

Long-term performance of Norway spruce in two provenance trials in Latvia

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Abstract

The Norway spruce is economically important tree species in the Baltic Sea region, covering large areas and being productive in pure plantations. The species is often regenerated with planting. It is important to choose not only productive, but also robust reproductive material with good adaptability in changing climate, hardiness and quality traits. The use of appropriate transferred provenances can be an option to increase forest productivity at final-harvest moment. Thus, it is necessary to know long-term fitness of different seedlots to increase climate change adaptation capacity. We examined two provenances trials in Western and Eastern Latvia at the age of 34 and 29 years, respectively. We assessed effect of provenance on growth performance, stem quality, and budburst time. In the milder climate of Western Latvia, superior growth showed certain northward-transferred, later flushing provenances from the Ukrainian Carpathian Mountains and Lithuania, resulting in by up to 35% higher basal area than the trial mean. No advantages were observed for early flushing Western Russian seedlots facing southward transfer. Latvian provenances showed variable performance regarding productivity and stem quality. In the harsher climate of Eastern Latvia, selection of productive local seedlots seemed reasonable option due to higher areal productivity and relatively lower proportion of trees with stem defects comparing with transferred material.

Keywords: long-term provenance study; flushing time; forking; seed transfer; adaptation ability

Introduction

The Norway spruce (*Picea abies* (L.) Karst.) is one of the most valuable tree species in the Baltic Sea region (Langvall 2011). It covers large forest areas, including highly productive Norway spruce plantations (Von Teuffel and Baumgarten 2004, Mullin et al. 2011, Westin and Haapanen 2013). Nevertheless, the species is vulnerable to climate change induced prolonged drought periods and more intense and frequent extreme wind events, which thereupon makes it susceptible to biotic risks, such as bark beetle outbreaks (Marini et al. 2017, Donis et al. 2018, Zeltnis et al. 2018, Bosela et al. 2020). As a result, Europe's forests are facing a decline of Norway spruce (Bosela et al. 2020).

Still, the species show high phenotypic plasticity (Schmidt-Vogt 1977), and assisted migration of tested genetic material suitable for future environmental conditions might mitigate negative climate change impact (Frank et al. 2017). Since planting of nursery stock is a commonly applied regeneration method for Norway spruce in the region (Jansons et al. 2015), identification and potential transfer of robust, adapted provenances with sufficient hardiness is crucial to secure profitability from improved productivity and benefit from initial investments in stand

establishment (Xiong 2010, Mullin et al. 2011, Westin and Haapanen 2013).

Traditionally, use of reproductive material with local origin for forest regeneration is considered to be the most optimal strategy (Aitken et al. 2008). Local genotypes are better adapted to certain conditions due to natural selection (Boshier et al. 2015). Therefore, common belief is that small transfer distances should maintain or enhance tree growth, while seed sources from long ecological distances might have worse performance (Matyas 1994, Gömöry et al. 2012). In Latvia, early evaluation of Norway spruce provenance trials showed advantages of local material regarding productivity and hardiness (Gailis 1993). However, collection of seeds from restricted sources may lead to reduced genetic diversity and limited adaptability (Boshier et al. 2015). Local provenances not necessarily include the optimal genotypes (Leinonen and Hänninen 2002). Use of appropriate transferred provenances is proved to increase forest productivity (Hannerz and Westin 2005, Mullin et al. 2011) and can supplement local seed sources, thus enhancing genetic diversity (Lindner et al. 2008).

To avoid potential risks of climate-induced damage, previous studies in Northern Europe have highlighted im-

portance of tree phenology in selection of most suitable provenances (Persson and Persson 1992, Skroppa and Magnussen 1993, Danusevicius and Persson 1998, Danusevicius and Gabrielavicius 2001, Leinonen and Hänninen 2002). Differences in tree growth and phenology are mainly related to temperature gradient and indicate adaptation to local environmental conditions (Howe et al. 2003, Aitken et al. 2008). Southern provenances of Norway spruce need higher temperature sum for budburst to be initiated, therefore in more northern places of utilization such seedlots flush later and are less prone to spring frost (Leinonen and Hänninen 2002). However, southernmost seedlots are characterized with delayed growth cessation, which has positive effect on productivity, but make trees susceptible to autumn frost damage (Skroppa and Magnussen 1993, Danusevicius and Persson 1998, Danusevicius and Gabrielavicius 2001). In contrast, northernmost origins have better cold hardiness, but trees flush early when transferred to milder climate, thus being prone to spring frost (Beuker 1994, Howe et al. 2003). In the end of summer, seedlings transferred southwards cease growth earlier, and overall growth period is shorter than for local provenances (Howe et al. 2003).

