Journal of Wood Science

ORIGINAL ARTICLE Open Access

The relationship among stress-wave-based wood stiffness and growth traits revealed by planting density trial with multiple genotypes in *Cryptomeria japonica*

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Abstract

Understanding the genetic and environmental factors influencing wood stiffness is essential for improving wood quality in plantation forestry. In this study, we investigated the phenotypic, genetic, and environmental variation in wood stiffness, measured as stress-wave-based modulus of elasticity (swMOE), in *Cryptomeria japonica*. Six genotypes were planted at three planting densities (7000, 3000, and 1700 trees/ha) in a field trial, and growth traits such as tree height, diameter at breast height (DBH), and bole height were measured at stand age 40. Using linear mixed models, we estimated variance components, broad-sense heritabilities, and correlations between swMOE and growth traits. We compared linear mixed models incorporating growth traits as covariates and examined their predictive accuracy for swMOE. Our results showed that swMOE was under relatively strong genetic control and was less influenced by planting density compared to growth traits. Among the growth traits tested, form ratio (tree height to diameter) exhibited the strongest positive correlation with swMOE at the phenotypic, genetic, and residual levels. Including form ratio as a covariate improved model fit and increased prediction accuracy across replications. These findings suggest that form ratio is both a biologically meaningful and practically useful trait for explaining and predicting wood stiffness of *C. japonica*. This approach has potential applications in genetic selection and wood property prediction in operational breeding and forest management.

Keywords *Cryptomeria japonica*, Stem stiffness, Stress wave velocity, Planting density

Introduction

Improving wood quality is a major objective of tree breeding both in Japan [1–4] and globally [5–9]. Among the various components of wood quality, wood stiffness is one of the most important traits for structural applications. *Cryptomeria japonica*, which accounts for 44% of all planted forests in Japan [10] and 36.6% of newly planted forest areas [11], has relatively low wood stiffness compared to other major commercial species in Japan, including *Larix kaempferi* and *Chamaecyparis obtusa* [12–14]. Improving stiffness in *C. japonica* has therefore become a key target for enhancing its material value.

Substantial genetic variation in wood stiffness has been reported in *C. japonica* [15–19], and the trait is known to be heritable [20–23]. Compared to growth traits, wood stiffness in *C. japonica* has shown relatively higher broad-sense and narrow-sense heritabilities [22, 24]. These findings suggest that genetically superior seedlings for wood stiffness can be produced through breeding by selecting

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elite clones as parental trees in seed orchards or as scion sources in grafting orchards.

However, wood stiffness is influenced not only by genetics, but also by growth characteristics such as height and diameter. At the species level, taller species possess grater stiffness when adjusted to equal specific gravity [25]. In *C. japonica*, clonal variation in the intra-clonal correlation between wood stiffness and diameter has been reported [20, 26]. While a positive genetic correlation between tree height and wood stiffness has been reported [27], the magnitude of this correlation is not high. A negative genetic correlation [27] and a negative phenotypic correlation [19] between stiffness and diameter have also been reported. Kijidani et al. [28] found that form ratio (height/diameter) was correlated with wood stiffness in 17 cultivars, although the strength of this relationship varied among cultivars.

Growth traits themselves are heritable but also highly sensitive to environmental conditions, often resulting in lower heritabilities than those of wood property traits [20, 22, 27, 29]. Growth traits can be influenced by a wide range of environmental factors, including climate conditions, and silvicultural practices such as initial spacing or thinning, as well as competition among neighboring trees. Consequently, wood stiffness may be indirectly affected by genetic and environmental factors through their effects on growth traits, in addition to its direct genetic and environmental determinants.

To improve the accuracy of wood stiffness prediction, it is essential to consider not only genetic variation, but also the effects of growth traits, and to incorporate these effects into predictive models. However, studies that address the genetic basis of the relationship between wood stiffness and growth traits are limited. Previous research has reported variations among local varieties in the relationship between form ratio and wood stiffness using over ten local varieties of *C. japonica* [28] and the relationship between wood stiffness and a wide range of growth conditions has also been examined [30]. Nonetheless, few studies have investigated how wood stiffness is influenced by growth traits across a wide range of growth states while accounting for genetic differences, due to the rarity of experimental materials that combine multiple genotypes and broad growth variation at the same age.

In this research, we estimated wood stiffness in standing trees based on stress wave velocity, which is known to correlate strongly with modulus of elasticity (MOE) [27, 31], and is also cost-efficient due to its non-destructive nature. We also measured growth traits for trees exhibiting diverse growth patterns, using multiple clones of *C. japonica* grown in a planting density trial. Using these data, we evaluated the relationship between wood stiffness and growth traits, and constructed predictive models for wood stiffness incorporating both genotype and growth characteristics. Here, we aimed to clarify how genetic and growth-related factors contribute to wood stiffness by jointly analyzing clonal genetic variation and growth trait effects, and to identify practical covariates for predicting wood stiffness in *C. japonica* trees.

Methods

Test site for measurement

We measured target traits of trees in a planting density test site located in Taragi Town, Kumamoto Prefecture, Japan (32°14′ N, 131°01′ E). The soil at the test site is classified as BD type (Brown forest soil—moderately moist type). The test site was established in 1980 using a randomized block design with three planting densities (7000, 3000, and 1700 trees/ha), each with two replicates (Fig. 1). Eight plus-tree clones were planted in a rectangular plot containing 72, 32, and 18 trees, corresponding to 7000 trees/ha, 3000 trees/ha, and 1700 trees/ha densities, respectively. Each measurement plot was surrounded by trees planted at the same time and the same density as the plot itself, with at least three surrounding rows serving as a buffer zone (Fig. 1). The two replicates were approximately 140 m apart in elevation and about 240 m apart in horizontal distance, with replicate 1 located at lower elevation. Thinning was never applied; however, three trees per plot were felled at the stand age of 33 for another experiment. In addition, some trees had fallen due to wind damage, causing survival rates to vary markedly among plots (Table S1). At the time of measurement, the average surviving tree densities were 1604.2, 1646.5, and 979.9 trees/ha for initial planting densities of 7000, 3000, and 1700 trees/ha, respectively. No branch pruning was conducted.

The three trees per plot felled for another test were genotyped using seven simple sequence repeat (SSR) markers, following the method described by Miyamoto et al. [32]. As a result, two pairs of plus-tree clones were identified, with each pair sharing the same genotype within the pair. In Kyushu Island, forestry based on vegetative propagation of *C. japonica* has a long history, and it is not uncommon for the same genotype to have been selected as differently named plus trees in different regions. Such duplication among plus trees has also been reported previously [33]. In this study, plus-tree clones with identical genotypes were treated as the same clone. Therefore, the number of distinct clones (genotypes) used in this research was six and the number of trees representing each of the two duplicated genotypes was doubled in each planting density.

