al., 2019; Oboite and Comeau 2019). Thus, in this study, we incorporated both climate variables and stand characteristics in exploring individual tree growth.

Machine learning techniques have been widely used and proved to be powerful tools in the field of forest management (Nunes et al., 2016; Wu et al., 2019), which could provide new solutions dealing with big data compared with traditional statistical methods (Christin et al., 2019). In particular, Artificial Neural Network models (ANN) performed well in predicting individual tree and forest growth (Ramazan et al., 2013). Numerous studies related to ANN have been employed for modelling tree or stand level attributes like tree height (Özçelik et al., 2013), tree volume (Lacerda et al., 2017), tree mortality (Bayat et al., 2019), stand biomass prediction (Nandy et al., 2017). The Deep Learning Algorithm (DLA) stands out from ANN as a more flexible artificial intelligence technique used in multi-dimensional data and in data mining (Ercanli, 2020). This artificial intelligence technology is aimed at achieving more accurate results by working like a human brain. It has the ability to learn and make decisions effectively and its complex

structures can contain 3–10 or more hidden layers and hundreds of neurons. However, we have found few studies that used the DLA method for modelling annual diameter growth while considering both stand and climate factors. The random forest (RF) algorithm is another nonparametric machine learning algorithm that performs well in classification and regression (Breiman, 2001). Previous studies suggested that the RF approach could generally produce results with higher accuracy and predictive abilities than other machine learning algorithms, such as ANN, boosted regression trees (BRT), K-nearest neighbor (KNN), and support vector machine (SVM) as well as traditional parametric algorithms (Weiskittel et al., 2011; Görgens et al., 2015; Kilham et al., 2019; Schratz et al., 2019; Zhao et al., 2019).

Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.), a native species with a capacity for fast growth, is widely planted in subtropical China (Zhang et al., 2013). Due to its excellent timber properties such as straight shape and high resistance to decay, Chinese fir has become one of the most important tree species in terms of wood production. Wang et al. (2012) reported that the carbon stock of Chinese fir plantations reached 238.5 Tg C during 2004–2008, occupying 4.32% of the total forest carbon in China. Therefore, an accurate prediction of tree growth and exploration of growth drivers of Chinese fir plantations would have significant implications for understanding forest dynamics in the face of future climate change. The aims for this research study are: (1) to model tree growth of Chinese fir with stand and climatic variables by using the DLA and RF methods; (2) to investigate whether the DLA or RF methods are more suitable for tree growth prediction; (3) to explore the specific impact of these stand and climatic variables on tree growth and rank their relative contributions; and (4) to disentangle the tree growth variation under different interactive effects of stand and climatic conditions.

2. Materials and methods

2.1. Study sites and data

In this study, the data were derived from permanent sample plots of Chinese fir stands, planted with bare-root seedlings and distributed at four provinces in subtropical China. The plantation establishment year was 1981 in Jiangxi, and 1982 in Fujian, Guangxi, and Sichuan province. Fujian, Jiangxi, and Sichuan provinces have a middle-subtropical climate while Guangxi province is characterized by a southern-subtropical climate.

Five plantation spacings were replicated three times for a total 15 plots in each province: spacing level A (2 m × 3 m, 1667 trees/ha), B (2 m × 1.5 m, 3333 trees/ha), C (2 m × 1 m, 5000 trees/ha), D (1 m × 1.5 m, 6667 trees/ha), and E (1 m × 1 m, 10,000 trees/ha). Every plot comprised a dimension of 20 × 30 m. Two rows of trees were set around each plot as a buffer to reduce interference. In Fujian, the field measurement was implemented every year from 1985 to 1990, and every 2 years from 1990 to 2010; In Jiangxi, the field measurement was implemented every year from 1985 to 1989, and every 2 years from 1989 to 2007; In Sichuan, the field measurement was implemented every year from 1985 to 1995, and every 2 or 3 years from 1995 to 2012; In Guangxi, the field measurement was implemented every year from 1990 to 1995, and every 2 years from 1995 to 2012. The field-measurements were carried out in the winter. All trees in a plot taller than 1.3 m were tagged and the corresponding DBH were measured. Fifty more trees were randomly selected to measure the height in each plot, and the average height of 6 tallest trees was calculated as the dominant height (Hd).

2.2. Stand factors

The annual mean diameter growth (ADG, in cm year^{-1}) was selected as a representative of individual tree growth and calculated as:

$$ADG = \frac{DBH_{i,2} - DBH_{i,1}}{Y} \tag{1}$$

where $DBH_{i,1}$ and $DBH_{i,2}$ (in cm) represents the diameter at breast height of i^{th} alive tree at the time of the first and the second measurement period, respectively; and Y denotes the time interval (in years) linking two successive measurements.

Four major categories of stand characteristics affecting tree growth were considered in this study including stand age (A), competition, site condition, and forest structural heterogeneity. Stand dominant height (Hd) usually serves as a measurement that represents site condition (Zhu et al., 2019). Several competition indices were utilized including: number of trees per hectare (N), stand basal area per hectare (Ba), quadratic mean diameter (Dq), the basal area of larger trees (BAL), stand density index (SDI), and relative diameter (RD = D/Dq) (Pretzsch and Biber, 2010; Zhang et al., 2017). SDI was defined to represent the relative component of live stocking according to individual size (Stage, 1968). Gini coefficient defined stand structure by represent structural heterogeneity and calculated using the tree DBH in a plot. A smaller value of Gini indicated a more homogeneous stand structure. The “ineq” package was used to calculate Gini coefficient in R (Zeileis, 2014).

We divided the stand age, Gini coefficient, and the basal area of larger trees (BAL) into three groups (Table 1) to analyze the effects of stand variables on the annual diameter growth (ADG). Table 2 provides the summary statistics of ADG and stand variables in each province.

2.3. Climate data

We used ClimateAP program to investigate the effect of climatic variables on diameter growth of Chinese fir plantations using climate data to provide a spatially interpolated estimation of climate data based on the site’s geographical attributes (Wang et al., 2012). Reports have concluded that precipitation and temperature are the fundamental climate variables affecting forest growth (Ford et al., 2017; Canham et al., 2018; Oboite and Comeau, 2019). Ten climate variables were selected as candidate dependent variables to fit tree-level growth model including annual precipitation (AP), mean annual temperature (MAT), winter mean minimum temperature (WMMT), mean coldest month temperature (MCMT), degree-days below 0 °C (DD0), degree-days above 5 °C (DD5), mean warmest month temperature (MWMT), summer mean temperature (SMT), summer mean maximum temperature (SMMT), and annual heat-moisture index (AHM) (Table 3).

To explore the main factors driving tree growth, 9 stand variables and 10 climatic variables were chosen to model the annual diameter growth. The variables were chosen by referring to previous studies (Galván et al., 2014; Ford et al., 2017; Jiang et al., 2018). In order to avoid the influence of multicollinearity among variables on model fitting, the variance inflation factor (VIF) test was used to screen candidate variables. In general, multicollinearity is eliminated among variables when $VIF < 5$ (Zhang et al., 2020a).

2.4. Deep learning model

Deep learning is a novel machine learning algorithm, which originated from a method of initializing weights proposed by Hinton et al.

Table 1
The three groups of the basal area of larger trees (BAL), age (A) and Gini coefficient (GC).

Stand variables	Groups		
Age (year)	Yong forest (A < 10)	Middle-aged forest (10 ≤ A < 20)	Mature forest (A ≥ 20)
BAL (m ² ha ⁻¹)	Low (Top 20% of BAL)	Middle (Medial 60% of BAL)	High (Bottom 20% of BAL)
Gini coefficient (-)	Small (GC < 0.1)	Middle (0.1 ≤ GC < 0.2)	Large (0.2 ≤ GC)

Table 2
Summary statistics of stand and tree characteristics by province.

Study sites	ADG		A		Hd		N		Ba		Dq		BAL		SDI		RD		Gini	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Fujian	0.90	0.42	15.45	7.50	11.28	5.52	6069	2670	38.19	22.08	9.29	4.50	23.44	18.58	1518	599	0.95	0.25	0.14	0.032
Guangxi	0.83	0.37	17.91	5.31	13.77	2.99	4481	2167	34.63	7.07	10.78	2.74	24.74	11.28	1322	297	0.96	0.24	0.14	0.017
Jiangxi	1.03	0.49	13.85	9.81	10.42	3.92	6100	2549	35.21	17.34	8.93	3.55	17.31	15.44	1374	640	0.96	0.26	0.16	0.029
Sichuan	0.96	0.35	14.43	6.95	10.66	3.84	5786	2577	27.56	11.81	8.24	2.95	22.06	11.22	1150	467	0.99	0.26	0.15	0.027
Total	0.92	0.47	14.72	7.07	11.18	4.50	5798	2603	34.06	17.35	9.10	3.73	21.79	15.37	1236	867	0.96	0.25	0.15	0.028

Note: ADG: annual diameter growth (cm year⁻¹); A: stand age (year); Hd: stand dominant height (m); N: number of trees per hectare; Ba: stand basal area (m² ha⁻¹); Dq: stand quadratic mean diameter (cm); BAL: the basal area of larger trees (m² ha⁻¹); SDI: stand density index; RD: relative diameter (cm); Gini: Gini coefficient of tree size (diameter) diversity.

Table 3
Summary statistics of climatic variables by province.

