ANALYSIS OF THE DOMINANT FACTORS THAT INFLUENCE GROWTH OF *LARIX GMELINII* FORESTS

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Abstract. Identification of environmental factors that strongly influence growth indicators (diameter at breast height, tree height and carbon density) for *Larix gmelinii* forests in the cold-temperate zone on the Greater Khingan Mountains, northeast China will provide an important reference for sustainable management of the forests. In this study, 75 plots were established in *L. gmelinii* forests during a forest inventory from 2015 to 2022. Sixteen environmental predictors, comprising climatic, edaphic, topographic, and biotic factors, were selected according to their ecological importance for *L. gmelinii* forests and peer-reviewed literature to determine their influence on the growth of *L. gmelinii* forests using linear fitting and redundancy analysis. Stocking degree had the strongest significant correlation with carbon density in the tree layer, which increased with increasing stocking degree. Solar radiation had the strongest significant positive correlation with stand average diameter at breast height. The stand average height was most strongly correlated with soil organic carbon content, with which it had a significant positive correlation. Stocking degree, solar radiation and soil organic carbon content were the dominant factors affecting the growth of *L. gmelinii* forests. Forest management should incorporate improved light and soil conditions and increase the stocking degree to promote growth of *L. gmelinii* forests.
Keywords: *diameter at breast height, total tree height, carbon density, linear fitting, redundancy analysis*

Introduction

Boreal forests are among the largest biomes on Earth and store more than 700 Pg carbon in the forest vegetation (Jiang et al., 2002), and provide global ecosystem services, such as climate regulation and carbon cycling (Gauthier et al., 2015). The boreal forests in China are mainly distributed on the Greater Khingan Mountains, which represent approximately 30% of China's total forests and account for one-third of the carbon stocks in Chinese forest ecosystems (Wang et al., 2001). These forests are the largest continuous coniferous forests in the cold-temperate zone of China (Liu et al., 2021), in which *Larix gmelinii* is the dominant tree species (Jiang et al., 2002). *L. gmelinii* forests, which account for more than 57% of the total Greater Khingan Mountains area, are the main contributor to carbon stocks in the forest ecosystem of this region and play an important role in maintaining the carbon balance of the ecosystem (Liu et al., 2020). Although *L. gmelinii* is of ecological importance, the growth of *L. gmelinii* in the Greater Khingan Mountains has declined and its distribution area has shifted northward owing to climate warming and human disturbance (Zhang et al., 2013).

Stand growth is essential for maintenance of a forest ecosystem as a sustainable carbon sink (Pugh et al., 2019). Stand growth is affected by both biotic and abiotic factors. Specifically, environmental factors affect the growth of stands by influencing tree photosynthesis (Bassow and Bazzaz, 1998), water utilization (Forner et al., 2018) and nutrient absorption (Bassirirad, 2000), among other processes, thereby affecting the carbon sink strength. Numerous abiotic factors can affect the growth of *L. gmelinii* stands, such as climate (Jiang et al., 2016), soil (Kuuluvainen et al., 1993) and topography (Bai et al., 2021). Climate is a primary limiting factor that determines the distribution and individual growth of tree species at a regional scale (Liu et al., 2023). The Greater Khingan Mountains Region is especially sensitive to climatic changes. Significant correlations between the growth of *L. gmelinii* and latitude, elevation and precipitation gradient have been reported (Jiang et al., 2016; Yasmeen et al., 2019). In addition, soil affects the growth of *L. gmelinii* forests, especially through elements that affect soil fertility, such as the carbon and nitrogen, and the soil pH. Increase in the soil nitrogen and phosphorus contents can accelerate the growth of trees (Prietzel et al., 2008). Among topographic factors, slope and aspect impact on the survival and growth of *L. gmelinii* seedlings. Slope and aspect influence the available phosphorus and potassium contents in the soil, thus causing differences in seedling survival (Huang et al., 2015). The growth of forests is a complex nonlinear process, which is affected by multiple biotic and abiotic factors rather than a single factor. It remains unclear which biotic and abiotic factors can jointly affect the growth of *L. gmelinii* forests. Understanding the factors that affect the growth of *L. gmelinii* forests is important for the assessment and prediction of the carbon sink function of the Greater Khingan Mountains Region.

Tree height (H), diameter at breast height (DBH) and other forest-structure parameters are examples of the important basic data recovered from a traditional forest resource survey, and are crucial for research on forest biomass estimation, forest carbon cycling, carbon flow and stand growth (Liu et al., 2018). In previous studies, a tree height–DBH model was constructed to estimate missing tree heights (Sumida et al., 2013) and for biomass estimation (Wang, 2006). Many studies have explored the impact of environmental factors on tree height and DBH (Wang et al., 2006) to provide a theoretical basis for the management and growth of trees. Forest carbon sequestration has become a focus of ecosystem research because of global climate change, and the ecological and environmental problems resulting from the sharp increase in the concentration of greenhouse gases, such as CO_2, in the Earth's atmosphere. Previous studies have estimated forest carbon storage (Pan et al., 2004; Paniagua-Ramirez et al., 2021; Sun and Liu, 2019) and the effects of climatic factors on the carbon budget (Finzi et al., 2020; Matthews et al., 2020). Carbon density as an index of forest carbon sinks has also been widely assessed (Jones and O'hara, 2011). Although there are many reasons to preserve forests, the protection of their carbon stocks and potential as future carbon sinks is a current policy priority (Mitchard et al., 2014).

On this basis, in the present study we conducted a comprehensive analysis, combining linear fitting and redundancy analysis (RDA), that included the three most important indicators of the growth of *L. gmelinii* forests, i.e., average diameter at breast height and average height of stands (Xie et al., 2022) as well as carbon density in the tree layer (Ahmad et al., 2021) as dependent variables, and the major abiotic and biotic factors affecting changes in *L. gmelinii* forests, namely, climatic, edaphic, topographic, and biotic factors, as independent variables. The factors were sorted according to their degree of impact on the growth of *L. gmelinii* forests, thereby determining the most

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important factors that influence *L. gmelinii* forests growth. The results contribute to an improved understanding of the impact of biotic and abiotic factors on *L. gmelinii* forests, and will increase the prediction accuracy for future growth of *L. gmelinii* forests and provide a theoretical basis for the adoption of effective measures to enhance the growth of *L. gmelinii* forests.

Materials and methods

Study area

The Greater Khingan Mountains are located in northeastern China (121°12′–127°00′E, 50°10′–53°33′N), covering an elevational range of 330–1750 m, and have an annual average temperature of −3°C and annual precipitation of 350–500 mm, most of which falls in May to October (Imbert et al., 2021). Snow cover lasts for 5 months and averages 300–500 mm and the frost-free period is shorter than 100 days (Liu et al., 2023; Xu, 1998). The region has a cold-temperate continental monsoon climate with a rainy summer and winter, a large temperature difference between day and night, and distinct montane climatic characteristics (Liu et al., 2020). The soil is mainly a brown coniferous forest soil with a depth of 15–20 cm and rich in organic matter (Imbert et al., 2021). Several other soil types present include dark brown soil, gray black soil, meadow soil, and swamp soil (Wang et al., 2001). The main tree species is *L. gmelinii*, followed by *Betula platyphylla* and *Populus davidiana*; the understory vegetation mainly includes *Ledum palustre*, *Rhododendron dauricum* and *Spiraea salicifolia*, and herbaceous plants mainly include *Filipendula palmata*, *Fragaria orientalis* and *Bupleurum longiradiatum* (Imbert et al., 2021).

