

Climate Change Effects On Height-Diameter Allometric Relationship Vary With Tree Species And Size For Larch Plantations In Northern And Northeastern China

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1 **Climate change effects on height-diameter allometric relationship vary with tree**
2 **species and size for larch plantations in northern and northeastern China**

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10 **Abstract:**

11 **Background:** Tree height-diameter relationship is very important in forest investigation, understanding
12 forest ecosystem structure and estimating carbon storage. Climate change may modify the relationship.
13 However, our understanding of the effects of climate change on height-diameter allometric growth is still
14 limited at large scale.

15 **Methods:** In this study, we explore how the climate change effects on height-diameter allometric
16 relationship vary with tree species and size for larch plantations in northern and northeastern China.
17 Based on the repeated measurement data of 535 plots from the 6th to 8th national forest inventory of
18 China, climate-sensitive tree height-diameter models of *Larix* plantations in north and northeast China
19 were developed by two-level nonlinear mixed effect (NLME) method. The final model was used to
20 analyze the height-diameter relationship of different *Larch* species under RCP2.6, RCP 4.5, and RCP8.5
21 climate change scenarios from 2010 to 2100.

22 **Results:** The values of R_{adj}^2 (adjusted coefficient of determination), MAE (mean absolute error) and
23 RMSE (root mean squared error) of the NLME models for calibration data were 0.92, 0.76m and 1.06m,
24 respectively. The inclusion of climate variables MAT (Mean annual temperature), CMD (Hargreaves
25 climatic moisture deficit) with random effects was able to increase R_{adj}^2 by 19.5% and reduce the AIC
26 (Akaike's information criterion), MAE and RMSE by 22.2%, 44.5% and 41.8%, respectively. The
27 climate sensitivity was ranked as *L. gmelinii* > the unidentified species group > *L. pincipis-rupprechtii* >
28 *L. kaempferi* > *L. olgensis* under RCP4.5, but *L. gmelinii* > *L. pincipis-rupprechtii* > the unidentified
29 species group > *L. olgensis* > *L. kaempferi* under RCP2.6 and RCP8.5.

30 **Conclusion:** According to the climate sensitivity, tree species could be classified as group I(*L. gmelinii*,
31 *L. principis-rupprechtii* and the unidentified species group) with large ΔH (from -4.77% to 18.17%) and
32 group II (*L. kaempferi* and *L. olgensis*) with small ΔH (from -6.37% to 9.4%). Large trees were more
33 sensitive to climate change than small trees.

34 **Key words:** nonlinear mixed-effects model; height-diameter model; climate change; climate-sensitive
35 growth model

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37 **Background**

38 Tree height-diameter (H-D) models are one of the most useful tools in forest management. Because
39 tree height measurement is time-consuming, expensive and difficult in over-crowded and dense forests, a
40 small number of trees are typically subsampled in practice to measure tree height, while D is measured
41 precisely for all trees in a plot (Zell 2018). Thus, H-D models are often constructed to predict missing
42 total height measurements for the rest of the trees. Numerous H-D models have been developed (Fang
43 and Bailey 1998; Huang, Price et al. 2000; Jayaraman and Zakrzewski 2001; Calama and Montero 2004;
44 Sharma and Yin Zhang 2004; Sharma and Parton 2007; Kroon, Andersson et al. 2008; Hulshof, Swenson
45 et al. 2015; Zang, Lei et al. 2016; Zell 2018; Zhang, Chhin et al. 2019; Bronisz and Mehtätalo 2020;
46 Ciceu, Garcia-Duro et al. 2020; Santiago-García, Jacinto-Salinas et al. 2020; Zhang, Sajjad et al. 2020).
47 Models showed that the H-D relationship was context-dependent, and dependent on genetic
48 characteristics (Kroon, Andersson et al. 2008), stand age (Sánchez, Varela et al. 2003), site condition
49 (Sharma and Yin Zhang 2004; Sharma and Parton 2007; Krisnawati, Wang et al. 2010; Zhang, Sajjad et
50 al. 2020), competition status (Calama and Montero 2004; Sharma and Yin Zhang 2004; Sharma and
51 Parton 2007; Ciceu, Garcia-Duro et al. 2020), silvicultural treatment (Saunders and Wagner 2008;
52 Russell, Amateis et al. 2010) and climate (Wang, Fang et al. 2006; Hulshof, Swenson et al. 2015; Fortin,
53 Van Couwenberghe et al. 2019; Zhang, Chhin et al. 2019).

54 Under the background of global change, the effects of climate change on forest growth were attained
55 great concerns (Hasenauer, Nemani et al. 1999; Kirschbaum 2000; Yang, Watanabe et al. 2006; Hartl-
56 Meier, Dittmar et al. 2014; Charney, Babst et al. 2016). However, how climate change alerts H-D
57 relationships has only recently been considered (Albert and Schmidt 2010; Hulshof, Swenson et al. 2015;

58 Fortin, Van Couwenberghe et al. 2019; Zhang, Chhin et al. 2019; Ng'andwe, Chungu et al. 2021). For
59 example, Hulshof, Swenson et al. (2015) developed mixed-effects models to test H-D allometric
60 differences due to climate and functional groups, and models showed that temperature, and some extent
61 precipitation, in part explained tree allometric variation. Climate variables can significantly explain the
62 variation of the relationship between tree height and diameter, and adding climate variables can improve
63 the prediction practicability of the model in the context of climate change. Zhang, Chhin et al. (2019)
64 developed tree level NLME model to explore height-diameter allometry of Chinese fir in relation to
65 climate and found that temperature was a key climate factor shaping height-diameter allometry, and
66 showed that tree heights increased with increasing mean annual temperature. Fortin, Van Couwenberghe
67 et al. (2019) developed generalized H-D models of 44 tree species across France and found that the
68 temperature effect was significant for 33 species and the precipitation effect was significant only for 7
69 species. They estimated that two-thirds of climate sensitive species are expected to be generally shorter
70 under RCP2.6 scenario.

71 However, the direction and magnitude of climatic effects on H-D relationships has further exploration
72 space. For example, Hulshof, Swenson et al. (2015) showed that the coefficient of MAT was negative
73 but the model developed by Zhang, Chhin et al. (2019) showed MAT has positive effects on H-D
74 allometry. Feldpausch, Banin et al. (2011) found that annual precipitation coefficient of variation, dry
75 season length, and mean annual air temperature were key drivers of variation in H-D allometry at the
76 pantropical and region scales. Ng'andwe, Chungu et al. (2021) found that temperature negatively
77 modulate H-D allometry in *Pinus merkusii* and *P. michoacana* in Zambia. Furthermore, how these
78 climatic effects differ among tree species and sizes of Larch are not well understood. The climate effects
79 on H-D relationship are likely to have an impact on tree stability, height estimation, yield prediction and
80 forest management decision, thus making it necessary to examine it under climate change.

81 Larch is an economically and ecologically important genus of tree species in China, especially in the
82 northern and northeastern Provinces. The area and volume of larch forests in Chinese forests amount to
83 6.50 and 6.77 per cent, respectively (State Forestry Administration 2014). Both empirical and process-
84 based models found that future climate change would affect stand growth, productivity, and biological
85 rotation of larch plantations (Shen, Lei et al. 2015; Lei, Yu et al. 2016; Zang, Lei et al. 2016; Xie, Wang
86 et al. 2017; Xie, Lei et al. 2020), but how climate change will modify the H-D relationship is unknown
87 yet. Therefore, the objectives of the study were: 1) to develop a climate-sensitive H-D model for larch

88 plantations in north and northeast China; 2) to examine the effects of future climate change on H-D
89 relationship among larch species and tree sizes. Quantifying the effects of climate change will help better
90 understand the H-D allometric relationship and adaptive forest management under climate change.