Study Sites	MAT		MCMT		AP		AHM		DDO		DD5		SMMT		WMMT		SMT	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Fujian	18.84	0.45	28.18	0.68	1.03	1.763	210	16.55	1.74	1.46	0.63	5023	157	32.21	0.53	4.59	18.29	0.83
Guangxi	22.28	0.22	28.27	0.45	1.07	1.494	182	21.88	2.34	1.79	0.83	6237	78.96	31.80	0.46	12.24	22.77	0.37
Jiangxi	18.12	0.37	28.44	0.86	1.30	1.610	163	17.66	1.84	3.39	1.88	4791	115	32.14	0.80	4.21	17.53	0.60
Sichuan	18.40	0.35	28.09	0.90	0.84	1.187	106	24.10	2.19	1.50	0.56	4870	125	30.61	0.66	7.23	18.65	0.56
Total	18.95	1.36	28.25	0.79	2.42	1.532	280	19.55	3.73	1.85	1.57	5071	476	31.72	0.94	6.16	18.74	1.74

Note: MAT: mean annual temperature (°C); MCMT: mean warmest month temperature (°C); AP: annual precipitation (mm); AHM: annual heat-moisture index; DDO: Degree-days below 0 °C, chilling degree days; DD5: Degree-days above 5 °C, chilling degree days; SMMT: summer mean minimum temperature (°C); WMMT: winter mean minimum temperature (°C); SMT: Spring (Mar.-May) mean temperature (°C).

(2006). DLA has grown rapidly since its inception and shows excellent performance in various applications in recent time, such as speech recognition and image classification. Thus, DLA has become the most widely used algorithm in artificial intelligence (AI). The artificial neural network (ANN) usually consists of an input layer, hidden layer (one or two as depends), and an output layer in the model structure. Originated from the ANN model, the DLA possesses an input layer, an output layer, and a more complex model structure by comprising many (3–10 or >10) hidden layers. Therefore, the DLA model can process high-dimensional data accurately and efficiently.

DLA methods were used for modelling annual diameter growth related with stand and climate variables in this study so as to achieve high accuracy of tree growth prediction. Furthermore, deep learning models have several key attributes that affect model performance: number of hidden layers and neuron numbers in each hidden layer, transfer function choice (between the two neurons, the transfer function takes the input signal and transforms it, and the transformed signal greater than the weight will be allowed to pass), and some parameter tuning. From our preliminary analyses on fitting results, the “Rectifier” function was chosen as the transfer function constitutes the DL regression model, which is consistent with the selection process of Ercanli (2020). Adaptive learning rate algorithm (ALRA), a method for optimizing model parameters and improving model self-learning from training data, was used to train the DLAs (Zeiler, 2012), with parameter *rho* and *epsilon* set to the default value to describe the initial rate of ALRA at 0.99 and 1×10^{-8} , respectively. The *epochs* parameter (defined as the number of iterations accepted in the training network) was set to 800 in model construction as this value achieved the best predictive results in various neural network analyses. The loss function choice (defined as a function seeking the minimum gap between observed and predicted values in training the DLAs) was set to the “Automatic” function, while the Gaussian distribution model based on the mean squared error was used for our regression objective.

Apart from these parameters of DLA, two additional parameters required special attention to obtain the best parameter estimation: the number of hidden layers in the network and the number of neurons existing in these hidden layers. In training DLAs, we set the hidden layer at eight levels from 3 to 10 and the number of neurons in each hidden layer was set at 10 (10, 20, 30, 40, 50, 60, 70, 80, 90 and 100 neurons). Consequently, 80 different DLA models were developed to predict annual tree diameter growth. The DLA models were constructed using *h2o* package based on R software (LeDell et al., 2021).

2.5. Random forest model

Except DLA models, random forest (RF) stands out as a nonparametric machine learning method which could be developed for both regression and classification (Breiman, 2001). In consideration of the strong performance of RF model in previous studies, RF algorithm was used as a regression model to fit tree growth with stand and climatic variables. RF works by creating a forest aggregated of decision trees, and each tree in the regression takes input from randomly selected subsets of the training data. Every decision tree in the random forest grows to its maximum without pruning till the end of the prediction has been reached decisively. The randomness of the random forest comes from the fact that the training samples of each decision tree are randomly selected by bootstrapping, and the attribute set of nodes splitting in each decision tree is also randomly selected.

RF has two main parameters that are most affected by parameter tuning: m_{try} (predictor numbers randomly chosen to split at each node in decision trees) and n_{tree} (decision tree numbers concluded in the random forest). The m_{try} was usually given its default value at one third of the number of all predictive variables (Yang et al., 2016). We set $n_{tree} = 1000$ as a replacement to minimize the model error during model development, as the default value of 500 has been shown to be incapable of stabilizing the model (Grimm et al., 2008).

2.6. Model performance evaluation

Five evaluation statistics were used to quantify the performance of each DLA and RF models and its ability to make accurate predictions, and included the coefficient of determination (R^2), the root-mean-square error (RMSE), the average of residuals (AR), the variance of residuals (VR) and the total relative error (TRE), which are listed as follows:

$$R^2 = \left\{ \frac{\sum_{i=1}^n (P_i - \bar{P})(O_i - \bar{O})}{\sqrt{\sum_{i=1}^n (P_i - \bar{P})^2} \sqrt{\sum_{i=1}^n (O_i - \bar{O})^2}} \right\}^2 \quad (2)$$

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (P_i - O_i)^2} \quad (3)$$

$$AR = \frac{\sum_{i=1}^n (O_i - P_i)}{n} \quad (4)$$

$$VR = \frac{\sum_{i=1}^n (O_i - P_i - \frac{\sum_{i=1}^n (O_i - P_i)}{n})^2}{n - 1} \quad (5)$$

$$TRE = \frac{\sum_{i=1}^n O_i - \sum_{i=1}^n P_i}{\sum_{i=1}^n P_i} \times 100 \quad (6)$$

where P_i and O_i represent the predicted and observed ADG; \bar{P} and \bar{O} indicate the mean values; and n denotes the total alive trees in a sample plot. The model with higher R^2 and lower $RMSE$, AR , VR and TRE usually reflects better performance. The model with the best comprehensive performance was selected for final prediction and the function to rank the relative importance for all retained predictors were based on the final model.

2.7. Sensitivity and interactive analysis

After the model comparison, ADG was predicted based on the final model. A sensitivity analysis was performed to explore the effect of independent variables on ADG through the *DALEX* package using R software (Biecek, 2018). On one hand, this procedure could provide the change of ADG of Chinese fir under the influence of a specific factor, while keeping other factors at their mean value. On the other hand, it is considered that the changes in tree growth are the result of multiple factors, instead of the accumulation of single factors. Therefore, how ADG changes under the interactive effect between stand and climatic variables is more worthy of exploration. In this section, we explored the changes of ADG under the interactions by using the *Random Forest* package in R software (Liaw and Wiener, 2002).

3. Results

We used annual diameter growth (ADG) as a measure of individual tree growth which ranged from 0.041 to 8.3 cm year⁻¹. Based on the VIF test, 6 variables were selected to develop the deep learning and random forest models including the basal area of larger trees (BAL), stand age (Age), Gini coefficient (Gini), and 3 climatic factors including summer mean maximum temperature (SMMT), annual precipitation (AP), and winter mean minimum temperature (WMMT).

3.1. Final model-Deep learning model

Based on the 6 variables which passed the VIF test, the fitting criteria of R^2 , RMSE, AR, TRE, and VR for the prediction results of 8 deep learning models and RF model are provided in Table 4 which represents the best performance models for each level of hidden layers. RF model did not obtain the highest accuracy (Table 4): $R^2 = 0.6509$, RMSE =

Table 4

The goodness-of-fit statistics (coefficient of determination (R^2), root mean square error (RMSE), average of residuals (AR), total relative error (TRE), and variance of residuals (VR) for the best predictive deep learning (DL) models under 8 levels of hidden layer and random forest (RF) model.

Hidden L	Neural	R^2	RMSE	AR	TRE	VR
3	70	0.5131	0.7105	0.0814	1.136	0.5753
4	60	0.5718	0.6524	0.0731	0.799	0.5279
5	60	0.5854	0.6383	0.0501	0.739	0.4950
6	80	0.5641	0.6691	0.0766	0.818	0.5518
7	60	0.6883	0.3913	0.0173	0.5248	0.3953
8	90	0.7332	0.3583	0.00919	0.2931	0.2019
9	70	0.6750	0.4114	0.0367	0.5578	0.4278
10	60	0.4647	0.7730	0.1104	1.238	0.6138
Random Forest model		0.6509	0.4693	0.0597	0.6375	0.4836

Note: Values in bold indicates the best performance.

0.4693, AR = 0.0597, TRE = 0.6375, and VR = 0.4836. RF ranked 4th among the 9 models. The model with 8 hidden layers and 90 neurons in each hidden layer achieved the best comprehensive performance, and represented the best predictive fitting results with $R^2 = 0.7332$, RMSE = 0.3583, AR = 0.00919, TRE = 0.2931, and VR = 0.2019, and further sensitivity and interaction analysis were carried out based on the prediction results of this final model. The other 7 models performed poorly in the evaluation phase, in which the model with 10 hidden layers and 60 neurons performed worst, with the following model results: $R^2 = 0.4647$, RMSE = 0.7730, AR = 0.1104, TRE = 1.238, and VR = 0.6138.

