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Genetic parameters of growth and quality traits in open-pollinated silver birch progeny tests

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Highlights

- Growth and stem quality traits were under strong genetic control.
- Weak genetic correlations between tree growth and stem quality were found.
- Strong age-age and type-B correlations suggest robust improvement over time and different environments.
- Simultaneous improvement of growth and stem quality might be applicable.

Abstract

Genetic parameters of growth and stem quality traits were estimated for open-pollinated silver birch *Betula pendula* Roth progenies in Latvia at the age of 10 and 14 years. Tree height and stem volume were found to be under strong genetic control at both inventories (narrow-sense heritabilities varied from 0.41 to 0.66). Mainly low heritabilities were found for stem defects, yet genetic control of branch diameter, stem straightness and overall stem quality varied from low to high depending on study site. High additive genetic coefficient of variation was found for stem volume (25.3–32.5%). Genetic correlations among growth traits were strong and positive (0.90–0.99). Mainly weak genetic correlations between growth and quality traits implied simultaneous improvement. Still, strong negative correlations between branch angle and stem straightness might result in enlarged knot size for straighter logs. The genetic age-age correlations were strong. Weak genotype by environment interaction and stability of best genotypes over different sites was indicated by strong genetic correlations between trials. Each growth or quality trait alone showed substantial improvement in terms of estimated genetic gain (up to 62% over trial mean for stem volume). Therefore, selection index combining both growth and stem quality may be developed.

Keywords *Betula pendula*; genetic gain; genetic parameters; tree breeding
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1 Introduction

In Latvia, comprehensive breeding of silver birch *Betula pendula* Roth was initiated in the middle of 1990s. For basic breeding material, 921 plus-trees and superior stand trees were phenotypically selected in 26 natural stands thorough the country, and their progeny tests were established in 1999 and 2000. Although breeding of coniferous species (Scots pine *Pinus sylvestris* L. and Norway spruce *Picea abies* (L.) H. Karst.) has longer history in Latvia, silver birch as a commercially important tree species is yet included in the long-term breeding program, aiming to develop seed production and raise the financial value of forests (Jansons 2008).

In the Eastern Baltic region, breeding activities in combination with appropriate silviculture (e.g. planting density) can result in highly productive silver birch stands for valuable plywood production (Stener and Hedenberg 2003), as confirmed by a clonal birch plantation in Central Latvia ready for harvest at the age of 40 years (Zeltiņš et al. 2018). The selection of genotypes must be based on the growth traits and stem quality traits such as stem straightness, desirable branch properties, and apical dominance (Stener and Hedenberg 2003). As indicated by mainly negligible genetic correlations between both types of traits (Koski and Rousi 2005; Stener and Jansson 2005), such simultaneous selection may be applicable. For plywood production, logs with no stem defects such as crooks, forking, and with knots as few as possible are required (Donaldson and Turner 2001; Heräjärvi 2001). For silver birch, growth traits have been reported to be mostly under strong genetic control (Stener and Hedenberg 2003; Stener and Jansson 2005), yet rapid growth not having strong negative effect on wood and stem properties (Dunham et al. 1999; Heräjärvi 2001; Heräjärvi 2004a and 2004b; Baliuckienė and Baliuckas 2006). In Scandinavia, heritability for growth traits found to vary considerably from 0.07 to 0.56 up to the age of 10 years, largely depending on planting site (Stener and Jansson 2005; Skrøppa and Solvin 2019). Moderate h^2 (cf. Falconer and Mackay 1996) for growth traits (0.20–0.39) reported in Scottish and Lithuanian studies (Malcolm and Worrell 2001; Baliuckienė and Baliuckas 2006). Genetic coefficients of variation (CV_a and CV_g), indicating level of genetic variability, reported to range from 4.6 to 20.5% for growth and from 9.8 to 15.1% for stem quality traits (Stener and Jansson 2005; Baliuckienė and Baliuckas 2006). Early selection has been justified by moderate to strong age-age genetic correlations for periods up to 17 years (Hagqvist and Hahl 1998; Stener and Hedenberg 2003; Stener and Jansson 2005), yet general information about long-term time trends for genetic control is limited (Stener and Hedenberg 2003).