We assessed two Norway spruce provenance trials at the age of 29 and 34 years, respectively. Most of provenance trials in Europe have been studied at juvenile age (Ulbrichová et al. 2015), but growth capacity can change over time (Budeanu et al. 2012, Zubizarreta-Gerendiain et al. 2012). Information about the long-term fitness of provenances and their reaction to climate-induced damage is necessary, especially to identify robust seedlots under changing climate, suitable to be utilized for assisted migration (Keskitalo et al. 2016, Zeltniš et al. 2016). Therefore, the aim of our study was to assess the long-term performance of Norway spruce provenances in two study sites with different climatic conditions.

Materials and methods

The study was carried out in two Norway spruce provenance trials located in the eastern and western part of Latvia, respectively (Figure 1).

Kalsnava

The Eastern Latvian trial Kalsnava (56°39'N; 25°54'E) was in the flat terrain ca. 110 m above sea level (a.s.l.), characterized with dominating continental climate (Laiviņš and Meleciš 2003). The mean annual temperature in the location is +6.0°C; the mean monthly temperature ranges from -6.4°C in February to +17.1°C in July. The mean annual precipitation is ca. 700 mm (Harris et al. 2014).

The experiment was established in 1985 on former agricultural land with normal moisture regime and fertile mineral soil, corresponding to *Oxalidos* forest type according to the Latvian forest typology (Bušs 1981). Four-years-old bare-rooted seedlings with initial density of 3,333 stems ha⁻¹ were planted in five randomized blocks. In 1995, systematic thinning was done retaining

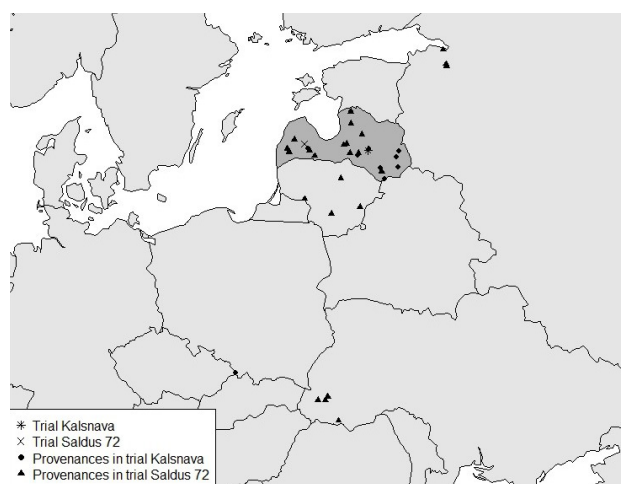


Figure 1. Provenance collection sites and location of studied trials Kalsnava and Saldus 72

Table 1. Overview of provenances in trial Kalsnava

Prove-nance	Geographical coordinates	Region	Num-ber of trees	Diameter at breast height (cm)		Branch diameter (mm)		Score of stem straightness		Proportion (%) of trees with		Basal area (m ² ha ⁻¹)
				mean**	SE***	mean	SE	mean	SE	spike knots	double leaders	
Bērzgale	56° 37'N 27° 32'E	Eastern Latvia	334	15.2	0.40	12.4	0.48	2.6	0.04	49.9	1.2	27.4
Dagda	56° 06'N 27° 31'E	Eastern Latvia	376	15.3	0.39	12.3	0.48	2.4	0.04	51.2	1.0	28.8
Janopole	56° 27'N 27° 23'E	Eastern Latvia	337	15.6	0.40	12.2	0.48	2.3	0.04	53.5	2.6	28.1
Jaunjelgava	56° 29'N 25° 20'E	Central Latvia	59	16.0	1.08	12.0	1.30	2.3	0.13	50.7	0.7	25.7
Kalsnava	56° 41'N 25° 55'E	Central Latvia	351	15.2	0.40	11.2	0.48	2.3	0.04	51.8	2.2	28.9
Kalupe	56° 06'N 26° 34'E	Central Latvia	319	15.4	0.41	11.8	0.49	2.4	0.04	46.4	1.8	31.5
Mazsalaca	57° 53'N 24° 59'E	Central Latvia	114	16.0	0.94	11.6	1.14	2.5	0.11	51.5	0.9	27.3
Silene	55° 44'N 26° 48'E	Central Latvia	343	15.4	0.40	11.9	0.49	2.5	0.04	45.7	1.0	26.3
Remte ^{SO}	56° 43'N 22° 41'E	Western Latvia	58	16.3	1.10	13.1	1.31	2.4	0.14	42.7	1.9	27.4
Istebna	49° 34'N 18° 52'E	Poland	95	17.1	0.94	12.8	1.14	2.5	0.11	68.6	3.5	27.0