Based on the final model, the effect of BAL on ADG was the largest, followed by A (age), Gini, SMMT, WMMT, and AP (Fig. 1). In addition, the final model had values of $R^2 = 0.7332$ and RMSE = 0.3583 cm/year (Fig. 2).

3.2. The effects of stand variables on ADG

From the results of sensitivity analysis, 3 stand variables all showed significant influence on ADG, but the magnitude and direction of the influence were not completely consistent (Fig. 3). As the most influential variable, the relationship between BAL (competition intensity) and ADG was negative. While the other five variables were kept constant, BAL's influence on ADG ranged from 0.93 to 1.68 cm/year (Fig. 3A). The sensitivity analysis curve of Age and ADG was similar to that of BAL, and had an inverted "J" shape. Moreover, the relationship between Age and ADG could be divided into two parts: for the first, ADG decreased rapidly with the increase of Age ($5 \leq \text{Age} < 10$); and second, the value of ADG

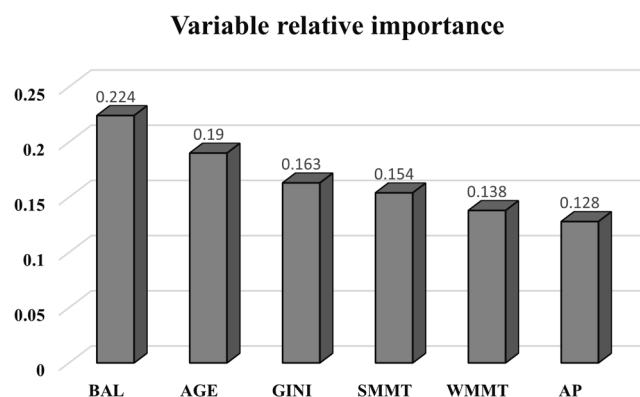


Fig. 1. Variable relative importance rank acquired from the final deep learning model, where variable importance was calculated as the relative proportion of each factor in model R^2 . These variables including the basal area of larger trees (BAL, m²ha⁻¹), age (A, year), Gini coefficient (Gini), summer mean maximum temperature (SMMT, °C), winter mean minimum temperature (WMMT, °C) and annual precipitation (AP, mm) explained 0.7332 of the diameter growth variation ($R^2 = 0.7332$).

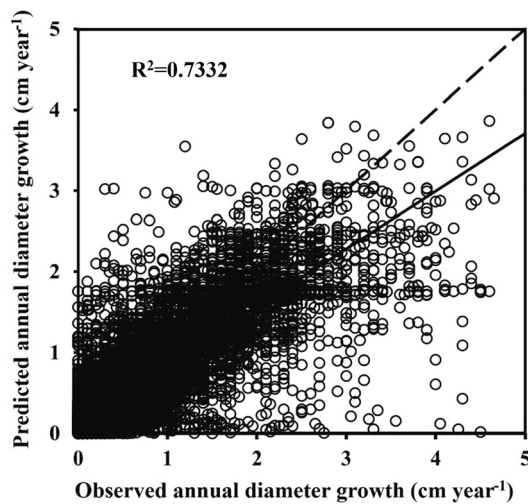


Fig. 2. Predicted and observed annual diameter growth. The solid line indicates the predicted value.

dropped slowly with further increase of Age (Age ≥ 10). The impact of Age on ADG ranged from 0.6 to 1.4 cm/year (Fig. 3B). In addition to BAL and Age, Gini (stand structure) is another stand variable that affects ADG greatly. The value of Gini under 0.13, and above 0.18 showed a gentle positive relationship with ADG, while a rapid growth of ADG occurs in $0.13 \leq \text{Gini} < 0.18$. The total range of ADG was 0.95–1.12 cm/year under the influence of Gini (Fig. 3C), while keeping other variables constant.

3.3. The effects of climate variables on ADG

Three climatic variables consisting of WMMT, SMMT, and AP were selected for model development (Fig. 1), and all showed great impact on individual tree growth. Overall, the influence of these three climate variables on ADG was dependent on a different range of values. On one hand, ADG decreased with increasing WMMT generally with several fluctuations in the curve, while the impact turned into a positive relationship between 9 and 10.9 °C clearly (Fig. 3D). On the other hand, ADG increased dramatically with the increase of SMMT within the range of 32–33.1 °C while decreased within the ranges of $30.7 < \text{SMMT} < 31.4$ and $\text{SMMT} > 33.1$ °C (Fig. 3E). As for the effect of annual precipitation (AP) on ADG, the sensitivity curve showed a similar pattern like SMMT. ADG increased with the increase of AP within the range of 1300–1650 mm and decreased with the increase of AP when $1100 < \text{AP} < 1300$ and $\text{AP} > 1850$ mm. Notably, a sharp decline of ADG happened around AP at 1700 mm followed by a sharp increase (Fig. 3F).

3.4. Climate influence on the relationship between stand factors and ADG

In general, the interaction curves were similar to the climate factor influence curves, but differences exist under the influence of stand variables. As the most influential factor on the tree growth, when we only consider the effects of BAL (competition intensity) on growth, the corresponding influence on ADG ranges from 0.93 to 1.68 cm/year (Fig. 3A). When taking climatic factors into account, we found that the peak value of ADG decreased from 1.68 to 1.48 cm/year, and the valley value decreased from 0.93 to 0.67 cm/year (Fig. 4; Fig. 3A). At the same time, we can clearly see that the difference of growth under middle and low competition intensity was significantly larger than that under middle and high competition intensity (Fig. 4).

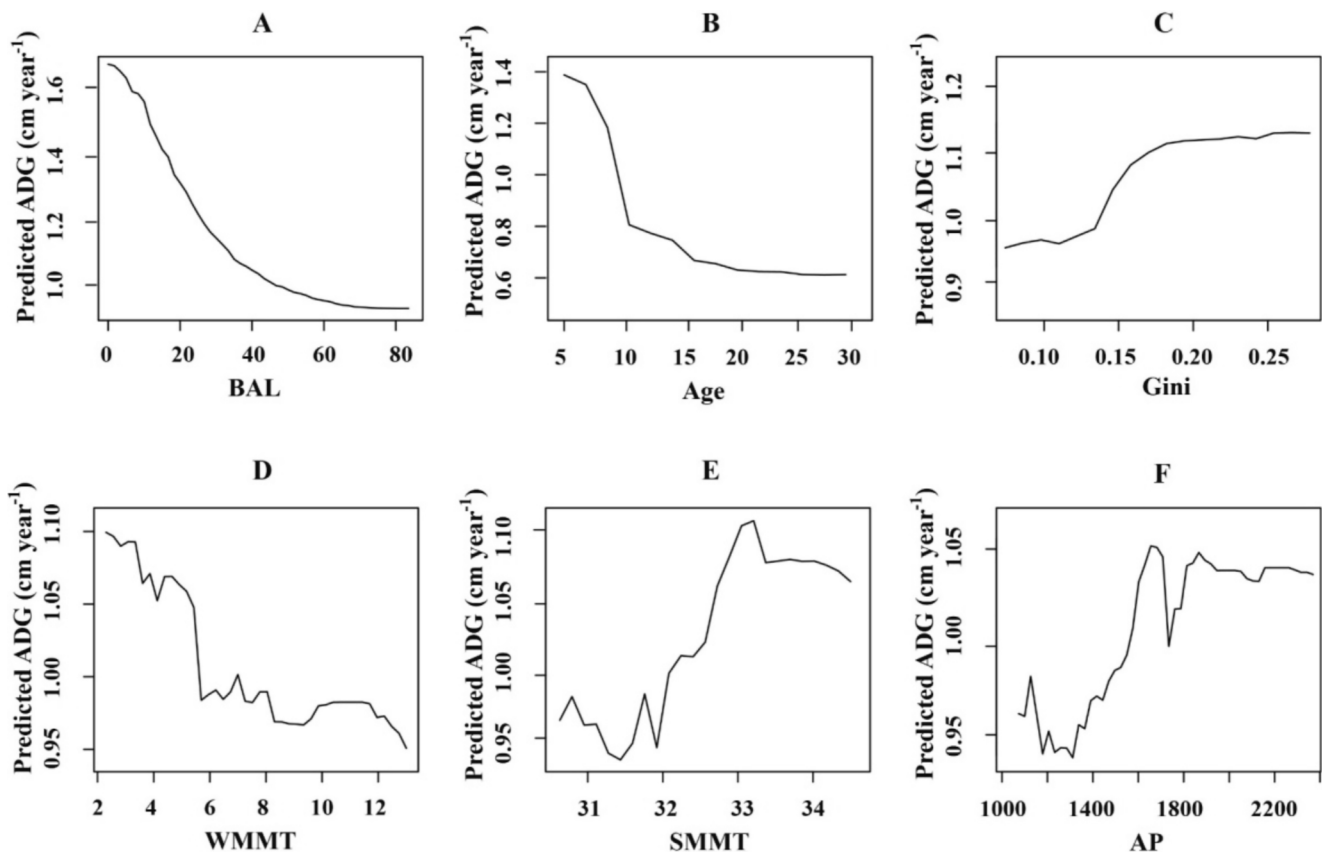


Fig. 3. Sensitivity analysis plot based on the predicted result from final deep learning model, showing the mean marginal influence of six explanatory variables the basal area of larger trees (BAL), age (A), Gini coefficient (Gini), winter mean minimum temperature (WMMT), summer mean maximum temperature (SMMT), and annual precipitation (AP) on annual diameter growth (ADG). Each graph represents the effect of variables on ADG, while the other variables were kept constant.

