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Genetic improvement of sawn-board shape stability in Scots pine (*Pinus sylvestris* L.)

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ABSTRACT

Adequate shape stability is a prerequisite for utilization of sawn boards in the building industry. This study investigated the possibility of indirect genetic improvement of Scots pine (*Pinus sylvestris* L.) sawn-board shape stability (specifically the bow, crook and twist) via selective breeding based on traits that can be non-destructively measured on standing trees. Relationships between shape stability and wood quality traits measured on logs and sawn boards were also determined. A total of 1896 standing trees from a 39-year-old Scots pine full-sib progeny test were non-destructively measured. A subset of 496 trees was harvested and sawn into 50 × 100 mm boards, the quality of which was assessed both non-destructively and destructively. Among the traits assessed on standing trees, grain angle (GRA) appeared to be the best predictor of sawn-board twisting and crooking ($r_A = 0.84$ and 0.62, respectively). The individual-tree narrow-sense heritability (h_i^2) was moderate for twist and GRA (0.37 and 0.40, respectively), low for bow (0.21) and very low for crook (0.05). Selective breeding targeting lower GRA would result in lower twist and crook but could also increase sawn-board density, stiffness and strength.

1. Introduction

Wood has been used as a construction material for centuries, mainly because of its wide availability, renewability and high specific strength. Shape and dimensional stability are crucial quality attributes of sawn board. In the construction industry, warping of sawn boards with poor shape stability often causes severe problems that can result in prioritizing other engineering materials over wood (Johansson et al., 1994). Among the various forms of warping, twisting is considered the most important. Twisting of sawn boards can to some extent be reduced by different modifications of the drying process such as applying an external load (Arganbright et al., 1978), additional steaming of boards (Frühwald, 2006), or using high temperatures (Kliger et al., 2005), whereas dimensional stability can be effectively improved by, e.g., tung oil treatment (He et al., 2019) or impregnation modification with furfuryl alcohol (Yao et al., 2017).

Several studies have indicated that twisting can be decreased by selective breeding targeting trees with a lower grain angle (e.g. Hallingbäck et al., 2008; Högberg et al., 2010). The GRA (i.e., spiral grain) is a measure of helical deviation from a longitudinal arrangement of wood fibers. Generally, conifers in the northern hemisphere develop a left-handed spiral grain first and, as they mature, switch to a right-handed direction (e.g. Harris, 1989; Säll, 2002). Although several hypotheses may explain why trees form a spiral grain, such as higher resistance to breaking, even distribution of sap (Kubler, 1991) or crown asymmetry due to phototropism (Skatter and Kucera, 1998), this phenomenon is not yet been fully understood.

Substantial genetic variation and moderate to high narrow-sense heritability (approximately 0.3–0.7) of GRA have been detected for different coniferous forest tree species (e.g. Hansen and Roulund, 1998; Gapare et al., 2007; Gaspar et al., 2008; Hallingbäck et al., 2010a; Högberg et al., 2014). Moreover, GRA has a strong positive genetic correlation with sawn-board twisting (Högberg et al., 2014) and nearly zero genetic correlations with growth traits and wood density (Hansen and Roulund, 1998; Hallingbäck et al., 2010a). These findings suggest that genetic selection for lower GRA results in trees producing sawn

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boards with low twist, while other traits remain unchanged. Only few studies on board shape stability have been performed at the genetic level because such studies require at least several hundred trees with known pedigree, arranged in a well-designed field test, to be harvested and processed into boards.

Recently, the Scots pine trees in the Swedish forest tree breeding program reached their half-rotation age and attained the minimum sawmillable dimensions. This created an opportunity for genetic studies targeting sawn boards as a final product. The main objectives of this study were to (1) assess the genetic variation and heritability of shape stability traits—crook (CRK), bow (BOW) and twist (TWI)—measured on Scots pine sawn boards and GRA measured under the bark of the respective standing trees, (2) estimate the relationships between shape stability traits or under-bark GRA with other wood quality and growth traits measured at different stages of wood processing, and (3) evaluate the possibility of improving sawn-board shape stability via selective breeding based on growth and wood quality traits non-destructively measured on standing trees, including the under-bark GRA.

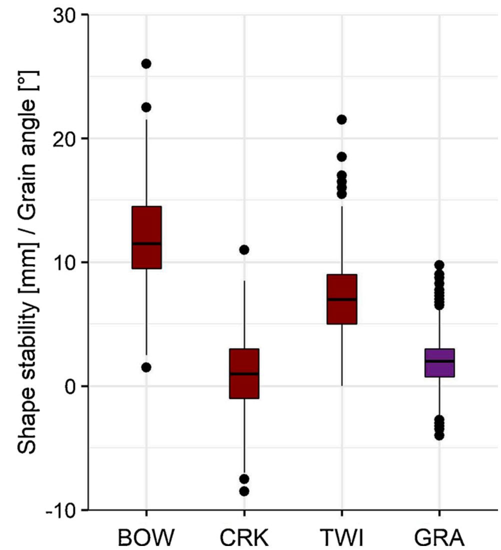

Fig. 1. Box plot of shape stability traits (bow, crook and twist) and grain angle.