91 **Methods**

92 **Tree height-diameter Data**

93 Tree H-D data used in this study were from 6th (year 2000), 7th (year 2005) and 8th (year 2010)
94 National Forest Inventories in 7 provinces (Beijing, Hebei, Shanxi, Liaoning, Jilin, Heilongjiang, and
95 Inner Mongolia) in north and northeast China. We selected only pure larch plantation plots to develop
96 the H-D model. The larch species presented in these plots are *L. gmelinii.*, *L. olgensis*, *L. kaempferi*, *L.*
97 *principis-rupprechtii*. In addition, there were trees not identified to specific species which were
98 recorded as larch. According to the protocol of NFI, heights of 3-5 medium trees were measured in each
99 plot. In total, 7304 pairs of H-D measurements in 535 plots were obtained across seven Provinces. Data
100 were split into two parts for model calibration and validation by the following method: each plot was
101 randomly allocated to a number between 1 and 535, and plots whose number were less than 20th
102 percentile of all plots were assigned as validation data (1609 pairs in 107 plots) and the rest were fitting
103 data (5695 pairs of H-D measurements in 428 plots). Summary statistics of tree and stand variables can
104 be found in Table 1. The scatter plot can be found in Figure 1.

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Table 1 Summary statistics for tree and stand variables by Provinces

Data	Province	Number of Plots	Number of tree observat ions	D (cm)	H (m)	AGE (a)	N (trees•ha ⁻¹)	BA (m ² •ha ⁻¹)
Calibr ation	Beijing	7	37	14.7(4.6)	9.3(2.3)	32.9(10.6)	561.9(418.5)	9.1(9.9)
	Hebei	72	3326	10.7(4.5)	7.9(2.2)	21.7(6.7)	1072.6(540.9)	9.3(7.3)
	Heilongjiang	96	706	14.5(5.3)	13(3.9)	27.9(9.7)	653.9(520.5)	4.6(4.6)
	Jilin	132	1058	12.9(4.7)	11.4(4.4)	25.2(9.9)	1032.2(565.3)	9.0(5.6)
	Liaoning	52	406	14.4(4.8)	13.5(4.5)	23.6(10.2)	1292.3(631.7)	13.5(8.6)
	Inner Mongolia	35	188	12.2(3.7)	10.1(3.2)	25.8(7.1)	855.1(617.7)	8.0(6.4)
	Shanxi	34	195	11.1(3.1)	8.7(2.8)	26.5(9.3)	1297.8(627.3)	9.4(7.7)
	total	428	5916	11.9(4.8)	9.6(3.8)	23.6(8.5)	977.2(610.6)	8.5(6.9)
Valida tion	Beijing	3	18	12.6(1.7)	9.2(1.6)	25.8(3.1)	816.8(469.2)	11.5(10.7)
	Hebei	12	620	11.4(3.8)	8.9(2.3)	24.8(7.6)	994.9(607.2)	8.5(5.4)
	Heilongjiang	27	193	15.2(5.0)	13.1(3.8)	29.5(9.8)	559.3(548.7)	6.0(6.3)
	Jilin	38	351	13.5(4.4)	11.9(4.0)	28.4(11.1)	904.2(532.9)	8.2(4.9)
	Liaoning	12	97	12.2(4.5)	11.3(5.4)	23.2(9.3)	1207.8(651.1)	17.7(7.0)
	Inner Mongolia	11	53	11.1(4.4)	9.1(4.1)	28(9.9)	1135.5(835.4)	7.3(6.4)
	Shanxi	4	21	9(1.8)	6.7(2.0)	17.9(4.2)	848.6(622.8)	7.3(6.3)
	total	107	1353	12.5(4.4)	10.4(3.8)	26.3(9.4)	902.6(626.8)	8.6(6.8)

120 Note: D, diameter at breast height; H, tree height; N, tree number per hectare; BA, basal area per hectare;
121 the numbers within parentheses are the standard deviation.

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123 **Figure 1 Scatter plot of tree height-diameter allometry by Larch species in 7 provinces.**

124 **Climate data**

125 The current climatic data for model calibration were downloaded from ClimateAP, which is an
126 application for dynamic local downscaling of historical and future climate data in Asia Pacific (Wang,
127 Wang et al. 2017). Seasonal and annual climate variables (averaged from 1980 to 2010) for a plot were
128 produced based on latitude, longitude, and elevation (Table 2).

Table 2. Descriptions of the candidate climatic variables

Variable	Description
AHM	Annual heat:moisture index
CMD	Hargreaves climatic moisture deficit
DD_0	Degree-days below 0°C
DD_18	Degree-days below 18°C
DD18	Degree-days above 18°C
DD5	Degree-days above 5°C
EMT / °C	Extreme minimum temperature over a 30-year period
EXT / °C	Extreme maximum temperature over a 30-year period
EREF	Hargreaves reference evaporation
MAP / mm	Mean annual precipitation (mm)
MAT / °C	Mean annual temperature
MCMT / °C	Mean coldest month temperature
MWMT / °C	Mean warmest month temperature
NFFD	The number of frost-free days
PAS / mm	Precipitation as snow between August in previous year and July in current year
TD / °C	Temperature difference between MWMT and MCMT, or continentality

130 For projections of future H-D relationship under expected climate change, we used the latest climate-
131 change scenarios of the 5th Assessment Report from the IPCC using a downscaled global climate model
132 (GCM) applied in three representative concentration pathways (RCPs), RCP2.6, RCP4.5, and RCP8.5
133 (Van Vuuren, Edmonds et al. 2011). These pathways represent the scenarios with low, medium and high
134 concentrations of greenhouse gases and predictive radiative forcing. The GCM model for future climate
135 scenarios used in the study was CNRM-CM5 (The Centre National de Recherches Météorologiques
136 Coupled global climate Model) (Voldoire, Sanchez-Gomez et al. 2013). Future climate data for the time
137 periods 2025 (average for 2010-2040), 2055 (average for 2040-2070) and 2085 (average for 2070-2100)
138 were also downloaded from the ClimateAP.

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142 **Selection of climate variables**

143 Principal Component Analysis (PCA) (Wold, Esbensen et al. 1987) can be an exploratory method used
144 for evaluation of the climatic variability and can be robust as an auxiliary technique when used in
145 combination with other statistical techniques (Scolforo, Maestri et al. 2013). We first used PCA method
146 to analyze the data for all climate variables. Owing to climate variables with different units, all variables
147 were standardized prior to PCA. Components explaining more than 80% of the variance were retained.
148 For each component, variables with large loading were selected for further analysis. These variables with
149 strong correlations with H and the least multicollinearity among them were served as options for
150 modelling.