In Fennoscandia, the silver birch breeding programs have resulted in substantial improvements of productivity and stem quality, genetic gains reaching 5–30% (Hagqvist and Hahl 1998; Rosvall et al. 2001; Jansson et al. 2017). In Latvia, the use of silver birch in plywood production, accounting for ca. 9% of total forest sector export value (Central Statistical Bureau of Latvia 2016) and being one of the leading branches of the wood processing industry (Liepins and Rieksts-Riekstins 2013) indicates the importance of birch breeding for the production of fast growing planting stock with desirable quality traits. However, comprehensive analysis of silver birch quantitative genetic parameters and potential genetic gains in the Eastern Baltic region is still lacking. Therefore, the aim of the study was to estimate genetic parameters for growth and stem quality traits in open-pollinated silver birch progeny trials at the age of 10 and 14 years.

Table 1. Description of the studied open-pollinated *Betula pendula* progeny trails.

Name	Latitude	Longitude	Altitude (m)	Planting year	No. of open-pollinated families assessed		No. of measured trees		No. of replications
					age 10	age 14	age 10	age 14	
Rembate	56°46′N	24°48′E	50	1999	637	637	46696	53032	3–5
Ukri	56°22′N	23°07′E	75	2000	639	657	9643	18371	10–93
Taurene	57°06′N	25°38′E	215	2000	612	621	11917	10964	10–77

2 Material and methods

For the progeny testing, the seeds were collected in years 1995–1998 from the plus-trees in 26 forest stands thorough the country (55°40′–58°05′N, 20°58′–28°14′E). Data were collected from three extensive silver birch open-pollinated progeny trials Taurene (57°06′N, 25°38′E), Ukri (56°22′N, 23°07′E), and Rembate (56°46′N, 24°48′E) (Table 1). In Ukri and Taurene, the field design was randomized blocks with single-tree plots in 10–93 and 10–77 replications, respectively, with spacing 2 × 2.5 m. Rembate was planted in a randomized complete block design with 32-tree four-row plots for each family in three to five replications with 2 × 2 m spacing (Table 1). The trial Rembate was established in spring 1999, but the trails Ukri and Taurene – in spring 2000 on former agricultural land with one-year-old containerized seedlings. All trials were characterized with dry silty soils and mesotrophic conditions comparable to *Oxalidosa* according to the Latvian forest typology (Bušs 1981).

The mildest climate was in Ukri, where the mean annual temperature (MAT) was 6.4 °C, the mean monthly temperature ranged from –4.4 °C to +17.4 °C in January and July, respectively; the mean annual precipitation (PRECIP) was ca. 630 mm (Harris et al. 2014). In Rembate, the MAT was 6.1 °C, the mean monthly temperature ranged from –5.0 °C to +17.4 °C; the PRECIP was 618 mm. Taurene trial was located in more continental climate of eastern Latvia (Laiviņš and Melecis 2003), where MAT was 5.1 °C, mean monthly temperature ranged from –6.3 °C to +16.9 °C; PRECIP was 670 mm (Harris et al. 2014).

2.1 Data collection

In all trials, evaluation was done at the age of 10 and 14 years. For the first evaluation, measurements from 68 256 trees were available for analysis (9643, 11 917, and 46 696 trees in Ukri, Taurene and Rembate, respectively). For the second evaluation, 82 367 trees were measured (18 371, 10 964, and 53 032 trees in Ukri, Taurene and Rembate respectively) (Table 1). During the first evaluation, for each individual a) tree height (H), b) diameter of the largest branch until the stem height of 2 m (BrD), and c) mean branch angle (BrA) was measured. Occurrence of spike knots (SpKn), double leaders (Doubl) and lost top (LostTop) were recorded as binary variables (1 – present, 0 – absent), and ordinal scores using 3-point-scale of stem straightness (StStr; bent, slightly bent, and straight) and overall stem quality (StQual; poor, intermediate, and good) were assessed. At the age of 14 years, H and diameter at breast height (DBH) were measured (except for Rembate, where H was not measured). Afterwards, stem volume (V) was calculated according to Liepa (1996). In trial Rembate, BrA was measured, but in Ukri and Taurene it was assessed using 3-point ordinal score (1 – from 65° to 90°; 2 – from 45° to 60°; 3 – from 0° to 40°). Occurrence of SpKn, Doubl, LostTop, and ordinal scores of StStr and StQual were assessed as described above.