2. Materials and methods

2.1. Study material and measurements

This study was conducted in a Scots pine full-sib progeny test “Älvkarleby” (#S22F791110E, 60°32’35″ N, 17°26’12″ E, 25 m a.s.l.) in central Sweden. The test was established by the Forestry Research Institute of Sweden (Skogforsk) in 1979 on a flat site with podzolic soil, by using 90 full-sib families of 24 parents crossed according to a partial diallelic design with each parent represented in as many as eight crosses. The trees, planted as 1-year-old seedlings with 2 × 2 m spacing, were arranged in a completely randomized block design comprising eight blocks, seven of which were included in the study. Details on the geographic origin of the parental trees are provided in Fundova et al. (2020).

All standing trees (1896) were assessed for diameter at breast height (DBH; 1.3 m) and stem straightness (STR; 9-point scale, where 9 is completely straight) and were drilled bark-to-bark approximately 1.2 m above the ground with a Resistograph IMLRESI PD300 micro-drill (Instrumenta Mechanic Labor, Germany) to assess wood density. Resistograph drilling profiles were linearly detrended and debarked to minimize bias in wood density estimates according to Fundova et al. (2018). Wood density (DEN_{TREE}) was calculated as the average value of the processed drilling profiles divided by four for better scaling. Standing-tree acoustic velocity (VEL_{TREE}) was measured between two probes hammered into a stem approximately 90 cm apart with a Hitman ST300 tool (Fiber-gen, New Zealand). The dynamic modulus of elasticity (MOE_d), representing wood stiffness, can be estimated from the acoustic velocity (VEL) and density (DEN) as

$$MOE_d = VEL^2 \cdot DEN \quad (1)$$

(Bucur, 2006). For the calculation of the standing-tree modulus of elasticity (MOE_{TREE}), VEL_{TREE} and DEN_{TREE} measured on standing trees were used in Eq. 1 (Fundova et al., 2019). GRA was measured under the bark with a wedge GRA gauge (Chalmers Institute of Technology, Sweden) gently hammered into a stem at breast height (Hannrup et al., 2003). A patch of bark was removed before each measurement. For every tree, measurements from two opposite sides (northern and southern) were combined to reduce bias caused by stem leaning (Harris, 1984; Hansen and Roulund, 1998). Positive and negative values were assigned to left-handed and right-handed grain, respectively (Hannrup et al., 2003). In all wood quality trait assessments, care was taken to avoid branches, compression wood or visible stem damage.

Bottom 3.3 m long sawlogs from 496 trees with DBH greater than 15 cm were felled during a systematic thinning and further studied. Acoustic resonance (f_{LOG}), induced by a hammer, was recorded with an Android application Resonance Log Grader (Fakopp Enterprise Bt., Hungary). The exact length (L) of all logs was measured and acoustic velocity (VEL_{LOG}) was calculated as $2 \cdot L \cdot f_{LOG}$. According to Eq. 1, the dynamic modulus of elasticity for logs (MOE_{LOG}) was estimated from VEL_{LOG} and DEN_{TREE}.

Afterward, the logs were sawn through the pith, thus producing two 50 × 100 mm boards per log. Two stacks of sawn boards (992), separated layer-wise by sticks, were weighted on top, covered with a roof and allowed to air-dry over the summer. In the autumn, shape stability, acoustic resonance, moisture content (MC) and weight were measured on all air-dried boards; the presence and extent of wane was also recorded. Shape stability traits, namely BOW, CRK and TWI (Fig. 1.A), were assessed on a right-angled flat table with a wedge with a millimeter scale. Only the upper 3 m of each board was considered to eliminate the variation in board length. BOW and CRK were measured as the maximum warping on a board’s face and along a board’s edge, respectively. For measuring TWI, the bottom end of a board was fixed, and the deviation of the top corner from the surface was scored. The direction of warping was taken into consideration by assigning positive and negative signs according to Mishiro and Booker (1988). At the same time as shape stability measurement, the MC of each board (mean at 15.3 %) was assessed by with a two-pin Delmhorst RDM-2S moisture meter according to Esping and Folkeson (1998).

An MTG Timber Grader (Brookhuis MicroElectronics) was used to measure acoustic resonance on sawn boards placed on two supports 3 m apart. The resonance frequency (f_{BOARD}) of an impulse generated by an integrated electric hammer was recorded, and the sawn-board acoustic velocity (VEL_{BOARD}) was calculated as $2 \cdot L \cdot f_{BOARD}$. The dynamic modulus of elasticity for sawn boards was determined according to Eq. 1 by using VEL_{BOARD} and the volumetric board density (DEN_{BOARD}), estimated as a board’s mass divided by its volume. Traits measured on pairs of boards were averaged so that one value per tree was used in further statistical analyses.