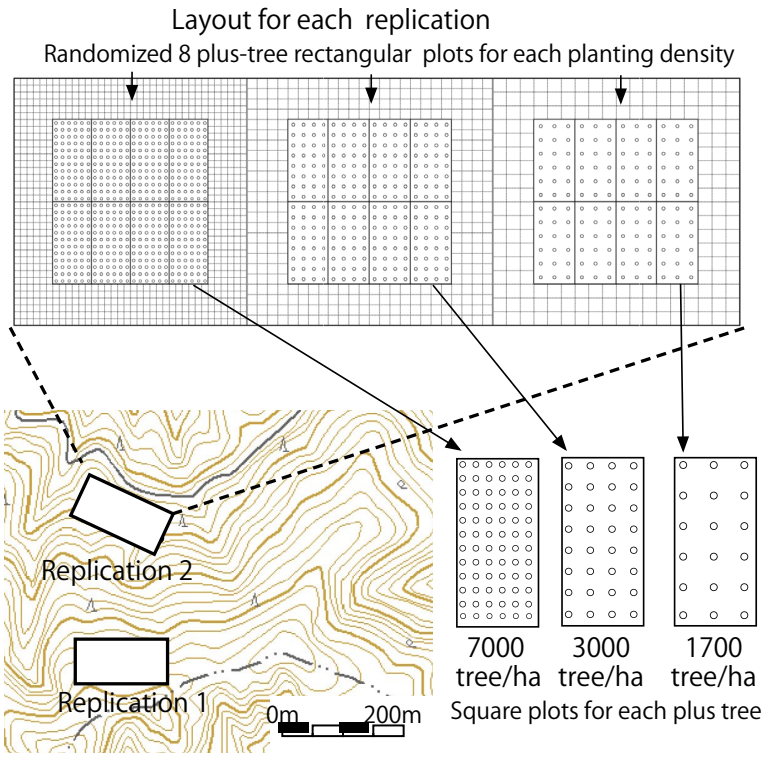


Fig. 1 Abstract map of the planting density trial. The trial consisted of two replications with three planting densities: 7,000, 3,000, and 1,700 trees/ha, corresponding to spacings of 1.2 m, 1.8 m, and 2.4 m between adjacent trees, respectively. The dimensions of each measuring plot were 7.2 m × 14.4 m. For each planting density, rectangular measurement plots were established for individual clones. Each group of eight adjacent measurement plots, corresponding to the three planting densities, was collectively surrounded by a buffer zone, in which trees were planted at the same time and the same density as the respective plots

Measurement of traits

At stand age 40, all surviving trees were measured for tree height (H), bole height (BH), diameter at breast height (DBH), and time of flight of stress waves. The number of measured trees ranged from 40 to 234, depending on genotype. H and BH were measured using a height measurement instrument (Vertex IV, Haglöf, Sweden), and DBH was measured using a caliper. Crown length (CL) was calculated as the difference between H and BH. Form ratio (FR) was calculated as the ratio of height to diameter (H/DBH). The time of flight of stress waves was measured using a TreeSonic Timer (Fakopp Enterprise Bt., Hungary). For each tree, time of flight was measured twice from two perpendicular directions, starting from the mountain side. The modulus of elasticity estimated from time of flight of stress waves (swMOE, MPa) was calculated using the following formula:

$$\mathrm{swMOE} = (\mathrm{DT}/t)^2 \times \rho \times 10^{-9},$$

where DT is the distance between the probes of TreeSonic Timer (1 m in this research), t is time of flight of stress wave (s), ρ is apparent basic density (assumed to be a constant of 900 kg/m^3 based on Ikeda [31]).

Statistical modeling

In this study, we applied several types of statistical models to address different analytical objectives. First, we used a linear mixed model for each trait, incorporating factors from the experimental design, to estimate variance components and broad-sense heritabilities. This allowed us to compare the degree of heritable and environmental variation among traits. Second, we fitted bivariate linear mixed models for swMOE and each growth trait to partition the observed phenotypic correlations into genetic and residual components, thereby clarifying the level at which the traits are correlated with swMOE. Third, we performed simple linear regression of swMOE on growth traits within each clone to explore how growth traits influence swMOE among individuals with the same genotype. Finally, we modeled swMOE using a linear mixed model including growth traits as covariates to assess whether incorporating these traits improves model performance. The improvement was further evaluated by cross-validation between replications.

Estimation of variance components and broad-sense heritabilities using linear mixed model

For estimation of variance components and broad-sense heritabilities (repeatabilities) for each trait, each trait was modeled using following linear mixed model:

$$y_{ijkl} = \mu + \mathrm{R}_i + \mathrm{PD}_j + \mathrm{R}_i \times \mathrm{PD}_j + \mathrm{G}_k + \mathrm{R}_i \times \mathrm{G}_k + \mathrm{PD}_j \times \mathrm{G}_k + \mathrm{P}_{ijk} + \mathrm{Resid}_{ijkl},$$

where y_{ijkl} is the phenotypic value of modeled trait for an individual tree, μ is overall mean, R_i is the effect of the ith replication, PD_j is the effect of planting density, $\mathrm{R}_i \times \mathrm{PD}_j$ is the interaction effect between PD_j andR_i, G_k is the effect of genotype (clone), $\mathrm{R}_i \times \mathrm{G}_k$ is the interaction effect between G_k andR_i, $\mathrm{PD}_j \times \mathrm{G}_k$ is the interaction effect between G_k atPD_j, P_{ijk} is the effect of plot, Resid_{ijkl} is the residual error. In the linear mixed models,R_i,PD_j, G_k and their interaction were all treated as categorical (nominal) variables. These factors represent group-level classifications rather than continuously measured values. Their effects were modeled as random effects to estimate the variance components associated with replication structure, planting conditions, and genetic differences among clones, and their interactions. In particular, G_k refers to the clonal identity of each tree, identified using SSR markers.