Sample plots and data collection

In this study, a systematic sampling method was employed. A total of 75 sample plots in *L. gmelinii* forests were established in the Greater Khingan Mountains Region from 2015 to 2022 (*Fig. 1*), with an area of 0.1 to 1.05 ha, distributed throughout the Greater Khingan Mountains (running across Inner Mongolia and Heilongjiang). The sample plots were representative of the existing site conditions and growth of *L. gmelinii* forests, containing trees growing in various sites and stand densities, and the tree age ranged from 13 to 140 years. For each plot, environmental factors, such as soil, topography, longitude, latitude and elevation, were recorded. For trees with DBH > 5 cm in the standard plots, each tree was inspected, we used the VERTEX IV hypsometer (Haglöf, Sweden) to aim at the DBH of the tree at a distance beyond the height of the tree, and then aimed at the top of the tree to measure the tree height, and the name of the tree species was recorded. After the survey of each plot was completed, the average diameter (D_g) of the trees in the plot was calculated (Crowther et al., 2016). Tree height curves were plotted based on the distribution of the average DBH and the average height of trees within each diameter range, and the average tree height (H_D) of each stand in each sample plot was determined from the tree height curves (for specific methods for plotting the tree height curves, see (West, 2009)). Based on D_g and H_D (with an error not exceeding ± 5%), three trees with an average trunk shape were selected as standard trees in each stand and the average stand age was estimated based on the age of the standard trees (see Liu et al. (2023) for the specific method). According to the information obtained from the sample plots, the environmental and growth indexes were obtained (*Fig. 2*).

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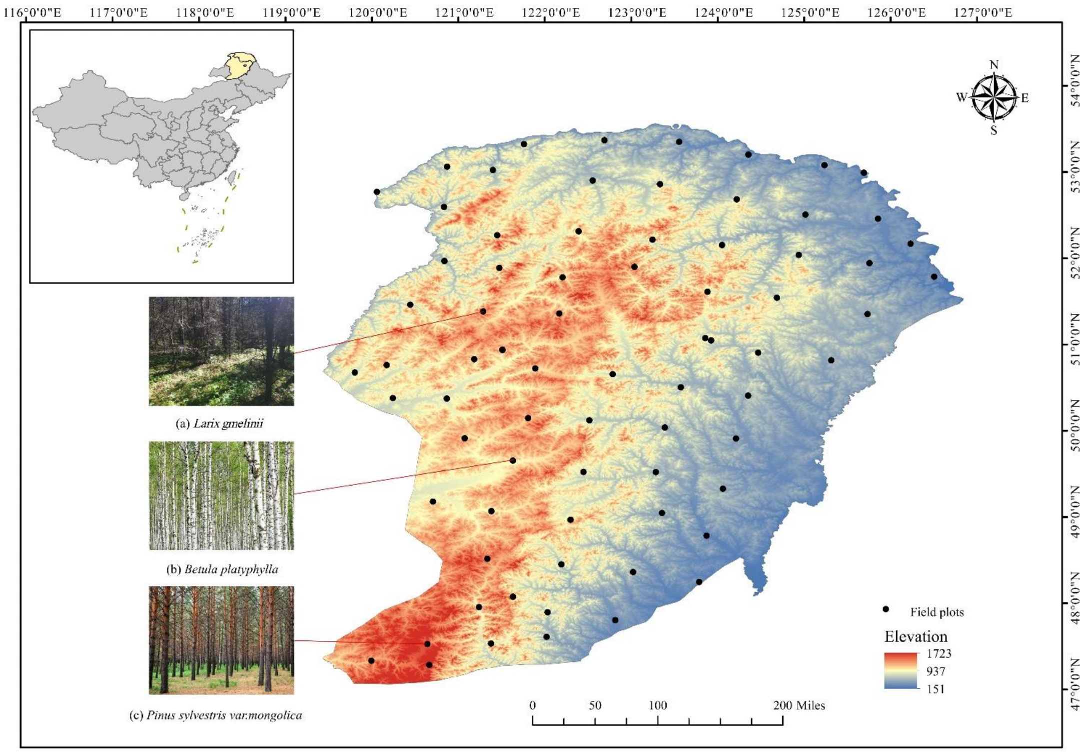

Figure 1. *Locations of the sampling sites of the 2015 to 2022 in the Greater Khingan Mountains, northeastern China. Larix gmelinii, Betula platyphylla and Pinus sylvestris var. mongholica forests are, three main forest types in the Greater Khingan Mountains*

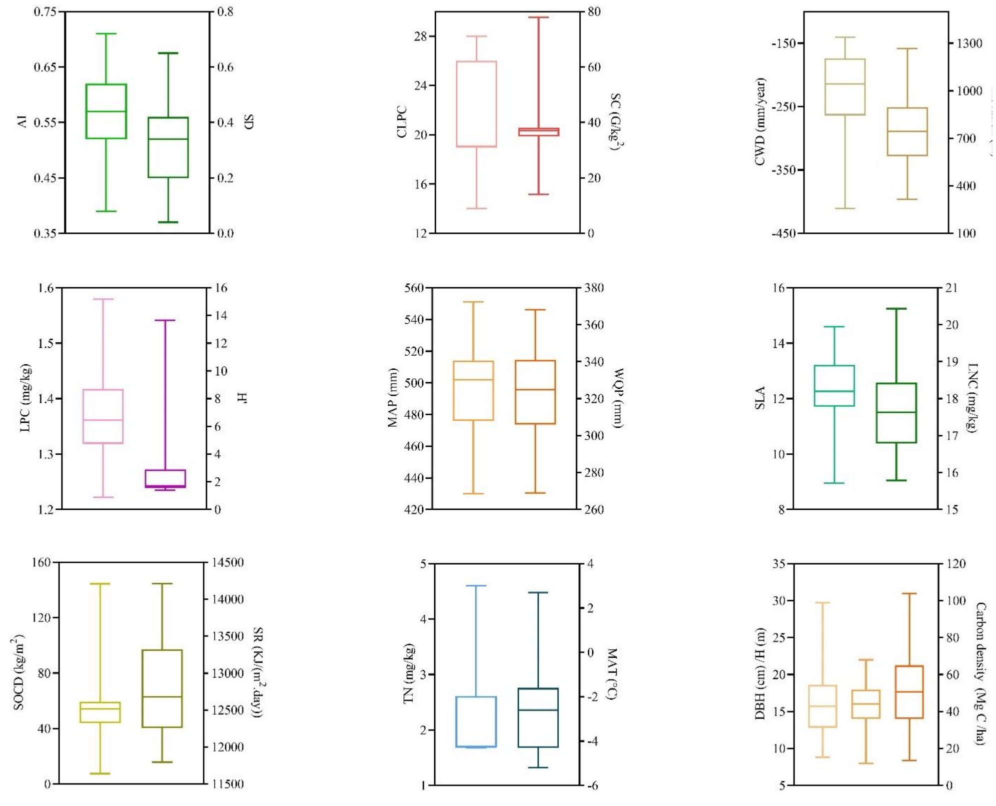

Figure 2. *Variations of environmental factors and growth factors for Larix gmelinii forests*

