



Genetic gains in wood property can be achieved by indirect selection and nondestructive measurements in full-sib families of Japanese cedar (*Cryptomeria japonica* D. Don) plus tree clones

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Abstract

• **Key message** We assessed the narrow-sense heredity and genetic gains of multiple traits obtained using the indirect selection method for progeny of *Cryptomeria japonica* D. Don by artificial crossing. Using stress wave velocity and Pilodyn penetration depth as indicative parameters, wood properties could be improved in future generations of *C. japonica* plus trees and forest breeding programs will become more efficient.

• **Context** To advance generations of *C. japonica* D. Don breeding populations, the narrow-sense heredity and genetic gain of traits of progenies are required to assess the practical genetic performance of parental trees and improve traits.

• **Aims** We assessed the genetic gains in both growth characteristics and wood properties by indirect selection using full-sib progenies of *C. japonica* plus trees produced through artificial crosses.

• **Methods** In 18-year-old progenies of 549 trees, we assessed growth characteristics, dynamic modulus of elasticity, basic density, stress wave velocity, and Pilodyn penetration depth. Genetic parameters were calculated using a mixed model and the breedR package.

• **Results** The genetic correlation between growth characteristics and wood properties was low. The efficiencies of indirect selection for dynamic modulus of elasticity by stress wave velocity and for basic densities by Pilodyn penetration depth were higher than those for growth characteristics by stress wave velocity and Pilodyn penetration depth, respectively. Strong correlations were found between the parental clonal values and breeding values of parental trees predicted from progeny using stress wave velocity and Pilodyn penetration depth.

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• **Conclusion** Using stress wave velocity and Pilodyn penetration depth as indicative parameters, future generations of *C. japonica* plus trees could produce superior wood properties. Growth characteristics and wood properties are independent; thus, both traits could be genetically improved compatibly.

Keywords Inheritance mode · Tree breeding · Basic density · Dynamic modulus of elasticity

1 Introduction

Wood property traits are of particular importance in forest tree breeding programs (Zobel and van Buijtenen 1989) because they are highly relevant to the physical and mechanical performance of wood products (Cown et al. 1995; Fujisawa 1998; Wessels et al. 2011). Modulus of elasticity (MOE) and wood density are the major traits that represent these mechanical properties. For example, MOE is strongly correlated with the breaking strength of wood (Castéra et al. 1996; Kijidani et al. 2010), whereas wood density is related to wood stiffness (Cown et al. 1995; Burdon et al. 2001). The latter also strongly affects tree carbon sequestration (Roderick and Berry 2001; Profft et al. 2009; Skovsgaard et al. 2011).

In most forest tree breeding programs, research that is aimed at simultaneously improving multiple traits, such as growth characteristics and wood properties, is ongoing (White et al. 2007). Improving multiple traits requires an understanding of both within- and among-tree variation for each trait as well as the genetic correlations among the traits of interest. Although good estimates of genetic parameters likely require a few hundred samples (Schimleck et al. 2019), wood property traits have generally been evaluated using surveys of felled trees, which is labor-intensive, expensive, and time-consuming. In addition, when using the standard destructive procedure that accompanies tree felling, it is difficult to obtain a sufficient number of samples from progeny or clonal tests because felling makes it difficult to continue the testing thereafter. Therefore, in many countries, nondestructive methods for investigating the traits of standing tree have been evaluated in major plantation tree species (Isik et al. 2011; Isik and Li 2003; Jones et al. 2005; Li et al. 2017; Pot et al. 2002; Raymond 2002; Schimleck et al. 2019; Wang et al. 1999; Wessels et al. 2011), and various nondestructive tools are now used in tree breeding programs and wood property breeding studies around the world (Apiolaza 2009; Schimleck et al. 2019).