Based on this model, variance components were calculated for each random effect. The broad-sense heritability (repeatability) of each trait was calculated using the following equation:

$$\mathrm{H}^2 = \frac{\sigma^2_{\mathrm{G}}}{\sigma^2_R + \sigma^2_{\mathrm{PD}} + \sigma^2_{\mathrm{R\times PD}} + \sigma^2_{\mathrm{G}} + \sigma^2_{\mathrm{R\times G}} + \sigma^2_{\mathrm{PD\times G}} + \sigma^2_{\mathrm{P}} + \sigma^2_{\mathrm{Resid}}},$$

where H^2 is broad-sense heritability,σ^2_G,σ^2_R,σ^2_{PD},$\sigma^2_{\mathrm{R\times PD}}$, $\sigma^2_{\mathrm{R\times G}}$,$\sigma^2_{\mathrm{PD\times G}}$,$\sigma^2_{\mathrm{P}}$, $\sigma^2_{\mathrm{Resid}}$ represent the variance components for genotype, replication, planting density, interaction between replication and planting density, interaction between replication and genotype, interaction between planting density and genotype, plot, and residuals, respectively. Model fittings were carried out using lmer() function in the lme4 package [34] in R.

Phenotypic, genetic, and residual correlations among traits using a bivariate linear mixed model

To estimate phenotypic, genetic, and residual correlation between swMOE and other traits, a bivariate linear mixed model was fitted. The model included trait-specific fixed intercepts and individual genetic effects, with unstructured covariance matrices specified for both genetic and residual components across traits. The model was formulated as follows:

$$\begin{bmatrix} y_{1i} \\ y_{2i} \end{bmatrix} = \begin{bmatrix} \mu_1 \\ \mu_2 \end{bmatrix} + \begin{bmatrix} g_{1i} \\ g_{2i} \end{bmatrix} + \begin{bmatrix} e_{1i} \\ e_{2i} \end{bmatrix},$$

where y_{1i} represents phenotypic value of one of the growth traits (H, DBH, BH, CL, or FL) and y_{2i} are the phenotypic value of swMOE for individual i. μ_1 and μ_2 are the fixed means, g_{1i} and g_{2i} are the random genetic effect, and e_{1i} and e_{2i} are the residuals. The genetic and residual effects were assumed to follow multivariate normal distributions:

$$g_i \sim \mathcal{N}\left(0, \begin{bmatrix} \sigma^2_{g_1} & \sigma_{g_{1,2}} \\ \sigma_{g_{1,2}} & \sigma^2_{g_2} \end{bmatrix}\right), \quad e_i \sim \mathcal{N}\left(0, \begin{bmatrix} \sigma^2_{e_1} & \sigma_{e_{1,2}} \\ \sigma_{e_{1,2}} & \sigma^2_{e_2} \end{bmatrix}\right).$$

In the above formulation, $\sigma^2_{g_1}$ and $\sigma^2_{g_2}$ are the genetic variances of trait 1 and trait2, respectively. $\sigma_{g_{1,2}}$ is the genetic covariance between trait 1 and trait 2. $\sigma^2_{e_1}$ and $\sigma^2_{e_2}$ are the residual variances of trait 1 and trait 2, respectively. $\sigma^2_{e_{1,2}}$ is the residual covariance between trait 1 and trait 2. The phenotypic correlation r_p, genetic correlation $\mathrm{r_g}$ and the residual correlation $\mathrm{r_e}$ between traits were calculated as:

$$r_p = \frac{\sigma_{g_{1,2}} + \sigma_{e_{1,2}}}{\sqrt{(\sigma^2_{g_1} + \sigma^2_{e_1}) \cdot \left(\sigma^2_{g_2} + \sigma^2_{g_2}\right)}}, r_g = \frac{\sigma_{g_{1,2}}}{\sqrt{\sigma^2_{g_1} \cdot \sigma^2_{g_2}}}, \quad r_e = \frac{\sigma_{e_{1,2}}}{\sqrt{\sigma^2_{e_1} \cdot \sigma^2_{e_2}}}.$$

Bivariate linear mixed models were fitted using ASReml-R [35].

Simple linear regressions of swMOE on growth traits within each clone

To further examine the relationships among swMOE and growth traits, we fitted following simple linear regression model separately for each clone:

$$y_i = \mu + \beta x_i + \mathrm{Resid}_i,$$

where y_i is the measured value of swMOE for the ith tree, μ is the intercept, β is the slope, x_i is the value of a growth trait (one of H, DBH, BH, CL or FR). Coefficients of determination (R^2) were calculated to assess the strength of the relationship between swMOE and each growth trait within clones. Linear regression was performed using the lm() function in R.

Modeling of swMOE using linear mixed models including growth traits as covariates

To analyze the effect of growth traits on swMOE, the following four linear mixed models were compared:

Null model:

$$y_{ij} = \mu + \mathrm{G}_i + \mathrm{Resid}_{ij}.$$

Full model (including block structure):

$$y_{ijkl} = \mu + \mathrm{R}_i + \mathrm{PD}_j + \mathrm{R}_i \times \mathrm{PD}_j + \mathrm{G}_k + \mathrm{R}_i \times \mathrm{G}_k + \mathrm{PD}_j \times \mathrm{G}_k + \mathrm{P}_{ijk} + \mathrm{Resid}_{ijkl}.$$

Fixed slope model:

$$y_{ij} = \mu + \sum_{m=1}^{M} \beta_m x_{m,ij} + \mathrm{G_i} + \mathrm{Resid}_{ij}.$$

Fixed + random slope model:

$$y_{ij} = \mu + \sum_{m=1}^{M} \beta_m x_{m,ij} + \mathrm{G_i} + \sum_{m=1}^{M} (\mathrm{G} \times x_m)_{i,ij} + \mathrm{Resid}_{ij},$$

where y_{ij} is swMOE value for the jth tree of the ith genotype, $x_{m,ij}$ represents the value of the mth growth trait (one of H, DBH, BH, CL or FR) for the jth tree of the ith genotype, and M is either 1 or 2 depending on the model. β_m is the fixed-effect slope for covariate x_m, $(\mathrm{G} \times x_m)_{i,ij}$ represents the genotype-specific random slope, $\mathrm{G_i}$ is the random intercept for genotype i, and $\mathrm{Resid_{ij}}$ is the residual error. R_i is treated as fixed factor in this analysis. Model selection was performed based on Akaike's information criterion (AIC) [36], comparing the four models across all covariate growth traits. To avoid overfitting and difficulty of interpretation, a maximum of two covariates was used in each model. For the model including two covariates, variance inflation factors (VIFs) were calculated to assess multicollinearity for each model.

Model fittings were carried out using lmer() function in lme4 package in R. The REML option in lmer() was set to FALSE for model comparison based on AIC. VIFs were calculated using vif() function from the car package [37].

Cross-validation among replication

To evaluate model generalizability for swMOE, cross-validation was conducted between the two replications. Three models were compared: a null model, a fixed slope model, and a fixed plus random slope model. Models were fitted using data from one replication, and evaluated on the other. Model performance was assessed using coefficient of determination (R^2) and root mean square error (RMSE). Model fittings and validation were carried out using lmer() function in lme4 package in R.