Notes: ^{SO} – seed orchard; * region according to Norway spruce seed zones in Latvia; ** least squared mean; *** standard error.

ca. 1600 stems ha⁻¹. The experiment was constituted of six local seedlots from the southeast part of Latvia, and four seedlots from forest stands and seed orchard in Latvia and Poland (Table 1).

In autumn 2010, for each living tree DBH was measured. Height measurements were impossible due to a very high stand density. Diameter of the thickest branch closest to breast height was measured. Stem straightness was evaluated using arbitrarily score in three-point scale: 1 = straight, 2 = one bend, 3 = two or more bends. As a bend was considered curvature with maximum deviation from straight line of at least 5 cm. Presence of spike knots and double leaders was assessed (1 = exist, 0 = not observed).

Saldus 72

Trial Saldus 72 (56°51' N; 22°31' E) was situated in a flat terrain with elevation of ca. 100 m a.s.l. The mean annual temperature in the location is +6.2°C; the mean monthly temperature ranges from -3.9°C in February to +16.8°C in July. The mean annual precipitation is ca. 707 mm (Harris et al. 2014). In this location, mild sea climate dominates (Laiviņš and Melecis 2003).

The trial was established in 1972 on former agricultural land with 2-years-old bare-rooted planting stock and initial density of 5,000 stems ha⁻¹ as recommended by IUFRO methodology (Rone 1984). The site could be characterized with mesotrophic mineral soil and normal moisture regime corresponding to *Hylocomiosa* or *Oxalidososa* forest type (Bušs 1981). Trees were planted in 15-tree-plots in eight replications. In 1991, systematic thinning was done retaining 50% of stems. In 2004, selective thinning had been done retaining ca. 950 stems ha⁻¹. The experiment is constituted of four local Western Latvian provenances, eight seedlots from Central Latvian seed zone, three seedlots from the Carpathian Mountains in Ukraine, three Lithuanian and four Western Russian provenances (Table 2).

In autumn 2004, for each living tree height and diameter at breast height (DBH) was measured and qualitative characteristics were evaluated. The presence of double leaders and spike knots was assessed as described above. Unfortunately, a storm in 2005 seriously damaged the trial; therefore, no more recent measurements were available.