151 **Basic H-D models**

152 The basic H-D model was from Zang et al. (2016) for the same tree species in the region and modified
153 as Eq. (1) which was a generalized H-D model with the inclusion of competition effects besides tree
154 diameter.

$$155 \quad H = 1.3 + (a_0 + a_1 BAL) \times (1 - \exp(-(b_0 + b_1 BAL) \times D))^c + \varepsilon \quad (1)$$

156 Where H is the total tree height (m), D is the diameter at breast height (cm), BAL is the sum of basal
157 area larger than a subject tree, a_0 , a_1 , b_0 , b_1 and c are model parameters, which have their own
158 biological characteristics, and ε is random error.

159 To evaluate the differences in height-diameter allometry among larch species, dummy variables S_m
160 were created: (1) $S_1 = 1$ denotes the *L. gmelinii*. and 0 the rest of cases; (2) $S_2 = 1$ denotes the *L.*
161 *olgensis* and 0 the rest of cases; (3) $S_3 = 1$ denotes the *L. principis-rupprechtii*. and 0 the rest of cases;
162 (4) $S_4 = 1$ denotes the *L. kaempferi*; and (5) the category which can not be identified was represent by
163 $S_1 = S_2 = S_3 = S_4 = 0$ as the reference.

164 Therefore, the model could be written as:

$$165 \quad H = f(\beta, S_m, D, BAL) + \varepsilon \quad (2)$$

166 Where β is the fixed-effect parameter vector, S_m was dummy variable denoting tree species, and
167 other variables are defined as above.

168 Nonlinear mixed-effects climate-sensitive H-D model

169 To quantify the climatic effects on the H-D allometry, the selected climate variables were added into
 170 the model by reparameterization for parameters in basic H-D model, and it could be written as:

$$171 \quad H = f(\beta, BAL, Climate, S_m, D) + \varepsilon \quad (3)$$

172 Where *Climate* was the climate variable vector selected by PCA and correlation analysis, and other
 173 variables were the same as mentioned above.

174 Owing to the correlated H-D observations in plots violating the principle of independence of error
 175 terms and the strong predictive ability of mixed effects model in forestry data (Calama and Montero 2004;
 176 Sharma and Parton 2007), the nonlinear mixed effected model can be an appropriate way to develop the
 177 climate sensitive H-D model which can be written as:

$$178 \quad H_{ijk} = f(\beta, D_{ijk}, BAL, Climate, S_m, u_i, u_{ij}) + \varepsilon_{ijk} \quad (4)$$

$$179 \quad u_i \sim N(0, \sigma_{province}^2), \quad u_{ij} \sim N(0, \sigma_{plot}^2).$$

180 Where H_{ijk} and D_{ijk} is the k^{th} individual tree height nested within j^{th} plot in the i^{th} province,
 181 u_i and u_{ij} is the province- and plot-level random effects, and ε_{ijk} is the random error. Other variables
 182 were the same as mentioned above.

183 The estimated random effect parameter u_i were calculated as follows:

$$184 \quad \hat{u}_i = \hat{\Psi} \hat{Z}_i^T (\hat{Z}_i \hat{\Psi} \hat{Z}_i^T + \hat{R}_i)^{-1} e_i \quad (5)$$

185 Where \hat{u}_i is the estimated prediction vector for random parameters, $\hat{\Psi}$ is the estimated $q \times q$
 186 variance-covariance matrix for among-unit variability, where q is the number of random effects
 187 parameters in the model, \hat{R}_i is the estimated $k \times k$ variance-covariance matrix for within-unit
 188 variability, \hat{Z}_i is the partial derivatives matrix with respect to the random parameters and e_i is the
 189 residual vector determined by the difference between the observed and predicted heights using model
 190 which only has fixed effects.

191 To account for the within-unit heteroscedasticity and autocorrelation in variance-covariance matrix
 192 (R_i), the variance-covariance matrix was determined as:

$$193 \quad R_i = \sigma^2 G_i^{0.5} \Gamma_i G_i^{0.5} \quad (6)$$

194 Where σ^2 is the value of residual variance of the estimated model, G_i is a diagonal matrix
 195 explaining the variance of within unit heteroscedasticity, Γ_i is a diagonal matrix accounting for within
 196 tree autocorrelation structure of errors, and AR(1) was used to reflect the within-tree autocorrelation

197 structure of errors for matrix Γ_i . To reduce the heterogeneity in variance, the variance power equation
 198 was determined as:

$$199 \quad \text{var}(\varepsilon_{ijk}) = \sigma^2 \widehat{H}_{ijk}^{2\gamma} \quad (7)$$

200 where, \widehat{H}_{ijk} is the estimated height of k^{th} tree nested in j^{th} plot in i^{th} province using fixed part
 201 of the mixed-effects model; γ is the parameter to be estimated; and σ^2 is the same as defined in Eq.6.
 202 Parameters in NLME models were estimated by restricted maximum likelihood implemented with ‘nlme’
 203 package in R software (Pinheiro, Bates et al. 2013).

204 When a new subject is available(for example, the one in the validation set), the model needs to be
 205 calibrated for this subject by using information about the subject to estimate the empirical best linear
 206 unbiased predictors (EBLUPs) of the random effects parameters (Meng and Huang 2009). The methods
 207 from Gordan was reference to compose the predict function in R (Nigh 2012; Team 2013).

208 Model evaluation and validation

209 The following statistics were employed for model evaluation and validation: the adjusted coefficient
 210 of determination (R_{adj}^2), Akaike’s information criterion (AIC), the mean absolute error (Scolforo, Maestri
 211 et al.), the root mean square error (RMSE).

$$212 \quad R_{adj}^2 = 1 - \frac{\sum_{i=1}^{n_i} \sum_{j=1}^{n_{ij}} \sum_{k=1}^{n_{ijk}} (H_{ijk} - \widehat{H}_{ijk})^2}{\sum_{i=1}^{n_i} \sum_{j=1}^{n_{ij}} \sum_{k=1}^{n_{ijk}} (H_{ijk} - \bar{H})^2} \times \frac{n-1}{n-p-1} \quad (8)$$

$$213 \quad MAE = \frac{\sum_{i=1}^{n_i} \sum_{j=1}^{n_{ij}} \sum_{k=1}^{n_{ijk}} |H_{ijk} - \widehat{H}_{ijk}|}{n} \quad (9)$$

$$214 \quad RMSE = \sqrt{\frac{\sum_{i=1}^{n_i} \sum_{j=1}^{n_{ij}} \sum_{k=1}^{n_{ijk}} (H_{ijk} - \widehat{H}_{ijk})^2}{n}} \quad (10)$$

$$215 \quad AIC = -2 \log Lik + 2k \quad (11)$$

216 Where n is the number of observations, \widehat{H}_{ijk} is k^{th} tree estimated height of nested in j^{th} plot nested
 217 in i^{th} province ; H_{ijk} is the k^{th} tree observed height nested in j^{th} plot nested in i^{th} province. \bar{H}
 218 is the observed mean height for all data, n_i , n_{ij} , n_{ijk} are the total number of the province, the plots
 219 nested in i^{th} province, k^{th} trees nested in the j^{th} plot nested in i^{th} province, p is the number of
 220 model parameters; and LL is the log-likelihood.