Japanese cedar, *Cryptomeria japonica* D. Don, is one of the most important plantation tree species in Japan. Through the national forest tree breeding program, about 3700 first-generation plus trees have been selected from natural forests and artificial plantations with a focus on stem volume and stem form. The selection of second-generation plus trees, which are superior

progenies of the first-generation plus tree clones, is ongoing. Pollination among selected second-generation plus tree clones will be conducted to set up a new breeding population and select for the third-generation plus trees in the future. In the second-generation plus tree selection criteria, both growth characteristics and wood property traits are major breeding targets. Evaluation of wood property traits in second-generation plus tree clones is performed using nondestructive procedures. The narrow-sense heritability of each trait and the genetic correlation among traits must be clarified if the improvement of multiple traits is to be optimized as generations of the breeding population advance. In addition, to advance wood property-focused breeding using nondestructive tools, it remains necessary to verify the usefulness of the nondestructive evaluation method based on full-sib progenies of the plus tree clones. Furthermore, it is not currently clear whether clonal values can be used as the proxy of the parental genetic abilities when selecting parents for controlled pollination among plus tree clones. The higher the ratio of additive effect over non-additive effect in wood property, the clonal value would well positively correlate with the breeding value. If this were the case, a large amount of data on the clonal wood properties of plus tree clones, which is often obtained in advance, could be utilized for the wood property breeding.

Previous studies on wood property inheritance and nondestructive evaluation methods for standing *C. japonica* trees have been mainly conducted using first-generation plus tree clones (Fukatsu et al. 2011; Fujisawa et al. 1992, 1994; Miyashita et al. 2009). Indeed, few data exist on the narrow-sense heritability of each trait, the genetic correlation between nondestructive evaluation values of standing tree and growth characteristics or wood properties, and the efficiency of indirect selection based on narrow-sense heritability.

In the present study, we evaluated optimal breeding strategies for improving both growth characteristics and wood properties using full-sib progenies of *C. japonica* plus tree clones. The specific research objectives in the study were to estimate (1) genetic gain by direct selection of multiple traits, (2) the phenotypic and genetic correlation among the traits, and (3) genetic gain by indirect selection of wood properties with nondestructive measurements, as well as to (4) compare the parental breeding wood property values estimated based on the progenies with their clonal wood property values.

2 Materials and methods

2.1 Plant materials

The progeny test site used in the present study was established in 1995 at the Forest Tree Breeding Center (36.69° N, 140.69° E), Forest and Forest Products Research Institute, Hitachi City, Ibaraki Prefecture. The test was designed to include unbalanced randomized complete blocks of six replications with 1.8×1.8 m spacing between trees (3000 individual/ha), mainly consisting of 45 full-sib families derived from eight sets of 4×4 half-diallel crosses using 32 *C. japonica* plus tree clones (Table 1). The number of trees in the experiment design was 2046 before the thinning. The thinning was conducted systematically, with an orthorhombic lattice pattern without paying attention to tree size in 2012 (stand age was 18 years), and the felled 549 full-sib progenies were used as the plant materials in the present study. There was a difference in the number of samples among parameters because the samples which were difficult to measure and calculate for each parameter were excluded (Table 2).

2.2 Growth characteristics and wood properties of standing trees

In November 2012, before thinning was performed, tree height (H; 0.1 m unit) and diameter at breast height (DBH; 0.1 cm unit) were measured at ~1.3 m above ground using a Vertex III (Haglof, Sweden) and caliper, respectively. Stress wave velocity (SWV; 1 m/s unit) was measured using a TreeSonic timer (FAKOPP, Hungary); specifically, start and stop sensors were installed, parallel to the axial direction of the trunk, at upper (1.7 m above ground) and lower (0.7 m above ground) positions, respectively (setting the section length to 1.0 m). SWV was measured in two perpendicular directions on the stem of standing trees. Measurements were taken five times each in one direction and the average value of 10 measured values was used as the individual value of each tree. Pilodyn penetration (PP; 0.1 mm unit) was measured using the Pilodyn 6J Forest instrument (Proceq Co., Switzerland) with an effective measurement range length of 0–40 mm and a pin diameter of 2.5 mm. During PP measurements, the device was first set facing the side of the standing tree's trunk in two perpendicular directions at breast height and then the pin was driven toward the pith. This PP measurement was performed once in each direction and without removing the bark, and the average of two measured values was used as the individual values for each tree.