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Carbon storage and density in biomass calculation

An allometric growth model enables estimation of the biomass of individual trees with high accuracy and can reduce destructive sampling of forest vegetation (Momo Takoudjou et al., 2018). Its core intention is to establish the correlation between biomass and DBH, and use tree height to calculate the biomass of an individual tree. In this study, the most typical (with D^2H as the independent variable) biomass allometric growth model $W = a(D^2H)^b$ was employed, where W is the biomass of each component, D is the diameter, H is the tree height, and a and b are model parameters. From the DBH and height of an individual tree in the sample plot, the biomass of different organs of an individual tree of the main tree species in the Greater Khingan Mountains was estimated was estimated using the fitted model parameters listed in *Table 1*. The biomass of each organ was summed to obtain the biomass of an individual tree. The biomass per unit area of the stand (Mg ha^{-1}) was calculated by adding the biomass of individual trees to the total biomass of the stand, and then dividing it by the area of the corresponding stand.

Table 1. *Parameter estimation from Zhou (2018) for different biomass components of the dominant tree species in Larix gmelinii forests on the Greater Khingan Mountains*

Tree species(group)	Organ	Eq. $W = a(D^2H)^b$		
		a	b	R^2
Larix gmelinii	Trunks	0.0242	0.9445	0.95
	Branches	0.0040	0.9272	0.95
	Leaves	0.0091	0.7482	0.95
	Roots	0.0110	0.8466	0.95
Betula platyphylla	Trunks	0.1040	0.7926	0.92
	Branches	0.0087	0.8855	0.91
	Leaves	0.0064	0.7453	0.91
	Roots	0.0155	0.8805	0.91
Other tree species	Trunks	0.0805	0.8063	0.94
	Branches	0.0669	0.6268	0.94
	Leaves	0.0961	0.6553	0.94
	Roots	0.2385	0.5227	0.97

W is the biomass of each component, D is the diameter, H is the tree height, and a and b are model parameters

Plant biomass is converted into carbon stocks based on the proportion of carbon in plant dry organic matter. In this study, the biomass per unit area was converted to carbon stock per unit area (Mg C ha^{-1}) according to a conversion coefficient of 0.5 (Fang et al., 2001). The carbon content slightly varies in different organs of the same tree species (Shen et al., 2016) and among the same component in different tree species (Johnson and Sharpe, 1983). It has been suggested that using a conversion factor of 0.5 would typically deviate by approximately 2%–3%, resulting in a systematic bias in carbon stock estimates of approximately 4%–6% (Thomas and Malczewski, 2007). Liu (2023) argue that this bias is small compared with the uncertainties associated with other forest carbon estimates. Furthermore, accurate carbon content data are not available for every type of vegetation biomass, so the default value of 0.5 is often used (Houghton et al., 1990).

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Environmental factor data

Data for mean annual temperature (MAT; °C), mean annual precipitation (MAP; mm), solar radiation (SR; kJ m^{-2} d^{-1}) and warmest quarter precipitation (WQP; mm) were obtained from the WorldClim database (https://www.worldclim.org) with spatial resolution of 30 s. Aridity index (AI) data were obtained from the Global Drought Index and Potential Evapotranspiration Climate Database (https://doi.org/10.6084/m9.figshare.7504448.v3) with spatial resolution of 30 s. Climatic water deficit (CWD; mm $year^{-1}$) data were sourced from http://chave.ups-tlse.fr/pantropical_allometry.htm with spatial resolution of 2.5 minutes. Using ArcGIS (version 10.2, ESRI Inc.), the smoothing spline algorithm was applied to normalize the CWD raster data, with spatial resolution of 30 s (Hutchinson and Bischof, 1983).

Biotic factor data

Specific leaf area

In each sample plot, three standard trees of the dominant tree species, that showed vigorous growth and were free of diseases and insect pests, were randomly selected for calculation of the specific leaf area (SLA). One healthy branch was sampled from each standard tree in each cardinal direction, i.e., east, south, west and north, and 30 bundles of 1-year-old pine needles free of diseases and insect pests were selected on each branch (thus meeting the requirements of a large sample). The collected pine needles were placed between two pieces of moist filter paper, then separately sealed in ziplock bags and stored in a thermal box. After their transport to the laboratory, the pine needles were removed from the ziplock bag and moisture on the needle surface was quickly absorbed with filter paper. The saturated fresh weight was measured with a 1/10,000 electronic balance (PTX-FA300, Huazhi Scientific Instrument Co. Ltd., Fuzhou, China) and a digital vernier caliper (SDZ5-0-300, Fidelity Technology Co. LT., Beijing, China) with an accuracy of 0.01 mm was used to measure the leaf length (LL) and mid-point leaf width (LD) for each bunch of pine needles. The pine needles were then dried in an oven at 65°C for 72 h to constant weight and the dry weight was measured (Łukowski et al., 2022). The specific leaf area was calculated by *Equations 1–3*:

Single-sided arc surface area of larch pine needles:

$$S_{\text{arc}} = \pi \times LD \times LL / 2 \quad \text{(Eq.1)}$$

Area of single bunch of *L. gmelinii* pine needles:

$$S = 2\, S_{\text{arc}} + 2LD \times LL \quad \text{(Eq.2)}$$

$$\text{SLA (cm}^2\text{ kg}^{-1}\text{) = leaf area (cm}^2\text{) / leaf dry weight (kg)} \quad \text{(Eq.3)}$$

Leaf nitrogen content

Dried pine needles used for SLA estimation were ground into fine powder. Approximately 0.1 g of the powder was added to a certain volume of a sulfuric acid–hydrogen peroxide mixture (H_2SO_4–H_2O_2) and digested reaction at 160°C to transform the sample into inorganic components. The sample was then diluted to a certain volume with deionized water and filtered to remove unwanted ions and impurities. An elemental

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analyzer (Elemental Vario EL III, Germany) was used to detect the nitrogen content in the sample solution. The Kjeldahl nitrogen determination method (Ordoñez et al., 2009) was used to determine the leaf nitrogen content (LNC). The leaf nitrogen content was calculated by *Equation 4*:

$$\text{LNC (g kg}^{-1}\text{)} = \text{total nitrogen in leaves (g) / leaf dry weight (kg)} \qquad \text{(Eq.4)}$$

Leaf phosphorus content

Dried pine needles used for SLA estimation were ground into fine powder. Approximately 0.1 g of the powder was added to a certain volume of nitric acid–hydrogen peroxide mixture (HNO_3–H_2O_2) and digested at 160°C transform the sample into inorganic components. Such sample was diluted to a certain volume with deionized water and filtered to remove unwanted ions and impurities. A continuous flow analyzer (SKALAR San++, The Netherlands) was used to detect the phosphorus content in the sample solution. The molybdenum–antimony resistance colorimetric method (Ordoñez et al., 2009) was used to determine the leaf phosphorus content (LPC). The leaf phosphorus content was calculated by *Equation 5*:

$$\text{LPC (g kg}^{-1}\text{)} = \text{total phosphorus in leaves (g) / leaf dry weight (kg)} \qquad \text{(Eq.5)}$$

Shannon–Wiener index

Biodiversity is commonly considered as species diversity. In this study, the Shannon–Wiener diversity index (*H'*) was used to quantify species diversity (including trees, shrubs and herbs) in the sample plots. The formula for calculation of the Shannon–Wiener diversity index was as *Equation 6*:

$$H' = -\sum_{i=1}^{s} p_i \log p_i \qquad \text{(Eq.6)}$$

where p_i is the proportion of the number of individuals of species i in the sample plot relative to the total number of individuals, and s is the number of species in the sample plot.