A four-point bending test was performed on one set of boards (496) according to the EN 408 standard (CEN, 2010b). The weakest section of each board was predicted by scanning the boards with WoodEye (Olsson et al., 2013) and placed between central loading points in a bending test setup (Fig. 2.A). Local ($MOE_{S.local}$) and global ($MOE_{S.global}$) moduli of elasticity and the modulus of rupture (MOR) representing mid-span and whole-span deflections and bending strength at rupture, respectively, were computed according to Eqs. 2,3 and 4, respectively.

$$MOE_{S.local} = \frac{3 a l_1^2 F}{4 b h^3 w} \quad (2)$$

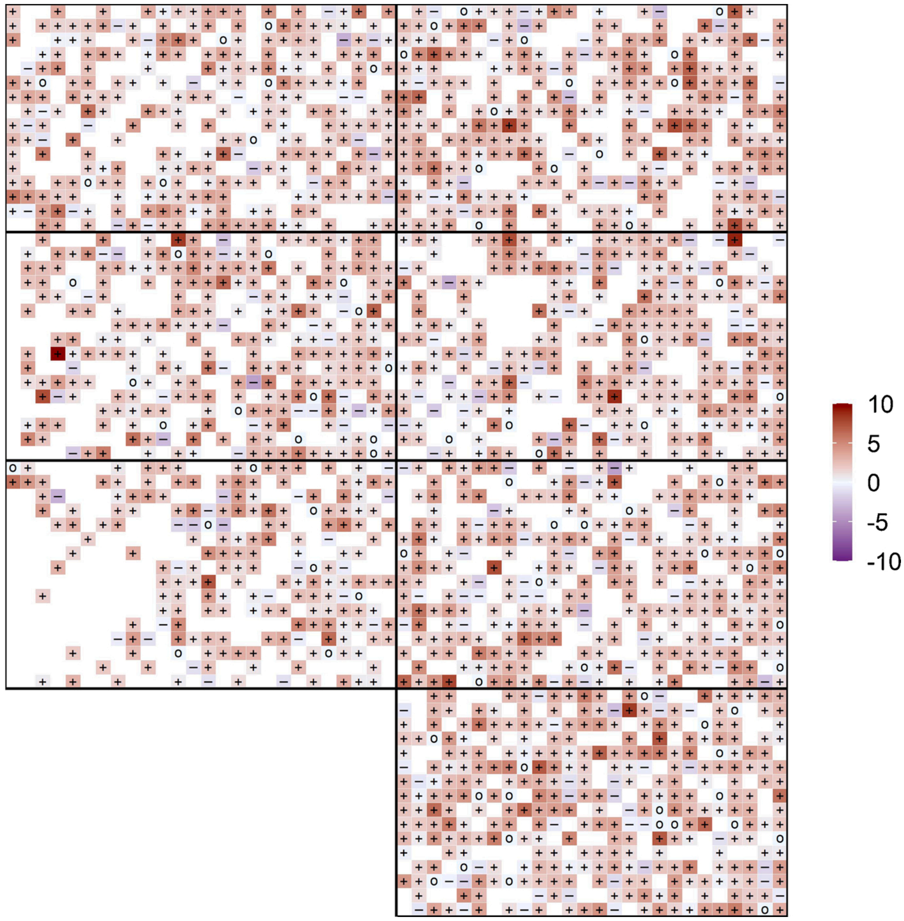

Fig. 2. Distribution of grain angle measurements on the experimental site. Signs +, – and ○ indicate positive (left-handed), negative (right-handed) and zero (straight) grain angle, respectively.

$$\mathrm{MOE}_{\mathrm{S.global}} = \frac{l^3F}{bh^3y}\left[\frac{3a}{4l} - \left(\frac{a}{l}\right)^3\right] \quad (3)$$

$$\mathrm{MOR} = \frac{3aF_{max}}{bh^2} \quad (4)$$

where F is an increase in applied load, F_{max} is the maximum load, b is board thickness, h is board width, a is the distance between loading and the nearest bearing point, l is the total distance between the bearing points, l_1 is the length of the central gauge, and w and y are local and global deformation increments, respectively (Fig. 2.A; further details can be found in Fundova et al. (2020)). Before the destructive testing, three measurements of MC were performed along each board with a two-pin moisture meter. The MC was adjusted to 12 % according to EN 384 (CEN, 2010a) for $\mathrm{MOE_S}$, whereas for $\mathrm{VEL_{BOARD}}$, $\mathrm{MOE_{BOARD}}$, $\mathrm{DEN_{BOARD}}$ and shape stability traits, simple regression analysis was used.

2.2. Statistical analysis

Variance and covariance components were estimated with the statistical package ASReml 4 (Gilmour et al., 2015) by fitting the response variables to the following linear mixed model:

$$y_{ijj'k} = \mu + B_i + G_j + G_{j'} + S_{jj'} + e_{ijj'k} \quad (5)$$

where $y_{ijj'k}$ is the k^{th} measurement for the jj'^{th} cross growing in the i^{th} block; B_i is the fixed effect of the block; G_j and $G_{j'}$ represent random general combining ability effects of the j^{th} female and the j'^{th} male, respectively; $S_{jj'}$ is the random specific combining ability effect of the j^{th} and j'^{th} parents; and $e_{ijj'k}$ is a random error term. The model was applied in a bivariate form so that a trait of interest was always paired with $\mathrm{DEN_{TREE}}$ because $\mathrm{DEN_{TREE}}$ was measured on all standing trees and thus would potentially help to improve estimates and reduce selection effects for the other trait (Wei and Borralho, 1998). Wane depth was used as a fixed covariate for variables measured on sawn boards except for the three shape stability traits, for which it was non-significant ($p > 0.05$).