2.2 Statistical analysis

Variance and covariance components for continuous traits were estimated using SAS MIXED procedure with the restricted maximum likelihood approach (REML) (Littel et al. 2006). Diagnostic plots were used to verify for normal distribution of residuals. For the binomial variables, a generalised linear mixed models applying binomial residual distribution and a "logit" link function were fitted. For the ordinal variables, ordinal logistic regression was fitted. The binary/categorical traits were analysed using the Generalized Linear Mixed (GLIMMIX) procedure (Littell et al. 2006). Standard errors were calculated using Dickerson's approximation (Dickerson 1969). For a combined-site analysis of Ukri and Taurene, which had similar experimental design and set of families, the following mixed model was used:

$$y_{ijkl} = \mu + S_i + B_j + F_k + SF_{ij} + \varepsilon_{ijkl}\,, \tag{1}$$

where y_{ijk} is the observation on the lth tree from the kth family in the jth block within the ith site; μ is the overall mean; S_i and B_j are the fixed effects of the ith site and the jth block within the ith site, respectively. The F_k and SF_{ik} are the random effects of the kth family and interaction of the ith site and the kth family, respectively, and ε_{ijkl} is the random residual effect. Preliminary analyses indicated significant effect for the family-by-site interaction for studied traits.

For an individual site analysis of Ukri and Taurene, following model was used:

$$y_{jkl} = \mu + B_j + F_k + \varepsilon_{jkl}\,, \tag{2}$$

where y_{jk} is the observation on the lth tree from the kth family in the jth block. For individual site analysis of Rembate, the model was complemented with an effect of the block and family interaction (a multiple-tree plot effect):

$$y_{jkl} = \mu + B_j + F_k + BF_{jk} + \varepsilon_{jkl}\,, \tag{3}$$

where BF_{jk} is a random interactive effect of the jth block and the kth family.

The estimates of narrow-sense individual-tree heritability (h^2) were obtained for each trait using the variance components from the individual and joint-site analysis described above (Falconer and Mackay 1996). The individual-tree narrow-sense heritability in the joint-site analysis of Ukri and Taurene was calculated as:

$$h^2 = \frac{4 \times \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{fs}^2 + \hat{\sigma}_\varepsilon^2}, \tag{4}$$

where h^2 is narrow-sense heritability, and $\hat{\sigma}_f^2, \hat{\sigma}_{fs}^2$ and $\hat{\sigma}_\varepsilon^2$ are the estimated variance components of family, family × site interaction and residual, respectively.

For an individual single-tree plot site, following formula was used:

$$h^2 = \frac{4 \times \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_\varepsilon^2}. \tag{5}$$

For a multiple-tree-plot design in Rembate, following formula was used:

$$h^2 = \frac{4 \times \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{fb}^2 + \hat{\sigma}_\varepsilon^2}, \tag{6}$$

where $\hat{\sigma}_{fb}^2$ is the estimated variance component of site × block interaction.

Additive genetic coefficient of variation (CV_a) describing the extent of genetic variability for the quantitative traits in each site (Falconer and Mackay 1996), was calculated as:

$$CV_a = \sqrt{4\hat{\sigma}_f^2} \cdot \frac{100}{\bar{x}}, \tag{7}$$

where $\bar{x}$ is the phenotypic mean.

Genetic correlations (type-A) between traits and age-age genetic correlations for each trait were estimated using formula:

$$r_G = \frac{\widehat{Cov}_{(xy)}}{\sqrt{\hat{\sigma}_{(x)}^2 \times \hat{\sigma}_{(y)}^2}}, \tag{8}$$

where $\hat{\sigma}_{(x)}^2$ and $\hat{\sigma}_{(y)}^2$ are a) the estimated genotypic variances for traits x and y, or b) the same trait variances at two different ages; and $\widehat{Cov}_{(xy)}$ is the estimated genotypic covariance between traits x and y or between two measurements of the same trait.

