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Differences in growth and wood density in clones and provenance hybrid clones of Norway spruce

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Abstract

The growing forest bioeconomy calls for enhancing wood production in Finland. Accordingly, we studied phenotypic differences and correlations for growth and wood density traits in 25 Norway spruce (*Picea abies* (L.) Karst.) genotypes grown in a field trial established in the 1970s in southeastern Finland. We also studied the effect of geographical origin of parent-trees. The clones represented six southern Finnish and two southwestern Russian clones, and three Finnish-Swiss, eight Finnish-German, three Finnish-Latvian and three Finnish-Estonian hybrid clones. Some local Finnish clones (e.g., V43) and provenance hybrid clones (e.g., Finnish-German V449 and V381) clearly displayed higher stem volume than the clone average and relatively high overall wood density (and wood biomass yield). The increase in latitudinal transfer distance of parent-trees compared to the latitude of the trial seemed to decrease the height, breast height diameter and stem volume, but the effect was not significant ($p > 0.05$). The overall wood density was affected significantly only by latitude of father parent trees ($p < 0.05$). Wood density traits showed clearly lower phenotypic variation compared to other traits. Contrary to our hypothesis, none of the studied hybrids show superior properties compared to the local Finnish clones.

Keywords: bioeconomy, biomass, phenotypic differences, stem volume, wood density

43 Introduction

44 More efficient wood production is called for in Finland and elsewhere in Europe to fulfill the
45 increasing demand for wood biomass in the growing forest bioeconomy, and to transfer towards a
46 low-carbon and resource-efficient society in which fossil resources are substituted by renewables
47 (The Finnish Bioeconomy Strategy 2014; Scarlat et al. 2015). At the same time, demand for
48 multiple-use of forests (e.g., for recreation and nature conservation) is increasing, and nature's
49 ecosystem services must be secured and maintained. In general, increasing demand for wood
50 biomass would increase environmental impacts due to the need to increase harvested forest area,
51 unless the average amount of harvested wood per hectare could be increased in commercial forests.
52 On the other hand, there are different ways to increase the resource-efficiency and wood production
53 per hectare, such as the use of improved seed and seedling material in forest regeneration, proper
54 spacing and thinning regimes, nitrogen fertilization and rotation length (Kellomäki et al. 2005;
55 Routa et al. 2013; Pyörälä et al. 2014; Kilpeläinen et al. 2016).

56 In Finland, Norway spruce (*Picea abies* (L.) Karst.) is an important raw material source for forest
57 bioeconomy as it accounts for 30% of the current volume of growing stock (Finnish Statistical
58 Yearbook of Forestry 2014). To improve the resource-efficiency in wood production and to fulfill
59 the growing demand of wood for forest bioeconomy, an increase of tailored wood production per
60 unit land area is needed. However, this requires better understanding of how the genotype affects
61 growth and wood property traits. In addition to genotype, environmental factors (e.g., temperature,
62 water, light and nitrogen availability), in interaction with forest management, affect the growth and
63 wood properties of tree stands (Kellomäki et al. 2005; 2008). Therefore, for the selection of suitable
64 genotypes for forest regeneration at different sites and regions, growth and wood properties should
65 both be considered. Adaptation capacity of genotypes in changing environmental conditions should
66 also be considered as it crucially affects the survival, growth, and properties of trees (Kellomäki et
67 al. 2005; 2008).

Until recently volume growth was typically used as a selection trait of primary importance in forest tree breeding, whereas less attention has been given to the genetic or phenotypic relationships among different growth and wood density traits (e.g., Karlsson and Rosvall 1993), despite these traits have a high inheritance and significant effect on the properties of wood products (Zobel and Buijtenen 1989; Zobel and Jett 1995; Skog et al. 2014). High wood density may be desirable, for example, for chemical pulp production (Ståhl 1998) and for gasification raw material (Wegner et al. 2010). However, selection of suitable genotypes for forest regeneration considering both high volume growth and wood density is a complicated task as genetic/phenotypic relationships observed between these traits are, in general, negative (Zobel and Jett 1995). Nonetheless, non-significant or weak positive relationships between these traits are observed, for example, in some Norway spruce clones (Zobel and Jett 1995; Bujold et al. 1996; Zubizarreta Gerendiain et al. 2007).

As selection for one trait will simultaneously affect other traits, different traits of interest should be evaluated simultaneously. For example, selection for both high stem volume and relatively high wood density may be possible by selection of genotypes with negligible relationships between these characteristics. Recently, Zubizarreta Gerendiain et al. (2007) found that some Finnish Norway spruce clones may have both a high stem volume and a relatively high wood density. Selection for both high stem volume and relatively high wood density may be possible also through hybridization (i.e. crossing local and foreign parent trees) and consequently the selection of hybrids combining these traits (Gerhold and Park 1986; Magnussen and Yeatman 1988; Ruotsalainen 2014).

The adaptation of different tree species and genotypes to climatic and site conditions is closely linked to geographic position (latitude, longitude and altitude) and photoperiod (Olsen 2010, Ruotsalainen 2010), which should also be considered in the selection of future seedling material (e.g., provenances, clones, hybrids) for practical forestry. This is because genotypes originating from milder climatic conditions (e.g., lower latitude and closer to sea level) tend to have, in general, longer growing periods and thus higher total growth (e.g., stem volume) associated with lower

wood density (White et al. 2007). This is opposite to the genotypes from harsh environments (Persson and Persson 1997; Skråppa and Hylen 1999). In overall, the success of different genotypes and differences between them can be determined at relatively young stage (Ruotsalainen 2010). Large improvement in volume growth over a rotation length and economic profitability of forestry may be expected by using improved seed/seedling material in forest regeneration (Ahtikoski et al. 2012; Ruotsalainen 2014).

We studied phenotypic differences for growth and wood density traits and their relationships in 25 Norway spruce clones and provenance hybrid clones grown in a field trial established in the 1970s in southeastern Finland. In addition, we studied how geographical origin of parent-trees affected different traits. The studied genotypes represented six southern Finnish and two southwestern Russian clones, and three Finnish-Swiss, eight Finnish-German, three Finnish-Latvian and three Finnish-Estonian hybrid clones. Based on the previous studies, we hypothesized that some hybrid clones could have higher growth (e.g., stem volume) and overall wood density than the local Finnish clones.

Materials and methods

Experimental data

The material for this research was collected from a Norway spruce trial established in 1974 in Imatra, southeastern Finland (28°48'E, 61°08'N, 60 m a.s.l.; 1300 growing degree days). The trial is located on agricultural soil with site fertility conditions typical for cultivation of Norway spruce on mineral soils. The spacing of trees in the trial was 2 m × 2.5 m, and 119 genotypes (clones and hybrid clones) were replicated in 20 blocks (4 repetition trees per block, 80 trees per genotype). Blocks were not expected to affect the performance of the genotypes on relative homogenous agricultural soil. Mother trees of clones and hybrid clones were produced through controlled crosses

between genotypes. The age of the mother trees varied from two to four years at the time of cloning, and this range was not expected to affect the results of this work (Rautanen 1995).