Results

Summary of phenotypic variation

The average values of measured traits for each replication were 16.8 m and 19.4 m for H, 24.0 cm and 22.9 cm for DBH, 11.1 m and 13.2 m for BH, and 6.81 GPa and 8.20 GPa for swMOE, in replication 1 and replication 2, respectively. Replication 2, which was located at the lower elevation (Fig. 1), exhibited greater tree height and higher swMOE.

The average values of each trait by genotypes and planting density are shown in Table S1, and the variation are shown in Fig. S1. DBH and CL tended to decrease as planting density increased. In contrast, no clear effect of planting density was observed for H and BH. FR tended to increase with increasing planting density. Although swMOE showed an increasing trend with increasing planting density, clonal differences remained prominent.

Variance components and broad-sense heritability

The variance components and broad-sense heritability for each trait are shown in Fig. 2. Among all traits, the proportion of variance explained by genotype was highest for swMOE, followed by H. The proportion of variance attributed to replication was most prominent in H, while that attributed to planting density was substantial in DBH and FR. Broad-sense heritability was highest for swMOE (0.634), followed by H (0.277). CL and BH

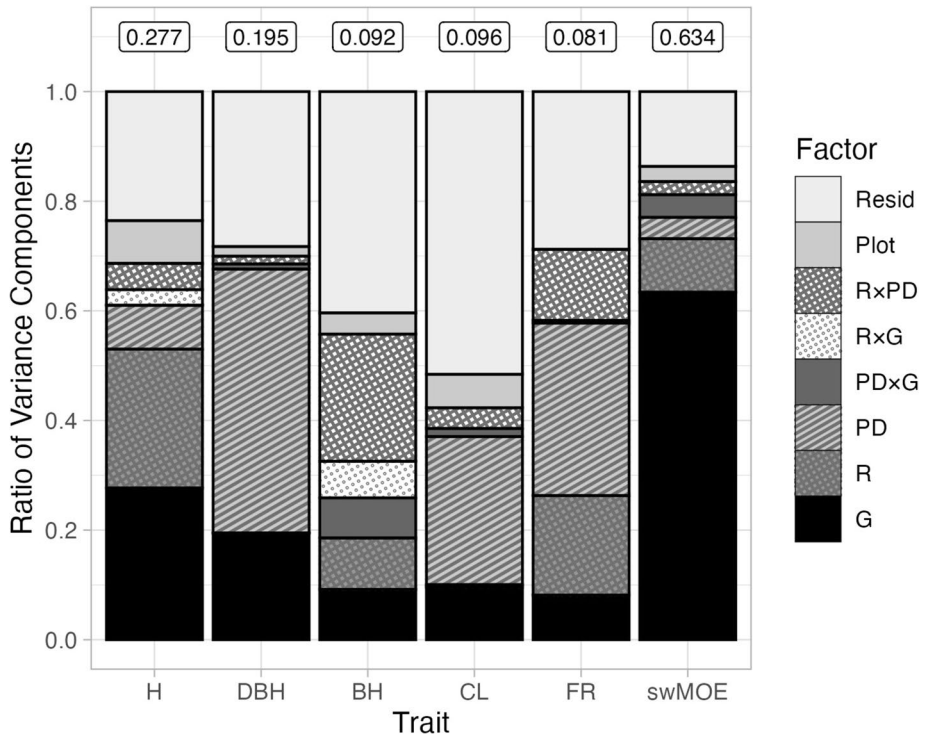


Fig. 2 Ratio of variance components and broad-sense heritabilities for each trait. Variance components were estimated using a linear mixed model fitted separately for each trait. The stacked bar plot shows the proportion of variance components attributed to genotype (G), replication (R), planting density (PD), their interactions (PD × G, R × G, R × PD), plot and residuals (Resid) for each trait. All factors were treated as random effects. Broad-sense heritability ($H.^2$) for each trait is shown above each bar. Traits include tree height (H), diameter at breast height (DBH), bole height (BH), crown length (CL), form ratio (FR), and stress-wave-based modulus of elasticity (swMOE)

showed lower heritabilities (0.092 and 0.096, respectively) compared to H and DBH (0.195). Although the broad-sense heritability of FR was low (0.081), its two component traits (H and DBH) used for the calculation showed relatively higher heritabilities.

Phenotypic, genotypic, and residual correlation

The Pearson's correlation coefficients among traits are shown in Fig. 3. Among the growth traits, DBH and FR exhibited the strongest correlation (−0.789), followed by DBH and CL (0.702). Although FR is mathematically derived from H and DBH, the correlation between H and FR was relatively low (0.059), indicating that DBH variation had a greater impact on FR in this study. H showed moderate correlation with BH, CL, and DBH. For swMOE, the highest correlation was observed with FR (0.503), followed by DBH (−0.361).

Given the significant correlation between swMOE and each of the growth trait, we used BLMM analysis to putatively divide this correlation into genetic and phenotypic contributions. The phenotypic, genetic, and residual correlations between each growth trait and swMOE are summarized in Table 1. DBH and CL showed negative phenotypic and residual correlation with swMOE, while their genetic correlations were close to zero or weakly positive. H exhibited very weak correlations with swMOE across all levels of correlation. Among all traits, form ratio (FR) showed the strongest positive correlations with swMOE, with a genetic correlation of 0.371 and a residual correlation of 0.731.

The coefficients of determination (R^2) for swMOE based on individual growth traits were calculated separately for each clone and for each growth traits by simple linear regression analysis (Fig. 4). For FR, the highest R^2 value among clones was 0.66, and mean R^2 across the six clones was 0.46. DBH showed the higher R^2 values than those obtained from directly measured traits such as H and BH, with mean R^2 of 0.27 across clones. H exhibited the lowest R^2 among all traits.