Soil data

Soil sampling points were set at the four corners of each sample plot and the soil profile at the sampling point (30 cm × 30 cm × 30 cm) was excavated. The litter on the soil surface was removed and the soil for analysis was taken from two layers, namely, the 0–10 cm layer and the 10–20 cm layer. A total of eight soil samples were collected from each plot (1 plot × 2 soil depths × 4 replicates). The soil samples from the same depth in each plot were mixed to obtain two soil samples from the different depths. Visible plant contaminants and small stones were screened out with a sieve (2 mm mesh) and then the screened soil samples were placed into sterile plastic bags for testing. In addition, soil profiles were collected in four quadrats within each sample plot, using a ring cutter from the 0–10 cm layer and the 10–20 cm layer, for determining the soil bulk density. The soil bulk density (g cm^{-3}) was determined using the oven drying method (Bittelli et al., 2021). The soil pH was measured with a pH meter with a soil/water mass ratio of 1:5 (w/v). The total nitrogen (TN) content was determined using

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the semi-micro Kjeldahl digestion method (Pruden et al., 1985). The content of organic carbon (SOC) in the soil was measured using the Mebius method (Nelson and Sommers, 1983). The clay content (CLPC) was determined with a laser particle size analyzer (Mastersizer 2000, Malvern, UK) (Chen et al., 2021).

The uppermost 0–20 cm soil layer contains most of the biologically active carbon (Crowther et al., 2016), especially in brown coniferous forest soil in the cold-temperate zone, and can store up to 57% of the total soil carbon (Jobbágy and Jackson, 2000). Therefore, the soil organic carbon density (SOCD) in the 0–20 cm surface layer was estimated, using *Equation 7* (Li et al., 2022):

$$SOCD = \sum_{i=1}^{n} T_i \times p_i \times C_i \times (1 - \theta\%) / 100 \quad \text{(Eq.7)}$$

where SOCD (kg m^{-2}) is the organic carbon density of the soil profile, θ is the content of gravel > 2 mm (volume %), p_i is the soil bulk density (g cm^{-3}) of the ith layer of the soil, C_i is the organic carbon content of the ith layer density (g kg^{-1}), T_i is the soil thickness of the ith layer (cm), and n is the total number of soil layers involved in the calculation.

Stocking degree

The ratio of the basal area per hectare of the actual stands to the basal area per hectare of the standard stands under the same site conditions (Liu et al., 2020) was calculated using *Equation 8*:

$$P = \frac{\sum G_{site}}{\sum G_{standard}} \quad \text{(Eq.8)}$$

where P is the stocking degree, G_{site} (m^2 hm^{-2}) is the basal area per hectare of the actual stands, and G_{standard} (m^2 hm^{-2}) is the basal area per hectare of the standard stands. The basal area of the standard stands was obtained from a standard forest inventory table (Agriculture and Forestry Planning Team of Inner Mongolia Autonomous Region, 1974).

Statistical analysis

The correlations between various biotic and abiotic factors (stocking degree, average annual precipitation, clay content, soil organic carbon density, elevation, soil organic carbon content, climatic water deficit, solar radiation, precipitation in the warmest season, total nitrogen content of the soil, aridity index, annual average temperature, specific leaf area, leaf nitrogen content, leaf phosphorus content and Shannon–Wiener diversity index) and stand growth (carbon density in the tree layer, D_g and H_D) were analyzed using a method combining linear fitting and RDA. Linear fitting describes the linear correlation between a dependent variable and one or more independent variables. In this study, the linear correlation between the stand growth factors and environmental factors was explored using the linear fitting method. In this process, the linear fitting was performed with IBM SPSS Statistics 19.0 software and plotted with SigmaPlot 14.0. The RDA method is a multivariable direct gradient

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analysis approach that was developed based on multiple linear regression models and has been widely applied in many fields, such as ecology (Rozas et al., 2009) and soil science (Qi et al., 2016). This method combines multiple regression analysis with principal component analysis (van den Wollenberg, 1977). It can effectively detect the correlation between multiple response variables and multiple explanatory variables, and better handle the complex impact of environmental factors on the structure and function of forest ecosystems in nature. Using the Canoco 5.0 software, a RDA analysis was performed and a Monte Carlo permutation test was conducted to evaluate the significance of the factors affecting stand growth. Only environmental variables that passed the Monte Carlo test ($p < 0.05$) were retained for further analysis (Chen et al., 2020). The RDA sorting chart showed the correlations between the indicators and predictors. An angle between the environmental variable and the response variable vector of greater than 90° indicates a negative correlation between the two; an angle less than 90° indicates a positive correlation; and an angle equal to 90° indicates that there is no correlation between the two. In addition, the longer the vector for an environmental variable, the greater the significance of the impact of the environmental variable on stand growth.

Results

Impact of biotic and abiotic factors on growth of Larix gmelinii forests in the Greater Khingan Mountains

Impact on stand average diameter at breast height

With increase in stocking degree and solar radiation, the average diameter at breast height of the *L. gmelinii* stands increased significantly ($p < 0.05$, *Fig. 3*). With increase in climatic water deficit, precipitation in the warmest season and aridity index, the average diameter at breast height showed a downward trend. Clay content, soil organic carbon density, soil organic carbon content, total nitrogen content of the soil and annual average temperature significantly ($p < 0.05$) affected the average diameter at breast height, but no obvious trend to increase or decrease was observed. The correlations of average diameter at breast height with specific leaf area, leaf nitrogen content, leaf phosphorus content, average annual precipitation, elevation, and Shannon–Wiener diversity index were not significant ($p > 0.05$).

Impact on stand average tree height

With increase in soil organic carbon content and aridity index, the average tree height of the stands increased (*Fig. 4*). Among these factors, soil organic carbon content had the most highly significant impact on the change in average tree height ($p < 0.05$). With increase in precipitation in the warmest season, annual average temperature, leaf nitrogen content, and leaf phosphorus content, the average tree height showed a downward trend. With increase in solar radiation, the average tree height showed an initial increase and a subsequent decreasing trend. Clay content, soil organic carbon density, climate water deficit, and total soil nitrogen content had a significant impact on average tree height ($p < 0.05$), but no obvious trend for increase or decrease in the average tree height of the stands with change in these factors was observed. Average annual precipitation, elevation, stocking degree, specific leaf area,

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and Shannon–Wiener diversity index had no significant impact on the average tree height ($p > 0.05$).