The studied genotypes represented six southern Finnish and two southwestern Russian clones, and three Finnish-Swiss, eight Finnish-German, three Finnish-Latvian and three Finnish-Estonian provenance hybrid clones (referred to hereafter as hybrids) (Table 1). In spring 2015, we randomly harvested eight to ten trees with a good cone crop for each genotype. Good cone crop was required for sample trees as their seed material was to be used for a follow-up study. The number of sample trees was taken to be enough for this type of cloned trial (see e.g., Zobel and Jett 1995). Sample trees were also previously harvested from this trial from some Finnish clones for research purposes (see e.g., Zubizarreta Gerendiain et al. 2007), but this was not expected to affect the growing conditions of our sample trees and consequently the results of this work. Related to the harvesting of sample trees, their height and stem diameters (at breast height, 1.3 m and at 6 m from the stem base) were measured for further calculation of the stem volume according to equations by Laasasenaho (1982). One sample disc from each sample tree was taken at a height of 1 m for measurements of intra-ring growth and wood property traits.

X-ray densitometry measurements

Radial wood segments 5 mm × 5 mm in size were cut in the south–north direction out of sample discs with a twin-blade circular saw. Thereafter, wood specimens were stored at fixed conditions, until they reached 12% moisture content (i.e., air dry). The wood specimens were then scanned in batches using a direct scanning ITRAX X-ray microdensitometer (Cox Analytical Systems, Göteborg, Sweden). ITRAX works with automatic collimator alignment (see Bergsten et al. 2001) at a geometrical resolution of 40 measurements per mm (0.025 mm × 1 mm). Based on previous

work by Zubizarreta Gerendiain et al. (2007), we used the standard X-ray intensity (30 kV, 35 mA) for X-ray measurements, with an exposure time of 20 ms.

The X-ray radiographic images were analyzed with the Density Profile Analyzer Package for Excel to determine intraring density profiles for each sample from pith to bark. This data was, then, processed by Excel macros (Microsoft, Redmond, Wash.) to determine from pith to bark for each individual ring: ring width (mm), earlywood and latewood widths (mm) and their percentages, mean wood density (g/cm^3), minimum and maximum wood densities (g/cm^3), earlywood and latewood densities (g/cm^3). Similar to previous work by Zubizarreta Gerendiain et al. (2007), the mean of the maximum and minimum intraring densities were used as a threshold for earlywood ($<$ mean) and latewood ($>$ mean) in each ring.

Data analyses

Growth and wood density values measured for each individual ring were used to calculate the weighted cross-sectional means for wood density (WD), earlywood density (EWD) and latewood density (LWD) for each sample tree (disc). In addition, mean widths of the annual ring (RW), earlywood (EWW) and latewood (LWW) widths were determined for each sample tree as well as latewood percentage (LWW%). Stem mass was calculated for each tree by multiplying stem volume with WD, following the approach used by Kilpeläinen et al. (2010). Phenotypic coefficient of variation (CV, %) was also calculated by normalizing the standard deviation (σ) by the mean (μ) of the variable (e.g., LWW, LWD) for each genotype ($\text{CV (\%)} = \sigma \times 100 / \mu$).

Statistical data analyses were undertaken in R software (R core team 2016). Differences in various growth traits (i.e. cross-sectional means for EWW, LWW, RW and LWW%, and final diameter at breast height, tree height, stem volume and stem mass, respectively) and wood density traits (i.e. weighted cross-sectional means for WD, EWD, LWD) between genotypes were tested with one-way analysis of variance (ANOVA). Pairwise analysis with a Tukey's test ($p < 0.05$) was applied

for height, LWW, LWW (%), EWD, LWD WD, and Dunnett's T3 test for D, V, SM, EWW, RW based on a test of the homogeneity of the variance (Levene's test of equality of error variances). Relationships between different growth and wood density traits were studied using phenotypic correlation instead of genetic correlation because of the small number of sample trees per genotype (see e.g., Zubizarreta Gerendiain et al. 2007). This was also suggested earlier by Hannrup et al. 2000.

The phenotypic correlations (r_p) between the property traits were computed by the Pearson's correlation method: $r_p = \sigma_{p1p2} / \sigma_{p1} \sigma_{p2}$, where σ_{p1p2} is the phenotypic covariance between properties 1 and 2 and σ_{p1} and σ_{p2} are the phenotypic standard deviations for properties 1 and 2. Correlations were expected to be significant at $p < 0.05$. The CV% and r_p were computed both for individual genotypes and as a mean of all the genotypes.

Linear mixed-effects modeling was used to study how the geographical origin of parent-trees affects diameter, height, stem volume and overall wood density of the genotypes. However, because of breeding approach, a co-linearity issue arises. This is because a change in the latitude is associated with a change in the longitude and the altitude. To avoid co-linearity between latitude and longitude, we did not include longitude of origin of parent-trees in our model. In a previous study by Barzdajn et al. (2016), no strong relationship was found between longitude and growth traits for European provenances of Scots pine (*Pinus sylvestris* L.). Furthermore, the breeding approach and the design of the trial does not allow direct estimates of the effect of altitude on the traits studied. Therefore, we used a transformation approach to adjust altitudinal climate effects in terms of latitude. This was done by assuming that each hundred-meter increase in altitude corresponds to one-degree latitude transfer to the north, following previous work by Laaksonen (1976). Similar to previous works of Matyas and Yeatman (1992) and Persson and Beuker (1997), in the final models we used differences between the revised latitude values (including altitude effect) of parent-trees origins and that of the trial as explanatory variables. In addition, there were

only nine to eleven independent observations per each geographical variable, which hinders investigation on the effects of multiple geographical factors on the studied traits within one model. Therefore, the following general design of mixed linear model was used:

$$y_{ijk} = \beta_o + \beta_1 x_{ijk} + a_i + b_{ij} + \varepsilon_{ijk} \quad (1)$$

where y_{ijk} a trait studied (Table 7), β_o is the intercept, β_1 is the fixed effect of the geographical variable x_{ijk} tested (x_{ijk} is adjusted latitude i either of mother or father parent-tree origin), a_i is the random effect of the geographical variable, b_{ij} is the random effect of genotype j , and ε_{ijk} is the error term (k stands for the individual trees within each genotype). The variability within each explanatory variable and between individual genotypes was estimated by using random intercepts in the models. Normality in the distribution of the residuals of final models was assessed using scatter and quantile-quantile plots. We applied lme4 package (Bates et al. 2015) for mixed-effects model analysis in R.

Results

Phenotypic variation in growth and wood density traits

Among the tree height, diameter at breast height and stem volume (Table 2), the lowest phenotypic variation was observed in height, followed by diameter and stem volume (range of overall means 5.5–23.4 %). Among the cross-sectional mean growth traits (Table 3), RW had the lowest phenotypic variation, followed by LWW and EWW (range 11.0–13.0 %). Among the cross-sectional mean wood density traits (Table 4), the lowest phenotypic variation was observed in LWD and EWD, followed by WD (range 3.7–4.3 %).