Modeling of swMOE including growth traits as covariates

Models predicting swMOE were fitted using various combinations of growth traits (H, DBH, BH, CL, FR) as fixed factors. These included fixed slope models that include one or two covariates, as well as fixed plus

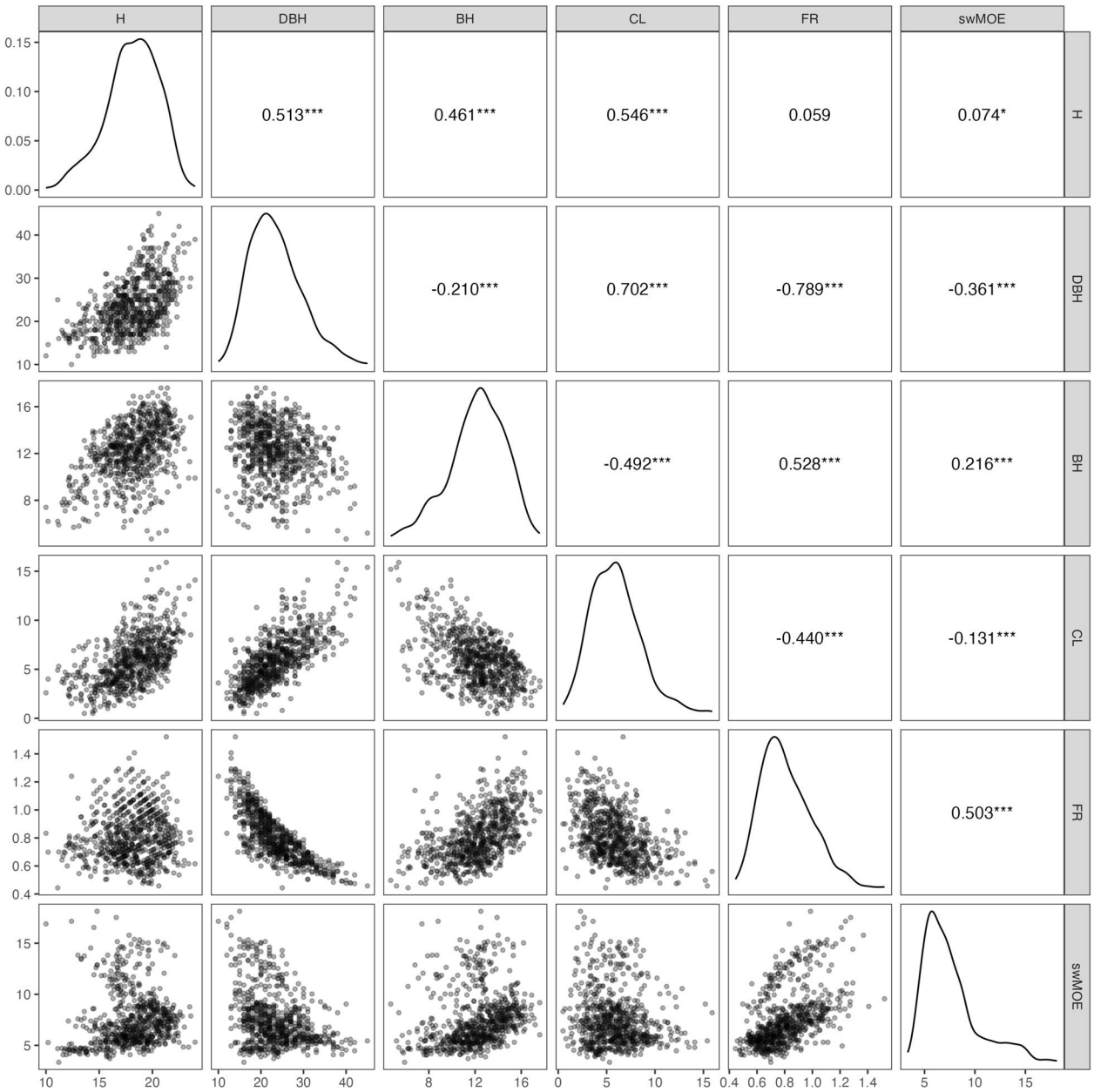


Fig. 3 Phenotypic correlations, distributions, and scatter plots among traits. Pairwise scatter plots (lower triangle), trait distributions (diagonal), and Pearson's correlation coefficients (upper triangle) among traits. Asterisks indicate significance levels: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). Trait abbreviations are the same as in Fig. 2

random slope models that additionally incorporated random slopes for each growth trait by clone. These models were compared with a null model including only clone as a genetic factor, and a full model that included replication, planting density, and their interaction as categorical fixed factors.

The AIC values of each model are shown in Table 2. The AIC for the null model was 2720.2 while that for the full model with design-based fixed factors was 2269.1. When H, DBH, BH or CL were used individually as covariates in fixed slope model, the AIC values improved compared to the null model but remained higher than that of the full model. In contrast, including FR as a covariate resulted

Table 1 Phenotypic, genetic, and residual correlation between growth traits and swMOE

Trait1	Trait2	Correlation		
		Phenotypic	Genetic	Residual
H	swMOE	0.115	0.162	0.069
DBH	swMOE	−0.292	0.006	−0.590
BH	swMOE	0.232	0.066	0.434
CL	swMOE	−0.100	0.259	−0.327
FR	swMOE	0.461	0.371	0.731

Phenotypic correlations, genetic correlations, and residual correlations between each growth trait and swMOE estimated using a bivariate linear mixed model. Trait abbreviations are the same as in Fig. 2

in a model with a lower AIC (2182.0) than the full model. When two covariates were included in the fixed slope model, the combination of H and FR yielded the lowest AIC value (2176.4). Furthermore, adding a random slope for FR by clone further reduced the AIC to 2135.9, and in the two-covariate model, H + FR resulted in the lowest AIC (2125.9) among all models tested.

The two-covariate models including both H and DBH, which are the components used to calculate FR, had higher AIC values than the models including FR alone, in both the fixed and fixed plus random slope models. The VIFs were below 2 in most cases and did not exceed 3.45, indicating no substantial multicollinearity issues in this analysis [38].

The best-fitting model among the single-covariate models, which included FR, is illustrated in Fig. 5, demonstrating that the slope of the FR-swMOE relationship varied among clones.

Prediction by cross-validation

The prediction accuracies of swMOE based on cross-validation between replications were analyzed (Table S2). Among single-covariate models, the fixed slope model using FR as a covariate achieved the best overall prediction performance, with the lowest average RMSE (1.24 GPa) and a high average R^2 of 0.834. When two covariates were used, the combination of DBH and FR resulted in the highest average R^2 (0.834), although the improvement over