2.3 Wood properties of logs

After measuring growth characteristics, SWV, and PP, thinning was conducted and 1.5-m-long logs were taken from the felled

Table 1 Diallel combinations of the samples used in this study

Female	Male		
	1531	1551	1579
1544	33 (30)	9 (8)	-
1531		2 (2)	14 (13)
1551			-
Female	Male		
	1565	1659	1552
1690	20 (17)	17 (15)	15 (14)
1565		5 (4)	1 (1)
1659			8 (7)
Female	Male		
	1543	1708	1557
1691	1 (1)	5 (4)	-
1543		5 (5)	1 (1)
1708			5 (4)
Female	Male		
	1566	1548	1538
1633	17 (15)	18 (13)	15 (11)
1566		25 (22)	7 (7)
1548			2 (2)
Female	Male		
	1578	1662	1726
1698	22 (19)	12 (11)	20 (18)
1578		21 (16)	24 (19)
1662			6 (5)
Female	Male		
	1577	1535	1715
1533	2 (2)	12 (11)	19 (18)
1577		9 (8)	20 (19)
1535			14 (14)
Female	Male		
	1707	1709	1727
1628	21 (18)	15 (14)	23 (20)
1707		18 (14)	21 (21)
1709			12 (12)
Female	Male		
	1719	1534	1539
1542	5 (2)	15 (14)	6 (4)
1719		1 (1)	2 (1)
1534			4 (2)

Values in the table represent the number of samples in a diallel combination. Values in parentheses represent the number of samples used in calculation for the average basic density (BD_{mean}), which was the smallest number of samples in this study

individuals at a height of 1.0–2.5 m above ground. The dynamic modulus of elasticity (DMOE; 0.1 GPa unit) was measured by the tapping method (Sobue 1986) using an FFT analyzer AD-3527 (A&D, Tokyo, Japan). After the DMOE was measured, 10-cm-thick disks were collected from the breast height region; these were stored in natural conditions until basic density (BD; 0.001 g/cm³ unit) was measured. Strip samples in two directions centered on the pith were prepared from each disk. The specimens (segments) used to measure BD were made from strips divided every five annual rings from the pith using a chisel. BD was calculated as the oven-dried weight divided by

Table 2 Growth traits and wood properties in the progenies of *Cryptomeria japonica* plus trees

Trait unit	H (m)	HDBH (cm)	DMOE (GPa)	BD _{mean} (g/cm ³)	BD1 (g/cm ³)	BD2 (g/cm ³)	BD3 (g/cm ³)	SWV (m/s)	PP (mm)
Mean	12.4	17.2	4.85	0.316	0.343	0.312	0.305	2667	18.9
Max.	18.2	32.9	7.85	0.416	0.488	0.439	0.409	3338	25.5
Min.	4.8	5.2	1.69	0.248	0.256	0.217	0.229	1870	13.0
S.D.	2.5	4.7	0.92	0.026	0.036	0.030	0.031	238	2.3
CV (%)	20.2	27.1	19.0	8.6	10.6	9.7	10.3	8.9	12.2
h^2	0.168	0.145	0.353	0.503	0.380	0.488	0.385	0.361	0.432
ΔG_x	0.4	0.7	0.32	0.013	0.014	0.015	0.012	86	1.0
Relative genetic gain (%)	3.4	4.0	6.7	4.1	4.0	4.7	3.9	3.2	5.2
n	548	549	547	479	488	488	488	545	549

Number of families =45

H tree height, DBH diameter at breast height (1.3 m above ground), $DMOE$ dynamic modulus of elasticity, BD_{mean} the average basic density of disks, $BD1$ the basic density of the region from the 1st to 5th rings on the pith side, $BD2$ the basic density of the region from the 6th to 10th rings on the pith side, $BD3$ the basic density of the region from the 11th to 15th rings on the pith side, SWV stress wave velocity, PP Pilodyn penetration depth, $S.D.$ standard deviation, CV coefficient of variance, h^2 narrow-sense heritability, ΔG_x genetic gain obtained by direct selection at selection intensity $i=1$, n number of the progenies measured for each trait

the green wood volume, which was measured by the water displacement method. $BD1$, $BD2$, and $BD3$ were defined as the basic densities of the segments containing the 1st to 5th, 6th to 10th, and 11th to 15th annual rings, respectively. BD was not measured outside of the 16th annual ring. The mean BD of the entire disk (BD_{mean}) was calculated by the weighted average method using the area of the $BD1$, $BD2$, and $BD3$ segments. All BDs (i.e., $BD1$, $BD2$, $BD3$, and BD_{mean}) were measured in two directions using two strips, and the mean value was used as the individual value of each BD .

For comparison with the parental breeding values of PP and SWV estimated based on the progenies (mentioned below), we used respective clonal values measured by Mishima et al. (2011).