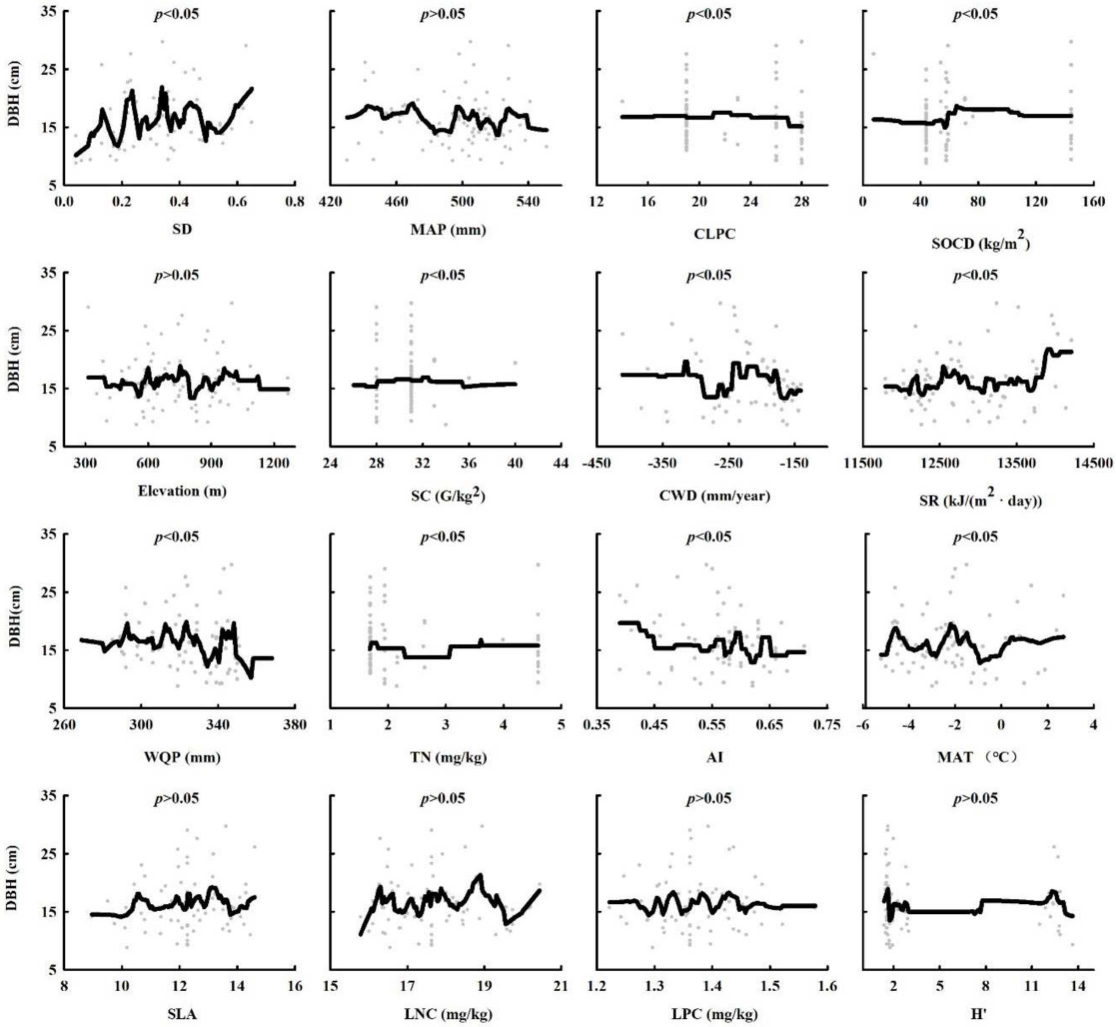

Figure 3. *Correlation between biotic and abiotic factors and average diameter at breast height in the tree layer of Larix gmelinii forests on the Greater Khingan Mountains. DBH, average diameter at breast height of the stands; MAT, average annual temperature; MAP, average annual precipitation; SR, solar radiation; WQP, precipitation in the warmest season; AI, aridity index; CWD, climatic water deficit; CLPC, clay content; SC, soil organic carbon content; TN total nitrogen content of soil; SOCD, soil organic carbon density; Elevation, elevation; SD, stocking degree; SLA, specific leaf area; LNC, leaf nitrogen content; LPC, leaf phosphorus content; H', Shannon–Wiener diversity index*

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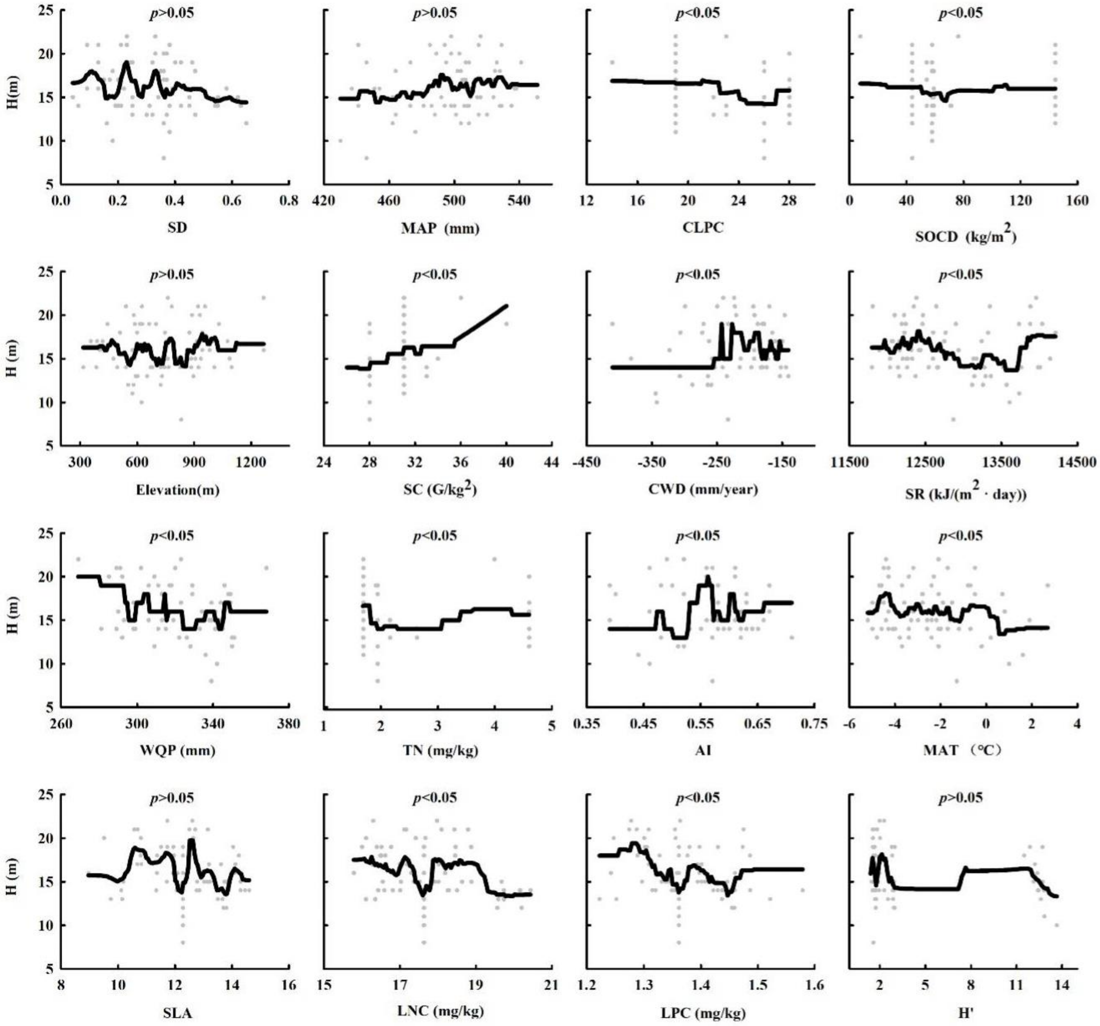