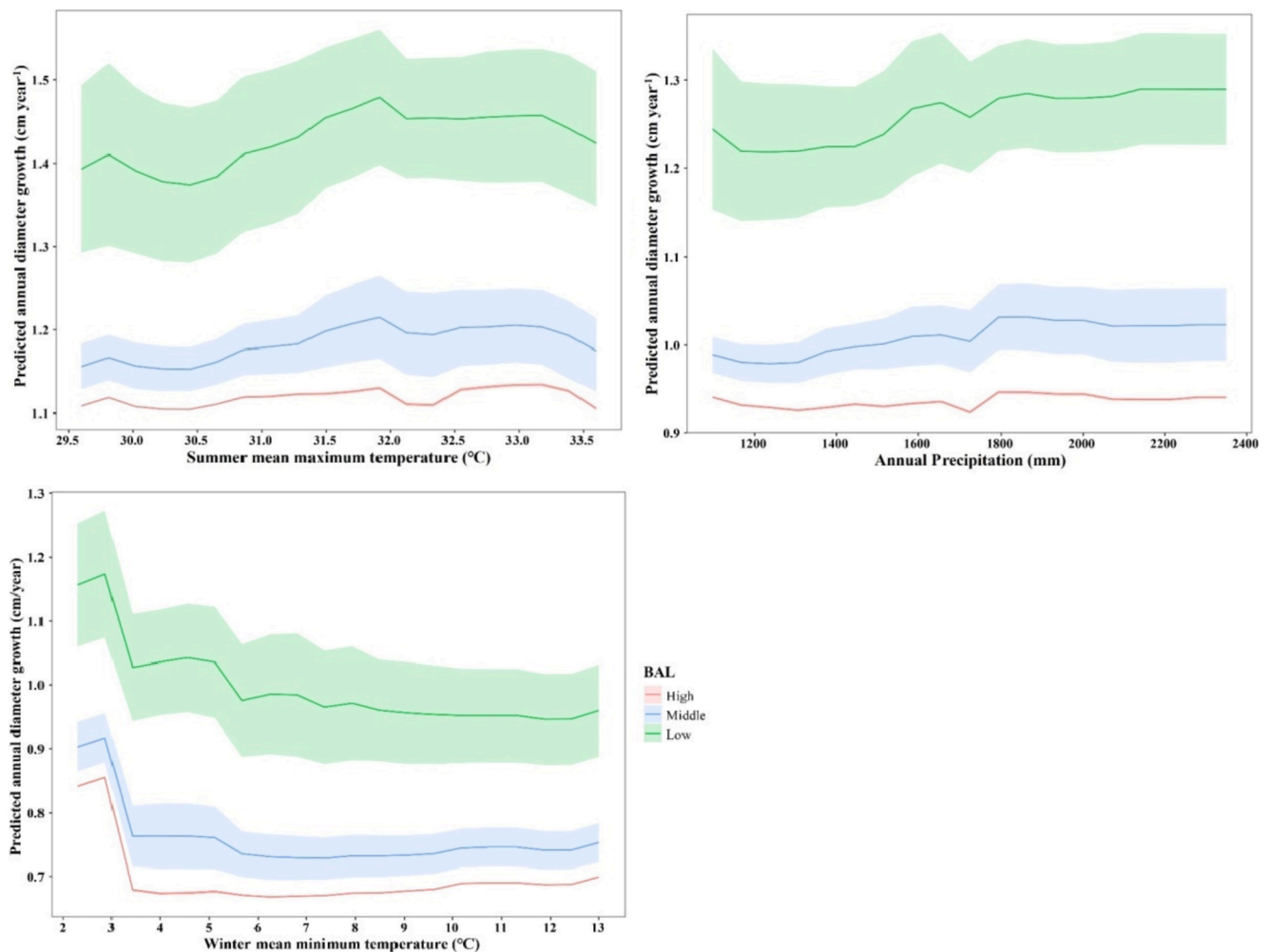


Fig. 4. Predicted annual diameter growth (ADG) from final deep learning model, and further analysis through random forest algorithm. Graphs demonstrated the interactive effect of basal area of larger trees (BAL) and three climatic factors on ADG when the other variables are kept at their average. Shaded areas represent a 95% confidence interval.

A similar pattern can be found in the interaction curve of Age (stand age) and climatic factors (Fig. 5). Young trees achieved the highest annual diameter growth, which was far more than the growth of middle-age trees under the same climate condition. The average growth difference was around 0.6 cm/year. Meanwhile, the difference of annual growth between middle-age and matured trees was small, and the mean growth difference under the climatic condition changes were nearly 0.05 cm/year (Fig. 5). The peak value of the three age groups increased from 1.40 to 1.55 cm/year, and the valley value decreased from 0.70 to 0.55 cm/year when taking climate factors into consideration (Fig. 5; Fig. 3B).

The results showed a positive correlation between Gini and ADG (Fig. 3C). Considering the effects of climatic variables, we found that there were small differences in tree growth between the stands with high and middle stand structure. The trees belonging to low stand structure forests always exert the lowest annual diameter growth (Fig. 6). The peak value of tree growth among all stand structure categories increased from 1.12 to 1.30 cm/year, and the valley value decreased from 0.95 to 0.77 under the influence of climatic factors (Fig. 6; Fig. 3C).

In addition, from the change of curves in the interaction diagrams, two more points could be concluded. Firstly, positive influences of climate conditions (SMMT and AP) tended to promote tree growth under low competition intensity, while negative relations with climate (WMMT) variables were more likely to decrease tree growth under high competition intensity (Fig. 4). Secondly, older trees were more likely to

be affected by climate conditions, which were reflected by a greater volatility in annual diameter growth when facing environmental variation. Most obviously, the negative effect of WMMT on old trees was significantly greater than that of young trees; however, the impact of WMMT on tree growth was negligible among all age categories when WMMT > 6 °C (Fig. 5).

4. Discussions

4.1. Model comparison

Based on 6 variables (i.e., BAL, Age, Gini, SMMT, WMMT, and AP), the RF model and 80 deep learning models were constructed for fitting annual diameter growth (ADG), in which the DL model with 8 hidden layers and 90 neurons achieved the best performance while the performance of RF model ranked 4th among all 9 models. Our results indicated that DLA might be superior to RF method in individual tree growth prediction based on multi-dimensional big data. Bond-Lamberty et al. (2014) studied the tree growth across the western United States using the RF method and found that the accuracy of RF models was not very high in predicting individual tree growth: their model only explained approximately 23%–44% diameter growth variation. Fiosina et al. (2019) compared deep learning (DL) and random forest (RF) methods and found that DL could significantly outperform classical random forest in prediction accuracy, given enough training data. However, the