221 Comparisons of H-D relationships among larch species under future climate change

222 For each plot, we produced 37 simulated trees with diameter from 5 cm (minimum value of D in
223 calibration data) to 41 cm (maximum value of D in calibration data), and these diameter values were set
224 to be evenly distributed. The values of BAL were obtained by mean value of each D with interval of 1cm
225 in calibration data. According to final nlme model with the inclusion of climate variables, tree heights
226 for a given D of all plots under different climate change scenarios were predicted. After the corresponding
227 H of each D is averaged, the H-D curves of different larch species under climate change scenarios were
228 generated. For observe how the climate change effect the H-D allometry in details, the relative change
229 of tree height ΔH was defined for comparisons with a given D (Eq. 12). Similarly, after the
230 corresponding ΔH of each D is averaged, the ΔH -D curves of different larch species were generated.

$$231 \quad \Delta H = \sum_1^n (H_{change} - H_{current}) / n \times H_{current} \quad (12)$$

232 Where n was the number of simulated trees. H_{change} and $H_{current}$ represent tree height value
233 predicted under future and current climate scenarios, respectively.

234 Results

235 Selected climate variables

236 Three principal components described 95.27% of the variability of the climate data (Table 3). For
237 component 1, the variables with absolute loading values > 0.3 were MAT, DD_0, DD5, DD_18 and
238 NFFD, so the component 1 mainly represents the temperature variability. For component 2, the variables
239 which absolute loading values > 0.3 were TD, MAP, AHM and CMD, so the component 2 represents the
240 moisture variability. For component 3, TD and PAS were chosen.

241 According to the loading, the most two important climate variables were selected which include MAT,
242 DD_18, CMD, MAP, TD, PAS. Table 4 presents the correlation between these climate variables and tree
243 height. Because of the collinearity between MAT, DD_18, MAP, TD and PAS. Finally, only MAT and
244 CMD were selected for further reparameterization using NLME. Summary statistics of MAT and CMD
245 can be found in Table 5.

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Table 3 PCA analysis result of the climate variables

	Comp.1	Comp.2	Comp.3
MAT	0.331	0.000	0.000
MWMT	0.265	0.248	-0.229
MCMT	0.282	-0.172	0.272
TD	-0.114	0.341	-0.43
MAP	0.000	0.394	0.338
AHM	0.147	-0.387	-0.262
DD_0	-0.302	0.104	-0.238
DD5	0.301	0.185	-0.14
DD_18	-0.329	0.000	-0.104
DD18	0.269	0.243	-0.183
NFFD	0.311	0.150	0.000
PAS	-0.172	0.265	0.388
EMT	0.287	-0.128	0.21
EXT	0.250	0.171	-0.357
Eref	0.249	-0.215	0.000
CMD	0.000	-0.444	-0.238
Accumulated variance	56.050	81.680	95.27

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Table 4 Pearson correlation coefficient matrix between H and climatic variables

Variables	CMD	TD	PAS	MAP	DD_18	MAT	H
CMD	1.000	-	-	-	-	-	-
TD	-0.424***	1.000	-	-	-	-	-
PAS	-0.673***	0.193***	1.000	-	-	-	-
MAP	-0.841***	0.141***	0.566***	1.000	-	-	-
DD_18	-0.041***	0.435***	0.421***	-0.358***	1.000	-	-
MAT	-0.004	-0.347***	-0.412***	0.390***	-0.995***	1.000	-
H	-0.503***	0.404***	0.329***	0.414***	0.070***	-0.029***	1.000

250

Note: *,p<0.05; **,p<0.01; ***,p<0.001.

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Table 5 Mean value of MAT and CMD under 3 climate change scenarios

MAT	Period:2010-2040	Period:2040-2070	Period:2070-2100
RCP2.6	3.95(2.40)	4.41(2.41)	4.53(2.43)
RCP4.5	3.92(2.43)	4.87(2.44)	5.70(2.42)
RCP8.5	4.14(2.42)	5.69(2.42)	7.44(2.36)
CMD	Period:2010-2040	Period:2040-2070	Period:2070-2100
RCP2.6	180.96(88.22)	164.38(75.68)	164.34(87.09)
RCP4.5	158.82(82.30)	142.16(77.02)	180.26(83.53)
RCP8.5	160.62(83.16)	186.03(82.88)	187.04(82.78)

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Note: The numbers within parentheses are the standard deviation

253

254 Final NLME h-d model with climatic variables

255 When climate variables were selected into the model, all the explanatory variables were determined.
256 Then, we tested all the combinations of dummy variables representing different species, climate variables
257 and Province- and plot- level random effects to parameters from the basic model (Eq. 1). The final model
258 with good convergence and the lowest AIC value was chosen for simulations. The climate variables were
259 set into parameter a and b , the tree species dummy variables and random effects were set into parameter
260 a .

261 Therefore, the equations 2 to 4 can be rewritten representing basic H-D model, climate-sensitive H-D
262 model, and climate-sensitive mixed-effect H-D model (Eq. 13-15).

$$263 \quad H_{ijk} = 1.3 + (a_0 + a_1BAL + \sum_{m=1}^4 f_m S_m)[1 - e^{b_0 D_{ijk} + b_1 BAL}]^c + \varepsilon_{ijk} \quad (13)$$

$$264 \quad H_{ijk} = 1.3 + (a_0 + a_1BAL + a_2MAT + a_3CMD + \sum_{m=1}^4 f_m S_m)[1 -$$
$$265 \quad e^{(b_0 + b_1BAL + b_2MAT + b_3CMD)D_{ijk}}]^c + \varepsilon_{ijk} \quad (14)$$

$$266 \quad H_{ijk} = 1.3 + (a_0 + a_1BAL + a_2MAT + a_3CMD + \sum_{m=1}^4 f_m S_m + u_i + u_{ij})[1 -$$
$$267 \quad e^{(b_0 + b_1BAL + b_2MAT + b_3CMD)D_{ijk}}]^c + \varepsilon_{ijk} \quad (15)$$

268 Where $f_1 \sim f_4$, $a_0 \sim a_3$, $b_0 \sim b_3$, c are the model parameters to be estimated; other variables are
269 defined as above.

270 Model comparison and evaluation

271 The fitting and validation results of the models are shown in Table 6. The base model (Eq.13) described
272 76% part of the variations in the height-diameter relationship when fitted the training data ($R_{adj}^2=0.76$).
273 When tree species dummy variable and province-specific, plot-specific random effects were included in
274 the base model, the climate variables contributed significantly to the variance of tree heights and R_{adj}^2
275 increased from 0.77 to 0.92 (Table 6). Training dataset showed similar results, and the inclusion of
276 climate variables (Eq. 14) resulted in the increase R_{adj}^2 by 3% and the reduce of AIC by 3%. Mixed
277 effect model (Eq. 15) also removed the heteroscedasticity of residuals (Figure 2).