Figure 4. *Correlation between biotic and abiotic factors and average tree height in the tree layer of Larix gmelinii forests on the Greater Khingan Mountains. H, average height of the stands; MAT, average annual temperature; MAP, average annual precipitation; SR, solar radiation; WQP, precipitation in the warmest season; AI, aridity index; CWD, climatic water deficit; CLPC, clay content; SC, soil organic carbon content; TN total nitrogen content of soil; SOCD, soil organic carbon density; Elevation, elevation; SD, stocking degree; SLA, specific leaf area; LNC, leaf nitrogen content; LPC, leaf phosphorus content; H', Shannon–Wiener diversity index*

Impact on carbon density in the tree layer

Significant differences were observed in the response of carbon density in the tree layer to different biotic and abiotic factors. The carbon density in the tree layer increased significantly with increase in stocking degree, elevation, solar radiation, and leaf nitrogen content ($p < 0.05$, *Fig. 5*). Among these factors, the carbon density showed the strongest increase with increase in stocking degree (maximum slope), which indicated that stocking degree had the strongest impact on the stand carbon density. The carbon density decreased significantly with decrease in soil organic carbon content and climatic water deficit ($p < 0.05$), and also declined with decrease in soil organic carbon density, aridity index and precipitation in the warmest season but the degree of decrease

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was relatively small; thus, soil organic carbon density and aridity index had little impact on the carbon density of *L. gmelinii* forests. The correlations of stand carbon density with annual average precipitation, specific leaf area, leaf phosphorus content, and Shannon–Wiener diversity index were not significant ($p > 0.05$).

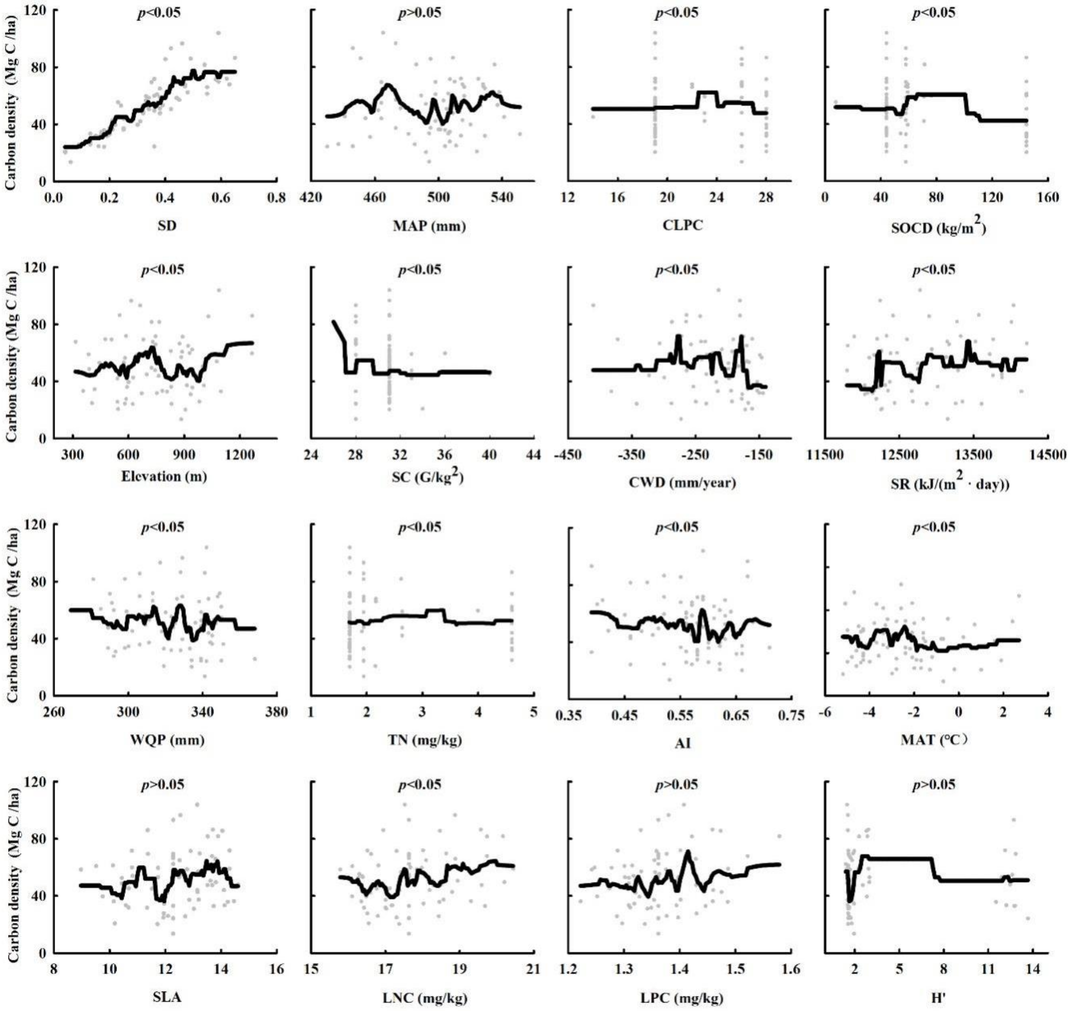

Figure 5. *Correlation between biotic and abiotic factors and carbon density of the tree layer in Larix gmelinii forests on the Greater Khingan Mountains. Carbon density, carbon density in the tree layer; MAT, average annual temperature; MAP, average annual precipitation; SR, solar radiation; WQP, precipitation in the warmest season; AI, aridity index; CWD, climatic water deficit; CLPC, clay content; SC, soil organic carbon content; TN total nitrogen content of soil; SOCD, soil organic carbon density; Elevation, elevation; SD, stocking degree; SLA, specific leaf area; LNC, leaf nitrogen content; LPC, leaf phosphorus content; H', Shannon–Wiener diversity index*

Redundancy analysis of the correlation between biotic and abiotic factors with stand growth