Local Finnish clone V43 had the largest stem volume and diameter (40.7 and 19.8 % higher than the mean over all genotypes). Finnish-Latvian hybrid V469 was the tallest (7.0 % higher than the mean). Also, Finnish-Latvian V471, Finnish-German V383 hybrids and local Finnish clone V48

were 4.3 to 6.7 % higher than the mean. Local Finnish clone V465, Finnish-German hybrids V449, V49 and V302 had 7.2 to 11.4 % larger diameters than the mean. Russian clone V327, local Finnish clone V465 and Finnish-German hybrids V382 and V49 had 15.7 to 21.3 % larger stem volumes than the mean (Table 2).

Local Finnish clone V43 had the largest RW (20.0 % higher than the mean). Also Finnish-German hybrids V49, V449, V302 had 8.8 to 10.8 % larger RW than the mean (Table 3). The Finnish-Swiss hybrid V455 had the highest WD (10.9 % higher than the mean), while Finnish-Latvian V471, Finnish-Swiss V456 and Finnish-German V447 hybrids had 5.4 to 6.9 % higher WD than the mean. Stem mass as calculated based on stem volume and overall wood density was the largest for the Finnish clone V43 (41.6 % higher than the mean) and Finnish-German hybrids V382 and V381 (Table 2).

Phenotypic correlations between growth and wood density traits

The phenotypic correlation between height, diameter at breast height and stem volume was strong and positive, ranging from 0.65 between diameter and height to 0.94 between diameter and stem volume ($p < 0.05$). The phenotypic correlation between the cross-sectional mean growth traits varied from weak to strong, and ranged from 0.28 between EWW and LWW to 0.96 between EWW and RW. Among cross-sectional mean wood density traits, the phenotypic correlation varied from 0.70 between EWD and LWD to 0.92 between EWD and WD. Phenotypic correlations between diameter and WD (-0.41) and between stem volume and WD (-0.35) were, in general, negative and moderate (Table 5). However, also negligible insignificant phenotypic correlations between these traits were observed for Finnish-German hybrids V49 and V448, Finnish-Latvian hybrids V471 and V469 and Finnish clones V47, V48 and V43 (Table 6).

238 *Effect of geographical origin of parent trees on different traits*

239 In general, the increase of revised latitudinal transfer distance of parent trees, compared to the
240 latitude of the trial tended to decrease the height, breast height diameter and stem volume, but the
241 effect was not significant ($p > 0.05$). The overall wood density was significantly affected only by
242 revised latitude (altitude effect considered) of the father parent tree ($p < 0.05$), a one-degree
243 increase of which decreased wood density by 0.006 g/cm^3 (Table 7).

244

245 **Discussion**

246 In this work we hypothesized that some provenance hybrid clones could simultaneously have both
247 higher stem volume and overall wood density than the local Finnish clones. However, the stem
248 volume and diameter were largest for local Finnish clone V43 (Figure 1). The Finnish-Latvian
249 hybrid V469 was the tallest. Calculated stem mass was largest for the Finnish clone V43 and
250 Finnish-German hybrids V382 and V381, in all of which WD was on average compared to all
251 genotypes. The growth and wood density traits of some of our Finnish clones were previously
252 studied also by Zubizarreta Gerendiain et al. (2007). This made us possible to compare their relative
253 success between two time periods. Similar to this study, the Finnish clone V43 had, according to
254 corresponding measurements made 10 years earlier, the largest diameter and stem volume of all
255 Finnish clones (also highest WD and second highest H). In addition, clone V465 improved its
256 ranking compared to the earlier study, unlike clone V47 (excluding WD). In both studies, the clones
257 V328 and V332, originating from southern and southwestern Finland, had the lowest WD.
258 However, the results of these two studies may not be fully comparable, as in our study one
259 additional criteria in sample tree selection was good cone crop as seeds were planned to be used for
260 a follow-up study in greenhouse and field conditions. These sampling criteria may have favored the
261 largest trees in sample tree selection and could explain some changes in ranking between clones. On

the other hand, neither in the previous study the suppressed trees were used as sample trees because they are usually harvested in first commercial thinning and not thus providing saw log sized wood.

In our study, wood density traits also showed considerably lower phenotypic variation compared to the growth traits, which is in line with earlier findings in Norway spruce and other coniferous species (for example Zobel and Jett 1995; Hannrup et al. 2004; Sofletea and Budeanu 2015). Phenotypic correlations for growth and wood density traits also revealed generally moderate and strong relationships. In particular, the relationship between stem volume and wood density was negative for most of studied genotypes. Thus, selection for one trait would simultaneously affect other traits as observed previously. This negative relationship between stem volume and wood density was also observed in earlier studies in Norway spruce (see e.g., Zobel and Jett, 1995; Raiskila et al. 2006).

Also in previous studies of Norway spruce, relatively large differences were observed for growth and wood density traits in different genotypes (e.g., Sofletea et al. 2015). It was also observed that growth of genotypes tend to decrease when the latitudinal transfer distance of parent-trees to the trial site increases. Andalo et al. (2005) observed this for White spruce (*Picea glauca* (Moench) Voss) and Barzdajn et al. (2016) for Scots pine. Also Kapeller et al. (2012) stated that geographical origin of parent trees (i.e., provenance) affects growth traits. However, in our study the change of latitudinal transfer distance of parent-trees (considering also altitude effect) compared to the latitude of the clonal trial did not explain performance of growth traits in different genotypes ($p > 0.05$). At the same time, in our study the transfer of father parent-tree genotypes from southward of Imatra negatively affected overall wood density ($p < 0.05$). Zubizarreta Gerendiain et al. (2009) reported similar kind of results in Norway spruce also in other Finnish trial. Unfortunately, the genotype crossing approach used in this work does not facilitate explaining these results in more detail.

In general, differences in the performance of genotypes at each trial site may also be partly explained by adaptation of parent-trees to certain environmental conditions, such as photoperiod (Ekberg et al. 1979) and prevailing temperature conditions of the growing season (Ståhl 1998; Skrøppa and Hylen 1999; Savva et al. 2006; Kapeller et al. 2013). In our work, the Finnish-German hybrids tend to show, on average, higher than the mean stem volume over all genotypes. This may imply that they can effectively utilize the growing season and adapt to prevailing climatic conditions in southeastern Finland. At the same time, all Finnish-Swiss and Finnish-Estonian hybrids showed relatively low growth and yield, revealing that they may cease growth earlier than other genotypes studied. The altitude differences of parent trees between the Finnish-German hybrids, and Finnish-Swiss and Finnish-Estonian hybrids, respectively, may partly explain these results. Under a warmer climate, the performance of different genotypes may also change in Northern Europe where the mean annual temperature is expected to increase 3 to 6 °C by 2100 (IPCC 2013).