For each variable, individual-tree narrow-sense heritability (h_i^2) and broad-sense heritability (H_i^2) were estimated as

$$h_i^2 = \frac{\sigma_A^2}{\sigma_P^2} = \frac{4\sigma_p^2}{2\sigma_p^2 + \sigma_f^2 + \sigma_e^2} \quad (6)$$

$$H_i^2 = \frac{\sigma_G^2}{\sigma_P^2} = \frac{4\sigma_p^2 + 4\sigma_f^2}{2\sigma_p^2 + \sigma_f^2 + \sigma_e^2} \quad (7)$$

where σ_A^2, σ_P^2, σ_G^2, σ_p^2, σ_f^2 and σ_e^2 are additive genetic, phenotypic, genotypic, parental, family and residual variance components, respectively. Standard errors were obtained with Taylor series expansion (Gilmour et al., 2015). Phenotypic and additive genetic correlations (r_{xy}) were estimated as

$$r_{xy} = \frac{\sigma_{xy}}{\sqrt{\sigma_x^2 \times \sigma_y^2}} \quad (8)$$

where σ_x^2 and σ_y^2 are phenotypic or additive genetic variances for traits x and y, respectively, and σ_{xy} is the phenotypic or additive genetic covariance between traits x and y, estimated by fitting a trivariate model

Table 1
Descriptive statistics for shape stability traits and grain angle (minimum, maximum and mean); phenotypic, additive genetic, dominance and genotypic standard deviations (σ_P, σ_A, σ_D and σ_G, respectively); and individual-tree narrow-sense (h_i^2) and broad-sense (H_i^2) heritability (standard errors in parentheses).

Trait	Units	Description	*Min*	*Max*	*Mean*	σ_P	σ_A	σ_D	σ_G	h_i^2	H_i^2
BOW	mm	Maximum bow	1.46	25.25	11.37	3.50	1.59	1.84	2.43	0.21 (0.10)	0.49 (0.15)
CRK	mm	Maximum crook	−9.94	12.38	1.44	3.64	0.76	0.00	0.76	0.05 (0.05)	0.05 (0.13)
TWI	mm	Maximum twist	−0.38	23.29	9.56	3.25	1.97	2.22	2.97	0.37 (0.13)	0.80 (0.17)
GRA	°	Grain angle under bark	−4.00	12.50	1.97	1.89	1.19	1.15	1.66	0.40 (0.11)	0.77 (0.11)

(Eq. 5) with DEN_{TREE} always being included. The correlated response (CR_{A_y}) to the selection for a target trait y was calculated as

$$CR_{A_y} = ih_{ix}r_{A_{xy}}\sigma_{A_y} \quad (9)$$

where i is the selection intensity, h_{ix} is the square root of the narrow-sense heritability for selection trait x, $r_{A_{xy}}$ is the additive genetic correlation between traits x and y, and σ_{A_y} is the additive genetic standard deviation for target trait y. The response from direct selection for trait y could be obtained by simplification of Eq. 9, where h_{ix} is exchanged for h_{iy}, and $r_{A_{xy}}$ is omitted.

3. Results and discussion

3.1. Range, variance and heritability

Descriptive statistics, variance and narrow- and broad-sense heritability estimates for shape stability traits measured on air-dried sawn boards and GRA measured on standing trees are summarized in Table 1 and visualized in Fig. 1. Descriptive statistics for other traits discussed in this study can be found in Fundova et al. (2020). Measurements of BOW ranged from 1.46 mm to 25.25 mm. The positive values indicated that deformations occurred only along the pith face (inner face) of the boards, which to a certain extent corresponded with the boards having been stored with the pith facing up. CRK exhibited both positive and negative values (from -9.94 to 12.38 mm) with a mean of 1.44 mm, thus suggesting that the occurrence of concave and convex deformations along a board's long edge was largely evenly distributed among boards. TWI ranged from 0.38 mm to 23.29 mm; positive TWI, i.e., with the top right side of a board raised when laid on the pith side, was more frequent and stronger than the negative TWI. Notably, the study material consisted of sawn boards produced from small-dimension logs obtained from systematic thinning. Because trees with small diameters contains relatively higher proportions of juvenile wood, their solid-wood products are susceptible to warping (Zobel and Sprague, 1998).

Note that comparisons of twisted and untwisted (control) samples have not been included in this study. In contrast to technical comparisons of materials, we focused on exploring natural variation (genetic and environmental), where defining control samples is difficult. Furthermore, the samples represented only a subset of centrally sawn bottom logs from trees grown in a relatively uniform and well defined environment. It is expected that a sample of fully mature trees at rotation age would harbor a phenotypic variation even greater than what is reported here. In this context, an untwisted "golden standard" control sample would appear as very narrow and artificial, and comparisons to such a control would therefore be meaningless.

The GRA measured on standing trees varied between -4° and 13°, with an average of 2 degrees. The positive values often observed in this study represent a left-handed orientation of the grain, which is typical of younger trees (Harris, 1989; Säll, 2002). A more pronounced GRA was expected in border trees than in trees inside stands (Wellner and Lowery, 1967); however, no pattern in GRA distribution was observed within the Älvkarleby site (Fig. 2).