Using the RDA method, the growth indicators for *L. gmelinii* forests (carbon density in tree layer, D_g and H_D) and the sixteen predictors were sorted. The eigenvalues of the first four axes in the sorting (*Table 2*) as well as correlations between the predictors with the

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sorting axis were obtained (*Table 3*). Based on the sorting results, the correlation coefficient between first axis and factors was 0.89 and that on the second axis was 0.59. Thus, the sorting results were considered to be reliable. The correlation between the combined variables of environmental factors represented by the first and second sorting axes and stand growth was significant ($p < 0.05$). The contribution of the sixteen factors to stand growth was 76.90%, the cumulative explanation of the total variation by the first four axes was 96.12%, and that of the first and second axes was 76.20%. Therefore, the first and second axes in the RDA could be used to explain the growth of *L. gmelinii* forests in the Greater Khingan Mountains. The results of the Monte Carlo permutation test showed that stand growth was significantly correlated with stocking degree, clay content, elevation, soil organic carbon content, aridity index, precipitation in the warmest season, solar radiation and average annual precipitation ($p < 0.05$, *Table 3*).

Table 2. *Summary statistics for each redundancy analysis axis*

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.7444	0.0176	0.0071	0.1921
Explained variation (cumulative)	74.44	76.2	76.91	96.12
Pseudo-canonical correlation	0.8942	0.5853	0.6333	0
Explained fitted variation (cumulative)	96.79	99.08	100	0

Table 3. *Correlation of predictors with redundancy analysis axes and Monte Carlo premutation test results*

Name	Explains %	Pseudo-*F*	*p*
Stocking degree	11.2	10.4	0.002
Clay content	5.4	5.7	0.018
Elevation	4.6	5.2	0.016
Soil organic carbon content	4.5	5.5	0.016
Aridity index	3.9	5.4	0.016
Climatic water deficit	1	2.4	0.094
Precipitation in the warmest season	0.7	4.3	0.014
Shannon-Wiener Diversity Index	0.7	1.8	0.17
Leaf nitrogen content	0.7	1.6	0.204
Leaf phosphorus content	0.6	1.5	0.234
Total soil nitrogen content	0.6	1.4	0.188
Average annual temperature	0.5	1.2	0.326
Soil organic carbon density	0.4	1.1	0.304
Specific leaf area	0.4	1.1	0.288
Solar radiation	0.3	3.8	0.362
Average annual precipitation	0.2	4.1	0.287

The vectors for stocking degree, solar radiation, leaf nitrogen content, leaf phosphorus content, clay content, aridity index, precipitation in the warmest season, and soil organic carbon content were longer than those for the other predictors (*Fig. 6*), indicating that these eight factors had the strongest impact on the growth of *L. gmelinii* forests. Among these predictors, the angles between stocking degree and carbon density, average diameter

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at breast height and solar radiation, and average tree height and soil organic carbon content were small and the vector directions were consistent (*Fig. 6*). The RDA analysis thus verified that stocking degree, solar radiation, and soil organic carbon content had a significant positive correlation with the growth indicators ($p < 0.05$).

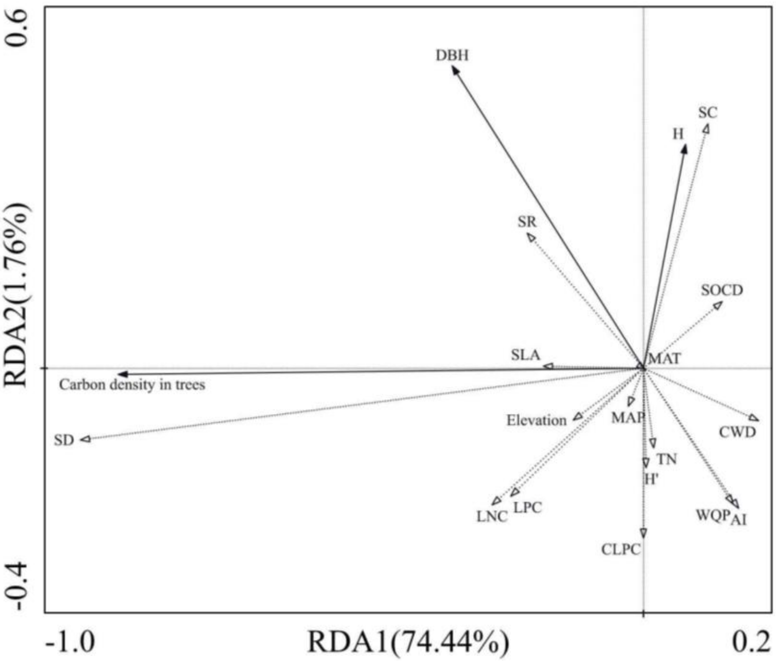

Figure 6. *Redundancy analysis plot of the impact of 16 predictors on stand growth of Larix gmelinii forests on the Greater Khingan Mountains. Carbon density in trees, carbon density in the tree layer; DBH, average diameter at breast height of the stands; H, average height of the stands; MAT, average annual temperature; MAP, average annual precipitation; SR, solar radiation; WQP, precipitation in the warmest season; AI, aridity index; CWD, climatic water deficit; CLPC, clay content; SC, soil organic carbon content; TN total nitrogen content of soil; SOCD, soil organic carbon density; Elevation, elevation; SD, stocking degree; SLA, specific leaf area; LNC, leaf nitrogen content; LPC, leaf phosphorus content; H', Shannon–Wiener diversity index*

Discussion

In the current research on the correlation between the carbon density in the tree layer and the stand density of *L. gmelinii* forests, the density of the stands was mostly considered as the tree density, through which the carbon density in the tree layer of *L. gmelinii* forests was assessed. However, the tree density does not truly reflect the carbon density in the tree layer of forests (Litton et al., 2004). The reason is that the carbon density in the tree layer differs when the average diameter of the trees in a natural forest differs, although the number of trees per unit area is identical. The size of forest trees may reflect the stocking degree of the stand, which is a relatively stable indicator for the density of the stands and is less strongly correlated with site conditions and stand age (Liu et al., 2020). The present analysis of the linear correlation between environmental factors and the growth of *L. gmelinii* forests revealed there is a significant ($p < 0.05$) positive correlation between stocking degree and carbon density in the tree layer (*Fig. 5*). The RDA results further confirmed the linear correlation results. Stocking degree was most strongly correlated with the carbon density in the tree layer, and the

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latter was enhanced with increase in the former (*Fig. 6*). Liu et al. (2020) reported that the inclusion of stocking degree significantly improves the accuracy of a stem taper model for *L. gmelinii*. A model that includes stocking degree can reflect the changes in shape along an entire trunk of *L. gmelinii*. The stocking degree is associated with the basal area and stock volume of the stand (Skovsgaard, 2009), and further affects the biomass and carbon density in the tree layer. The findings of Liu et al. (2020) confirm the reliability of the present results from a mechanistic perspective. Of course, if the research focus is an artificial forest, the number of trees per unit area is similar or uniform, the average diameter of the forest trees shows limited variation, and variation in the carbon density in the tree layer is relatively small, then the tree density may be selected as an indicator to reflect the carbon density in the tree layer. For example, previous studies (Gevaña et al., 2017; Wirabuana et al., 2021) have reported that, as the stand density increases, the carbon stock in the tree layer will also gradually increase.