In this work, some Finnish-German (V449, V381, V382, V383) and Finnish-Latvian (V469) hybrids showed both relatively high stem volume and overall wood density (Figure 2), despite negative relationship existing between these traits. Thus, hybridization could offer means to affect different traits (e.g., Gerhold and Park 1986; Magnussen and Yeatman 1988; Ruotsalainen 2014). However, based on some previous studies no general superiority has been expected from hybrids compared to the best parent-trees (see e.g. Ekberg et al. 1982; Gerhold and Park 1986). In fact, we found that local Finnish clone V43 had the highest stem volume and relatively high wood density while showing a negligible relationship between these traits. Saranpää (2003) also reported this negligible relationship, as did Zubizarreta Gerendiain et al. (2007) for the local Finnish clone V43 at a younger age in this same trial. However, a negligible relationship between these two traits does not necessarily mean that genotype has good performance in given growing conditions (see, e.g., Finnish clones V47 and V48, and Finnish-Latvian hybrid V471). In our study, Finnish clone V465

showed high stem volume and relatively high wood density and moderate negative correlation between these traits. On the other hand, resin canals and resin itself contribute to wood density values if not removed from softwoods like Norway spruce. This may be the case, particularly for stress induced resin canals (Nagy et al 2000, Schmidt et al. 2011). Thus, the anatomical structure of wood should also be studied when planning to choose appropriate genotypes for further breeding based on wood density. This research still also lacks study on parent-trees, thus not making it possible to determine the contribution of the parents' genotypes to different traits.

Conclusions

Our research revealed differences in growth and wood density in studied Finnish and Russian clones and provenance hybrid clones. It also demonstrated that by using proper genotypes for forest regeneration, we could enhance wood production, which in turn is needed to sustainability satisfy the growing demand for wood by forest bioeconomy. Selection for both high stem volume and relatively high wood density may be possible, for example, by selecting hybrids with these traits. This may be done also by selection of genotypes with a negligible relationship between them; such as the most productive genotype in our study, local Finnish clone V43. At the same time, the possibility exists to encounter genotypes, such as V465, with high stem volume, relatively high wood density and a negative relationship between these traits. In our study, the Finnish clone V43 showed the highest stem volume and relatively high wood density as well as low variation of the different traits studied, as was observed also in a previous study by Zubizarreta Gerendiain et al. (2007). However, as high wood density may be due to factors like high resin amount, the anatomy of wood should be taken into account in breeding before selecting genotypes based on their wood density. We also plan to study the anatomy of wood for genotypes used in this study (e.g., Finnish clone V43) in further studies, as well as the growth and adaptation capacity of the next tree

generation of genotypes used in this study under changing environmental condition in greenhouses and field experiments, i.e. based on seed material provided from cones of our sample trees. Research of this type is required as increasing wood demand for bioeconomy will call for more detailed understanding on the raw material properties of wood for any kind of usage.

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- 489

490 **Table 1.** Genotypes (Gtype) and the geographical origin of parent trees. In parenthesis for altitude
 491 variable are shown mean altitude values used for the modeling.

Gtype	Geographical origin	Geographical location and elevation: mother parent tree			Geographical location and elevation: father parent tree			Sample trees/clones
		Latitude (N)	Longitude (E)	Altitude m	Latitude (N)	Longitude (E)	Altitude m	
Finland × Switzerland (F × S)								
V454	1/E1845 Muonio × E1771 Wintschgau	67° 58'	23° 40'	150-250 (200)	46° 30'	10° 25'	< 800 (799)	9
V455	3/E1845 Muonio × E1771 Wintschgau	67° 58'	23° 40'	150-250 (200)	46° 30'	10° 25'	< 800 (799)	10
V456	4/E1845 Muonio × E1771 Wintschgau	67° 58'	23° 40'	150-250 (200)	46° 30'	10° 25'	< 800 (799)	10
Finland × Germany (F × G)								
V447	6/E1832 Rovaniemi × E1770 Spiegelau	66° 29'	25° 40'	250	48° 57'	13° 25'	700–800 (750)	10
V448	8/E1832 Rovaniemi × E1770 Spiegelau	66° 29'	25° 40'	250	48° 57'	13° 25'	700–800 (750)	10
V449	10/E1832 Rovaniemi × E1770 Spiegelau	66° 29'	25° 40'	250	48° 57'	13° 25'	700–800 (750)	10
V49	E5520 Loppi × E1893 Carlsfeld	60° 37'	24° 26'	120	50° 24'	12° 35'	900	10
V302	H3270 Loppi × E1766 Carlsfeld	60° 37'	24° 26'	120	50° 24'	12° 35'	900	10
V381	K1413 Pieksänmaa × E1890/2 Schielbach	62° 23'	27° 04'	160	50° 24'	12° 18'	400–600 (500)	10
V382	K1413 Pieksänmaa × E1890/6 Schielbach	62° 23'	27° 04'	160	50° 24'	12° 18'	400–600 (500)	10
V383	K1411 Pieksänmaa × E1890/8 Schielbach	62° 23'	27° 04'	160	50° 24'	12° 18'	400–600 (500)	9
Finland × Latvia (F × L)								
V469	E2672 Loppi × E943/2 Goldingen	60° 44'	24° 30'	120	57° 38'	22° 00'	< 100 (99)	9
V470	E2672 Loppi × E943/3 Goldingen	60° 44'	24° 30'	120	57° 38'	22° 00'	< 100 (99)	9
V471	E2672 Loppi × E943/6 Goldingen	60° 44'	24° 30'	120	57° 38'	22° 00'	< 100 (99)	10

Russia (R)								
V325	513/2 Pskov Oblast				57° 48'	28° 26'	100–200 (150)	10
V327	513/8 Pskov Oblast				57° 48'	28° 26'	100–200 (150)	10
Finland × Estonia (F × E)								
V386	K1420 Pieksänmaa × E949/1 Perawald	62° 22'	27° 04'	160	58° 00'	27° 30'	< 100 (99)	9
V388	K1420 Pieksänmaa × E949/4 Perawald	62° 22'	27° 04'	160	58° 00'	27° 30'	< 100 (99)	10
V389	K1420 Pieksänmaa × E949/5 Perawald	62° 22'	27° 04'	160	58° 00'	27° 30'	< 100 (99)	9
Finland (F)								
V47	Tree157, +8 Pornainen	60° 29'	25° 30'	30				10
V328	E2969/5 Pornainen	60° 29'	25° 30'	30				10
V332	E2937/4 Pöytyä	60° 43'	22° 51'	90				9
V43	Tree300, + 44 Michikkälä	60° 47'	27° 30'	60				9
V48	Tree92, + 44 Michikkälä	60° 47'	27° 30'	60				10
V465	E3821/1 Ruokolahti	61° 19'	28° 55'	100				10
Total no. of trees								242

Table 2. Statistics for total height (H), diameter at breast height (D), stem volume (V) and stem mass (SM) for the genotypes. Different letters indicate differences among genotypes ($p < 0.05$)