The genotype × environment interaction (G × E) for studied traits was evaluated by estimating type-B genetic correlations (r_B) between two experiments (Bourdon 1977). Considering similar experimental design and set of the same families, the type-B genetic correlation between Ukri and Taurene was calculated as (Lu and Charrette 2008):

$$r_B = \frac{\widehat{Cov}_{(a1a2)}}{\sqrt{\hat{\sigma}_{(a1)}^2 \times \hat{\sigma}_{(a2)}^2}}, \tag{9}$$

where $\widehat{Cov}_{(a1a2)}$ is the covariance between genotypic effects of the same traits in different sites, and $\hat{\sigma}_{(a1)}^2$ and $\hat{\sigma}_{(a2)}^2$ are genotypic variances for the same traits in each of the trails, respectively. Both r_G and r_B with their standard errors were estimated by multivariate REML using the MIXED procedure of SAS (Piepho and Möhring 2011) extending univariate mixed models described above.

Breeding values were estimated for each trait to evaluate gain from selection of the best families. We obtained general combining ability (GCA) values of parents by a Best Linear Unbiased Predictors (BLUP) procedure in SAS using the analytical models defined above. Since parent can only transmit half of its genes to its progeny (Falconer and Mackay 1996), breeding values (BV) of families were calculated as double BLUPs. Since the linear predictors for the binary traits from the generalized mixed models were calculated on a logit scale, predicted probabilities of stem defects for families were estimated by applying the inverse of the link function (Littell et al. 1996). Genetic gains, assuming the selection intensity of 10% (as commonly used in tree breeding practice in Latvia), were estimated from BV as the percentage over the trial means.

Table 2. Narrow sense heritabilities (h^2) and type-B genetic correlations (r_B) with standard errors (SE) (all r_B are significant $p < 0.01$) in the studied open-pollinated *Betula pendula* progeny trials at the age of 10 and 14 years.

	h^2 ± SE								r_B ± SE
Trial	Taurene		Ukri		Rembate		Ukri & Taurene together		
Age (years)	10	14	10	14	10	14	10	14	14
H	0.37 ± 0.03	0.45 ± 0.04	0.47 ± 0.04	0.64 ± 0.04	0.30 ± 0.07	na	0.37 ± 0.03	0.52 ± 0.03	0.94 ± 0.02
DBH	na	0.45 ± 0.04	na	0.52 ± 0.03	na	0.12 ± 0.02	na	0.42 ± 0.03	0.89 ± 0.03
V	na	0.41 ± 0.03	na	0.53 ± 0.03	na	na	na	0.41 ± 0.03	0.97 ± 0.03
BrD	0.24 ± 0.03	na	0.20 ± 0.03	na	0.10 ± 0.03	na	0.17 ± 0.02	na	na
BrA	0.33 ± 0.03	0.83 ± 0.19	0.27 ± 0.03	0.61 ± 0.07	0.30 ± 0.03	0.31 ± 0.03	0.25 ± 0.02	0.37 ± 0.1	0.78 ± 0.12
SpKn	0.07 ± 0.02	0.08 ± 0.02	0.06 ± 0.02	0.05 ± 0.01	0.04 ± 0.03	0.07 ± 0.02	0.07 ± na	0.06 ± 0.02	na
Doubl	0.29 ± 0.07	0.05 ± 0.06	0.04 ± 0.03	0.19 ± 0.04	0.08 ± 0.04	0.27 ± 0.05	0.1 ± na	na	na
LostTop	0.09 ± 0.03	0.04 ± 0.02	0.06 ± 0.03	0.05 ± 0.01	0.12 ± 0.03	0.06 ± 0.02	0.05 ± 0.04	0.02 ± 0.01	na
StStr	0.45 ± 0.05	0.35 ± 0.05	0.41 ± 0.05	0.45 ± 0.05	0.32 ± 0.05	0.39 ± 0.05	0.40 ± 0.06	0.4 ± 0.05	0.97 ± 0.05
StQual	0.15 ± 0.03	0.35 ± 0.05	0.11 ± 0.03	0.21 ± 0.03	0.14 ± 0.03	0.26 ± 0.04	0.10 ± 0.03	0.23 ± 0.03	0.89 ± 0.08