2.4 Statistical analysis

Pearson's correlation coefficients were calculated between traits as phenotypic correlations. The variance component and breeding value for each trait was estimated with a linear mixed model (Eq. 1) using the restricted maximum likelihood method (REML):

$$Y_{ijkl} = \mu + B_i + G_{jkl} + S_{kl} + B_i \times S_{kl} + e_{ijkl} \quad (1)$$

Here, Y_{ijkl} is a measurement value, μ is the general mean, B_i is a fixed effect of the block i , G_{jkl} is a random effect of the general combining ability (GCA) of an individual j for parents k and l , S_{kl} is a random effect of the specific combining ability (SCA) of parents k and l , $B_i \times S_{kl}$ is a random interaction effect for block i and parents k and l , and e_{ijkl} is a random residual effect. The abovementioned parameters of variances were estimated by the REML method. The random factors and

individual tree breeding values were obtained by an "animal model" of best linear unbiased prediction (BLUP).

The narrow-sense heritability (h^2) of each trait was estimated by Eq. 2:

$$h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_s^2 + \sigma_{bs}^2 + \sigma_e^2} \quad (2)$$

Here, σ_g^2 , σ_s^2 , σ_{bs}^2 , and σ_e^2 are the variance components of GCA, SCA, the interaction of block \times SCA, and the residual, respectively.

The genetic correlation between trait x and trait y was estimated using Eq. 3:

$$r_{g(x,y)} = \frac{COV_{g(x,y)}}{\sqrt{\sigma_{g(x)}^2 \times \sigma_{g(y)}^2}} \quad (3)$$

Here, $r_{g(x,y)}$ is the genetic correlation of trait x and trait y , $COV_{g(x,y)}$ is the covariance of trait x and trait y , and $\sigma_{g(x)}^2$ and $\sigma_{g(y)}^2$ are the variances of trait x and trait y , respectively. The variance components and genetic parameters, such as the narrow-sense heritability, genetic correlation, and breeding value, were calculated using the R package breedR (Munoz and Sanchez 2019) in R 3.6.1 (R Core Team 2019).

We also estimated the genetic gain obtained by direct selection and indirect selection for growth characteristics and wood properties. The genetic gain obtained by direct selection was calculated using Eq. 4:

$$\Delta G_x = i \times h_{(x)}^2 \times \sigma_{g(x)} \quad (4)$$

Here, ΔG_x is the genetic gain of trait x , i is the selection intensity, $h^2(x)$ is the narrow-sense heritability of trait x , and $\sigma_{g(x)}$ is the standard deviation of the GCA effect at trait x . The genetic gain obtained by indirect selection was calculated with Eq. 5:

$$\Delta G_{x(y)} = i \times h_{(y)}^2 \times r_{g(xy)} \times \sigma_{g(x)} \quad (5)$$

Here, $\Delta G_{x(y)}$ is the genetic gain of trait x by selection with trait y , $h_{(y)}^2$ is the narrow-sense heritability of trait y , and $r_{g(x,y)}$ is the genetic correlation between traits x and y . In both calculations, selection intensity $i=1$ was applied (Falconer and Mackay 1996). The percentage of the genetic gain by direct selection from the mean of target trait x (relative genetic gain) and the efficiency of genetic gain by indirect selection compared to direct selection were calculated according to Fukatsu et al. (2015).

To examine the usefulness of evaluating parental abilities using clones, the parental breeding values obtained from the REML/BLUP procedures (described above) and the clonal values measured by Mishima et al. (2011) were correlated to calculate correlation coefficients for PP and SWV. In their study, three ramets were basically measured and used as the clonal value.

3 Results

3.1 Growth characteristics and wood properties

Data on growth characteristics and wood properties are given in Table 2. BD values decreased in the order of BD1, BD2, and BD3. The coefficient of variation (CV) of each wood property (8.6–19.0%) was less than the CV of each growth characteristic (20.2–27.1%). The narrow-sense heritability for each wood property ($h^2=0.353$ – 0.503) was higher than that of H and DBH ($h^2=0.168$ and 0.145 , respectively). The relative genetic gains from direct selection (with selection intensity $i=1$) for growth characteristics and wood properties were similar (3.2–6.7%), as shown in Table 2. The ratio of variance components is shown in Fig. 1. The ratio of SCA was smaller than that of GCA for all traits.