Gtype	Geographical origin	D, cm [*]			H, m			V, m ³ [*]			SM, kg [*]		
		Mean $\pm$ SD	% [†]	CV, %	Mean $\pm$ SD	% [†]	CV, %	Mean $\pm$ SD	% [†]	CV, %	Mean $\pm$ SD	% [†]	CV, %
V454	F $\times$ S	17.7 $\pm$ 1.2 befghj	91.6	6.9	16.82 $\pm$ 1.09 ab	93.2	6.5	0.196 $\pm$ 0.041 befgh	74.0	21.1	82.1 $\pm$ 15.3 begijkl	75.3	18.7
V455	F $\times$ S	15.6 $\pm$ 2.2 begj	80.7	14.0	16.81 $\pm$ 1.06 ab	93.1	6.3	0.161 $\pm$ 0.059 befg	60.8	36.5	73.5 $\pm$ 24.7 befghijkl	67.4	33.6
V456	F $\times$ S	17.3 $\pm$ 3.5 bcdefghj	89.6	20.1	17.51 $\pm$ 0.94 bcd	97.0	5.4	0.214 $\pm$ 0.099 abcdefgh	80.8	46.2	91.0 $\pm$ 34.2 bcdefghijkl	83.5	37.6
V447	F $\times$ G	19.3 $\pm$ 2.0 bcdefghj	100.1	10.5	18.12 $\pm$ 1.29 bcde	100.4	7.1	0.249 $\pm$ 0.052 bcdefgh	94.1	20.9	110.4 $\pm$ 22.9 bcdefghijkl	101.2	20.7
V448	F $\times$ G	20.1 $\pm$ 1.8 cdefghj	103.7	8.8	17.91 $\pm$ 0.73 bcde	99.2	4.1	0.269 $\pm$ 0.058 abcdefgh	101.4	21.5	105.7 $\pm$ 22.5 bcdefghijkl	97.0	21.3
V449	F $\times$ G	21.0 $\pm$ 2.3 acdefghj	108.5	11.1	18.30 $\pm$ 1.07 bcde	101.3	5.9	0.305 $\pm$ 0.081 abcdefgh	115.0	26.7	127.1 $\pm$ 30.8 acdefghijkl	116.6	24.2
V49	F $\times$ G	21.3 $\pm$ 1.8 acdfhj	110.1	8.3	18.55 $\pm$ 0.96 cde	102.7	5.2	0.322 $\pm$ 0.060 acdgh	121.3	18.6	123.9 $\pm$ 23.0 acdfhijkl	113.6	18.6
V302	F $\times$ G	21.5 $\pm$ 2.7 acdefghj	111.4	12.4	17.08 $\pm$ 0.79 bc	94.6	4.6	0.284 $\pm$ 0.090 abcdefgh	107.3	31.6	102.7 $\pm$ 26.7 bcdefghijkl	94.2	26.0
V381	F $\times$ G	20.4 $\pm$ 2.3 acdefghj	105.4	11.1	18.31 $\pm$ 1.54 bcde	101.4	8.4	0.306 $\pm$ 0.083 abcdefgh	115.4	27.1	129.9 $\pm$ 33.5 acdefghijkl	119.2	25.8
V382	F $\times$ G	20.5 $\pm$ 2.4 acdefghj	106.1	11.6	18.38 $\pm$ 1.09 bcde	101.8	5.9	0.320 $\pm$ 0.087 acdefgh	120.8	27.1	135.5 $\pm$ 32.4 acdfghijkl	124.3	23.9
V383	F $\times$ G	20.2 $\pm$ 1.9 acdefghj	104.6	9.4	18.92 $\pm$ 1.01 de	104.8	5.3	0.292 $\pm$ 0.059 acdefgh	110.0	20.4	123.6 $\pm$ 24.0 acdefghijkl	113.4	19.4
V469	F $\times$ L	20.2 $\pm$ 0.5 cdfghj	104.5	2.4	19.32 $\pm$ 0.58 e	107.0	3.0	0.290 $\pm$ 0.021 cdfgh	109.2	7.2	124.9 $\pm$ 9.8 acdfjkl	114.6	7.9
V470	F $\times$ L	17.9 $\pm$ 2.9 abcdefghj	92.8	16.4	18.39 $\pm$ 1.98 bcde	101.8	10.8	0.239 $\pm$ 0.077 abcdefgh	90.2	32.3	101.2 $\pm$ 30.0 abcdefghijkl	92.8	29.6
V471	F $\times$ L	18.3 $\pm$ 1.4 bcdefghj	94.7	7.4	18.82 $\pm$ 0.83 de	104.3	4.4	0.251 $\pm$ 0.036 bcdefgh	94.7	14.3	109.5 $\pm$ 15.9 cdefghijkl	100.5	14.5
V325	R	19.8 $\pm$ 1.7 cdefghj	102.4	8.3	18.05 $\pm$ 0.85 bcde	100.0	4.7	0.276 $\pm$ 0.053 acdefgh	104.1	19.1	101.1 $\pm$ 16.3 bcdefghijkl	92.8	16.2
V327	R	20.5 $\pm$ 2.4 acdefghj	106.1	11.9	18.65 $\pm$ 1.22 cde	103.3	6.5	0.307 $\pm$ 0.074 acdefgh	115.7	24.1	119.9 $\pm$ 27.6 acdefghijkl	110.0	23.0
V386	F $\times$ E	18.9 $\pm$ 1.8 bcdefghj	97.6	9.5	18.66 $\pm$ 0.83 cde	103.4	4.4	0.263 $\pm$ 0.049 bcdefgh	99.2	18.8	110.7 $\pm$ 18.5 cdefghijkl	101.5	16.7

* Dunnett's T3 test was applied here due to the heterogeneity of variance. In other cases Tukey's test was applied.

† Values are the percentages of the genotype means relative to the mean of all 25 genotypes.

V388	F × E	17.1 ± 1.6 befghj	88.4	9.3	16.98 ± 0.66 abc	94.1	3.9	0.192 ± 0.040 befgh	72.3	21.0	81.0 ± 15.4 begijkl	74.3	19.1
V389	F × E	18.1 ± 2.0 bcdefghj	93.8	10.9	18.31 ± 0.80 bcde	101.4	4.4	0.236 ± 0.056 bcdefgh	88.9	23.8	100.6 ± 19.4 bcdefghijkl	92.3	19.3
V47	F	18.1 ± 1.0 bfghj	93.6	5.4	17.64 ± 0.72 bcde	97.7	4.1	0.237 ± 0.031 bcdefgh	89.3	13.0	99.0 ± 13.5 bcdefghijkl	90.8	13.6
V328	F	20.0 ± 1.7 cdefghj	103.5	8.3	18.42 ± 1.10 bcde	102.0	6.0	0.283 ± 0.059 acdefgh	106.7	20.7	109.4 ± 22.2 bcdefghijkl	100.4	20.3
V332	F	16.1 ± 2.6 bdefghj	83.1	16.2	15.54 ± 0.81 a	86.1	5.2	0.170 ± 0.067 bdefgh	64.2	39.2	62.7 ± 23.6 beghl	57.5	37.6
V43	F	23.1 ± 0.8 aceh	119.8	3.4	18.66 ± 0.82 cde	103.4	4.4	0.373 ± 0.043 ach	140.7	11.7	154.4 ± 18.1 acdfk	141.6	11.7
V48	F	19.5 ± 1.4 cdefghjk	100.9	7.1	19.27 ± 0.82 e	106.7	4.3	0.286 ± 0.054 acdefgh	107.8	18.8	117.1 ± 23.8 acdefghijkl	107.4	20.3
V465	F	20.7 ± 2.2 acdefghj	107.2	10.5	17.93 ± 1.39 bcde	99.3	7.8	0.308 ± 0.071 acdefgh	116.1	23.2	128.3 ± 29.3 acdefghijkl	117.7	22.8
All genotypes		19.3 ± 1.9	100.0	10.0	18.05 ± 1.00	100.0	5.5	0.265 ± 0.060	100.0	23.4	108.9 ± 22.9	100.0	21.7

Table 3. Statistics for ring width (RW), earlywood (EWW) and latewood width (LWW), latewood percentage (LWW %), for the genotypes.