H – height, DBH – diameter at breast height, V – stem volume, SpKn – spike knots, Doubl – double leaders, LostTop – lost top, StStr – stem straightness, BrD – branch diameter, BrA – branch angle, StQual – stem quality.

3 Results

The survival was high at both measurement times in Rembate (>80%) and Ukri (>90%), yet lower in Taurene (>60%). At the age of 10 years, the means for H in Taurene and Ukri were the same (6.7 m), and other measured traits and proportion of trees with stem defects were similar. In Rembate, H was lower (5.5 m), and proportion of trees with SpKn was ca. three times lower than in the both other trials. At the age of 14 years, mean H was somewhat advanced ahead for Ukri comparing to Taurene (12.3 m and 11.5 m, respectively), yet other traits were stably alike. In Rembate, proportion of trees with SpKn had increased and was high (ca. 60%) and similar to both other trials. In all trials, proportion of trees with SpKn and LostTop was rather high (>50%), while only 6–12% of trees had Doubl.

The estimated narrow-sense heritability (h^2) varied among the variables, generally being higher for growth traits than stem quality (Table 2). The highest h^2 was estimated for H, DBH, V (0.30–0.64), except low value (0.12) for DBH in Rembate. Similarly high h^2 had StStr (0.35–0.45), while StQual, BrD, and Doubl had generally lower values (0.04–0.35). Heritability for BrA varied considerably (0.25–0.83) depending on site and year, but LostTop showed the overall lowest values (0.02–0.12). The genetic coefficient of variation CV_a for H ranged between 8.5 and 15.0% at age of 10 years, while DBH showed ca. two times higher genetic variation in Ukri and Taurene (20.6 and 18.7%, respectively), yet being around the same in Rembate (9.3%) (Table 3). Rather high CV_a was estimated for V, ranging from 25.3 to 40.3% in Rembate and Ukri, respectively. Branch angle showed low degree of genetic variation in all trials (3.7–6.4%) (Table 3).

The estimates of r_G among growth traits were similar and high in all studied trials (0.90–0.99) (Table 4), yet having mainly low to moderate genetic correlations with stem quality traits ($-0.10 < r_G < 0.40$). Branch angle had moderate to strong negative correlations with StStr and StQual ($-0.67 < r_G < -0.45$), which both strongly correlated with each other (0.83–0.84). Rather high positive correlations between SpKn and Doubl (0.60–0.74) were found. Still, stem quality traits generally had low to moderate genetic correlations with each other (Table 4). Genetic age-age correlations for traits measured at both inventories were mostly strong (>0.78) in all trials. Estimated type-B genetic correlations between Ukri and Taurene were high (0.78–0.97) for both growth and stem quality traits (Table 2). Considering low h^2 values, age-age and type-B correlations for SpKn, Doubl, and LostTop were not estimated.

For growth traits, selection of top 10% families resulted in GG% of 9.6–26.6% for H and DBH, while reaching 25.3–61.6% for V. Similar to h^2 values, GG% were generally lower for stem quality traits: 8.6–21.2% for StStr, 5.5–10.3% for StQual, 6.9–18.2% for BrD, 1.6–9.1% for BrA. Estimated GG% for the stem defects (Doubl and LostTop) varied notably among the trials and years, ranging from 5.2 to 58.3%.

Table 3. Genetic coefficients of variation for quantitative traits (CV_a) in the studied open-pollinated *Betula pendula* progeny trials at the age of 10 and 14 years.