3.2 Phenotypic and genetic correlations between traits

The phenotypic and genetic correlations between traits are shown in Table 3. A strong positive phenotypic correlation was observed between SWV and DMOE ($r=0.847$), whereas the phenotypic correlation between PP and BD_{mean} was strongly negative ($r=-0.729$). Correlations between PP and BD1, BD2, and BD3 gave coefficients of -0.429 , -0.632 , and -0.768 , respectively; these negative correlations were stronger at the bark side and weaker at the pith side. A strong

positive genetic correlation was also observed between SWV and DMOE ($r_{g(x,y)}=0.901$). The genetic correlations between PP and BD values, namely BD1, BD2, BD3, and BD_{mean} , were again negative and largely strong, especially at the bark side, -0.534 , -0.730 , -0.870 , and -0.797 , respectively. The phenotypic and genetic correlations between growth characteristics (H and DBH) and wood properties measured after felling were weaker than the respective correlations with wood properties measured from standing trees.

3.3 Efficiency of indirect selection

The efficiencies of indirect selection (with a selection intensity of $i=1$) for growth characteristics and wood properties are presented in Table 4. The efficiency of indirect selection for DMOE by SWV (1.10) was higher than that for each BD (0.19–0.30). On the other hand, the efficiencies of indirect selection for BDs by PP (0.60–0.97) were higher than that for DMOE (0.11). Among the BD values, BD3 had the highest indirect selection efficiency value (0.97).

The efficiencies of indirect selection for H and DBH by SWV (0.56 and 0.50) were lower than that for DMOE (1.10). Similarly, the efficiencies of indirect selection for H and DBH by PP (0.13 and 0.55) were lower than those obtained for BDs (0.60–0.97).

3.4 Relationship between parental breeding values predicted by the progenies and their clonal values

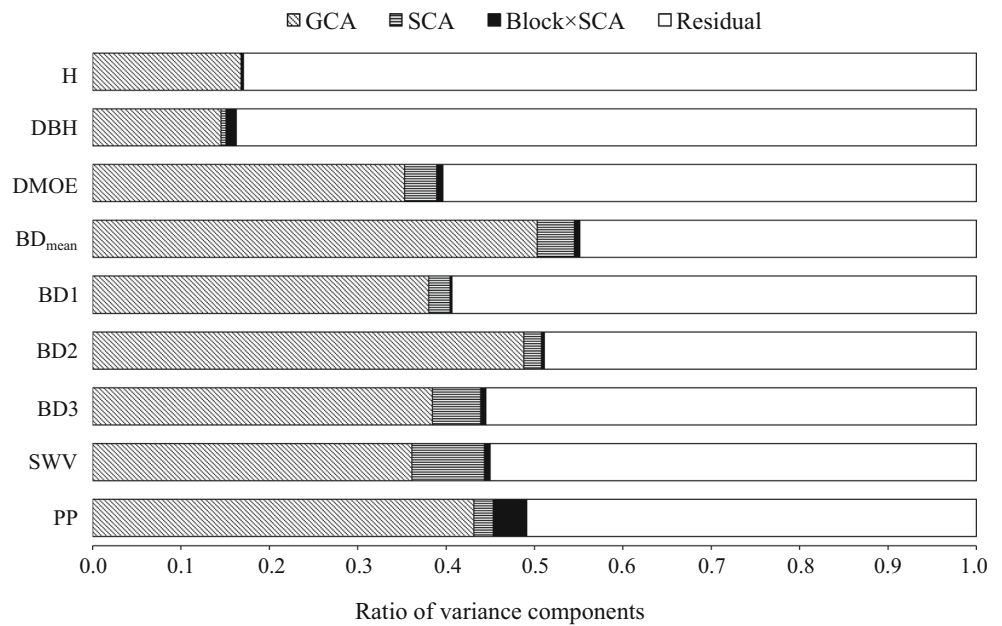
For SWV and PP, correlations between parental breeding values predicted by the progenies and clonal values were assessed. For both SWV and PP, positive correlations ($r=0.75$ and $r=0.69$, respectively Fig. 2), were found between these values.

4 Discussion

4.1 Inheritance for each trait

In the present study, the variance component ratios were calculated for growth characteristics (H and DBH) and wood properties (DMOE, BDs, SWV, and PP). The larger ratio of variance component of GCA than that of SCA for growth characteristics and wood properties (Fig. 1) have also been reported in other coniferous species including *Pinus taeda* L. (Isik and Li 2003; Isik et al. 2011), *Pinus radiata* D. Don (Gapare et al. 2010), and *Larix kaempferi* (Lamb.) Carr. (Fukatsu et al. 2015). In general, these results indicated that the genetic performance of a parent is additively transmitted to its progeny (White et al. 2007). Therefore, it would be possible to select superior progenies from superior parents for both growth characteristics and wood properties in *C. japonica*.