The phenotypic standard deviations observed for the shape stability traits were similar (3.25–3.64 mm), whereas their additive genetic deviations varied substantially (0.76–1.97 mm), as did their heritability.

Table 2
Additive genetic and phenotypic correlations of shape stability traits (bow, crook and twist) with growth and wood quality traits (standard errors in parentheses).

	Genetic correlations			Phenotypic correlations		
	BOW	CRK	TWI	BOW	CRK	TWI
DBH	−0.24 (0.30)	**−0.54** (0.24)	−0.09 (0.28)	0.02 (0.05)	**−0.21** (0.05)	**0.12** (0.05)
STR	**0.74** (0.19)	−0.17 (0.31)	−0.05 (0.28)	**0.17** (0.05)	**−0.12** (0.04)	−0.06 (0.05)
GRA	0.26 (0.29)	**0.62** (0.22)	**0.84** (0.09)	−0.02 (0.05)	**0.15** (0.04)	**0.53** (0.03)
DEN_{TREE}	−0.07 (0.30)	**−0.65** (0.23)	−0.32 (0.25)	0.03 (0.05)	−0.04 (0.05)	−0.06 (0.05)
DEN_{BOARD}	0.18 (0.30)	−0.34 (0.30)	−0.36 (0.25)	**0.11** (0.05)	**−0.08** (0.04)	**−0.10** (0.05)
VEL_{TREE}	−0.53 (0.37)	−0.49 (0.40)	−0.21 (0.36)	**−0.10** (0.05)	−0.06 (0.04)	**−0.13** (0.04)
VEL_{LOG}	−0.43 (0.32)	−0.07 (0.34)	0.15 (0.31)	**−0.18** (0.05)	0.00 (0.05)	−0.08 (0.05)
VEL_{BOARD}	−0.44 (0.30)	−0.22 (0.38)	0.01 (0.32)	**−0.30** (0.04)	0.01 (0.05)	**−0.14** (0.05)
MOE_{TREE}	−0.24 (0.31)	**−0.62** (0.26)	−0.30 (0.26)	−0.06 (0.05)	−0.06 (0.05)	**−0.13** (0.05)
MOE_{LOG}	−0.04 (0.32)	−0.56 (0.31)	−0.08 (0.29)	**−0.11** (0.05)	0.01 (0.05)	−0.05 (0.05)
MOE_{BOARD}	−0.33 (0.34)	−0.40 (0.38)	−0.12 (0.32)	**−0.22** (0.05)	−0.02 (0.05)	**−0.16** (0.05)
$MOE_{S.local}$	−0.61 (0.38)	−0.59 (0.48)	−0.24 (0.34)	**−0.17** (0.05)	0.05 (0.05)	**−0.20** (0.05)
$MOE_{S.global}$	−0.59 (0.42)	−0.96 (0.55)	−0.54 (0.31)	**−0.20** (0.05)	0.03 (0.05)	**−0.23** (0.05)
MOR	−0.19 (0.37)	**−0.74** (0.35)	−0.37 (0.29)	−0.07 (0.05)	−0.01 (0.05)	**−0.12** (0.05)

Note: Correlations with magnitudes greater than two times the standard errors are highlighted in bold.
BOW – maximum bow, CRK – maximum crook, TWI – maximum twist, DBH – diameter at breast height, STR – stem straightness, GRA – grain angle, DEN_{TREE} – adjusted resistograph density, DEN_{BOARD} – volumetric board density, VEL_{TREE} – standing-tree acoustic velocity, VEL_{LOG} – felled-log acoustic velocity, VEL_{BOARD} – sawn-board acoustic velocity, MOE_{TREE} – standing-tree dynamic modulus of elasticity, MOE_{LOG} – felled-log dynamic modulus of elasticity, MOE_{BOARD} – sawn-board dynamic modulus of elasticity, $MOE_{S.local}$ – local static modulus of elasticity, $MOE_{S.global}$ – global static modulus of elasticity, MOR – modulus of rupture. Descriptive statistics and heritability for these traits can be found in Fundova et al. (2020).

TWI demonstrated the highest (0.37), and CRK demonstrated the lowest (0.05), narrow-sense heritability, thus reflecting the magnitude of their additive genetic variances. The narrow-sense heritability for BOW was somewhat low (0.21). A comparable study on Norway spruce (*Picea abies* (L.) H. Karst.) has reported similar narrow-sense heritability (0.34) for TWI but lower heritability for BOW (0.10) and completely absent heritability for CRK (Högberg et al., 2014). Broad-sense heritability for TWI was as high as that observed in a radiata pine (*Pinus radiata* D. Don) clonal trial (0.80 and 0.86, respectively) (Cown et al., 2004).

Compared with sawn-board shape stability traits, GRA has been substantially better studied at the genetic level. The observed narrow-sense heritability (0.40) was in accordance with that reported in studies on Scots pine (Hannrup et al., 2003; Högberg et al., 2010) and

Table 3
Additive genetic and phenotypic correlations of grain angle with growth and wood quality traits (standard errors in parentheses).