Table 2. Overview of provenances in trial Saldus 72

Provenance	Geographical coordinates	Region	Number of trees	Stem volume (m ³)		Budburst score		Proportion (%) of trees with		Basal area (m ² ha ⁻¹)
				mean**	SE***	mean	SE	spike knots	double leaders	
Augstroze	57° 30'N 24° 59'E	Central Latvia*	16	0.203	0.023	1.7	0.24	3.9	4.0	16.0
Bānūži	57° 09'N 25° 34'E	Central Latvia*	19	0.224	0.022	2.4	0.20	10.8	0.0	22.5
Bēne	56° 28'N 23° 03'E	Central Latvia*	21	0.268	0.021	2.7	0.13	4.4	2.3	29.8
Jaunkalsnava	56° 41'N 25° 55'E	Central Latvia*	21	0.229	0.021	2.6	0.16	8.2	0.0	24.0
Mazsalaca	57° 53'N 24° 59'E	Central Latvia*	15	0.199	0.024	2.0	0.26	12.6	0.0	11.5
Ogre	56° 49'N 24° 36'E	Central Latvia*	22	0.252	0.020	2.5	0.17	9.6	2.4	24.2
Raņķi	56° 51'N 24° 46'E	Central Latvia*	24	0.220	0.020	2.6	0.15	2.4	0.0	23.9
Sece 1	56° 33'N 25° 24'E	Central Latvia*	25	0.283	0.020	2.8	0.13	1.8	1.9	36.1
Sece 2	56° 33'N 25° 24'E	Central Latvia*	24	0.224	0.020	2.6	0.14	2.2	4.5	23.1
Taurkalne	56° 33'N 24° 56'E	Central Latvia*	24	0.249	0.020	2.7	0.14	3.6	0.0	31.1
Zaļumi	55° 58'N 26° 37'E	Central Latvia*	12	0.245	0.027	2.7	0.17	0.0	0.0	21.4
Aizpute	56° 42'N 21° 36'E	Western Latvia*	19	0.223	0.022	2.4	0.20	13.8	5.7	25.2
Blīdene	56° 38'N 22° 47'E	Western Latvia*	21	0.224	0.021	2.4	0.20	2.1	2.1	27.9
Kalvene	56° 36'N 21° 42'E	Western Latvia*	21	0.262	0.021	2.2	0.21	6.0	3.1	24.8
Kuldīga	56° 59'N 21° 58'E	Western Latvia*	20	0.211	0.021	2.2	0.21	18.7	3.1	15.2
Druzhnoselskiy 44	59° 20'N 30° 04'E	Western Russia	20	0.209	0.021	1.5	0.18	10.8	5.6	21.0
Druzhnoselskiy 54	59° 20'N 30° 04'E	Western Russia	21	0.244	0.021	1.4	0.16	6.5	0.0	27.3
Kartashevskaya	59° 24'N 30° 02'E	Western Russia	22	0.247	0.020	1.5	0.17	8.3	2.1	27.6
Orlinsk	59° 51'N 29° 53'E	Western Russia	20	0.257	0.021	1.8	0.20	2.4	0.0	26.5
Nemenčine	54° 50'N 25° 29'E	Lithuania	22	0.241	0.020	2.9	0.06	8.9	4.7	24.5
Panevėžys	55° 45'N 24° 28'E	Lithuania	22	0.274	0.021	2.7	0.13	2.3	2.3	31.6
Prienai	54° 38'N 23° 57'E	Lithuania	17	0.212	0.023	2.5	0.22	3.0	9.4	15.7
Smalininkai	55° 06'N 22° 31'E	Lithuania	15	0.284	0.024	2.5	0.20	14.7	0.0	24.2
Bohdan	48° 02'N 24° 19'E	Ukrainian Carpathians	18	0.276	0.023	2.4	0.20	8.7	9.1	27.6
Huklivyi	48° 41'N 23° 14'E	Ukrainian Carpathians	18	0.212	0.022	1.8	0.25	21.6	11.1	13.0
Myslivka	48° 48'N 23° 45'E	Ukrainian Carpathians	20	0.292	0.021	2.8	0.10	19.6	5.7	27.4
Torun	48° 41'N 23° 37'E	Ukrainian Carpathians	18	0.292	0.023	2.8	0.11	0.0	6.2	32.6

Notes: * region according to Norway spruce seed zones in Latvia; ** least squared mean; *** standard error.

For the trial, data about budburst in the spring 1994 was available. Budburst was evaluated using a 3-point score: 1 = the length of the young shoot exceeds 1 cm (early flushing); 2 = buds are ready to burst; bud bursting is starting (average flushing); 3 = no flushing observed (late flushing) (Gailis 1993).

Data analysis

The whole data analysis was conducted in program R, v.3.3.1 (R Core Team 2019). To assess yield in trial Saldus 72, the stem volume of trees was calculated according to the formula for Norway spruce (Liepa 1996):

$$V = 0.00231h^{0.78193}DBH^{0.34175\ln(h)+1.18811}, \quad (1)$$

where V is the stem volume (m³), h is the tree height (m), and DBH is the stem diameter at breast height (cm).

We did mixed effects analysis of the relationship between studied traits and provenance or provenance region:

$$y_{ijk} = \mu + P_i + r_j + p_k + \varepsilon_{ijk}, \quad (2)$$

where y_{ijk} is the response variable, P_i is the fixed effect of provenance or provenance region, r_j is the random effect of replication, p_k is the random effect of plot, and ε_{ijk} is the residual error. For the growth traits, we used linear mixed effect model (Bates et al. 2014). For the binomial variables (presence of spike knots and double leaders), generalized linear mixed model applying binomial residual distribution and “logit” link function was fitted using the analytical model in Equation 2 (Bolker et al. 2009). For arbitrary score of stem straightness and budburst time, an ordinal logistic regression was applied to the analytical model in Equation 2 (Scott Long 1997). We performed analysis with R packages *lme4* (Bates et al. 2014) and *ordinal* (Christensen 2015). Considering unbalanced data structure, we obtained the least-square means of studied traits for provenances using package *lsmeans* (Lenth 2016). Tukey’s honestly significant difference (HSD) multiple comparison test was used to determine significant differences between the pairs of seedlots. On the provenance level, we estimated correlations between studied variables for each study site using Pearson’s correlation coefficient. We calculated basal area (BA, m² ha⁻¹) for each provenance based on the least-square means of DBH and the number of trees to represent areal productivity comparable in both experiments.

Table 3. Region mean values for studied traits in trial Kalsnava

Region	Diameter at breast height (cm)		Branch diameter (mm)		Score of stem straightness		Proportion (%) of trees with	
	mean	SE	mean	SE	mean	SE	spike knots	double leaders
Central Latvia	15.4 ^A	0.33	11.6 ^A	0.42	2.4 ^A	0.03	48.3 ^A	1.1 ^A
Eastern Latvia	15.4 ^A	0.33	12.3 ^B	0.42	2.4 ^A	0.03	51.6 ^{AB}	1.1 ^A
Istebna	17.1 ^A	0.94	12.8 ^{AB}	1.14	2.5 ^A	0.13	68.6 ^B	3.4 ^A
Western Latvia	16.3 ^A	1.09	13.1 ^{AB}	1.31	2.4 ^A	0.15	42.7 ^{AB}	2.2 ^A

Note: Characters in superscript show significant differences ($p \leq 0.05$) between regions for each trait.

Results

Kalsnava

At the age of 29 years, 43.6% of initially planted trees in the trial had been retained. Mean DBH ± standard deviation (SD) was 15.4 ± 3.8 cm. Provenance did not significantly affect neither DBH ($p = 0.40$) nor branch diameter ($p = 0.14$). Due to maintained high stand density, provenance mean DBH deviation from trial mean was low, reaching +2.8% and -0.4% for the best and worst seedlots, respectively. However, significant differences for branch diameter were observed between two provenance regions – Central and Eastern Latvia ($p = 0.02$). In general, transferred provenances from Poland (Istebna) and Western Latvia (Remte) had the largest DBH (Table 1 and 3). No differences in DBH on regional basis were observed between Eastern and Central Latvia (Table 3). Estimated basal area per hectare in the trial was 28.6 m² ha⁻¹. Like DBH, variation in BA among provenances was rather low, ranging between 31.5 m² ha⁻¹ (+10.2% relative to the trial mean) and 25.7 m² ha⁻¹ (-10.1%) for Istebna and Bērzgale, respectively (Table 1).

Regarding stem quality, the presence of double leaders and spike knots was not affected by provenance ($p \geq 0.13$). At regional level, proportion of trees with spike knots was significantly higher ($p = 0.03$) for Polish seedlot Istebna (68.6%) than Central Latvian provenances (48.3%). The presence of double leaders was negligible, reaching 2.2% for Western Latvia (Table 3). The most pronounced differences among provenances ($p < 0.01$) were observed for arbitrary score of stem straightness. The straightest stems had Janopole, Kalsnava and Kalupe (mean score 2.3), while Bērzgale (mean score 2.6) were the least qualitative. However, no regional differences for stem straightness were observed due to variation within one region of seedlot origin (Table 3).

The only significant correlation ($r = 0.66$, $p = 0.04$) was observed between the proportion of trees with spike knots and double leaders. Despite insignificance, moderate positive correlations were observed between DBH and presence of both stem defects ($0.51 < r < 0.57$), as well as between DBH and branch diameter ($r = 0.62$) (Table 4).