Fig. 1 The ratio of variance components for each trait. The abbreviations for traits are listed in Table 2. Additional definitions: *GCA* general combining ability, *SCA* specific combining ability, *Block × SCA* interaction effect between block and *SCA*, *Residual* random residual effect



Although there have been many reports of broad-sense heritability in *C. japonica* (Fujisawa et al. 1992, 1994; Fukatsu et al. 2011; Miyashita et al. 2009), there are few data on narrow-sense heritability for wood properties. The repeatability of wood properties such as dynamic modulus of elasticity and basic density is known to be higher than that of growth characteristics such as tree height and diameter at breast height (Fujisawa et al. 1992, 1994; Fukatsu et al. 2011; Miyashita et al. 2009). In the present study, the narrow-sense heritability of each wood property in both logs and standing trees was also higher than that for the measured growth characteristics (Table 2). Therefore, in *C. japonica*, the phenotypes of wood properties appear to be affected less than the growth characteristics by environmental factors. Results such as this have also been reported for other coniferous species, e.g., *P. taeda* (Isik and Li 2003), *P. radiata* (Gapare et al.

2010; Kumari et al. 2002), *Pinus sylvestris* L. (Hong et al. 2014), and *L. kaempferi* (Fukatsu et al. 2015). Taken together, these results suggested that the inheritance of wood properties observed in the present study would be common to coniferous species. Again, this shows that superior progenies from superior parents could be selected for both growth characteristics and wood properties in *C. japonica*.

4.2 Efficiency of nondestructive measurement of wood properties

Here, a nondestructive wood property measurement method was assessed for its efficiency when evaluating the additive genetic performance for next-generation breeding with the progeny of *C. japonica* plus tree clones. High absolute values for phenotypic correlations

Table 3 Phenotypic and genetic correlation coefficients obtained from correlations between each trait

		Genetic correlation coefficients								
Trait		H	DBH	DMOE	BD _{mean}	BD1	BD2	BD3	SWV	PP
Phenotypic correlation coefficients	H		0.790	0.218	0.124	0.184	0.204	0.071	0.317	0.079
	DBH	0.808		0.106	-0.074	-0.001	0.033	-0.165	0.263	0.300
	DMOE	0.023	-0.237		0.347	0.438	0.319	0.262	0.901	-0.092
	BD _{mean}	-0.287	-0.331	0.283		0.786	0.948	0.918	0.224	-0.797
	BD1	-0.458	-0.489	0.321	0.729		0.717	0.604	0.253	-0.534
	BD2	-0.187	-0.196	0.223	0.920	0.615		0.833	0.248	-0.730
	BD3	-0.175	-0.43	0.202	0.873	0.452	0.735		0.158	-0.870
	SWV	0.238	0.029	0.847	0.096	0.056	0.085	0.091		0.040
	PP	0.395	0.410	-0.043	-0.729	-0.429	-0.632	-0.768	0.124	

The abbreviations for traits are listed in Table 2

Table 4 Genetic gains of indirect selection and efficiency of the genetic gain for each trait (with selection intensity $i=1$)

x	y	$\Delta G_{x(y)}$	Efficiency of indirect selection
H	SWV	0.4	0.56
DBH	SWV	0.7	0.50
DMOE	SWV	0.44	1.10
BD _{mean}	SWV	0.003	0.23
BD1	SWV	0.005	0.30
BD2	SWV	0.004	0.26
BD3	SWV	0.003	0.19
H	PP	0.1	0.13
DBH	PP	0.7	0.55
DMOE	PP	0.04	0.11
BD _{mean}	PP	0.010	0.78
BD1	PP	0.009	0.60
BD2	PP	0.011	0.72
BD3	PP	0.013	0.97

x represents the direct selection traits and y represents the indirect selection traits for x . $\Delta G_{x(y)}$ is the genetic gain obtained by indirect selection. The abbreviations for traits are listed in Table 2