278

279 **Figure 2 Residuals vs predicted values for different H-D models based on calibration data**

280

281

Table 6 Parameter estimates and statistics for equations (13)-(15)

	parameter	parameter definition	Eq.(13)	Eq.(14)	Eq.(15)
fixed-effects parameters	a_0		21.382(0.000)	21.460(0.000)	19.772(0.000)
	b_0		0.078(0.000)	0.088(0.000)	0.106(0.000)
	c_0		1.616(0.000)	1.545(0.000)	2.083(0.000)
	a_1	BAL	-0.137(0.000)	-0.085(0.000)	-0.111(0.000)
	a_2	MAT		1.322(0.000)	0.259(0.0381)
	a_3	CMD		-0.021(0.000)	-0.030(0.000)
	b_1	BAL	0.001(0.000)	0.001(0.000)	0.005(0.000)
	b_2	MAT		-0.005(0.000)	0.003(0.0024)
	b_3	CMD		0.000(0.07)	0.000(0.000)
	f_1	<i>L. gmelinii</i>	-5.137(0.000)	-3.790(0.000)	0.216(0.898)
	f_2	<i>L. olgensis</i>	3.234(0.000)	3.317(0.000)	1.879(0.013)
	f_3	<i>L. kaempferi</i>	-4.944(0.000)	-2.951(0.000)	0.865(0.050)
	f_4	<i>L. principis-rupprechtii</i>	2.557(0.000)	2.319(0.000)	0.226(0.735)
	Variance components	$\sigma_{province}$			
σ_{plot}					2.700
model performance					
	γ				0.674
	AIC		23007.83	22368	17911.4
Fitting set	R_{adj}^2		0.77	0.79	0.92
Fitting set	MAE(m)		1.37	1.28	0.76
Fitting set	RMSE(m)		1.82	1.72	1.06
Validation set	MAE(m)		1.5	1.44	1.38
Validation set	RMSE(m)		2.03	1.93	1.8

283 Note: $\sigma_{province}$ and σ_{plot} are the variance for the random parameters u_i and u_{ij} , respectively; γ is

284 the parameter of correlation structure. AIC was the Akaike's information criterion.

285

286

287 H-D relationships among larch tree species and tree sizes under future climate change

288 Results showed different effects of climate variables on parameters a_0 and b_0 , denoting the maximum
289 and relative change of tree height with diameter (Table 6). Parameter a_1 was significantly negative
290 indicating the increasing BAL will reduce the maximum height. The coefficient a_2 of MAT for parameter
291 a was significantly positive which means that the rising MAT will increase the maximum tree height.
292 This was also shown in Figure 3 where all H-D curves of different species became steeper under RCP2.6
293 and RCP 4.5 from 2010 to 2070. However, parameter b_2 was negative indicating that the rising MAT will
294 lower the tree height with the same diameter and there is a threshold for the effect of temperature on H-
295 D relationship of larch species. Parameter a_3 was significantly negative indicating the decreasing
296 precipitation will reduce the maximum height. Both CMD and BAL showed marginal effects on H-D
297 relationship since b_1 and b_3 were nearly zero.

298 Table 6 showed that all parameters of tree species dummy variables $f_1 \sim f_4$ were positive, but f_1 and f_4
299 were not significant, indicating that *L.olgensis* and *L.Kaempfer* had significant difference with
300 unidentified group, which was also illustrated in Figure. 3. Coefficient f_2 was the largest indicating that
301 the maximum of tree height is the largest for *L.olgensis*.

302 MAT increases with the time and the temperature under RCP8.5 is largest followed by RCP4.5 and
303 RCP2.6. The precipitation under RCP8.5 is smallest and has the steepest slope followed by RCP4.5 and
304 RCP2.6. Figure 4 showed the Δ H-D curve of larch species under climate scenarios RCP2.6, RCP4.5 and
305 RCP8.5. Generally, tree species can be obviously classified as two groups in terms of Δ H, which are
306 group I (*L. gmelinii* group, *L. pincipis-rupprechtii* and the unidentified larch species) and group II (*L.*
307 *kaempferi* and *L. olgensis*). They showed strong (Δ H from -4.77% to 18.17%) and weak (Δ H from -
308 6.37% to 9.40%) responses to climate change, respectively. The values of Δ H for Group I were positive
309 which indicated that future climate change increased tree height compared with current climate with the
310 exception of RCP 2.6 from 2010 to 2040 and RCP8.5 from 2040-2100. However, the values of Δ H were
311 complicated varying from negative to positive with the increasing diameter for Group II.

312 It can be observed that Δ H varied with tree diameter. Generally, large trees showed large Δ H values,
313 but there were different responses to climate among larch species. For tree species group I, the Δ H
314 increased with the increase of tree DBH in small and medium sizes and kept stable in large size. For
315 group II, the absolute Δ H increased with the increase of tree DBH, but changed from negative to positive

316 Mean absolute ΔH value of tree height with diameter among larch species under different climate
317 scenarios in period 2010 to 2100 (mean value of the absolute ΔH in period 2010 to 2040, 2040 to 2070
318 and 2070 to 2100) was shown in Figure 5. It can be observed that the climate sensitivity of larch species
319 was ranked as *L. gmelinii* > *L. pincipis-rupprechtii* > the unidentified species group > *L. olgensis* > *L.*
320 *kaempferi* under RCP2.6 and RCP8.5, and the sensitivity was larger under RCP8.5 than that under RCP2.6.
321 However, the sensitivity was ranked as *L. gmelinii* > the unidentified species group > *L. pincipis-*
322 *rupprechtii* > *L. kaempferi* > *L. olgensis* under RCP4.5.

323 **Figure 3 Relationship between tree height and DBH of larch species under different climate**
324 **change scenarios**

325

326 **Figure 4 Relative change of tree height with diameter among larch species under different climate**
327 **scenarios**

328

329 **Figure 5 Mean absolute ΔH values of height with diameter among larch species under different**
330 **climate scenarios**

331 **Discussion**

332 **Climate-sensitive H-D model**

333 The climate-sensitive H-D allometry model with a two-level NLME approach at the province and plot
334 levels was developed for larch plantations in the study. Results showed that a two-level mixed-effects
335 model with the inclusion of climate variables provided better performance compared to fixed-effects
336 model without climate variables, which could also be found in other reports (Sharma and Parton 2007;
337 Zang, Lei et al. 2016; Zhang, Chhin et al. 2019; Bronisz and Mehtätalo 2020; Ciceu, Garcia-Duro et al.
338 2020). In this study, using mixed-effects model and including climate variables was able to increase R_{adj}^2
339 by 19.5% and reduce the AIC, MAE and RMSE by 22.2%, 44.5% and 41.8% for fitting set, respectively.
340 The residual heterogeneity was also reduced. Owing to the correlation among tree height-diameter
341 observations, fixed-effect model would lead to biased variance of the parameter estimates and thus
342 invalidate the hypothesis tests (Pinheiro, Bates et al. 2013). Mixed effect modelling approach can be an
343 appropriate solution to this problem (Calama and Montero 2004; Sharma, Vacek et al. 2016). Similarly,

344 Vizcaíno-Palomar, Ibáñez et al. (2017) reported that inclusion of climate variables and random effects
345 reduce the AIC by 9.0%. Sharma, Vacek et al. (2016) reported that inclusion of random effects was able
346 to increase the R_{adj}^2 by 9.2% and reduce the AIC and RMSE by 7.8% and 25%, respectively.