Different letters indicate differences among genotypes ($p < 0.05$)

Gtype	Geographical origin	EWW, mm*			LWW, mm			LWW, %			RW, mm*		
		Mean ± SD	%†	CV, %	Mean ± SD	%†	CV, %	Mean ± SD	%†	CV, %	Mean ± SD	%†	CV, %
V454	F × S	1.80 ± 0.25 acdefghjk	94.3	13.7	0.61 ± 0.08 bcd	97.7	13.6	28.17 ± 3.60 bcdefg	104.6	12.8	2.41 ± 0.28 acdefghj	95.1	11.6
V455	F × S	1.39 ± 0.20 acfk	72.8	14.1	0.60 ± 0.09 bc	96.2	15.7	32.81 ± 4.07 g	121.9	12.4	1.99 ± 0.24 adgh	78.6	11.9
V456	F × S	1.66 ± 0.53 abcdefghjk	86.9	32.2	0.64 ± 0.06 bcde	103.3	9.3	31.27 ± 5.38 efg	116.1	17.2	2.30 ± 0.56 abcdefghj	90.9	24.5
V447	F × G	1.83 ± 0.20 cdefghjk	95.8	11.1	0.75 ± 0.05 e	119.6	7.0	32.66 ± 2.40 fg	121.3	7.3	2.57 ± 0.22 cdefghj	101.6	8.6
V448	F × G	2.05 ± 0.20 bdefghjk	107.6	9.5	0.58 ± 0.08 b	93.0	13.3	24.47 ± 2.92 abcd	90.9	11.9	2.63 ± 0.21 cdefghj	104.0	8.2
V449	F × G	2.07 ± 0.27 bcdefghjk	108.7	13.0	0.72 ± 0.09 cde	114.9	13.1	27.32 ± 2.73 abcdefg	101.5	10.0	2.79 ± 0.33 bcdefghj	110.2	11.7

* Dunnett’s T3 test was applied here due to the heterogeneity of variance. In other cases Tukey’s test was applied.

† Values are the percentages of the genotypes means relative to the mean of all 25 genotypes.

V49	F × G	2.15 ± 0.16 bdfghjk	112.9	7.2	0.60 ± 0.05 bc	96.1	9.0	22.83 ± 1.54 ab	84.8	6.7	2.75 ± 0.17 bcefhj	108.8	6.0
V302	F × G	2.17 ± 0.39 bcdefghjk	113.9	18.1	0.63 ± 0.12 bcde	101.4	19.4	24.21 ± 5.67 abc	89.9	23.4	2.81 ± 0.39 bcdefghj	110.8	14.0
V381	F × G	2.03 ± 0.26 bcdefghjk	106.3	12.6	0.68 ± 0.09 bcde	108.9	12.9	28.34 ± 2.58 bcdefg	105.3	9.1	2.71 ± 0.32 bcdefghj	106.9	11.9
V382	F × G	1.97 ± 0.32 bcdefghjk	103.4	16.1	0.60 ± 0.06 bc	96.1	9.4	25.98 ± 3.07 abcde	96.5	11.8	2.57 ± 0.34 abcdefghj	101.6	13.3
V383	F × G	1.99 ± 0.21 bcdefghjk	104.5	10.5	0.65 ± 0.06 bcde	104.4	9.9	27.23 ± 3.12 abcdef	101.1	11.5	2.64 ± 0.23 bcdefghj	104.5	8.8
V469	F × L	1.98 ± 0.13 efghjk	103.6	6.7	0.62 ± 0.05 bcde	99.9	8.1	25.45 ± 1.69 abcd	94.6	6.7	2.60 ± 0.13 cdefghj	102.7	5.0
V470	F × L	1.68 ± 0.36 abcdefghjk	88.2	21.6	0.57 ± 0.07 b	92.1	11.5	28.30 ± 5.36 bcdefg	105.1	18.9	2.26 ± 0.40 acdefghj	89.2	17.7
V471	F × L	1.70 ± 0.11 acfhjk	89.0	6.6	0.61 ± 0.09 bcd	97.9	14.3	27.67 ± 2.34 abcdefg	102.8	8.5	2.31 ± 0.17 adegghj	91.2	7.2
V325	R	2.07 ± 0.15 bdefghjk	108.3	7.1	0.66 ± 0.12 bcde	106.4	18.5	24.70 ± 2.84 abcd	91.8	11.5	2.73 ± 0.22 bceefghj	107.8	8.2
V327	R	2.03 ± 0.26 bcdefghjk	106.4	12.8	0.61 ± 0.06 bc	97.3	10.3	25.53 ± 3.55 abcd	94.8	13.9	2.64 ± 0.28 bcdefghj	104.2	10.5
V386	F × E	1.86 ± 0.22 cdefghjk	97.5	11.6	0.59 ± 0.11 bc	94.6	19.3	25.64 ± 3.34 abcde	95.2	13.0	2.45 ± 0.29 acdefghj	96.8	11.7
V388	F × E	1.72 ± 0.21 acefghjk	90.1	12.2	0.57 ± 0.06 b	91.7	10.9	26.95 ± 3.57 abcde	100.1	13.3	2.29 ± 0.21 adefghj	90.5	9.3
V389	F × E	1.82 ± 0.26 acdefghjk	95.6	14.1	0.57 ± 0.05 b	91.8	8.5	25.98 ± 3.40 abcde	96.5	13.1	2.40 ± 0.26 acdefghj	94.7	11.0
V47	F	1.73 ± 0.20 acefghjk	90.7	11.7	0.68 ± 0.08 bde	109.4	11.5	30.21 ± 4.16 defg	112.2	13.8	2.41 ± 0.21 acdefghj	95.3	8.7
V328	F	2.03 ± 0.30 bcdefghjk	106.3	14.8	0.59 ± 0.08 bc	94.3	13.6	24.86 ± 3.87 abcd	92.3	15.6	2.62 ± 0.33 bcdefghj	103.3	12.6
V332	F	1.66 ± 0.36 abcdefghjk	86.9	21.7	0.42 ± 0.07 a	68.0	16.4	22.19 ± 5.35 a	82.4	24.1	2.08 ± 0.39 acdefghj	82.3	18.8
V43	F	2.31 ± 0.12 bdgj	120.8	5.2	0.73 ± 0.07 de	117.7	9.7	25.67 ± 2.12 abcde	95.3	8.3	3.04 ± 0.14 bcfj	120.0	4.6
V48	F	2.02 ± 0.15 bdefghjk	106.1	7.6	0.55 ± 0.08 b	89.0	13.5	25.26 ± 2.57 abcd	93.8	10.2	2.58 ± 0.19 cdefghj	101.9	7.3
V465	F	1.97 ± 0.25 bcdefghjk	103.3	12.8	0.74 ± 0.08 e	118.4	11.1	29.37 ± 2.37 cdefg	109.1	8.1	2.71 ± 0.31 bcdefghj	107.0	11.3
All genotypes		1.91 ± 0.24	100.0	13.0	0.62 ± 0.10	100.0	12.4	26.92 ± 3.34	100.0	12.5	2.53 ± 0.27	100.0	11.0