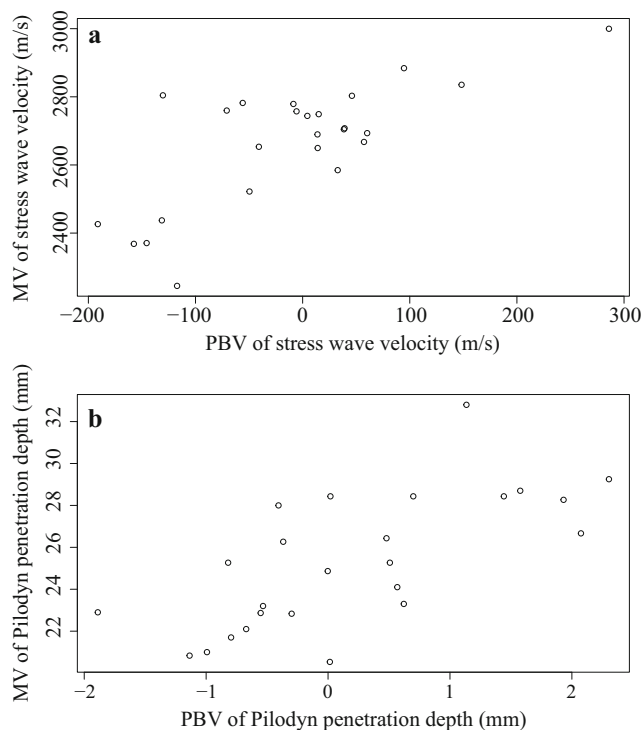


Fig. 2 Scatter plot of measured parental clonal values (MV) and parental breeding values estimated from standing wood properties of artificial cross family traits (PBV). **a** Stress wave velocity (m/s). Pearson's correlation coefficient = 0.75 ($P < 0.001$). **b** Pilodyn penetration depth (mm). Pearson's correlation coefficient = 0.69 ($P < 0.001$). For both traits, measured values in the parental clone (MV) are plotted against the breeding values of the parental clone (PBV), and each value is representative of the parental clone

between SWV and DMOE and between PP and BDs (Table 3) were also reported between stress wave velocity and dynamic modulus of elasticity in *C. japonica* (Miyashita et al. 2009) and other coniferous species (Chen et al. 2015; Ishiguri et al. 2008; Schimleck et al. 2019; Wessels et al. 2011, 2015). Additionally, similar relationships between Pilodyn penetration depth and basic density have been reported in *C. japonica* (Fukatsu et al. 2011; Miyashita et al. 2009) and other conifers (Cown 1978; Cown and Hutchison 1983; Chen et al. 2015; dos Santos et al. 2016; Ishiguri et al. 2008; Schimleck et al. 2019). Obtaining a genetic correlation between two traits is an important aspect of validating a correlated response to selection or indirect selection among traits (White et al. 2007). In the present study, genetic correlations between SWV and DMOE and between PP and BD_{mean} were evident (Table 3). In addition, the efficiencies of indirect selection for DMOE by SWV and for BD_{mean} by PP (Table 4) suggest that, in forest tree breeding programs, *C. japonica* with high dynamic modulus of elasticity or high average basic density can be selected effectively using stress wave velocity and Pilodyn penetration depth as indirect selection indices. In addition, the genetic correlation between PP and BD3 was higher than between PP and either BD1 or BD2, indicating that it is possible to evaluate outer basic density (near the bark) accurately using Pilodyn penetration depth.

For both phenotypic and genetic correlations, correlation coefficients were low between SWV and BDs and between PP and DMOE (Table 3). The lower efficiency of indirect selection for BDs selected by SWV and for DMOE selected by PP and a weak genetic correlation between DMOE and BDs could be occurred because, in a previous study of *C. japonica*, dynamic modulus of elasticity was more strongly correlated with the microfibril angle of the S₂ layer in latewood tracheids than with wood density (Hirakawa et al. 1997); thus, it appears to be difficult to improve wood density in this species using stress wave velocity as an indirect selection criterion. On the other hand, the genetic correlation between wood density and stress wave velocity has been reported to be strong in other coniferous species such as *P. radiata*, *Picea abies* (L.) Karst., and *L. kaempferi* (Apiolaza 2009; Chen et al. 2015; Fukatsu et al. 2015). Additionally, a positive correlation has been reported between dynamic modulus of elasticity and wood density in *L. kaempferi* (Ishiguri et al. 2008; Nakada et al. 2005; Tumenjargal et al. 2020). These findings suggest that the relationship between dynamic modulus of elasticity and wood density differs depending on tree species. Therefore, appropriate procedures for wood property breeding should be chosen according to species.