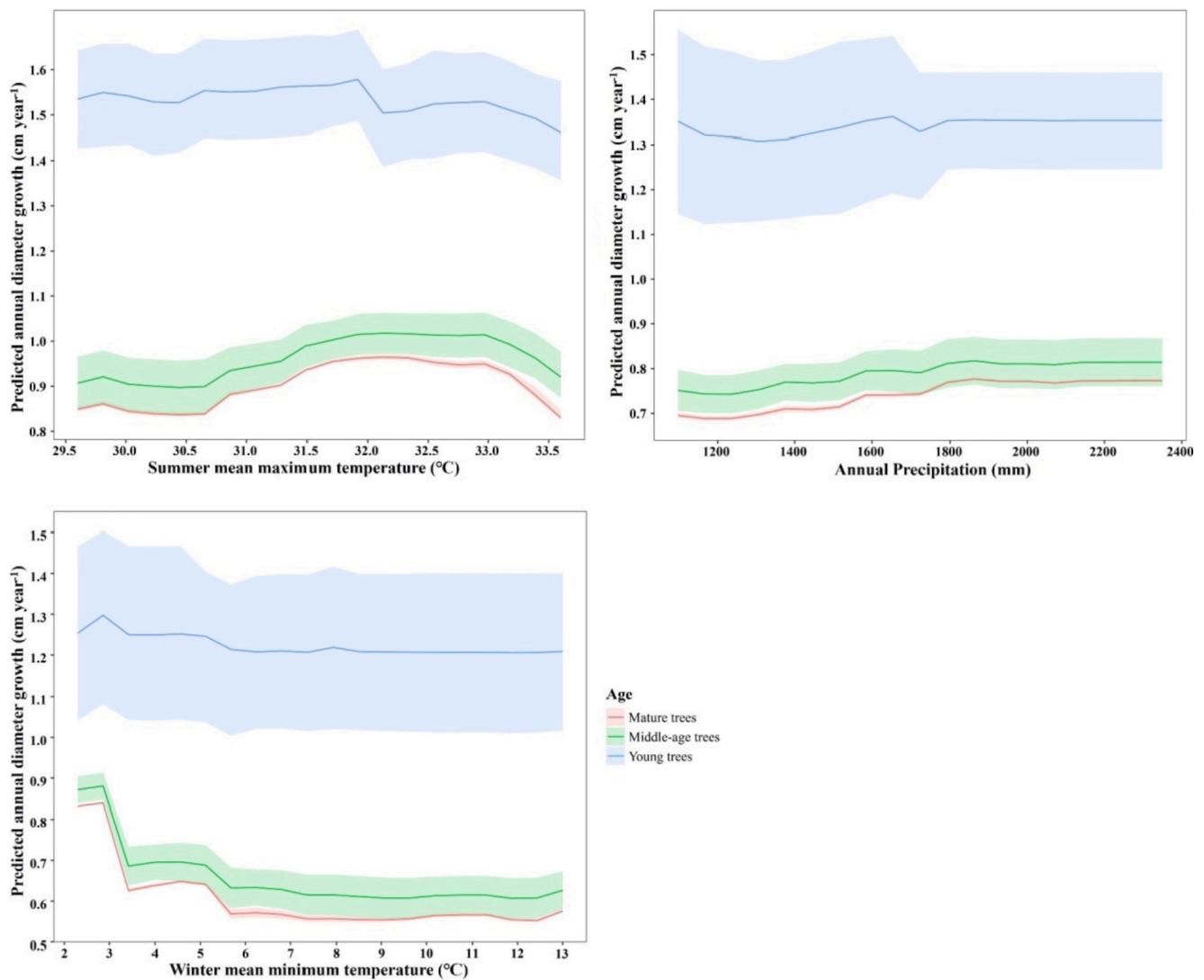


Fig. 5. Predicted annual diameter growth (ADG) from final deep learning model, and further analysis through random forest algorithm. Graphs demonstrated the interactive effect of stand age (Age) and three climatic factors on ADG when other variables are kept constant at their mean values. Shaded areas represent 95% confidence interval.

accurate prediction of DLA is still a “black box”, lacking necessary explanations. By contrast, some scholars proposed two methods to improve the interpretability of RF: the relative importance of predictive variables and the partial dependence plot (Breiman, 2001; Friedman, 2001). In other words, we cannot obtain both accuracy and explanation by only one machine learning method so far.

It is worth noting that DL models with more neurons in each hidden layer (neurons ≥ 60) tend to achieve better performance (Ercanli, 2020). Meanwhile, from the value of the average residual (AR) of model fitting, the prediction results of deep learning models tend to be underestimated (Table 4; Fig. 2).

4.2. Tree growth in response to climate factors

Climate factors have been considered as vital drivers of tree growth (Macias et al., 2006; Hlásny et al., 2017; Quadri et al., 2021; Zhirnova et al., 2021). In this study, Chinese fir tree growth was greatly affected by climatic factors mainly associated with SMMT, AP and WMMT. However, the influence of these three climatic factors on tree growth was not always positive or negative (Fig. 3), which was dependent on specific ranges of the climatic conditions. Results showed that tree growth increased with increasing SMMT, generally, while growth

decreased when $30.7 < \text{SMMT} < 31.4$ and $\text{SMMT} > 33.1$ °C (Fig. 3E). Liu et al. (2020) concluded that the positive response of tree growth to summer temperature might be caused by increased photosynthesis. However, when rising temperatures exceed the growth optimum, excessive photorespiration would increase consumption of carbohydrate reserves and further inhibits tree growth. Previous studies considered that WMMT might exert a more complex growth pattern for tree growth (Ryan, 2010; Wilmking et al., 2020). With an increase in WMMT, our results showed that tree growth decreased markedly first followed by a gentle reduction and then returning to an increase, and lastly, further increment of WMMT result in a growth decrement (Fig. 3D). The above phenomenon can be explained by the following research studies. Decreased winter temperature could lead to an inhibition of tree growth by causing bud damage, frost desiccation and reduced root activity (Luo et al., 2017). Furthermore, increased winter temperature could result in less frost damage to roots and leaves (Chen et al., 2015a; Su et al., 2015), and thereby advance the onset of growth. Gea-Izquierdo et al. (2012) reported that increased winter temperatures could lead to biomass loss of individuals through enhanced respiration rate and further causing a reduction in growth.

The tree growth in response to annual precipitation was significant in our study and AP exerted a positive association with tree growth when

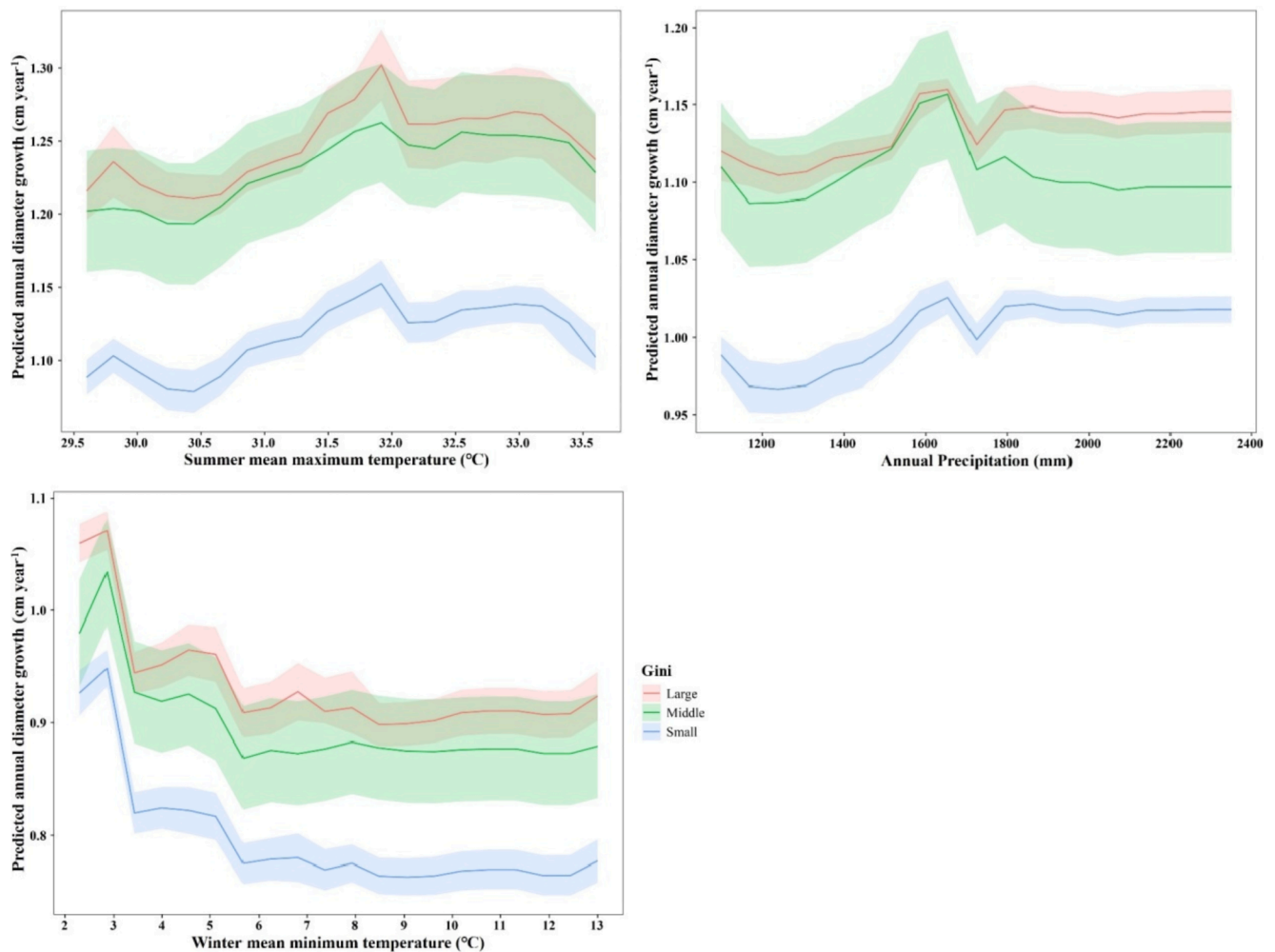


Fig. 6. Predicted annual diameter growth (ADG) from final deep learning model, and further analysis through random forest algorithm. Graphs demonstrated the interactive effect of stand structural diversity (Gini) and three climatic factors on ADG when the other predictors are kept constant. Shaded areas represent a 95% confidence interval.

1300 < AP < 1650 (Fig. 3F), while more precipitation during the range of 1100 < AP < 1300 and AP > 1850 led to a decrease in growth. Many studies have proved that precipitation was an important driver of tree growth (Canham et al., 2018; Devi et al., 2020). However, the importance of water resources to growth varied by regional climatic conditions. The positive driving force of rainfall would not be as strong compared with temperature in humid regions (Zheng et al., 2012; Chen et al., 2015b; Su et al., 2015). In addition, it is understandable that excessive rainfall leads to a reduction in radial growth (Dannenberg et al., 2019), for high annual precipitation and a concomitant increase in cloud cover, would likely shorten the photoperiod.

4.3. Tree growth in response to stand variables

In this study, stand structure represented by the Gini coefficient, showed a positive relation with tree growth (Fig. 3C), which was consistent with Vanhellemont et al. (2018). High stand structural heterogeneity might promote tree growth by exploiting unused space and light (De Boeck et al., 2006), thereby improving water and resources utilization (Silva Pedro et al., 2017; Jactel et al., 2018). However, for regions with poor site conditions, trees might be incapable of utilizing the underlying resources created by structural heterogeneity. In other words, the relationship between stand structure and growth may not be obvious and may even be negative, which is dependent on the environment of the study area (Jactel et al., 2018). Notably, our study sites

are not lacking water or soil nutrients, and Chinese fir is a light-demanding species. Thus, it is understandable that tree growth increases with an increase in stand structural complexity.