Trial	Taurene		Ukri		Rembate	
Age (years)	10	14	10	14	10	14
H	10.4	8.5	11.4	5.5	7.5	na
DBH	na	18.7	na	10.3	na	4.7
V	na	32.5	na	20.1	na	na
BrD	16.2	na	12.6	na	4.3	na
BrA	4.4	na	4.7	na	3.2	1.9

H – height, DBH – diameter at breast height, V – stem volume, BrD – branch diameter, BrA – branch angle.

Table 4. Genetic correlations (standard errors in brackets) in combined Ukri and Taurene (the upper diagonal part) and in Rembate (the lower diagonal part) open-pollinated *Betula pendula* progeny trials at the age of 14 years.

	DBH	V	SpKn	Doubl	LostTop	StStr	BrA	StQual
H	0.92 (0.01)	0.94 (0.01)	0.43 (0.07)	0.23 (0.07)	0.05 (0.09)	–0.10 (0.05)	0.26 (0.06)	0.16 (0.06)
DBH		0.99 (0.00)	0.39 (0.07)	0.20 (0.07)	0.10 (0.09)	–0.06 (0.05)	0.22 (0.06)	0.17 (0.06)
V	na		0.39 (0.07)	0.23 (0.07)	0.06 (0.09)	–0.06 (0.05)	0.23 (0.06)	0.17 (0.06)
SpKn	0.13 (0.13)	na		0.60 (0.11)	0.08 (0.20)	–0.29 (0.08)	–0.02 (0.09)	–0.51 (0.07)
Doubl	–0.10 (0.11)	na	0.74 (0.11)		–0.51 (0.11)	0.03 (0.08)	–0.12 (0.09)	–0.16 (0.08)
LostTop	0.10 (0.13)	na	–0.06 (0.14)	–0.49 (0.11)		–0.69 (0.09)	0.52 (0.11)	–0.58 (0.09)
StStr	0.02 (0.09)	na	–0.39 (0.10)	–0.08 (0.09)	–0.71 (0.09)		–0.67 (0.05)	0.83 (0.03)
BrA	0.00 (0.25)	na	–0.01 (0.10)	0.09 (0.09)	0.28 (0.10)	–0.57 (0.06)		–0.45 (0.07)
StQual	0.40 (0.24)	na	–0.67 (0.09)	–0.28 (0.08)	–0.62 (0.08)	0.84 (0.04)	–0.48 (0.07)	

H – height, DBH – diameter at breast height, V – stem volume, SpKn – spike knots, Doubl – double leaders, LostTop – lost top, StStr – stem straightness, BrA – branch angle, StQual – stem quality.

4 Discussion

The survival was high in Rembate and Ukri (>80%), yet lower in Taurene (>60%), which was most likely affected by the insufficient moisture in dry summer after the establishment due to the fine textured soil in the trial (Sutinen et al. 2002). However, first years after planting, necessary weed control was applied sufficiently to eliminate further mortality induced by weed competition (Ferm et al. 1994; Hynynen et al. 2010). In all trials, proportion of trees with SpKn and LostTop was rather high (>50%), while only 6–12% of trees had Doubl, seemingly not affected by different continentality of the studied trials (Laiviņš and Melecis 2003). Viherä-Aarnio and Velling (1999) reported 13% of trees with SpKn. Similar to Viherä-Aarnio and Velling (1999), most of the trees had at least a light stem sweep.