Table 4. Statistics for weighted average wood density (WD), earlywood (EWD) and latewood (LWD) densities for the genotypes. Different letters indicate differences among genotypes ($p < 0.05$)

Gtype	Geographical origin	EWD, g/cm ³			LWD, g/cm ³			WD, g/cm ³		
		Mean $\pm$ SD	% ⁵	CV, %	Mean $\pm$ SD	% ⁵	CV, %	Mean $\pm$ SD	% ⁵	CV, %
V454	F $\times$ S	0.338 $\pm$ 0.017 defgh	101.0	5.0	0.633 $\pm$ 0.029 bcde	100.5	4.6	0.421 $\pm$ 0.025 defg	101.7	5.9
V455	F $\times$ S	0.364 $\pm$ 0.013 j	108.8	3.6	0.656 $\pm$ 0.017 de	104.2	2.6	0.459 $\pm$ 0.018 h	110.9	3.9
V456	F $\times$ S	0.344 $\pm$ 0.020 fgh	102.8	5.9	0.642 $\pm$ 0.034 bcde	102.0	5.3	0.438 $\pm$ 0.037 fgh	105.7	8.4
V447	F $\times$ G	0.338 $\pm$ 0.005 efgh	101.1	1.5	0.658 $\pm$ 0.019 de	104.5	3.0	0.443 $\pm$ 0.008 gh	106.9	1.9
V448	F $\times$ G	0.322 $\pm$ 0.016 bcde	96.1	5.0	0.617 $\pm$ 0.019 bc	97.9	3.0	0.394 $\pm$ 0.020 abcde	95.1	5.1
V449	F $\times$ G	0.337 $\pm$ 0.009 cdefgh	100.7	2.7	0.638 $\pm$ 0.021 bcde	101.4	3.3	0.419 $\pm$ 0.012 defg	101.2	2.9
V49	F $\times$ G	0.318 $\pm$ 0.007 abcd	95.0	2.1	0.612 $\pm$ 0.017 b	97.1	2.7	0.385 $\pm$ 0.010 ab	93.0	2.5
V302	F $\times$ G	0.300 $\pm$ 0.012 a	89.5	4.1	0.571 $\pm$ 0.021 a	90.7	3.6	0.366 $\pm$ 0.023 a	88.3	6.4
V381	F $\times$ G	0.334 $\pm$ 0.011 bcdefgh	99.9	3.4	0.657 $\pm$ 0.024 de	104.4	3.6	0.426 $\pm$ 0.017 fg	102.8	4.1
V382	F $\times$ G	0.345 $\pm$ 0.016 fghj	103.2	4.6	0.655 $\pm$ 0.033 cde	104.1	5.0	0.426 $\pm$ 0.026 fg	102.9	6.1
V383	F $\times$ G	0.342 $\pm$ 0.019 efgh	102.1	5.5	0.648 $\pm$ 0.032 bcde	102.9	5.0	0.425 $\pm$ 0.027 fg	102.7	6.3
V469	F $\times$ L	0.352 $\pm$ 0.012 hj	105.3	3.5	0.662 $\pm$ 0.015 e	105.2	2.2	0.431 $\pm$ 0.013 fgh	104.2	3.1
V470	F $\times$ L	0.343 $\pm$ 0.015 fgh	102.4	4.0	0.649 $\pm$ 0.014 bcde	103.0	2.2	0.429 $\pm$ 0.023 fg	103.6	5.3
V471	F $\times$ L	0.351 $\pm$ 0.009 ghj	104.9	2.6	0.659 $\pm$ 0.014 e	104.7	2.1	0.436 $\pm$ 0.013 fgh	105.4	2.9
V325	R	0.302 $\pm$ 0.012 a	90.3	3.9	0.569 $\pm$ 0.022 a	90.4	3.8	0.368 $\pm$ 0.016 a	88.9	4.5
V327	R	0.316 $\pm$ 0.014 ab	94.4	4.5	0.616 $\pm$ 0.029 b	97.9	4.7	0.392 $\pm$ 0.021 abcd	94.7	5.4
V386	F $\times$ E	0.351 $\pm$ 0.010 ghj	104.8	2.8	0.632 $\pm$ 0.027 bcde	100.4	4.2	0.423 $\pm$ 0.011 efg	102.0	2.7
V388	F $\times$ E	0.345 $\pm$ 0.010 fghj	103.2	2.9	0.640 $\pm$ 0.018 bcde	101.7	2.9	0.424 $\pm$ 0.014 fg	102.5	3.3
V389	F $\times$ E	0.352 $\pm$ 0.011 ghj	105.1	3.3	0.656 $\pm$ 0.029 cde	104.1	4.5	0.430 $\pm$ 0.018 fg	103.9	4.2
V47	F	0.331 $\pm$ 0.010 bcdefg	98.9	3.0	0.620 $\pm$ 0.030 bcd	98.4	4.9	0.418 $\pm$ 0.017 defg	101.0	4.1
V328	F	0.325 $\pm$ 0.013 bcdef	97.0	4.1	0.579 $\pm$ 0.024 a	92.0	4.1	0.387 $\pm$ 0.016 abc	93.5	4.1
V332	F	0.317 $\pm$ 0.010 abc	94.8	3.2	0.565 $\pm$ 0.032 a	89.8	5.7	0.371 $\pm$ 0.014 a	89.5	3.9
V43	F	0.333 $\pm$ 0.005 bcdefgh	99.5	1.5	0.649 $\pm$ 0.011 bcde	103.0	1.8	0.414 $\pm$ 0.009 cdefg	100.0	2.1
V48	F	0.332 $\pm$ 0.013 bcdefgh	99.4	4.0	0.637 $\pm$ 0.028 bcde	101.1	4.4	0.409 $\pm$ 0.017 bcdef	98.8	4.2
V465	F	0.334 $\pm$ 0.018 bcdefgh	99.8	5.3	0.620 $\pm$ 0.022 bcd	98.4	3.5	0.418 $\pm$ 0.023 defg	100.9	5.4
All genotypes		0.335 $\pm$ 0.012	100.0	3.7	0.630 $\pm$ 0.023	100.0	3.7	0.414 $\pm$ 0.018	100.0	4.3

⁵ Values are the percentages of the genotype means relative to the mean of all 25 genotypes.