Saldus 72

At the age of 34 years, 20.0% of initially planted trees were retained after last thinning. Mean stem volume ± SD was 0.240 ± 0.008 m³. The study site included larger set of

Table 4. Provenance mean Pearson correlation coefficients (bottom left triangle) and their *p* values (upper right triangle) for the analysed traits in trial Kalsnava

	Diameter at breast height	Branch diameter	Stem straightness score	Proportion of trees with spike knots	Proportion of trees with double leaders
Diameter at breast height	1	0.05	0.34	0.09	0.13
Branch diameter	0.62	1	0.29	0.64	0.33
Stem straightness score	0.34	0.37	1	0.57	0.82
Proportion of trees with spike knots	0.57	0.17	0.20	1	0.04
Proportion of trees with double leaders	0.51	0.35	-0.08	0.66	1

Note: Significant ($p \leq 0.05$) correlations highlighted in bold.

provenances from more diverse places of origin than Kalsnava trial, and differences for growth performance among provenances were more pronounced and significant for stem volume ($p < 0.01$). Among the most productive provenances were seedlots from the Carpathian Mountains in Ukraine – Myslivka, Torun and Bohdan (stem volume were 0.292, 0.292 and 0.276 m³, respectively) – as well as Lithuanian provenance Smalininkai (0.284 m³) and Central Latvian seedlot Sece 1 (0.283 m³). The poorest growth we found for provenances Mazsalaca and Augstroze from Central Latvia (0.203 m³ and 0.199 m³, respectively), and for Druzhnoselskiy 44 (0.209 m³) from Western Russia (Table 2).

Regarding stem volume, provenance variation from trial mean reached +21.5% and -17.0% for the best and the worst performing seedlots, respectively. In general, provenances within one region showed variable performance, thus no significant differences among regions were observed ($p = 0.10$). For instance, Sece 1 was among the best performing provenances, while neighbouring Sece 2 had stem volume below average. Still, northward-transferred seedlots from the Ukrainian Carpathians and Lithuania tended to have larger stems than those of Latvian and Western Russian origins (Table 5).

Estimated trial mean BA was 24.1 m² ha⁻¹. The highest BA was estimated for Sece 1, reaching 36.1 m² ha⁻¹, or +49.8% comparing to the trial mean. For Myslivka, Panevežys and Torun, 27.4, 31.6, and 32.6 m² ha⁻¹ was calculated, respectively. The lowest BA was in Mazsalaca,

namely 11.5 m² ha⁻¹ or -52.1% comparing to the trial mean (Table 2).

The presence of spike knots and double leaders was not affected by provenance ($p > 0.14$). Like Kalsnava, the proportion of trees with double leaders was rather low for all provenances and ranged from 0% for a number of seedlots to 11.1% for Huklivyi from the Carpathians (Table 2). At the regional level, occurrence of double leaders was significantly more probable ($p = 0.01$) for the Carpathian (7.9%) than Central Latvian provenances (1.3%) (Table 5), though remaining rather low. The presence of spike knots was generally higher and reached 19.6% for Carpathian provenance Myslivka (Table 2).

The most pronounced differences among provenances as well as provenance regions (both $p < 0.01$) were for the arbitrary score of budbursts. The earliest flushing was Western Russian provenances Druzhnoselskiy 54, Druzhnoselskiy 44, and Kartashevskaya (mean budburst score: 1.4, 1.5, and 1.7, respectively). Other regions could be characterized with rather late budburst; the region mean score ranged from 2.4 to 2.7 for Western Latvia and Lithuania, respectively (Table 5). Lithuanian provenance Nemenčine and Carpathian seedlots Myslivka and Torun were the latest flushing, having significantly later budburst time than Western Russian provenances, Augstroze from Central Latvia and Huklivyi from the Carpathians (Table 2).

At the provenance level, the budburst score had significant positive relationship with stem volume ($r = 0.46$,

Table 5. Region mean values for the studied traits in trial Saldus 72

Region	Stem volume (m ³)		Budburst score		Proportion (%) of trees with	
	mean	SE	mean	SE	spike knots	double leaders
Central Latvia	0.234 ^A	0.010	2.5 ^B	0.07	4.9 ^A	1.3 ^A
Lithuania	0.252 ^A	0.013	2.7 ^B	0.08	6.2 ^A	4.1 ^{AB}
Ukrainian Carpathians	0.267 ^A	0.013	2.6 ^B	0.11	11.6 ^A	7.9 ^B
Western Latvia	0.237 ^A	0.012	2.4 ^B	0.10	7.8 ^A	3.2 ^{AB}
Western Russia	0.239 ^A	0.013	1.5 ^A	0.11	6.4 ^A	1.8 ^{AB}

Note: Characters in superscript show significant differences ($p \leq 0.05$) between regions for each trait.