	Correlation with GRA	
	Genetic	Phenotypic
DBH	−0.26 (0.24)	**−0.26** (0.03)
STR	0.06 (0.25)	**−0.11** (0.03)
DEN_{TREE}	**−0.49** (0.19)	**−0.16** (0.03)
DEN_{BOARD}	−0.35 (0.23)	−0.04 (0.04)
VEL_{TREE}	−0.44 (0.28)	**−0.29** (0.02)
VEL_{LOG}	0.17 (0.29)	−0.08 (0.05)
VEL_{BOARD}	0.05 (0.29)	**−0.12** (0.05)
MOE_{TREE}	**−0.50** (0.20)	**−0.27** (0.03)
MOE_{LOG}	−0.17 (0.26)	−0.06 (0.04)
MOE_{BOARD}	−0.12 (0.29)	**−0.11** (0.04)
$MOE_{S.local}$	−0.35 (0.30)	**−0.14** (0.04)
$MOE_{S.global}$	**−0.67** (0.27)	**−0.16** (0.04)
MOR	−0.47 (0.26)	**−0.09** (0.04)

Note: Correlations with magnitudes greater than two times the standard errors are highlighted in bold.
GRA – grain angle under bark, DBH – diameter at breast height, STR – stem straightness, GRA – grain angle, DEN_{TREE} – adjusted resistograph density, DEN_{BOARD} – volumetric board density, VEL_{TREE} – standing-tree acoustic velocity, VEL_{LOG} – felled-log acoustic velocity, VEL_{BOARD} – sawn-board acoustic velocity, MOE_{TREE} – standing-tree dynamic modulus of elasticity, MOE_{LOG} – felled-log dynamic modulus of elasticity, MOE_{BOARD} – sawn-board dynamic modulus of elasticity, $MOE_{S.local}$ – local static modulus of elasticity, $MOE_{S.global}$ – global static modulus of elasticity, MOR – modulus of rupture.

Table 4
Additive genetic (above diagonal) and phenotypic (below diagonal) correlations among shape stability traits (standard errors in parentheses).

	BOW	CRK	TWI
BOW	1	0.04 (0.39)	0.05 (0.33)
CRK	−0.02 (0.04)	1	**0.87** (0.20)
TWI	−0.07 (0.05)	**0.14** (0.04)	1

Note: Correlations with magnitudes greater than two times the standard errors are highlighted in bold.
BOW – maximum bow, CRK – maximum crook, TWI – maximum twist.

other conifer species (Costa e Silva et al., 2000; Gapare et al., 2007; Gaspar et al., 2008; Steffenrem et al., 2009; Hallingbäck, 2010; Hallingbäck et al., 2010a; Högberg et al., 2014). Nevertheless, higher narrow-sense (Hansen and Roulund, 1998; Kennedy et al., 2013), and lower broad-sense (Hansen and Roulund, 1997; Hannrup et al., 2002) heritability have also been reported.

The broad-sense heritability values for TWI, GRA and BOW were twice those of their narrow-sense heritability values in this study, thus suggesting considerable non-additive genetic variance. Substantial non-additive effects are commonly observed for growth traits (Baltunis et al., 2009; Berlin et al., 2019) but rarely observed for wood quality traits (Chen et al., 2020).

3.2. Additive genetic (r_A) and phenotypic (r_P) correlations

Sawn-board shape stability traits were considered the target traits for genetic improvement in this study. Such traits cannot, however, be measured until the wood is processed, thus making their direct selection infeasible. Their improvement can be accomplished through indirect selection based on selection traits, i.e., traits that provide reliable information about the target traits and can be non-destructively measured on young standing trees. Furthermore, knowledge of among-trait relationships is essential, because selection for one trait affects other genetically correlated traits in favorable or unfavorable ways.

Additive genetic and phenotypic correlations are presented in Tables 2–4, and the relationships between measured GRA and shape stability traits are visualized in Fig. 3. The strongest additive genetic as well as phenotypic correlation (0.84 and 0.53, respectively) was observed between sawn-board TWI and stranding-tree GRA. Similar findings have been reported for Norway spruce ($r_A = 0.93$, $r_P = 0.54$) (Högberg et al., 2014) and Scots pine ($r_P = 0.54$) (Högberg et al., 2010); a stronger phenotypic correlation (0.7) has been reported for hybrids of slash and Caribbean pine (*Pinus elliottii* Engelm. × *P. caribaea* Morelet) (Harding et al., 2008). A positive genetic correlation (0.62) with GRA was also found for CRK. The results suggest that the TWI and CRK of sawn boards could be decreased by selection for lower GRA measured on standing trees.

A strong additive genetic correlation (0.74) was estimated between BOW and STR, thus suggesting that trees with straighter stems produce sawn boards with greater bow. In contrast, Högberg et al. (2014), using the same 9-point scale for assessing STR, have observed a weakly negative non-significant correlation (-0.21). Among the shape stability traits, only CRK exhibited non-zero correlations (r_A = -0.54, r_P = -0.21) with DBH, i.e., trees with larger stems tended to have less crooked boards.