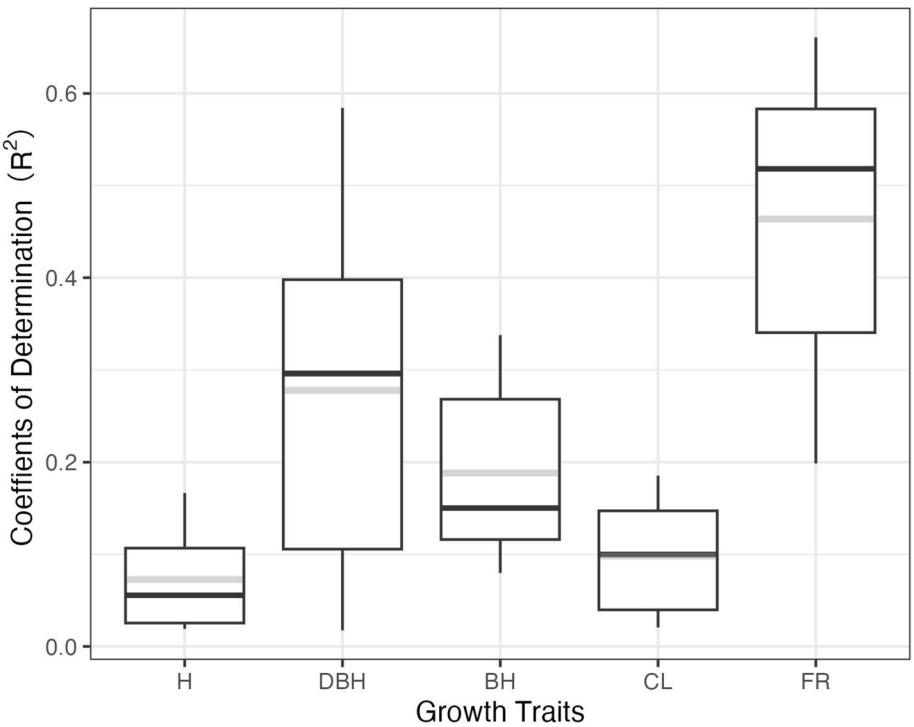


Fig. 4 Coefficients of determination (R^2) for swMOE explained by growth traits in each clone. R^2 values were obtained from simple linear regression models fitted separately for each clone, with swMOE as the response variable and each growth trait as the predictor. Boxplots show the variation in R^2 across clones for each growth trait ($n = 6$ for each boxplot). Trait abbreviations are the same as in Fig. 2. Black horizontal lines indicate the median R^2, and gray horizontal lines indicate the mean R^2

Table 2 Comparison of linear mixed models predicting swMOE based on Akaike's information criterion (AIC)

Explanatory variables	AIC	Number of continuous covariates	Is include random slope(s)	Variance inflation factor
Null model				
G	2720.2	0	F	-
Full model				
G + PD + R:PD + G + R:PD:G	**2269.1**	0	F	1.72
Fixed slope model				
H + G	2718.8	1	F	-
DBH + G	2420.9	1	F	-
BH + G	2575.2	1	F	-
CL + G	2642.8	1	F	-
FR + G	**2182.0**	1	F	-
H + DBH + G	2229.6	2	F	1.29
H + BH + G	2572.2	2	F	1.12
H + CL + G	2572.2	2	F	1.42
H + FR + G	**2176.4**	2	F	1.00
DBH + BH + G	2364.3	2	F	1.17
DBH + CL + G	2397.9	2	F	2.13
DBH + FR + G	2180.2	2	F	3.45
BH + CL + G	2572.2	2	F	1.61
BH + FR + G	2183.6	2	F	1.49
CL + FR + G	2179.5	2	F	1.35
Fixed + random slope model				
H + G + H:G	2715.5	1	T	-
DBH + G + DBH:G	2386.0	1	T	-
BH + G + BH:G	2568.2	1	T	-
CL + G + CL:G	2638.5	1	T	-
FR + G + FR:G	**2135.9**	1	T	-
H + DBH + G + H:G + DBH:G	2175.5	2	T	1.01
H + BH + G + H:G + BH:G	2563.4	2	T	1.01
H + CL + G + H:G + CL:G	2560.3	2	T	1.03
H + FR + G + H:G + FR:G	**2125.9**	2	T	1.00
DBH + BH + G + DBH:G + BH:G	2321.3	2	T	1.00
DBH + CL + G + DBH:G + CL:G	2362.8	2	T	1.09
DBH + FR + G + DBH:G + FR:G	2129.2	2	T	1.08
BH + CL + G + BH:G + CL:G	2559.0	2	T	1.04
BH + FR + G + BH:G + FR:G	2134.1	2	T	1.02
CL + FR + G + CL:G + FR:G	2133.6	2	T	1.01

"G" represents genotype (clone), "PD" planting density, and "R" replication (block), "H" tree height, "DBH" diameter at breast height, "BH" bole height, "CL" crown length, "FR" form ratio. Bold values indicate the lowest AIC within each combination of model type and number of continuous covariates

single-covariate FR model was minimal. In most cases, fixed slope models outperformed fixed plus random slope models in terms of both R^2 and RMSE.

The null model and best-performing fixed slope single-covariate model using FR, both trained on replication 2 and applied to replication 1, are shown in Fig. 6. The null model, which included only genotype, was unable to explain within-clone variation in swMOE (Fig. 6a), whereas the FR-based model successfully captured intra-clonal differences (Fig. 6b).

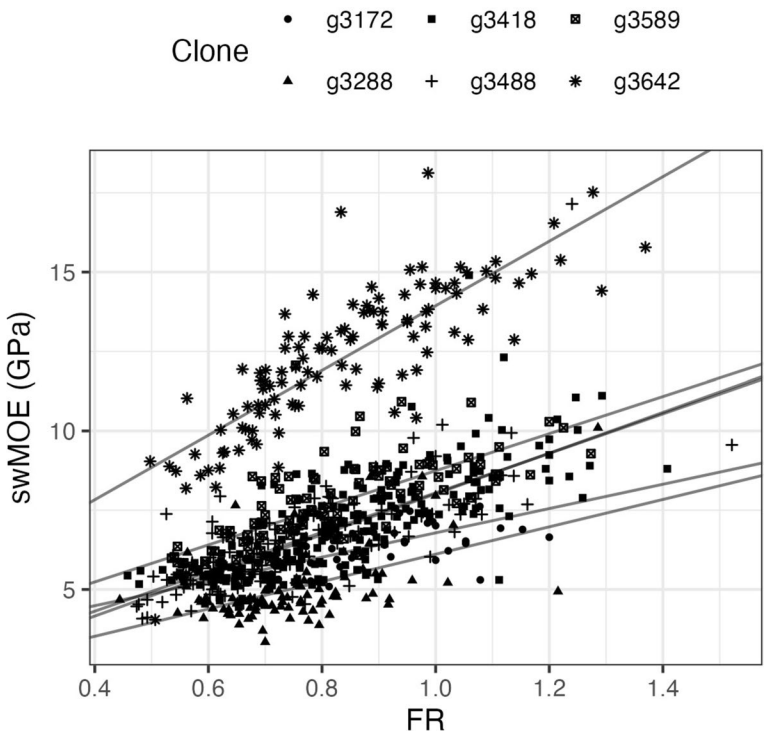


Fig. 5 Best-fitting fixed plus random slope model of swMOE with form ratio (FR) as a covariate. Results from the linear mixed models including form ration (FR) as a covariate are shown. The model includes both a fixed slope and a random slope for each clone. The scatter plot showing the relationship between form ratio (FR) and swMOE for individual trees across six clones. Each point represents an individual tree, with symbol shapes indicating clone identity. Solid lines represent the fitted regression lines combining the fixed slope and clone-specific random slopes

Discussion

In this research, we estimated wood stiffness in standing trees using stress wave velocity, measured as swMOE and recorded growth traits for trees exhibiting diverse growth patterns in planting density trial involving six clones (genotypes). Using these data, we evaluated the relationship between wood stiffness and growth traits, and modeled wood stiffness from the perspective of both genotype and growth traits for predictive purposes. Our study is strengthened by a large sample size, which enhances the robustness and the generalizability of the modeling results.