347 The climate variables including MAT and CMD significantly affected H-D relationship but the effect
348 was not very strong which was in line with the previous studies (Hulshof, Swenson et al. 2015; Fortin,
349 Van Couwenberghe et al. 2019; Zhang, Chhin et al. 2019). Temperature usually affects the growth season
350 and growth rate of tree height. Low temperature will hinder the division and specialization of cambium
351 and meristem cells, thus accumulating more nutrients and carbohydrates and distributing them to the
352 trunk, therefore the shape of tree changed (Kilpeläinen, Peltola et al. 2006). Fortin, Van Couwenberghe
353 et al. (2019) pointed out that the mean temperature from March to September affected H-D relationship
354 of most French species. Temperature was not a marginal effect that can be overlooked and its effect was
355 also quadratic so that an optimal temperature existed. Ng'andwe, Chungu et al. (2021) also found that
356 increasing temperature beyond the optimum for *Pinus merkusii* and *P. michoacana* will reduce the tree
357 growth and increase the rotation age. Similarly, in this study, MAT modified parameters a_2 and b_2
358 positively and negatively, respectively, which also indicated that there was an optimal temperature for
359 larch tree height. Zhang, Chhin et al. (2019) reported that MAT was the dominant climatic factor in
360 modulating height-diameter allometry of Chinese fir, and the effect of MAT and MWMT were positively
361 associated with tree height. Larch in the region begins to grow in May, and the growth speed reaches the
362 maximum in July, then gradually slows down until it stops growing (Wang, Wang et al. 1992). Therefore,
363 the temperature in May and the precipitation in the previous year are very important for the height growth
364 of larch. Our results showed that CMD had significant effects on H-D relationship. The coefficient of
365 CMD, a_3 , was negative which indicated that the height decreases with the increase of water deficiency.
366 This was consistent with previous study (Zhou, Lei et al. 2019) which found that the precipitation from
367 the previous October to the current April significantly promoted the height growth of Mongolian pine.
368 Sang, Sebastian - Azcona et al. (2019) also found that the negative and positive effects of CMD on the
369 height of white spruce trees in northern Canada.

370 Besides climate, H-D relationship was affected by multiple biotic and abiotic variables, for example
371 genetic characteristics (Kroon et al., 2008), stand age (Sánchez et al., 2003), site condition (Sharma and
372 Yin Zhang, 2004; Sharma and Parton, 2007; Zhang et al., 2020), competition status (Calama and Montero,
373 2004; Sharma and Yin Zhang, Ciceu et al., 2020). Considering the inclusion of other stand factors will

374 aggravate the model complexity, we only use diameter and BAL as the independent variable for ensuring
375 more stable convergence. Other methods like machine learning were worthy of further exploration in
376 future study.

377 The impact of climate change on H-D relationship by larch species and tree size

378 Our model simulations showed that the effects of climate change on H-D relationship varied with larch
379 species. Generally, ΔH -D curves of larch species can be obviously classified as two groups, which are
380 group I (*L. gmelinii* group, *L. principis-rupprechtii* group and the unidentified species group) and group
381 II (*L. kaempferi* and *L. olgensis*). They showed strong (ΔH from -4.77% to 18.17%) and weak (ΔH from
382 -6.37% to 9.40%) response to future climate change, respectively. Under warmer and drier climatic
383 conditions, *L. kaempferi* and *L. olgensis* will grow thicker and shorter than the rest of the tree species group,
384 and their ΔH s are lower than those of group I for a given tree diameter. This may due to these two tree
385 species are moisture loving species (Wang *et al.*, 1992). Under drought stress, the hydraulic conductivity
386 of the xylem of the trunk suffers irreversible loss. Therefore, the lack of water during the growing season
387 allows to allocate more resources for the growth of diameter (Ryan and Yoder 1997). Compared with
388 group II, group I is more resistant. As the temperature increases, more resources will be allocated to the
389 growth of the height than the diameter, thus trees would be higher. Previous studies also supported this
390 result (Aiba and Kitayama 1999; THORNLEY 1999; Schelhaas 2008; Zhang, Wang *et al.* 2020).

391 ΔH also varied with tree diameter under future climate change. For tree species group I, ΔH increased
392 for small and medium sizes and kept stable for large sizes. This may be resulted from the limited height
393 growth of trees with large diameter because of the limits to tree height (Koch, Sillett *et al.* 2004). For tree
394 species group II, ΔH increased with the increasing DBH, but changed from negative to positive,
395 indicating that small trees will grow short but large trees high. Campbell, Magnussen *et al.* (2021)
396 reported that large trees were most sensitive to annual climate fluctuations. From the perspective of
397 competition, larger trees in a stand have more competitive advantages than smaller trees while the smaller
398 neighbor trees do not influence the growth of larger trees (Cannell *et al.*, 1984). Under the warmer and
399 drier climate in the future, due to the developed root system of the big trees, their growth will not be
400 affected by the lack of water, and the growth of small trees may face drought stress. McDowell, Pockman
401 *et al.* (2008) pointed out that plants can avoid water damage caused by drought through stomatal closure,

402 leading to carbon starvation and a cascade of down-stream effects. Seedlings or small trees are more
403 likely to inhibit growth or even die due to hydraulic failure. The phenomena of changing from negative
404 to positive for ΔH of *L. kaempferi* and *L. olgensis* along with increasing diameter support this conclusion.

405 **Conclusions**

406 Two-level climate-sensitive NLME model was developed for larch plantations in north and northeast
407 China in this study which showed biological and statistical reasonability. MAT, CMD, was the dominant
408 climatic factor in modulating height-diameter allometry of larch plantations. Model simulation showed
409 that the climate sensitivity of H-D allometry varied with tree species and diameter. According to the
410 climate sensitivity, tree species could be classified as group I (*L. gmelinii*, *L. principis-rupprechtii* and the
411 unidentified species group) with large ΔH (from -4.77% to 18.17%) and group II (*L. kaempferi* and *L.*
412 *olgensis*) with small ΔH (from -6.37% to 9.4%). Large trees were more sensitive to climate change than
413 small trees.

414

415 **Declarations**

416 **Ethics approval and consent to participate**

417 The authors declare that the study was not conducted on endangered, vulnerable or threatened species.
418 The authors declare that they obtained the informed consent from human participants involved in this
419 study.

420 **Consent for publication**

421 All authors gave their informed consent to this publication and its content.

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424 **Availability of data and material**

425 The datasets generated during and/or analysed during the current study are available from the

426 corresponding author on reasonable request.

427 **Authors' contributions**

428 Q.G. Xu: Data preparation, Data analysis, Writing, review & editing; X. D. Lei: Conceptualisation,
429 Funding, Writing, review & editing; H. Zeng and W. S. Zeng: Data collection, review & editing.