In the present study, CRK showed strong to moderate negative additive genetic correlations (from -0.40 to -0.96) with all MOE estimates. Moderate negative genetic correlations were also observed between BOW and all estimates of VEL and static MOE (from -0.43 to -0.61), and between TWI and $MOE_{S.global}$ (-0.54). These relationships indicate that

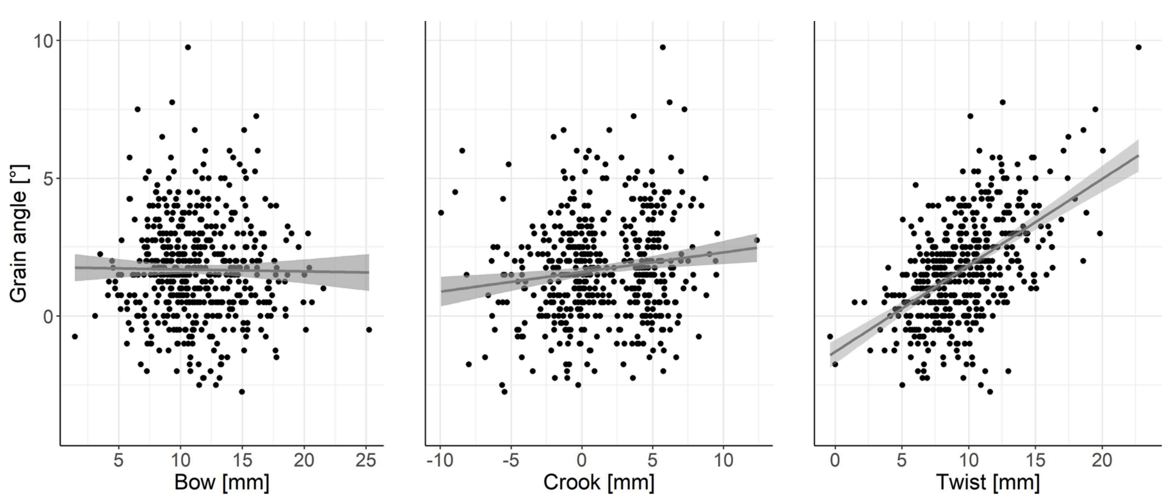

Fig. 3. Relationships of grain angle measured on standing trees with shape stability traits (bow, crook and twist) measured on sawn boards and adjusted to 12 % moisture content.

Table 5
Correlated genetic response of shape stability traits to selection based on stem diameter and several wood quality traits non-destructively measured on standing trees (1% selection intensity). The arrows indicate the desired direction of intended selection.

Selection traits		Response in selection traits	Response in target correlated traits		
			BOW [mm]	CRK [mm]	TWI [mm]
DBH	↑	15.19 %	−0.50	−0.57	−0.23
DEN_{TREE}	↑	10.97 %	−0.19	−0.89	−1.07
VEL_{TREE}	↑	0.89 %	−0.51	−0.24	−0.25
MOE_{TREE}	↑	11.28 %	−0.48	−0.63	−0.74
GRA	↓	−2.02°	−0.70	−0.85	−2.80

BOW – maximum bow, CRK – maximum crook, TWI – maximum twist, DBH – diameter at breast height, DEN_{TREE} – adjusted resistograph density, VEL_{TREE} – standing-tree acoustic velocity, MOE_{TREE} – standing-tree dynamic modulus of elasticity, GRA – grain angle under bark.

shape stability traits, particularly BOW and CRK, affect wood stiffness to some degree. Nevertheless, such inferences should be made with caution, because the correlation estimates were associated with high standard errors (0.26–0.55), thus indicating lower accuracy. Moreover, the phenotypic correlations were only weakly negative or even close to zero (-0.30 to 0.05). CRK was moderately correlated (r_A = -0.65) with DEN_{TREE} estimated on standing trees, whereas genetic correlations between BOW and wood density were close to zero. In contrast, genetic correlation of BOW was moderately positive with specific gravity in *Eucalyptus grandis* (0.52) (Santos et al., 2004) and moderately negative (-0.66) with Pilodyn penetration in Norway spruce (Högberg et al., 2014), thus suggesting a positive relationship between BOW and wood density. CRK and TWI were strongly genetically correlated (0.87) in this study, whereas neither correlated with BOW.

Previous studies have reported no or weak genetic correlation of GRA with DBH (Hannrup et al., 2003, 2004; Steffenrem et al., 2009) or with STR (Hansen and Roulund, 1998; Hallingbäck, 2010), in accordance with the results of this study. On the other hand, the negative genetic correlation (-0.49) of GRA with resistograph-based DEN_{TREE} was in contrast to its positive correlations with X-ray density reported in maritime pine (*Pinus pinaster* Ait.) (0.55) (Gaspar et al., 2008) and volumetric and X-ray density in Norway spruce (~0.6) (Steffenrem et al. 2009). A moderate negative genetic correlation (-0.35) was also observed between GRA and air-dried DEN_{BOARD} in this study, whereas a nearzero correlation between the two traits was estimated by Högberg et al. (2014). Moreover, moderately negative genetic correlations of GRA with VEL_{TREE}, MOE_{TREE}, $MOE_{S.global}$ and MOR were found (-0.44 to -0.67); however, the estimation errors were considerable for these correlations (0.20 to 0.28). In comparison, a weak negative genetic correlation between GRA and MOE_{TREE} has been observed in Norway spruce (Nguyen, 2019). Negative but very weak genetic correlations of GRA with VEL^2_{TREE}, static MOE and MOR have also been reported for Sitka spruce (*Picea sitchensis* (Bong.) Carrière) (Kennedy et al., 2013). The correlations indicate that higher GRA is associated with lower density, strength and stiffness, in agreement with findings from other studies (e.g. Cown et al., 1995; Pope et al., 2005; Ivković et al., 2009).