4.1 Genetic parameters

In the Baltic sea region, heritabilities for growth and stem quality of common forest tree species Scots pine and Norway spruce reported to vary from 0.05 to 0.25 (Velling 1982; Haapanen et al. 1997; Hannrup et al. 1998; Olsson and Ericsson 2002; Jansons et al. 2006). In our study, h^2 for growth traits were mainly moderate to high, and genetic correlation among them were strong, supported by earlier findings in Latvia (Zeltiņš et al. 2018). Considering that the genes controlling each of growth traits might be strongly correlated (Searle 1961), selection may be based on tree height, which possessed the highest h^2. In earlier studies, estimated h^2 and broad-sense heritability H^2 of corresponding traits for silver birch reported to vary widely from low to high (Nepveu and Velling 1983; Malcolm and Worrell 2001; Stener and Jansson 2005; Zeltiņš et al. 2018). In Norway, narrow-sense heritability h^2 of six-years-old open-pollinated families estimated to be rather low, i.e. 0.09 and 0.17 for H and DBH, respectively (Skrøppa and Solvin 2019). In the present study, high heritability values and low variety among trails for growth traits might correspond to relatively homogenous growing conditions on agricultural land sufficiently maintained after establishment. Thus, genetically determined differences were better revealed comparing to forestland (Haapanen 1996; Hannrup et al. 2004). Although h^2 values from individual-site analysis are commonly overestimated and higher comparing to joint-site estimates (Hodge and White 1992; Haapanen 2001; Wu et al. 2008), our estimates of Ukri and Taurene together were close to heritabilities in separate sites. In contrast, insufficient maintenance, subsequent uneven survival and heterogeneous growth conditions commonly reported to result in low heritability indices with low accuracy, reducing benefits from tree breeding (Haapanen 1996; Mäkinen 1996; Talbot 1997; Nummi 1999; Olsson and Ericsson 2002; Koski and Rousi 2005). Nevertheless, mainly low h^2 for such stem defects as SpKn, Doubl and LostTop (0.04–0.29) coincides with earlier findings (Stener and Hedenberg 2003; Zeltiņš et al. 2018), suggesting relatively weak genetic control and strong prevailing effect of such environmental factors as drought, frost or biotic damage (Malcolm and Worrell 2001; Stener and Hedenberg 2003).

Stener and Jansson (2005) reported low h^2 and H^2 values (0.09–0.27) for StStr in a series of up to 10 years old silver birch clonal and progeny trials. Although StQual had low h^2 values (0.10–0.15) at the age of 10 years (Table 2), moderate to high heritabilities (0.21–0.45) and rather weak genetic correlations (Table 4) with growth traits for both StStr and StQual implied substantial improvement for wood quality in our study. In addition, generally moderate negative correlations between StQual and stem defects suggests that selection based on inclusive ordinal score of stem quality traits might reduce occurrence of stem defects despite low heritabilities of them, thus improving timber quality and increasing amount of merchantable wood (Agestam et al. 1998; Möttönen 2005). Mainly weak genetic correlations reported among quality traits as well as between growth and quality traits, likely related to rather low genetic variance of the latter ones (Koski and Rousi 2005; Stener and Jansson 2005). In Scotland, straight stems found to be associated with superior volume growth (Malcolm and Worrell 2001), yet not observed in our study. Similar to previous findings in Sweden and Latvia (Stener and Jansson 2005; Zeltiņš et al. 2018), BrD and BrA possessed high heritabilities. However, the substantial negative correlations between BrA and StStr might result in enlarged knot size for straighter logs, thus reducing technical quality (Niemistö 1995a). Larger BrD had been commonly reported as negative effect for fast growing silver birch (Niemistö 1995b, Stener and Jansson 2005), suggested to be mitigated with sufficient planting density of at least 1600 trees ha^{-1} for smaller knot size and improved wood strength (Niemistö 1995a; Dunham et al. 1999). Nevertheless, study in 40-years old low-density clonal silver birch plantation in Latvia showed possibility to obtain high-quality plywood applying wide (5 × 5 m) initial spacing (Zeltiņš et al. 2018).

Besides heritability, considerable CV_a (20.1–32.5%) suggested potential of breeding to improve V (Table 3). Lower CV_a values for stem quality traits comparing to growth traits coincide with results in Lithuania, where CV_a for StStr and BrA was ca. 13% (Baliuckienė and Baliuckas 2006). In a recent study of low-density clonal plantation, estimated CV_g for H was almost three times lower (3.2%) than CV_a in the present study (on average, ca. 8%) (Zeltiņš et al. 2018). It might be partly explained with remarkable differences in initial spacing (5 × 5 and 2 × 2.5 m in clonal plantation and our study sites, respectively), since genetic variance can be higher in closer spacing (Franklin 1979; Euler et al. 1992). Nevertheless, similar CV_a for H reported in north Sweden (Stener and Jansson 2005). Generally higher estimated CV_a values for DBH as for H were similar to results in Swedish progeny tests (14 and 8% for DBH and height, respectively) (Stener and Jansson 2005).