In this study, swMOE exhibited stronger genetic control compared to growth traits (Fig. 3). Fujisawa et al. [24] reported a broad-sense heritability of 0.64 of dynamic MOE in logs from 21 to 26-year-old *C. japonica* stands, and Miyashita et al. [22] reported broad-sense heritabilities 0.78 for stress wave velocity and 0.81 for dynamic MOE for logs from 10-year-old *C. japonica* trees. Our results, a broad-sense heritability of 0.63, is consistent with these previous findings. From another perspective, more than 30% of the variation in swMOE was attributed to environmental factors. Among these factors, planting density had only a minor effect on swMOE (Fig. 3). However, some clones tended to show higher swMOE under higher planting density (Fig. S1e). Similar trends have been reported previously. Tsushima et al. [17] found that MOE of log was slightly higher at denser initial spacing using six local cultivars of *C. japonica*. Fukuchi et al. [30] found that stress wave velocity increased with planting density in a local variety of *C. japonica*. Ishiguri et al. [39] also showed that MOE increased with planting density, from 1500 trees/ha to 6000 trees/ha for *C. japonica*. Roth et al. [40] in *Pinus taeda*, and Erasmus et al. [41] in *Pinus patula*, observed a similar trend, with higher planting density leading to increased stress wave velocity.

In contrast, growth traits were more susceptible to environmental factors than swMOE, and the magnitude of these effect varied among traits. The effect of planting density, a controllable environmental factor in forest management, was smaller for H compared to DBH and crown length (CL) (Fig. 2). Tsushima et al. [17] reported no differences in tree height within each *C. japonica* cultivars grown in different spacing. Sato et al. [42] reported that the effect of planting density on H remained small over time, while its effect on DBH increased with age in *C. japonica*. Our results align with this finding, showing a small planting density effect on H and more pronounced effect on DBH at stand age 40. Dickens and Will [43] reported that in *Pinus elliottii*, tree height is suppressed

at high planting density, though to a lesser degree than diameter growth. Fukuchi et al. [30] observed a clear reduction in tree height with increasing planting density (376–10,000 trees/ha) using Nelder plot in *C. japonica*. Although planting density effect had a weaker influence on H compared to genotype (Fig. 2) in our study, high planting density tended to reduce tree height (Fig. S1, Table S1), a trend supported by previous research. Our results contribute to this body of knowledge by confirming that while planting density affects tree height, the effect is relatively modest. Interaction effects between clone and planting density were small for both H and DBH, suggesting that the influence of planting density on these traits was largely consistent across genotype in *C. japonica*.

Planting density is an artificial and controllable environmental factor in plantation forestry. However, its effects are not uniform across individual trees. After planting, trees grow under competitive pressure from neighboring individuals, and growth variation can arise even among trees with the same planting density and genotype. Therefore, it is important to understand how variations in growth traits——such as tree height, diameter, bole height, crown length, as well as combinations of these traits——affect wood stiffness in order to clarify the sources of genetic variation in wood stiffness and to improve its prediction.

From a biomechanical perspective, tall and slender trees require stiffer wood to avoid buckling under self-loading [44]. Relationships between tree form (e.g., form ratio or crown projection area) and wood stiffness have been reported at the species level in conifers [45]. In *C. japonica*, Kijidani et al. [28] examined 17 local cultivars and found that most showed a positive relationship between wood stiffness and form ratio (H/DBH). Our results support these findings: form ratio, representing stem slenderness, showed the highest R^2 values for each clone (Fig. 4), derived from a large-scale planting density trial that allowed us to evaluate wide range of growth states. At the genetic level, Mishima et al. [46] reported a weak positive clonal correlation ($r=0.103$) between DBH and stress wave velocity based on 745 plus trees of *C. japonica,* and Yasuda et al. [27] also reported a weak positive genetic correlation ($r=0.263$) in *C. japonica*. In our study, no genetic correlation was detected between DBH and swMOE (Table 1), which is consistent with previous reports in indicating that the genetic association between these traits is weak. However, we observed a large residual correlation between swMOE and growth traits such as DBH and form ratio (Table 1, Fig. 4). These results