430 **Competing interests**

431 The authors declared that they have no conflicts of interest to this work.

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Figures

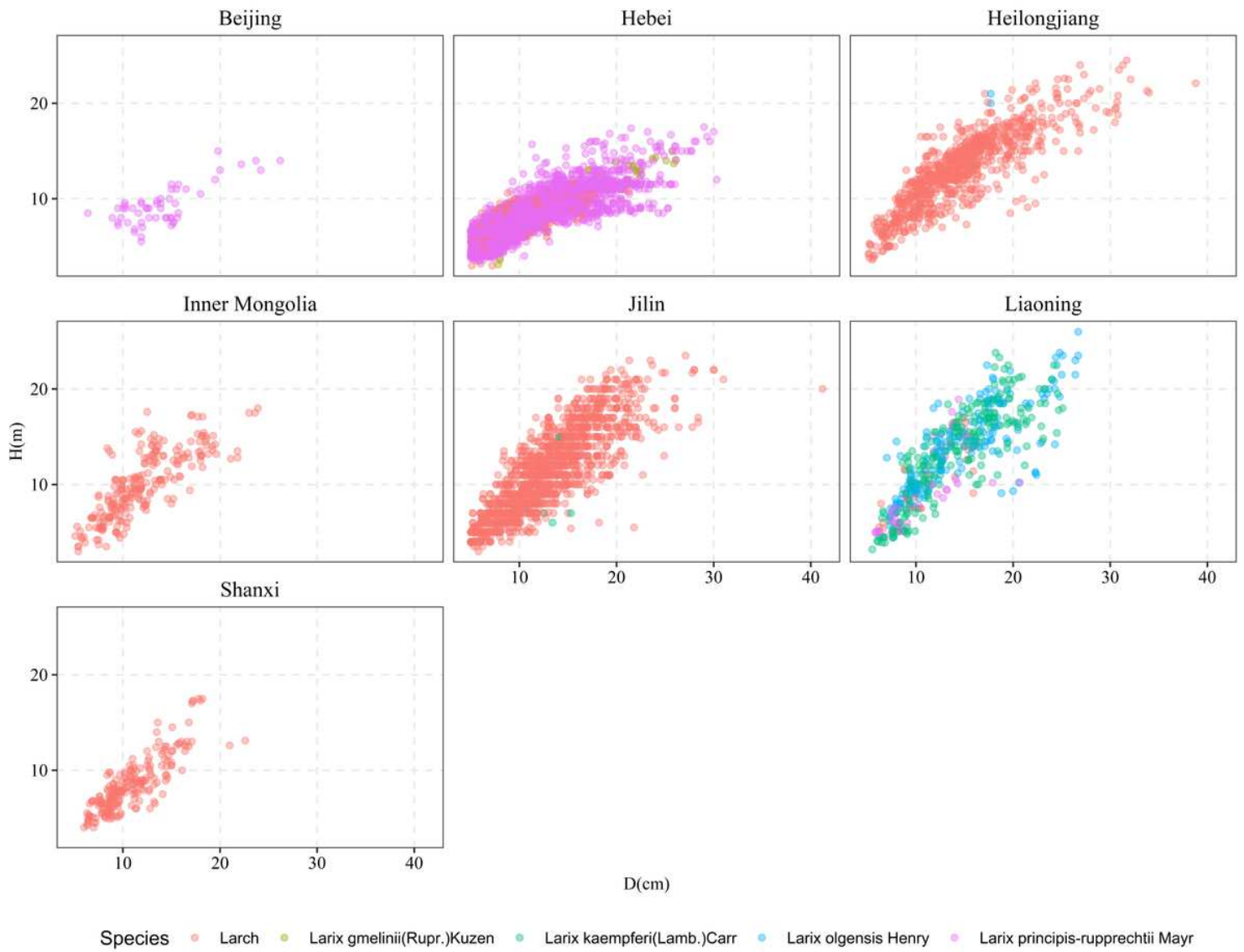


Figure 1

Scatter plot of tree height-diameter allometry by Larch species in 7 provinces.