Estimated GG% confirmed general trends for h^2 and CV_a discussed above, reaching the highest values for V (25.3–61.6%), while being overall lower for stem quality (1.6–21.2%). Such estimates are over the means of trials instead of general population due to the lack of control plots, and thereby gains over forest stands might be higher (Malcolm and Worrel 2001). Nevertheless, selection of genotypes should compromise improved productivity with sufficient quality as well as improved performance in different growth conditions (Matheson and Cotterill 1990), especially when the aim is to produce high-quality silver birch timber for plywood industry (Hynynen et al. 2010). As indicated by single-trait gains, CV_a values (Table 3) and mainly weak r_G between growth and quality traits (Table 4), further development of index for simultaneous selection of both growth and stem quality traits may be possible.

4.2 Genotype by environment interaction

The studied traits showed low G × E interaction, indicated by strong type-B correlations for all studied traits ($r_B \geq 0.78$) between trials Ukri and Taurene (Table 2). Contradictory results have been reported previously: from strong and significant correlations between trials even in rather different environments (Stener and Hedenberg 2003; Stener and Jansson 2005) to substantial genotype by site interaction (Baliuckienė 2009). However, the accuracy of r_B might not be high (Bourdon 1977; Haapanen 1996), often related to inappropriate design of progeny trials, which has insufficient number of replications not following natural patterns of growing conditions (Haapanen 1996). Still, high type-B correlations with rather low standard errors for growth traits and low variation of h^2 for the same trait among trails discussed above indicated stability of performance over different environments, as well as appropriate experimental design.

Another relevant question regarding experimental design is the use of single-tree- or multiple-tree (block) plots. In general, single-tree plots in Ukri and Taurene had higher estimated heritabilities for growth traits and BrA than block-plots in Rembate (Table 2). Single-tree plots in many replications allow assessing genetic differences in statistically effective way (White et al. 2007), since progenies of plus-trees are represented in possibly wide range of competition and growing conditions within a trial (Haapenen 1992; Haapanen 1995). However, inter-tree competition among different genotypes may exaggerate estimated genetic variance for growth traits promoting initially fast growing families (Malcolm and Worrell 2001; Vergara et al. 2004; Gould and Marshall 2010). In the present study, growth traits might be somewhat affected by competition in the single-tree-plot trials Ukri and Taurene, since estimates from the block plots in Rembate were lightly lower. Still, estimates from more trials would be needed for generalized conclusions.

Stener and Hedenberg (2003) stressed general lack of information about age-age correlations for silver birch. In our study, the genetic age-age correlations for traits measured at the age of 10 and 14 years were mainly strong, implying as accurate selection for the respective traits at the first measurement time as at the second inventory. Nevertheless, strong correlations between so close ages are not very informative about long-term trends. Still, strong age-age correlations have been indicated for V for up to three decades in southern Finland (Hagqvist and Hahl 1998). There have been reported correlations ranging from 0.75 to 0.86 between the ages of 9 and 26 years; correlation of 0.94 between the ages of 5 and 10 years, and 0.84 between the age of 11 and 18 years for tree height (Stener and Hedenberg 2003). Stener and Jansson (2005) found moderate to strong age-age correlations (0.60–0.99) for H and quality traits.

5 Conclusions

Growth and stem quality traits were mostly under strong genetic control, yet occurrence of stem defects – spike knots, double tops and lost top – were more affected by environmental factors. Weak positive genetic correlations between growth traits and inclusive stem quality score indicated potential for improved productivity and wood quality simultaneously. Still, improvement for stem straightness might increase stem knottiness. Strong genetic correlations between different study trials, as well as strong age-age correlations indicated stability for improvements of silver birch planted on former agricultural land. Considerable single-trait gains, additive genetic coefficient of variation values, and mainly weak genetic correlations between growth and quality traits suggest further development of selection index for simultaneous improvement of both growth and stem quality.

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