3.3. Correlated response to selection

The correlated response of shape stability traits to selection based on traits non-destructively measured on standing trees is provided in Table 5. Selection aiming at higher DBH, DEN_{TREE}, VEL_{TREE} and MOE_{TREE} as well as lower GRA resulted in lower BOW, CRK and TWI. The greatest potential improvement in shape stability traits was achieved for TWI (-2.8 mm) as a response to a selection for lower GRA (decreased by 2.0°). Selection for higher resistograph-density (DEN_{TREE}) also resulted in a considerable improvement in TWI (-1.1 mm). Furthermore, selection for either a lower GRA or higher DEN_{TREE} led to improvement in

Table 6
Correlated genetic response (%) of important sawn-board traits to selection for lower grain angle (1% selection intensity). The arrow indicates the desired direction of intended selection.

Selection trait	Response in target correlated traits				
	DBH	DEN_{BOARD}	$MOE_{S.local}$	$MOE_{S.global}$	MOR
GRA ↓	5.10	2.11	4.53	6.11	7.10

GRA – grain angle under bark, DBH – diameter at breast height, DEN_{BOARD} – volumetric board density, $MOE_{S.local}$ – local static modulus of elasticity, $MOE_{S.global}$ – global static modulus of elasticity, MOR – modulus of rupture.

CRK (-0.9 mm for both), and GRA also appeared to be suitable for improvement in BOW (-0.7 mm).

GRA, non-destructively measured on standing-trees, appears to be the best choice for genetic improvement of sawn-board shape stability. Selection for lower GRA also appeared to have a positive effect on sawn-board density, stiffness and strength (Table 6), similarly to the selection for DEN_{TREE}, MOE_{TREE} or STR (Fundova et al., 2020). Studies on GRA in single annual rings have designated GRA as a suitable trait for very early selection (Fujimoto et al., 2006; Gapare et al., 2007; Hallingbäck et al., 2010b, 2018). In the case of Scots pine, the removal of bark before GRA measurements would not be necessary, because the bark of young Scots pine trees is more papery than that of older trees, which is thick and scaly. Consequently, omitting bark removal in the measuring procedure would substantially decrease the workload and the risk of fungal infection.

4. Conclusion

This study investigated the genetics and potential for genetic improvement of sawn-board shape stability traits through selective breeding. TWI, BOW and CRK demonstrated moderate, low and very low (0.37, 0.21 and 0.05) narrow-sense heritability, respectively, thus reflecting the magnitude of their additive genetic variances. Their improvement by direct selection is, however, not possible, because their assessment requires the trees to be felled. Among the traits non-destructively measured on standing trees, under-bark GRA ($h_i^2 = 0.40$) appeared to be a reliable trait for indirect improvement of sawn-board shape stability traits. Selection focusing on lower GRA would result in lower CRK and TWI and could also result in higher sawn-board density, stiffness and strength. Consequently, the requirements for utilization as construction lumber would be met by a higher percentage of sawn boards and thus the profitability of the forestry and wood processing industry would increase.

CRediT authorship contribution statement

Irena Fundova: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Henrik R. Hallingbäck:** Methodology, Validation, Investigation, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Gunnar Jansson:** Writing - review & editing, Supervision, Project administration, Funding acquisition. **Harry X. Wu:** Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors reported no declarations of interest.

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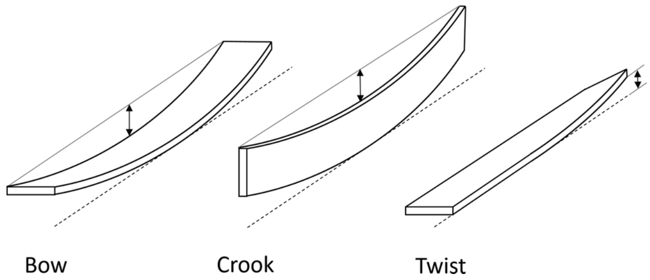

Fig. A1. Three shape stability traits (bow, crook and twist) measured on sawn boards.

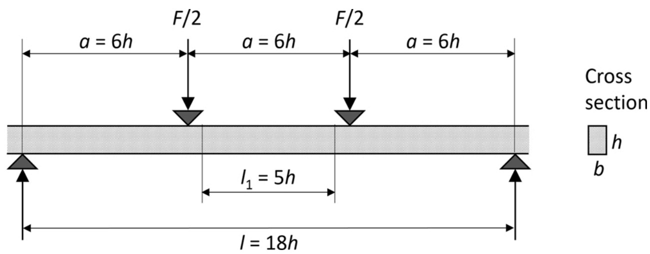

Fig. A2. Schema of a four-point bending test according to EN408, where F is the load increment, a is the distance between load points, l_1 is the central gauge length, l is the test span, h is the board width and b is the board thickness.

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Appendix A

See Figs. A1 and A2

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