Age was another main driver of tree growth which has been confirmed by other studies (e.g., Chen et al., 2016). Derived from the sensitivity analysis, tree growth decreased rapidly with the increase of Age (5 ≤ Age < 10), and a further increase in age would cause growth to decline slowly (Age ≥ 10) (Fig. 3 B). The results might indicate that the negative effects of age on tree growth were greater for young trees rather than older trees.

Competition intensity has been considered as the main driving factor influencing diameter growth (Aakala et al., 2013; Buechling et al., 2017; Jiang et al., 2018). In our study, the variable importance ranking showed that the basal area of larger trees (BAL) exerted the most important influence on Chinese fir growth (Fig. 1), which was consistent with previous studies (Zhang et al., 2020b; Hatami et al., 2020). Nevertheless, the relationship between competition and tree growth can have different response patterns. Some studies suggested that competition could be a driving force influencing individual growth but it doesn't play a major role (Calama et al., 2019; Wang et al., 2021). Liang et al., (2019) hold the opinion that other factors mediate the relation between growth and competition intensity, such as latitude for instance. In fact, the mediating effect of latitude on competition is also reflected in geographical and environment characteristics, such as the interaction between competition and climatic factors, and this dimension was also

explored in this paper. We used the basal area of larger trees (BAL) to measure tree-level competition, and results indicated that the tree growth decreased with an increase in BAL (Fig. 3A). Based on our analysis, we found that younger trees belonging to young forests have low BAL and tend to achieve high diameter growth rate. Other studies also concluded similar results: for instance, Oboite and Comeau (2019) investigated the western boreal forest and found that competition (BAL) had a negative effect on black spruce growth. Ford et al. (2017) studied the montane forests in western North America and found individual tree growth was strongly constrained by competition (BAL).

4.4. Climate factors modulate the response of tree growth to stand conditions

Age, competition intensity, stand structure, and climate are the main factors driving tree growth. However, these factors do not act independently on individual growth, but by means of interactions (Calama et al., 2019). The tree growth of Chinese fir varied with climatic factors under different stand conditions. Combining the results of sensitivity and interaction analysis, the general trend of individual trees in response to climate factors kept constant under the impact of varied stand conditions, while climatic variables modulated the response of tree growth to different site conditions, which was consistent with Tomás et al., (2017). Moreover, as the greatest impact factor, highest annual diameter growth was associated with the lowest BAL (Fig. 3A), and tree growth ranged from 0.93 to 1.68 cm/year. When considering the climatic factors, the trend of growth decreasing with increasing BAL did not change. At the same time, we could clearly see that trees under low competition intensity achieved the highest radial growth, which was much higher than the growth under middle and high competition intensity (Fig. 4). The difference of growth between middle and high competition intensity was small, which might indicate that the negative effects on growth gradually decreased across a low to highly competitive gradient. In terms of the growth range, we found that tree growth decreased from 0.93 to 1.68 to 0.67–1.48 cm/year under the influence of climate. This suggested that climate factors might exacerbate the negative effects of competition on growth (Oboite and Comeau, 2019).

The response of tree growth to competitive intensity and age was very similar no matter whether climate conditions were considered or not (Figs. 3, 4, and 5). Tree growth decreased with increasing age, and young trees achieved the highest diameter growth (Fig. 5). The difference lies in the growth range. Among all three age categories, the value of tree growth range varied from 0.60 to 1.40 to 0.55–1.55 cm/year, the peak value of growth increased from 1.40 to 1.55 cm/year, while valley value decreased from 0.60 to 0.55 cm/year. It was expected that climate conditions would promote the growth of younger trees but restrain the growth of older trees, and that climatic factors might intensify the negative effect of age on tree growth.

In contrast, tree growth under different stand structural conditions (represented by three levels of the Gini coefficient) showed a different response pattern to climate conditions, and the curves representing annual diameter growth of trees with high and middle stand structural heterogeneity were close, and higher than the growth of trees with low stand structure (Fig. 6). Jactel et al. (2018) suggested that the positive correlation between stand structure and tree growth could be eliminated by poor site conditions, and this might provide an explanation for this phenomenon. The growth range influenced stand structure by transforming annual diameter growth from 0.95 to 1.12 to 0.77–1.30 cm/year when climate was not considered versus considered, respectively (Fig. 3C; Fig. 6). Results suggested that climatic factors might amplify the effect of stand structural heterogeneity on growth, including the reduction of the positive effect of low stand structure, and expanding the promotional effect of high stand structure on growth. In addition, we found that positive climate change (i.e., SMMT and AP) tended to promote tree growth at low-level competition intensity, compared with the other two competition categories. Trees in a higher competitive

environment were more likely to suffer damage under climate deterioration (i.e., WMMT), leading to a greater growth decline. Older trees were more likely to be affected by climate conditions. In particular, the negative effect of WMMT on older trees was significantly greater than that of younger trees. Our study results indicated that suitable site and climate conditions are the prerequisites for high growth of individual trees.

Based on our study, competition was the most influential variable on tree diameter growth, and trees under weak competition level tend to achieve higher growth increments, which indicated the balance between competition and tree growth should be considered whether through thinning or low-density afforestation. Older trees were more sensitive to climate variables, especially the negative effect of climatic stress. Therefore, we should pay more attention on developing adaption strategies for older trees to enhance their resilience to extreme weather, such as extreme summer or winter temperatures. Trees under high stand structure diversity tend to achieve higher annual diameter growth. Thus, suitable replanting and thinning measures can be carried out to promote single tree growth.

5. Conclusion

Exploring how stand and climatic factors impact tree growth of Chinese fir plantations is of great importance. Here we used the random forest algorithm (RF) and deep learning approach (DLA) to model the individual tree growth with stand age, competition intensity and stand structure and three climatic variables which were acquired from long-term spacing trials in subtropical China. Results showed the model with 8 hidden layers, and 90 neurons in each hidden layer achieved the best comprehensive performance. Further sensitivity analysis and interactive effect analysis were carried out based on the prediction results of the deep learning model. Results showed that individual tree growth of Chinese fir increased with an increase in stand structural diversity (Gini), but decreased with an increase in competition intensity (BAL) and stand age (Age). Moreover, BAL had the greatest influence on diameter growth among all the variables.

Meanwhile, the relationships between tree growth and three climatic variables were not constant, which was dependent on the range of values of each climatic factor. In addition, we found that: (i) Climatic conditions might exacerbate the negative effects of competition on growth; (ii) Climate conditions could promote the growth of younger trees but restrain the growth of older trees; (iii) With the climate variables considered, the value of tree growth under high and middle stand structural heterogeneity were similar, and was significantly higher compared with trees under low stand structural complexity; (iv) Positive influences of climate variables tended to promote tree growth under lower competition while growth of trees dealing with high competition were more likely to suffer under climate deterioration; and (v) Older trees were more sensitive to climate conditions since middle-age and mature trees were more vulnerable to the change of WMMT. Our findings provide important implications for understanding the mechanisms of tree growth of Chinese fir plantations in the face of future climate change.

CRedit authorship contribution statement

Zhen Wang: Writing – original draft. **Xiongqing Zhang:** Conceptualization, Supervision, Writing – review & editing. **Jianguo Zhang:** Review and improve the manuscript. **Sophan Chhin:** Review and improve writings.

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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References