Table 5. Phenotypic correlations (r_p) between yield, growth, and wood density traits: diameter (D), height (H), stem volume (V), earlywood width (EWW), latewood width (LWW), ring width (RW), earlywood density (EWD), latewood density (LWD) and overall wood density (WD) over all genotypes.

	H	V	EWW	LWW	RW	EWD	LWD	WD
D	0.65*	0.94*	0.86*	0.39*	0.87*	-0.40*	-0.10	-0.41*
H		0.75*	0.52*	0.22*	0.52*	-0.07	0.21*	-0.08
V			0.80*	0.36*	0.81*	-0.33*	-0.04	-0.35*
EWW				0.28*	0.96*	-0.55*	-0.16*	-0.58*
LWW					0.53*	0.02	0.08	0.24*
RW						-0.48*	-0.12	-0.44*
EWD							0.70*	0.92*
LWD								0.77*

Note: *, $p < 0.05$

Table 6. Phenotypic correlations (r_p) between overall wood density (WD) and following variables: diameter (D), height (H), volume (V), earlywood width (EWW), latewood width (LWW), ring width (RW), earlywood density (EWD) and latewood density (LWD) for each genotype.

Gtype	Geographical origin	Phenotypic correlation of WD with							
		D	H	V	EWW	LWW	RW	EWD	LWD
V454	F × S	-0.35	-0.63	-0.52	-0.59	0.46	-0.38	0.91*	0.75*
V455	F × S	-0.50	-0.16	-0.56	-0.63	0.05	-0.51	0.95*	0.06
V456	F × S	-0.80*	-0.73*	-0.84*	-0.89*	-0.18	-0.86*	0.93*	0.88*
V447	F × G	-0.22	-0.17	-0.23	-0.53	-0.15	-0.53	0.83*	0.36
V448	F × G	-0.03	-0.63	-0.10	-0.33	0.71*	-0.05	0.94*	0.59
V449	F × G	-0.75*	-0.64*	-0.74*	-0.82*	-0.51	-0.82*	0.87*	0.37
V49	F × G	-0.11	-0.12	-0.07	-0.41	0.23	-0.31	0.87*	0.67*
V302	F × G	-0.56	-0.84*	-0.72*	-0.68*	0.76*	-0.44	0.59	0.54
V381	F × G	-0.28	-0.49	-0.29	-0.19	0.19	-0.10	0.95*	0.65*
V382	F × G	-0.68*	-0.06	-0.46	-0.72*	0.13	-0.65*	0.95*	0.77*
V383	F × G	-0.30	-0.34	-0.32	-0.77*	0.30	-0.61	0.96*	0.74*
V469	F × L	0.05	-0.14	-0.01	-0.49	0.06	-0.481	0.93*	0.39
V470	F × L	-0.86*	-0.82*	-0.85*	-0.80*	-0.04	-0.73*	0.89*	-0.02
V471	F × L	-0.07	0.25	-0.03	-0.84*	-0.10	-0.62	0.82*	0.68*
V325	R	-0.54	-0.73*	-0.68*	-0.35	0.50	0.04	0.85*	0.77*
V327	R	-0.38	0.09	-0.29	-0.77*	0.26	-0.66*	0.97*	0.47
V386	F × E	-0.78*	-0.21	-0.72*	-0.46	-0.14	-0.40	0.84*	0.39
V388	F × E	-0.79*	-0.36	-0.66*	-0.76*	0.07	-0.72*	0.89*	-0.10
V389	F × E	-0.95*	-0.89*	-0.94*	-0.89*	-0.27	-0.92*	0.95*	0.47

V47	F	0.04	-0.47	0.00	-0.37	0.29	-0.24	0.73*	0.55
V328	F	-0.33	-0.29	-0.17	-0.44	0.15	-0.37	0.92*	0.22
V332	F	-0.43	-0.59	-0.46*	-0.61	0.28	-0.51	0.96*	-0.37
V43	F	0.20	-0.11	-0.08	-0.51	0.44	-0.22	0.61	0.21
V48	F	0.12	0.44	0.20	0.21	0.76*	0.47	0.92*	0.56
V465	F	-0.39	-0.31	-0.27	-0.68*	0.08	-0.53	0.97*	0.76*

Note: *, $p < 0.05$

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Table 7. Statistical characteristics of linear mixed-effect models for diameter (D), height (H), stem volume (V) and weighted average wood density (WD), based on transformed latitudinal transfer of mother parent tree genotypes (dtlatM) and father parent tree genotypes (dtlatF) with respect to the Imatra trial site.

	D, cm			H, m			V, m ³			WD, g/cm ³		
	estimates	p-values	95% CI	estimates	p-values	95% CI	estimates	p-values	95% CI	estimates	p-values	95% CI
x = dtlatM												
β_o	19.73	< 0.001	18.58–20.87	18.07	< 0.001	17.42–18.69	0.279	< 0.001	0.250–0.308	0.401	<0.001	0.386–0.415
β_1	–0.16	0.309	–0.43–0.12	–0.06	0.482	–0.2–0.10	–0.006	0.175	–0.013–0.001	0.004	0.071	0.0004–0.0076
var (a_i)	1.30 ²		0.00–2.24	0.79 ²		0.00–1.29	0.030 ²		0.000–0.055	0.018 ²		0.005–0.029
var (b_{ij})	1.19 ²		0.73–2.02	0.51 ²		0.29–0.99	0.035 ²		0.021–0.028	0.013 ²		0.008–0.020
var (ε_{ijk})	2.02 ²		1.84–2.22	1.03 ²		0.95–1.14	0.063 ²		0.058–0.069	0.019 ²		0.017–0.021
x = dtlatF												
β_o	19.84	< 0.001	18.44–21.26	17.99	< 0.001	17.24–18.75	0.281	< 0.001	0.242–0.322	0.397	<0.001	0.382–0.412
β_1	0.20	0.361	–0.20–0.62	0.005	0.968	–0.21–0.23	0.006	0.312	–0.005–0.018	–0.006	0.025	–0.010–0.002
var (a_i)	1.41 ²		0.00–2.35	0.82 ²		0.00–1.32	0.040 ²		0.000–0.067	0.011 ²		0.000–0.022
var (b_{ij})	1.10 ²		0.64–1.89	0.48 ²		0.25–0.91	0.030 ²		0.016–0.052	0.017 ²		0.012–0.026

$\text{var}(\varepsilon_{ijk})$	2.20^2		1.84–2.22	1.03^2		0.95–1.14	0.063^2		0.058–0.069	0.019^2		0.017–0.021
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Figure 1. Stem volume (top), wood density (middle) and stem mass (bottom) calculated for individual genotypes as a percentage of the overall mean (solid line). Legend F, S, G, R, E. in Table 1

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Figure 2. Relationship between mean stem volume (x-axis) and wood density (y-axis). The vertical and horizontal lines are the overall mean stem volume and wood density, respectively, for the 25 genotypes. Legend F, S, G, R, E. in Table 1