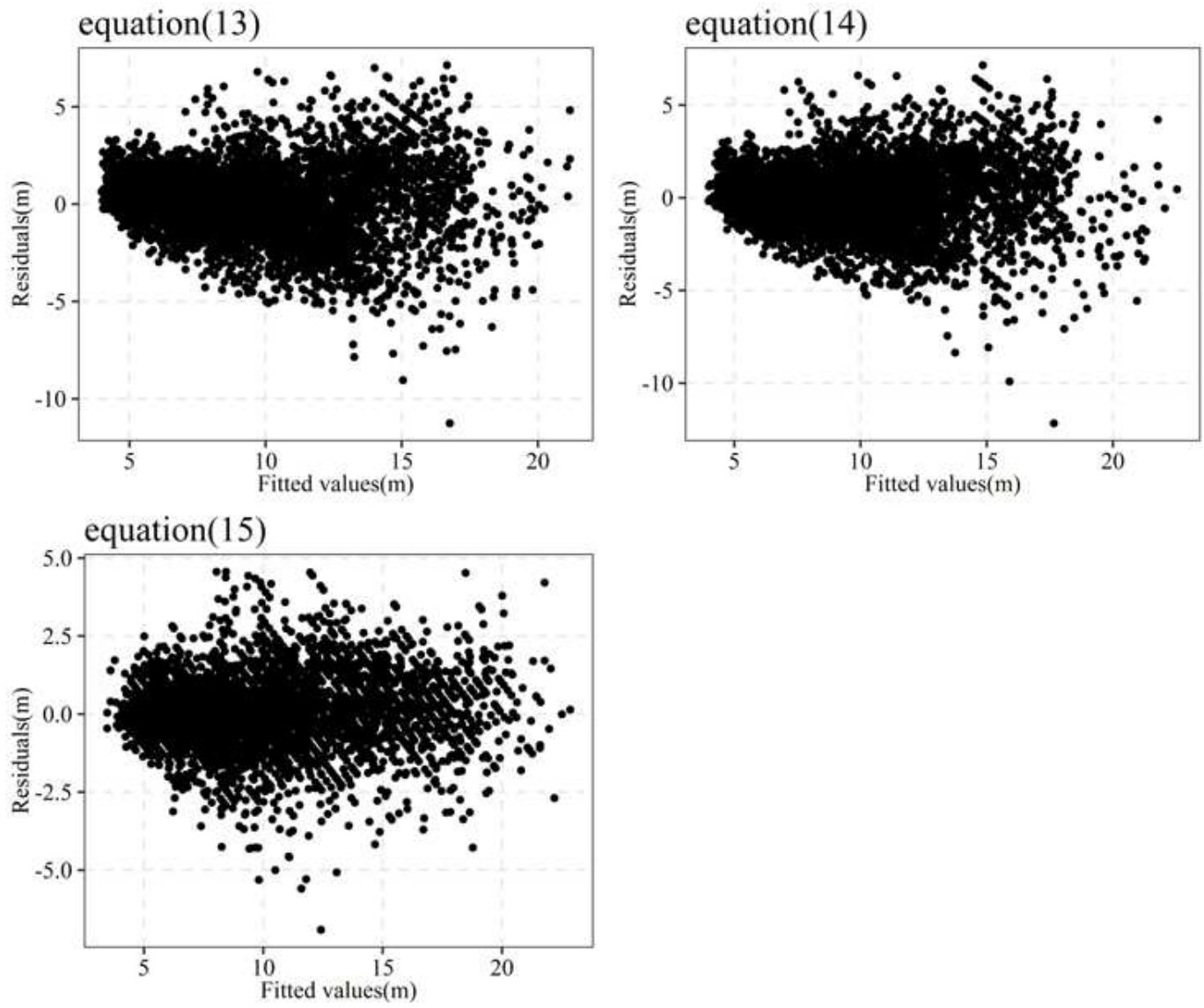


Figure 2

Residuals vs predicted values for different H-D models based on calibration data

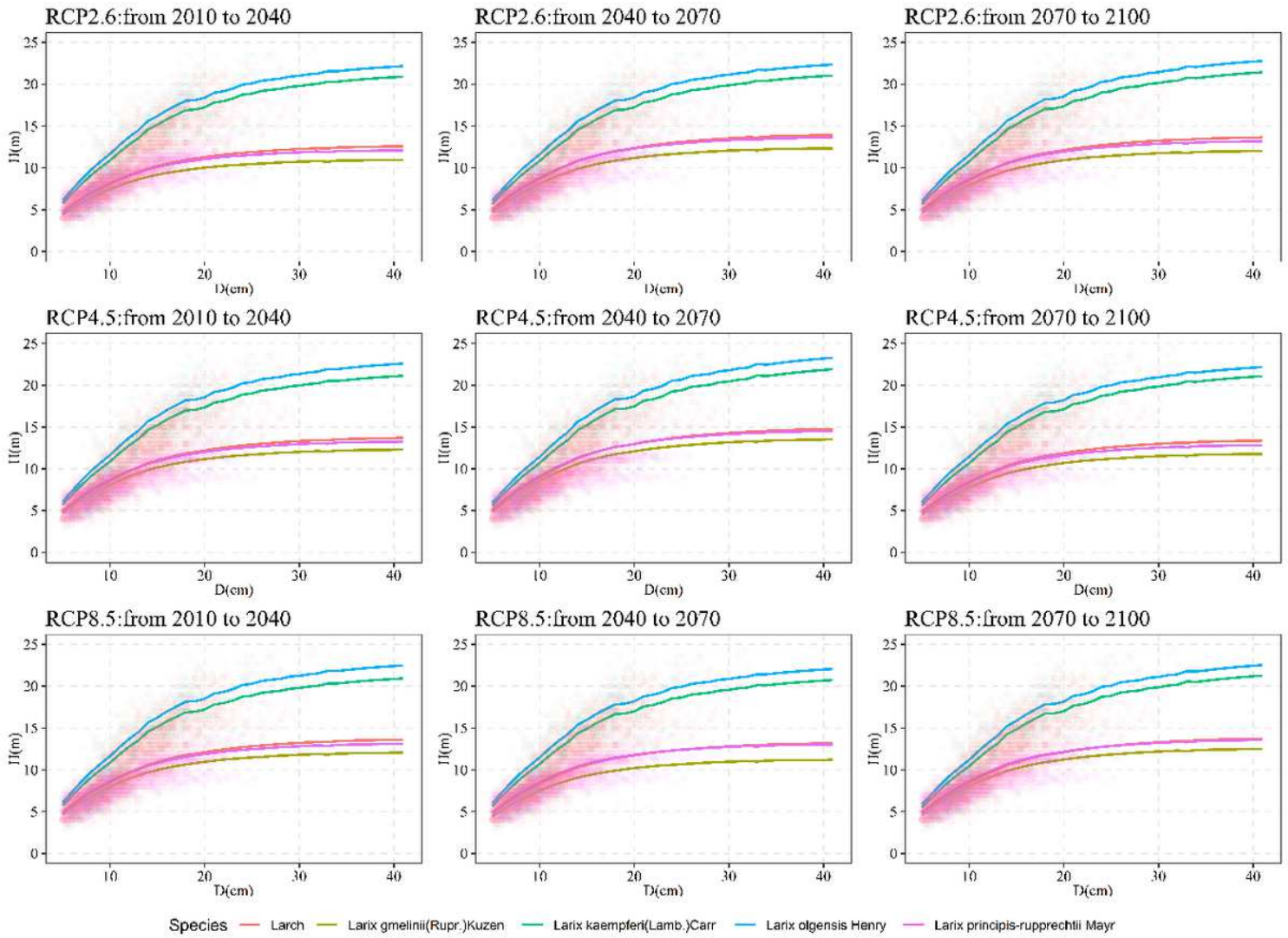


Figure 3

Relationship between tree height and DBH of larch species under different climate change scenarios

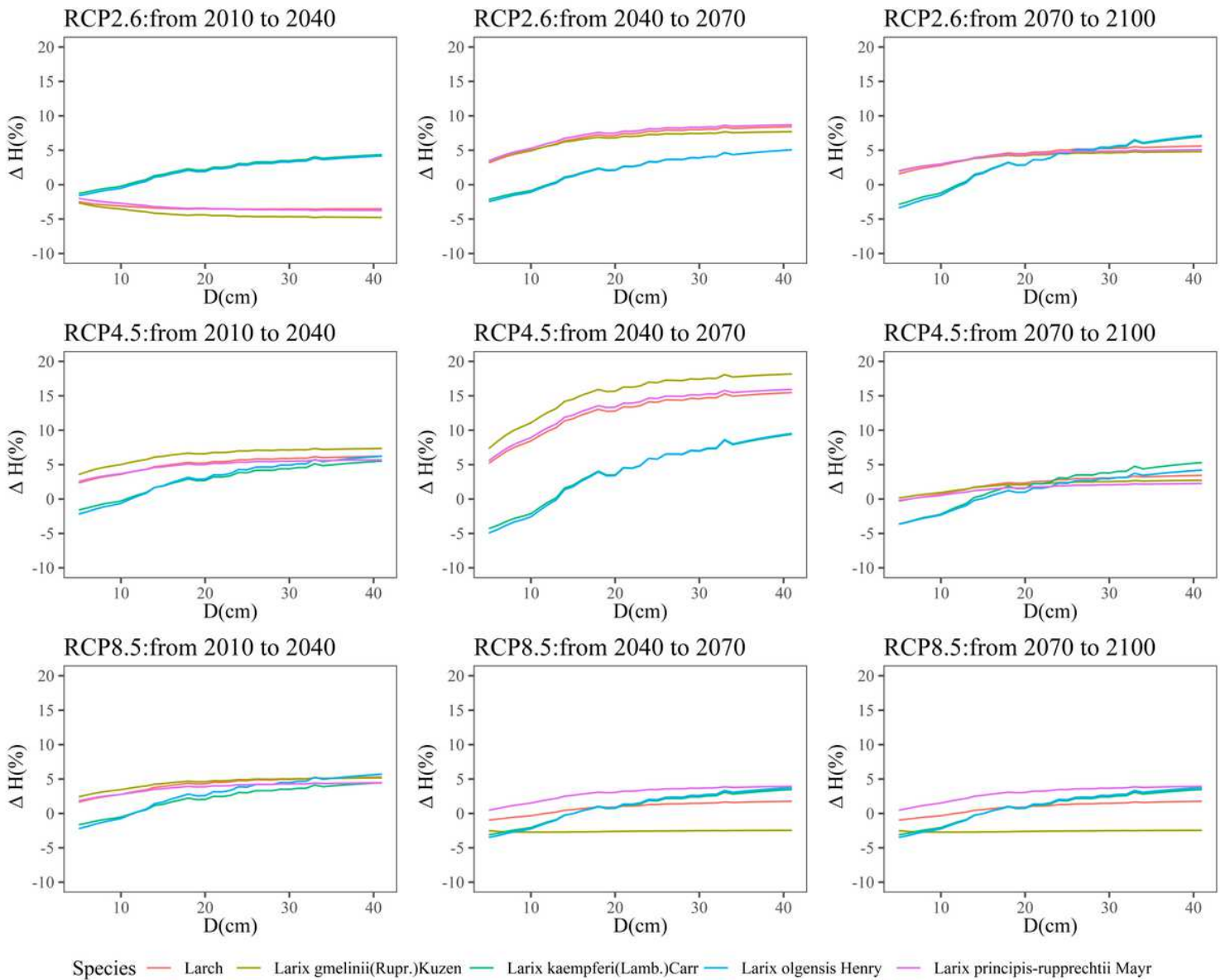


Figure 4

Relative change of tree height with diameter among larch species under different climate scenarios

Figure 5

Mean absolute ΔH values of height with diameter among larch species under different climate scenarios