- Aakala, T., Fraver, S., D'Amato, A.W., Palik, B.J., 2013. Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. *For. Ecol. Manage.* 308, 128–135.
- Bayat, M., Ghorbanpour, M., Zare, R., Jaafari, A., Thai Pham, B., 2019. Application of artificial neural networks for predicting tree survival and mortality in the Hyrcanian forest of Iran. *Comput. Electron. Agr.* 164, 104929. <https://doi.org/10.1016/j.compag.2019.104929>.
- Biecek, P., 2018. DALEX: Explainers for Complex Predictive Models in R. *J. Math. Learn. Res.* 19 (84), 1–5.
- Bond-Lamberty, B., Rocha, A.V., Calvin, K., Holmes, B., Wang, C., Goulden, M.L., 2014. Disturbance legacies and climate jointly drive tree growth and mortality in an intensively studied boreal forest. *Glob. Chang. Biol.* 20 (1), 216–227.
- Breiman, L., 2001. Random Forests. *Mach. Learn.* 45, 5–32.
- Buechling, A., Martin, P.H., Canham, C.D., Piper, F., 2017. Climate and competition effects on tree growth in Rocky Mountain forests. *J. Ecol.* 105 (6), 1636–1647.
- Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78, 1958–1965.
- Calama, R., Conde, M., de-Dios-García, J., Madrigal, G., Vázquez-Piqué, J., Gordo, F.J., Pardos, M., 2019. Linking climate, annual growth and competition in a Mediterranean forest: *Pinus pinea* in the Spanish Northern Plateau. *Agric. For. Meteorol.* 264, 309–321.
- Canham, C.D., Murphy, L., Riemann, R., McCullough, R., Burrill, E., 2018. Local differentiation in tree growth responses to climate. *Ecosphere* 9 (8). <https://doi.org/10.1002/ecs2.2018.9.issue-810.1002/ecs2.2368>.
- Chen, F., Yuan, Y., Wei, W., Yu, S., Wang, H., 2015a. Tree-ring response of subtropical tree species in southeast China on regional climate and sea-surface temperature variations. *Trees* 29 (1), 17–24.
- Chen, F., Yuan, Y.-J., Yu, S.-L., Zhang, T.-W., 2015b. Influence of climate warming and resin collection on the growth of Masson pine (*Pinus massoniana*) in a subtropical forest, southern China. *Trees* 29 (5), 1423–1430.
- Chen, H.Y.H., Luo, Y., Reich, P.B., Searle, E.B., Biswas, S.R., Enquist, B., 2016. Climate change-associated trends in net biomass change are age dependent in western boreal forests of Canada. *Ecol. Lett.* 19 (9), 1150–1158.
- Christin, S., Hervet, É., Lecomte, N., Ye, H., 2019. Applications for deep learning in ecology. *Methods Ecol. Evol.* 10 (10), 1632–1644.
- Copenhaver-Parry, P.E., Cannon, E., 2016. The relative influences of climate and competition on tree growth along montane ecotones in the Rocky Mountains. *Oecologia* 182 (1), 13–25.
- Crookston, N.L., Rehfeldt, G.R., Ferguson, D.E., Warwell, M., 2008. FVS and global warming: a prospectus for future development. Crookston, N.L., Fort Collins, CO, pp. 7–16.
- Curto, R.D.A., Mattos, P.P.d., Braz, E.M., Péllico Netto, S., 2021. Growth and retrospective analysis of competition in an overstocked stand of *Araucaria angustifolia*. *For. Ecol. Manage.* 483, 118766. <https://doi.org/10.1016/j.foreco.2020.118766>.
- Dannenberg, M.P., Wise, E.K., Smith, W.K., 2019. Reduced tree growth in the semiarid United States due to asymmetric responses to intensifying precipitation extremes. *Sci. Adv.* 5, 20157.
- De Boeck, H.J., Nijs, I., Lemmens, C.M.H.M., Ceulemans, R., 2006. Underlying effects of spatial aggregation (clumping) in relationships between plant diversity and resource uptake. *Oikos* 113 (2), 269–278.
- Devi, N.M., Kukarskih, V.V., Galimova, A.A., Mazepa, V.S., Grigoriev, A.A., 2020. Change evidence in tree growth and stand productivity at the upper treeline ecotone in the Polar Ural Mountains. *For. Ecosyst.* 7, 7.
- Ercanli, 2020. Innovative deep learning artificial intelligence applications for predicting relationships between individual tree height and diameter at breast height. *For. Ecosyst.* 7 (02), 3–20.
- Fiosina, J., Fiosins, M., Bonn, S., 2019. Deep learning and random forest-based augmentation of SRNA expression profiles. *Lect. Notes Comput. Sci.* 11490, 159–170.
- Flake, S.W., Weisberg, P.J., 2019. Fine-scale stand structure mediates drought-induced tree mortality in pinyon-juniper woodlands. *Ecol. Appl.* 29 (2). <https://doi.org/10.1002/eap.2019.29.issue-210.1002/eap.1831>.
- Ford, K.R., Breckheimer, I.K., Franklin, J.F., Freund, J.A., Kroiss, S.J., Larson, A.J., Theobald, E.J., HilleRisLambers, J., 2017. Competition alters tree growth responses to climate at individual and stand scales. *Can. J. For. Res.* 47 (1), 53–62.
- Forrester, D.I., 2019. Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. *For. Ecol. Manage.* 447, 139–157.
- Forrester, D.I., Ammer, C., Annighofer, P.J., Barbeito, I., Bielak, K., Bravo-Oviedo, A., Hurt, V., 2018. Effects of crown architecture and stand structure on light absorption in mixed and monospecific *Fagus sylvatica* and *Pinus sylvestris* forest along a climate gradient through Europe. *J. Ecol.* 106, 746–760.
- Forrester, D.I., Bauhus, J., 2016. A review of processes behind diversity-productivity relationships in forests. *Curr. For. Rep.* 2, 45–61.
- Friedman, J.H., 2001. Greedy function approximation: a gradient boosting machine. *Annu. Stat.* 29 (5), 1189–1232.
- Galván, J.D., Camarero, J.J., Gutiérrez, E., Zuidema, P., 2014. Seeing the trees for the forest: drivers of individual growth responses to climate in *Pinus uncinata* mountain forests. *J. Ecol.* 102 (5), 1244–1257.
- Gea-Izquierdo, G., Fonti, P., Cherubini, P., Martin-Benito, D., Chaar, H., Canellas, I., 2012. Xylem hydraulic adjustment and growth response of *Quercus canariensis* Willd. to climatic variability. *Tree Physiol.* 32 (4), 401–413.
- Görgens, E.B., Montagni, A., Rodriguez, L.C.E., 2015. A performance comparison of machine learning methods to estimate the fast-growing forest plantation yield based on laser scanning metrics. *Comput. Electron. Agr.* 116, 221–227.
- Grimm, R., Behrens, T., Märker, M., Elsenbeer, H., 2008. Soil organic carbon concentrations and stocks on Barro Colorado Island-Digital soil mapping using Random Forests analysis. *Geoderma* 146 (1–2), 102–113.
- Guo, Q., Ren, H., 2014. Productivity as related to diversity and age in planted versus natural forests. *Global Ecol. Biogeogr.* 23 (12), 1461–1471.
- Hatami, N., Lohmander, P., Moayeri, M.H., Limaçei, S.M., 2020. A basal area increment model for individual trees in mixed continuous cover forests in Iranian Caspian forests. *J. For. Res.* 31 (1), 99–106.
- Hinton, G.E., Osindero, S., Teh, Y.-W., 2006. A fast-learning algorithm for deep belief nets. *Neural Comput.* 18 (7), 1527–1554.
- Hlásky, T., Trombik, J., Bošafa, M., Merganič, J., Marušák, R., Šebeň, V., Štěpánek, P., Kubista, J., Trnka, M., 2017. Climatic drivers of forest productivity in Central Europe. *Agric. For. Meteorol.* 234–235, 258–273.
- Huang, J.-G., Stadt, K.J., Dawson, A., Comeau, P.G., Auge, H., 2013. Modelling growth-competition relationships in trembling aspen and white spruce mixed boreal forests of western Canada. *Plos One* 8 (10), e77607.
- Jactel, H., Gritti, E.S., Drössler, L., Forrester, D.I., Mason, W.L., Morin, X., Pretzsch, H., Castagnérol, B., 2018. Positive biodiversity-productivity relationships in forests: climate matters. *Biol. Lett.* 14 (4), 20170747. <https://doi.org/10.1098/rsbl.2017.0747>.
- Jiang, X., Huang, J.-G., Cheng, J., Dawson, A., Stadt, K.J., Comeau, P.G., Chen, H.Y.H., 2018. Interspecific variation in growth responses to tree size, competition and climate of western Canadian boreal mixed forests. *Sci. Total Environ.* 631–632, 1070–1078.
- Kilham, P., Hartebrodt, C., Kandler, R.G., 2019. Generating tree-level harvest predictions from forest inventories with random forests. *Forests* 10 (1), 20.
- Kunstler, G., Albert, C.H., Courbaud, B., Lavergne, S., Thuiller, W., Vieilledent, G., Zimmermann, N.E., Coomes, D.A., 2011. Effects of competition on tree radial-growth vary in importance but not in intensity along climatic gradients. *J. Ecol.* 99, 300–312.
- Kweon, D., Comeau, P.G., 2019. Relationships between tree survival, stand structure and age in trembling aspen dominated stands. *For. Ecol. Manage.* 438, 114–122.
- Lacerda, T.H.S., Cabacina, C.D., Araújo Júnior, C.A., Maia, R.D., Lacerda, K.W.d.S., 2017. Artificial neural networks for estimating tree volume in the Brazilian savanna. *Cerne* 23 (4), 483–491.
- LeDell, E., Gill, N., Aiello, S., Fu, A., Candel, A., Click, C., Kraljevic, T., Nykodym, T., Abotoun, P., Kurka, M., Malohlava, M., 2021. H2o: R Interface for the “H2o” Scalable Machine Learning Platform.
- Liang, H., Huang, J.-G., Ma, Q., Li, J., Wang, Z., Guo, X., Zhu, H., Jiang, S., Zhou, P., Yu, B., Luo, D., 2019. Contributions of competition and climate on radial growth of *Pinus massoniana* in subtropics of China. *Agric. For. Meteorol.* 274, 7–17.
- Liaw, A., Wiener, M., 2002. Classification and Regression by randomForest. *R News* 2 (3), 18–22.
- Liu, J.Y., Zhang, R., Xu, X., Fowler, J.C., Miller, T.E.X., Dong, T., 2020. Effect of summer warming on growth, photosynthesis and water status in female and male *Populus cathayana*: implications for sex-specific drought and heat tolerances. *Tree Physiol.* 40 (9), 1178–1191.
- Luo, D., Huang, J.-G., Jiang, X., Ma, Q., Liang, H., Guo, X., Zhang, S., 2017. Effect of climate and competition on radial growth of *Pinus massoniana* and *Schima superba* in China's subtropical monsoon mixed forest. *Dendrochronologia* 46, 24–34.
- Luo, Y., Chen, H.Y.H., 2011. Competition, species interaction and aging control tree mortality in boreal forest. *J. Ecol.* 99, 1470–1480.
- Macias, M., Andreu, L., Bosch, O., Camarero, J.J., Gutiérrez, E., 2006. Increasing aridity is enhancing silver fir (*Abies Alba* Mill.) water stress in its south-western distribution limit. *Clim. Change* 79 (3–4), 289–313.
- Mainwaring, D.B., Maguire, D.A., 2004. The effect of local stand structure on growth and growth efficiency in heterogeneous stands of ponderosa pine and lodgepole pine in central Oregon. *Can. J. For. Res.* 34 (11), 2217–2229.
- McElhinny, C., Gibbons, P., Brack, C., Bauhus, J., 2005. Forest and woodland stand structural: its definition and measurement. *For. Ecol. Manage.* 218, 1–24.
- McRoberts, R.E., Winter, S., Chirici, G., Hauk, E., Pelz, D.R., Moser, W.K., Hatfield, M.A., 2008. Large-scale spatial patterns of forest structural diversity. *Can. J. For. Res.* 38 (3), 429–438.
- Morin, X., 2015. Species richness promotes canopy packing: A promising step towards a better understanding of the mechanisms driving the diversity effects on forest functioning. *Funct. Ecology* 29 (8), 993–994.
- Navarro-Cerrillo, R.M., Manzanedo, R.D., Rodriguez-Vallejo, C., Gazol, A., Palacios-Rodríguez, G., Camarero, J.J., 2020. Competition modulates the response of growth to climate in pure and mixed *Abies pinsapo* subsp. *Maroccana* forest in northern Morocco. *For. Ecol. Manage.* 459, 117847.
- Nandy, S., Singh, R., Ghosh, S., Watham, T., Kushwaha, S.P.S., Kumar, A.S., Dadhwal, V. K., 2017. Neural network-based modelling for forest biomass assessment. *Carbon Manage.* 8 (4), 305–317.