4.3 Relationship between the breeding values predicted by progenies and the clonal values of parental plus trees

By evaluating the genetic performance of the parental clones that contribute to the next generation, it is possible to plan the appropriate mating designs necessary for constructing next-generation breeding populations. In the present study, for SWV and PP, positive correlations were observed between the breeding values of the parent predicted from progenies and the clonal values of the first-generation plus trees (Fig. 2). These results indicate that, based on clonal values, it is possible to select superior parents for mating and superior families from existing breeding populations, which originated from artificial crossing between plus tree clones, before performing progeny tests with high accuracy. In *C. japonica*, wood properties for most of the first-generation plus tree clones have already been evaluated by stress wave velocity and Pilodyn penetration depth using their ramets (e.g., Mishima et al. 2011). Given the large amount of existing data on clonal wood properties, wood property improvement can be driven forward efficiently in *C. japonica* breeding programs.

4.4 Relationships between growth characteristics and wood properties

The weak genetic correlations among growth characteristics and wood properties (Table 3) and the lower efficiency of indirect selection for H and DBH by SWV and PP (Table 4) suggest that individuals with superior growth characteristics and wood properties can be selected, and that it would be possible to achieve genetic improvement in both growth characteristics and wood properties simultaneously. The weak phenotypic correlations between growth characteristics and wood properties in the present study are consistent with findings of previous *C. japonica* studies (Fujisawa et al. 1992, 1994; Fukatsu et al. 2011; Miyashita et al. 2009).

4.5 Application to tree breeding for wood properties in *C. japonica*

The results of the present study suggest that the growth characteristics of *C. japonica* (H and DBH) and the wood properties of its logs (DMOE and BD) are genetically independent; therefore, it should be possible to select *C. japonica* individuals with both superior growth and wood qualities. A progeny which has both superior traits may be produced by artificially mating a parent with superior growth and a one with superior wood property. Moreover, stress wave velocity and Pilodyn penetration depth, both of which are nondestructive measurements, were shown to be effective indices for evaluating dynamic modulus of elasticity and average basic density, respectively. Currently, the selection of second-generation

C. japonica plus trees from a breeding population consisting of the progenies of the first-generation plus tree clones is underway. After the conventional evaluation of superior trees based on growth characteristics, by applying stress wave velocity and Pilodyn penetration depth during selection, it may be possible to select superior second-generation plus tree candidates, in terms of growth characteristics and wood properties, efficiently, and nondestructively.

The relatively large GCA component and positive correlation between the parental breeding values predicted from progenies and clonal values suggests that the clonal value of wood properties obtained by nondestructive measurements could be used as a proxy of the breeding value, i.e., a measure of genetic performance as parent which has been conventionally obtained by the progeny test. *C. japonica* has already been comprehensively evaluated for clone of first-generation plus trees, and we thought that this evaluation can be effectively used for future selection and creation of the next generation. Clonal values as the parental genetic performance also suit seed production in seed orchards, in which random mating of parents is assumed. In other words, by creating a seed orchard from *C. japonica* second-generation plus tree clones with superior growth characteristics and wood properties, it may be possible to produce *C. japonica* seedlings with superior growth characteristics and wood properties.

5 Conclusions

In this study, we clarified the genetic gains in wood property by indirect selection using nondestructive measurements based on full-sib families derived from half-diallel crosses of *C. japonica* plus tree clones. We showed that the growth characteristics and wood properties of *C. japonica* could be improved independently and that stress wave velocity and Pilodyn penetration depth were effective indirect selection indices for breeding. Indeed, stress wave velocity and Pilodyn penetration depth have become indispensable indicators of wood property improvement in forest tree breeding programs. Since the relationship between growth characteristics and wood properties differs depending on tree species, genetic evaluation must be performed after selecting an appropriate indirect evaluation method according to the tree species or age.

We also showed that clonal wood property data in first-generation plus tree clones is useful for advancing the breeding of this species. Second-generation plus tree clones, which have been selected and propagated from breeding populations, are currently preserved and evaluated for growth traits. In addition, assessing the wood properties of these trees in the clonal archives using nondestructive measurements would provide further data for use when breeding the next advanced generation. Based on these nondestructive measurements and

clonal wood properties data, it should be possible to advance *C. japonica* breeding more effectively and efficiently.

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

Declaration

Conflict of interest The authors declare that they have no conflict of interest.

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