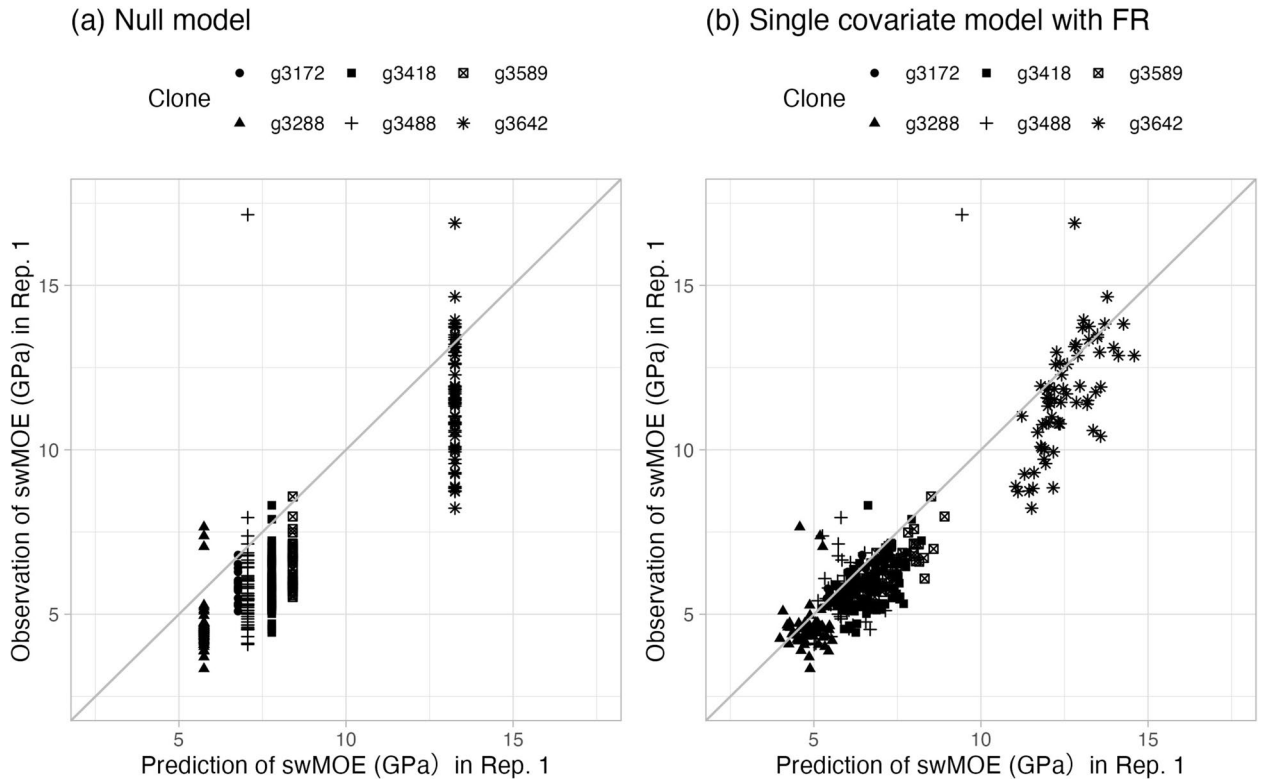


Fig. 6 Cross-validation results of swMOE prediction from replication 2 to replication 1. **a** Prediction using the null model, which included only genotype as a random effect. **b** Prediction using the best-performing fixed slope model, which included form ratio (FR, H/DBH) as a covariate. Gray diagonal lines represent the reference line where predicted values equal observed values (x = y)

emphasize the importance of distinguishing between genetic and environmental contributions when analyzing trait relationships.

In general, phenotypes are shaped by the combined effects of genotype and environment, and their interaction [47]. In tree breeding, environmental variation is typically treated as noise—stemming from site, replications, tree plot effects—which is one-off and difficult to reproduce, and one of the goals is to estimate genetic values by removing these environmental effects. However, wood formation is influenced not only by genetics but also by growth status, which reflect resource allocation and physiological conditions such as photosynthate production and hormone levels [48], and stimulation by gravity by tree form [49], among others. Growth itself is also a phenotype influenced by both genotype and environment, and in the context of genetic analysis for wood properties, growth traits can be considered environmental covariates influencing wood formation.

In this study, we decomposed variation in swMOE using a linear mixed model structure that included genetic intercepts, continuous growth trait covariates, genotype-by-covariate interactions modeled as random slopes, and residuals (Table 2). Among the tested covariates, form ratio (H/DBH) provided the best model fit. Furthermore, the random slope model for form ratio outperformed the fixed slope model, suggesting that the relationship between form ratio and swMOE varies among genotypes (Table 2). These results indicate that swMOE is determined by four major components: genotype-specific baseline stiffness (genetic intercepts), the overall effect of form ratio (fixed slope), genotype-by-form ratio interactions (random slope), and residual variation which includes unexplained environmental factors.

From a predictive perspective, however, including random slopes for each genotype slightly reduced prediction accuracy (Table S2). In prediction modeling, overfitting can be a concern [50], and simpler model often preferred. Nevertheless, incorporating form ratio as a fixed covariate clearly improved prediction accuracy compared to the null model. Thus, form ratio is confirmed to be a key predictor of wood stiffness, from both model fitting and prediction standpoints.

In practical applications, predicting wood properties at newly planted sites is critical for planning lumber production and estimating economic return. In this study, swMOE showed high heritability (broad-sense heritability = 0.634), suggesting that genetic information of planted clones can be valuable for predicting wood stiffness at operational sites. However, the actual swMOE may still be influenced by individual growth conditions. Compared to swMOE, tree height and diameter are less heritable, but much easier to measure, especially with the advancement of remote sensing technologies such as laser scanning [51]. When combined with information on planted clones or families, models incorporating form ratio may offer practical value for predicting wood stiffness in operational forestry.

The mechanisms underlying the relationship between form ratio and wood stiffness are not yet fully understood. At the anatomical level, wood stiffness is known to be influenced by microfibril angle of cell wall and wood density [18, 52]. Microfibril angle has been linked to gravitational signaling mediated by auxin [53]. Funada et al. [54] reported the level of endogenous auxin levels decreased with a reduction in crown proportion in *C. japonica*. Kijidani et al. [55] also found that both crown length and distance from a crown base significantly influence auxin level in the stem. In our results, form ratio was a better predictor of swMOE than models based on crown length and bole height combined (Table 2), suggesting that form ratio may reflect factors associated with microfibril angle and wood stiffness, possibly including auxin-mediated response to gravitational stimuli. However, since auxin affects multiple developmental processes, it is also possible that auxin levels influence both form ratio and swMOE independently. While our results suggest a strong statistical association, the underlying physiological mechanism remains unclear. Further research is required to examine whether and how form ratio contributes causally to microfibril angle or wood stiffness, including direct measurements of anatomical traits and hormone levels.

Conclusion

In this study, we demonstrated that wood stiffness (swMOE) in *Cryptomeria japonica* is under relatively strong genetic control and is strongly influenced by growth traits—particularly the form ratio (H/DBH)—based on data from a planting density trial with a large number of trees per clone. These findings highlight the importance of form ratio to clarify the mechanism that forms the phenotypic, genotypic, and environmental variation in wood stiffness, and suggest that form ratio is a reliable covariate for explaining and predicting intra-genotypic variation in wood stiffness.

Abbreviations

MOE	Modulus of elasticity
SSR	Simple sequence repeat
H	Tree height
BH	Bole height
DBH	Diameter at breast height
CL	Crown length
FR	Form ratio
swMOE	Modulus of elasticity estimated from time of flight of stress waves
AIC	Akaike's information criterion
VIF	Variance inflation factor
RMSE	Root mean square error

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s10086-025-02220-1.

Supplementary material 1.

Acknowledgements
The test site used in this study was established and maintained by the National Forests of Japan in collaboration with the Forest Tree Breeding Center, Forestry and Forest Products Research Institute. We thank the members of these organizations for their dedicated efforts.

Author contributions
EF was a major contributor in writing the manuscript. KY collected and analyzed stress wave velocity, KM collected and analyzed growth trait. MK collected and analyzed growth traits. All authors read and approved the final manuscript.

Funding
This work was supported by JSPS KAKENHI Grant Number 22H02411.

Data availability
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests
The authors declare that they have no competing interests.

Received: 27 April 2025 Accepted: 11 July 2025
Published online: 01 August 2025

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