- Nunes, M.H., Gørgens, E.B., Hernandez Montoya, A.R., 2016. Artificial intelligence procedures for tree taper estimation within a complex vegetation mosaic in Brazil. *PLoS One* 11 (5), e0154738.
- Oboite, F.O., Comeau, F.G., 2019. Competition and climate influence growth of black spruce in western boreal forest. *For. Ecol. Manage.* 443, 84–94.
- Özçelik, R., Diamantopoulou, M.J., Crecente-Campo, F., Eler, U., 2013. Estimating Crimean juniper tree height using nonlinear regression and artificial neural network models. *For. Ecol. Manage.* 306, 52–60.
- Pretzsch, H., Biber, P., 2010. Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. *Can. J. For. Res.* 40 (2), 370–384.
- Prior, L.D., Bowman, D.M.J.S., 2014. Across a macro-ecological gradient forest competition is strongest at the most productive sites. *Front. Plant Sci.* 5, 260.
- Quadri, P., Silva, L.C.R., Zavaleta, E.S., 2021. Climate-induced reversal of tree growth pattern at a tropical treeline. *Sci. Adv.* 7 (22), eabb7572.
- Ramazan, O., Diamantopoulou, M.J., Crecente-Campo, F., Eler, U., 2013. Estimating Crimean juniper tree height using nonlinear regression and artificial neural network models. *For. Ecol. Manage.* 306, 52–60.
- Ryan, M.G., 2010. Temperature and tree growth. *Tree Physiol.* 30 (6), 667–668.
- Schratz, P., Muenchow, J., Iturririx, E., Richter, J., Brenning, A., 2019. Hyperparameter tuning and performance assessment of statistical and machine-learning algorithms using spatial data. *Ecol. Modell.* 406, 109–120.
- Silva Pedro, M., Rammer, W., Seidl, R., Roxburgh, S., 2017. Disentangling the effects of compositional and structural diversity on forest productivity. *J. Veg. Sci.* 28 (3), 649–658.
- Stage, A.R., 1968. A tree-by-tree measure of site utilization for grand fir related to stand density index. *USDA For. Serv. Res. Note INT-77*, 7p. Intermountain Forest & Range Experience Station, Ogden, UT.
- Staudhammer, C.L., LeMay, V.M., 2001. Introduction and evaluation of possible indices of stand structural diversity. *Can. J. For. Res.* 31 (7), 1105–1115.
- Sterba, H., Ledermann, T., 2006. Inventory and modelling for forests in transition from even-aged to uneven-aged management. *For. Ecol. Manage.* 224, 278–285.
- Su, H., Axmacher, J.C., Yang, B.o., Sang, W., 2015. Differential radial growth response of three coexisting dominant tree species to local and large-scale climate variability in a subtropical evergreen broad-leaved forest of China. *Ecol. Res.* 30 (4), 745–754.
- Vanhellemont, M., Bijlsma, R.-J., De Keersmaeker, L., Vandekerckhove, K., Verheyen, K., 2018. Species and structural diversity affect growth of oak, but not pine, in uneven-aged mature forests. *Basic Appl. Ecol.* 27, 41–50.
- Wang, B., Wei, W., Xing, Z., You, W., Niu, X., Ren, X., Liu, C., 2012a. Biomass carbon pools of *Cunninghamia lanceolata* (Lamb.) Hook. forests in subtropical China: Characteristics and potential. *Can. J. For. Res.* 27 (6), 545–560.
- Wang, T., Hamann, A., Spittlehouse, D.L., Murdock, T., 2012b. Climate WNA-high-resolution spatial climate data for western North America. *J. Appl. Meteorol. Cli.* 51, 16–29.
- Wang, Z., Zhang, X., Chhin, S., Zhang, J., Duan, A., 2021. Disentangling the effects of stand and climatic variables on forest productivity of Chinese fir plantations in subtropical China using a random forest algorithm. *Agric. For. Meteorol.* 304–305, 108412. <https://doi.org/10.1016/j.agrformet.2021.108412>.
- Weiskittel, A.R., Crookston, N.L., Radtke, P.J., 2011. Linking climate, gross primary productivity, and site index across forests of the western United States. *Can. J. For. Res.* 41 (8), 1710–1721.
- Wilmking, M., Buras, A., Metslaid, S., Kaczka, R., Trouillier, M., Harvey, J.E., Janecka, K., 2020. Higher winter-spring temperature and winter-spring/summer moisture availability increase Scots pine growth on coastal dune microsites around the south Baltic sea. *Front. For. Glob. Change* 3, 578912.
- Wu, C., Chen, Y., Peng, C., Li, Z., Hong, X., 2019. Modeling and estimating aboveground biomass of *dacrydium pierrei* in China using machine learning with climate change. *J. Environ. Manage.* 234, 167–179.
- Wyckoff, P.H., Clark, J.S., 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. *J. Ecol.* 90, 604–615.
- Yang, R., Zhang, G., Liu, F., Lu, Y., Yang, F., Yang, M., Zhao, Y., Li, D., 2016. Comparison of boosted regression tree and random forest models for mapping topsoil organic carbon concentration in an alpine ecosystem. *Ecol. Indic.* 60, 870–878.
- Zeileis, A., 2014. Ineq: Measure Inequality, Concentration, and Poverty (Version 0.2e13). Retrieved from <http://CRAN.R-project.org/package=ineq>.
- Zeiler, M.D., 2012. Adadelta: an adaptive learning rate method. arXiv preprint arXiv:1212.5701.
- Zhang, H., Wang, K., Zeng, Z., Du, H., Zou, Z., Xu, Y., Zeng, F., 2019. Large-scale patterns in forest growth rates are mainly driven by climatic variables and stand characteristics. *For. Ecol. Manage.* 435, 120–127.
- Zhang, X., Cao, Q., Duan, A., Zhang, J., 2017. Modeling tree mortality in relation to climate, initial planting density, and competition in Chinese fir plantations using a Bayesian logistic multilevel method. *Can. J. For. Res.* 47 (9), 1278–1285.
- Zhang, X., Duan, A., Zhang, J., 2013. Tree biomass estimation of Chinese fir (*Cunninghamia lanceolata*) based on Bayesian method. *PLoS One* 8 (11), e7986.
- Zhang, X., Wang, H., Chhin, S., Zhang, J., 2020a. Effects of competition, age and climate on tree slenderness of Chinese fir plantations in southern China. *For. Ecol. Manage.* 458, 117815.
- Zhang, X., Wang, Z., Chhin, S., Wang, H., Duan, A., Zhang, J., 2020b. Relative contribution of competition, stand structure, age, and climate factors to tree mortality of Chinese fir plantation: long-term spacing trials in southern China. *For. Ecol. Manage.* 465, 118103.
- Zhao, Q., Yu, S., Zhao, F., Tian, L., Zhao, Z., 2019. Comparison of machine learning algorithms for forest parameter estimations and application for forest quality assessments. *For. Ecol. Manage.* 434, 224–234.
- Zheng, Y., Zhang, Y., Shao, X., Yin, Z.Y., 2012. Temperature variability inferred from tree-ring widths in the Dabie mountains of subtropical central China. *Trees* 26, 1887–1894.
- Zhirnova, D.F., Belokopytova, L.V., Meko, D.M., Babushkina, E.A., Vaganov, E.A., 2021. Climate change and tree growth in the Khakass-Minusinsk Depression (South Siberia) impacted by large water reservoirs. *Sci. Rep.* 11, 14266.
- Zhu, G., Hu, S., Chhin, S., Zhang, X., He, P., 2019. Modelling site index of Chinese fir plantations using a random effects model across regional site types in Hunan province, China. *For. Ecol. Manage.* 446, 143–150.