The present RDA showed that solar radiation was most strongly correlated with the average diameter at breast height of the stands (D_g), and that the average diameter at breast height increased with the increase in solar radiation (*Fig. 6*). This finding is consistent with the conclusion drawn by Dong et al. (2012) that the stand growth rate is positively correlated with changes in the incident solar radiation. Tian et al. (2018) revealed that heat and water status are strongly correlated with indicators of tree growth, and that solar radiation, as the driving force of heat and water status, is strongly associated with the regulation of physiological processes, such as tree leaf stomatal opening and photosynthesis. *L. gmelinii* forests are mainly affected by the cold-temperate continental monsoon climate. The growing season is short, usually from June to October. During this period, light energy utilization peaks between 06:00 and 07:00 in the morning and between 17:00 and 19:30 in the evening, which are the periods when *L. gmelinii* absorbs solar radiation and converts it into organic dry matter most efficiently (Zhou, 2011). In addition, due to the abundant rainfall in this climatic zone, cloudy and rainy days are more frequent during the rainy season from June to August, which increases the incidence of scattered and reflected radiation, and the water vapor pressure deficit is smaller and the light energy utilization rate is higher (Urban et al., 2007), which are conducive to growth of *L. gmelinii* forests.

The RDA results also showed that the average tree height was most strongly correlated with soil organic carbon content, and the tree height increased with the increase of the latter (*Fig. 6*). This finding confirmed the results of Wang et al. (2013). A possible reason is that increase in the soil organic carbon content is conducive to improvement of the soil quality and increase in soil fertility, which in turn would promote the growth of *L. gmelinii* forests. Previous research has shown that the soil nutritional status is crucial for the growth of *L. gmelinii* forests, and that the soil nitrogen and phosphorus contents have a strongly promotive effect on stand growth (McNab, 1989). Compared with other regions, the soil organic carbon content is higher in the region where *L. gmelinii* forests are located. The temperature in this region is relatively low and microbial activity is suppressed, which is conducive to the accumulation of organic matter (Oades, 1988) The organic carbon in the soil in this region is mainly concentrated in the surface layer (0–10 cm depth), which is more conducive to the growth of *L. gmelinii* forests, which have shallow root systems. In addition, the soil organic carbon content is relatively high in the region where *L. gmelinii* forests are located, and their living environment is relatively superior. The better the site conditions are, the higher the average tree height of the stand will be

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(West, 2009). The present finding that the soil organic carbon content showed a significant positive correlation with average tree height further supports this statement.

The present study clarified the impacts of sixteen biotic and abiotic factors, and the nature of their influence on the growth of *L. gmelinii* forests. Stocking density was most strongly correlated with the carbon density in the tree layer of *L. gmelinii* forests, solar radiation was most strongly correlated with the average diameter at breast height of the stands, and soil organic carbon content was most strongly correlated with the average tree height of the stands. By optimizing the management of the stocking density, the carbon density in the tree layer of *L. gmelinii* forests can be increased, thereby promoting carbon accumulation, which is of practical importance for sustainable forest management.

Conclusions

There was a significant positive correlation between stocking degree and the carbon density of *L. gmelinii* forests, indicating that stocking degree is a primary driver of changes in carbon density. This study provides a basis for optimizing the carbon storage capacity of forest ecosystems by adjusting stand stocking degree. Solar radiation had the most significant effect on DBH among the environmental factors and was positively correlated with increased radiation intensity. Additionally, our findings establish a substantial positive correlation between soil organic carbon content and average tree height in the forests, underscoring the benefits of increasing soil organic carbon content for the growth of *L. gmelinii* forests. Our results suggest that the growth of *L. gmelinii* forests is influenced not only by stocking degree but also by environmental conditions such as water, heat, and soil. However, it remains unclear whether trees with an average DBH beyond the current study range (5–35 cm) can maintain similar relationships with these environmental factors. Further expanded studies are necessary to better understand the complex interactions between forest growth and environmental factors.

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APPENDIX

Analysis of the dominant factors that influence growth of *Larix gmelinii* forests

Table A1. *The GPS positions and the elevations of the sampling sites*

Sample plot	Longitude (°)	Latitude (°)	Elevation (m)	Sample plot	Longitude (°)	Latitude (°)	Elevation (m)	Sample plot	Longitude (°)	Latitude (°)	Elevation (m)
1	124.3565	53.20109	362	26	124.2128	49.90789	332	51	121.5101	50.93967	830
2	125.2366	53.07754	417	27	122.4485	49.52086	592	52	121.5112	50.93522	830
3	125.6913	52.99045	242	28	123.2865	49.51986	441	53	121.185	50.82863	777
4	124.2214	52.68235	582	29	124.0619	49.32595	399	54	121.8915	50.72069	846
5	125.0161	52.50539	362	30	122.2989	48.96628	914	55	122.1691	51.35872	884
6	125.8554	52.45775	355	31	123.3565	49.04511	403	56	121.2882	51.38182	999
7	126.2322	52.16718	347	32	123.8718	48.78236	289	57	122.2076	51.77762	792
8	123.2463	52.21472	643	33	122.1928	48.44929	495	58	122.3923	52.31211	745
9	124.0509	52.15224	498	34	123.0218	48.35962	401	59	122.5545	52.90025	487
10	124.9391	52.03751	475	35	123.7871	48.24497	274	60	123.3338	52.85719	580
11	125.7564	51.94249	366	36	122.0335	47.89404	509	61	123.5555	53.34906	352
12	126.5061	51.78456	293	37	122.8169	47.80226	277	62	122.6914	53.36755	540
13	123.0382	51.89877	944	38	120.7081	49.17707	762	63	121.4007	53.0228	460
14	123.8825	51.61082	706	39	121.3836	49.06698	740	64	120.0591	52.76949	417
15	124.6865	51.54111	574	40	121.3363	48.51459	981	65	121.76	53.32249	652
16	125.7345	51.35214	434	41	120.6647	47.28301	1097	66	120.8355	52.59416	492
17	123.8577	51.07355	670	42	119.9947	47.331	965	67	120.8708	53.0611	622
18	123.9258	51.04697	560	43	120.6427	47.5263	1087	68	121.4504	52.26584	716
19	124.4692	50.9044	544	44	121.3788	47.53164	613	69	121.4746	51.88671	862

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20	125.3149	50.81602	420	45	122.022	47.60896	477	70	120.444	51.46065	574
21	122.7866	50.65471	601	46	121.2396	47.95311	744	71	120.8401	51.96671	457
22	123.5743	50.50325	451	47	121.632	48.07374	941	72	119.8033	50.67459	680
23	124.3528	50.40597	416	48	121.0752	49.91167	831	73	120.1713	50.75993	743
24	122.5167	50.11989	586	49	121.631	49.65242	771	74	120.2438	50.37731	732
25	123.3901	50.03712	443	50	121.8085	50.14538	884	75	120.8675	50.37238	662

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