Table 6. Provenance mean Pearson's correlation coefficients (bottom left triangle) and their *p* values (upper right triangle) for the analysed traits in trial Saldus 72

	Stem volume	Budburst score	Proportion of trees with spike knots	Proportion of trees with double leaders
Stem volume	1	0.02	0.42	0.77
Budburst score	0.46	1	0.29	0.94
Proportion of trees with spike knots	-0.16	-0.21	1	0.13
Proportion of trees with double leaders	-0.06	-0.02	0.30	1

Note: Characters in superscript show significant differences ($p \leq 0.05$) between regions for each trait.

$p = 0.02$), implying higher yield for later flushing seedlots. In contrast to trial Kalsnava, at the provenance level, the proportion of trees with both stem defects did not have significant correlation ($r = 0.30$, $p = 0.13$) (Table 6).

Discussion and conclusions

The two studied sites represented the rather mild coastal climate of Western Latvia and the harsher, more continental climate of Eastern Latvia (Laiviņš and Melcis 2003, Harris et al. 2014). We could not compare both trials directly, since the different sets of provenances were planted, different silvicultural treatments were applied, and different traits were measured at each site. Nevertheless, some trends associated with provenance transfer could be indicated and interpreted in both trials.

In both study sites, transferred provenances tended to show superior growth performance in terms of DBH and stem volume (Tables 1 and 3). In Kalsnava, the seedlots from Poland and Western Latvia were superior though not significantly better comparing to Central and Eastern Latvian provenances (Table 2). Most likely, the dense spacing did not allow different genotypes to fully manifest themselves (Hynynen et al. 2010). In Saldus 72, the leaders were seedlots from the Ukrainian Carpathians and Lithuania (Table 5). The estimated basal area per hectare was by up to 35% higher for the most productive provenances comparing to the trial mean. In general, Latvian seedlots showed high variability of growth, indicating potential narrow-scale local adaptation and varying adaptability within a single region (Mullin et al. 2011, Boshier et al. 2015). It has been noticed that seedlots with local origin not always have the most appropriate genotypes for growing conditions in a particular site (Leinonen and Hänninen 2002).

The growth superiority for provenances from the Baltic region and the Carpathian Mountains has been commonly reported, even in North America (Holst 1963, Krutzsch 1974, Fowler and Coles 1978, Persson and Persson 1992, Persson and Persson 1997, Giertych 2007). Northward transfer of such provenances as Istebna or Carpathian seedlots is proved to result in enhanced growth due to more efficient utilization of the available vegetation period than local provenances do (Suvanto et al. 2016). In our study, significant correlation between stem volume and budburst in Saldus 72 confirmed previously reported later flushing of productive seedlots with more southern origins (Table 6), which have better performance due to later growth cessation and are less affected by spring frost (Balut and Sabor 1993, Skroppa and Magnussen 1993, Danusevicius and Gabrilavicius 2001, Hannerz and Westin 2005). However, increased presence of a) trees with double leaders for Carpathian seedlots in Saldus 72 (Table 5), and b) trees with spike knots for Istebna in Kalsnava trial (Table 3) might indicate that terminal buds of those trees had been injured by autumn frost at young age because of late growth cessation and delayed onset of hardiness development. Such frost in-

jury results in formation of double leaders and spike knots (Søgaard et al. 2011). Besides, trial Kalsnava had considerably higher proportion of trees with spike knots comparing to Saldus 72 (51.2% and 7.7%, respectively). We explain it with milder climate and subsequently less frequent frost injuries in the latter trial. Since formation of stem defects is determined by both environment and genotype (Persson and Persson 1997), overall high incidence of spike knots on site with high frost risks in Kalsnava highlights necessity to select appropriate provenance, which has a balance between productivity and time of autumn hardiness. Otherwise, the increased occurrence of double leaders and spike knots affects wood quality at mature age and subsequent economic value (Xiong 2010), subtracting benefits of increased productivity. Evaluation of Norway spruce provenances at juvenile age has shown increased frost damage for late flushing Carpathian seedlots in southeast Latvia (Rone 1984). In Saldus 72, where frost injury risks are lower, utilizations of late flushing provenances from more southern origins have resulted in overall superior performance over local seedlots at the age of 34 years. Although being statistically significant, increase in presence of double leaders was practically negligible (Table 2). Carpathian provenances reported to be among best performing in similar growing conditions in Southern Sweden (Persson and Persson 1992).

Western Russian provenances from Leningrad region, which faced southward transfer and were particularly early flushing (Table 5), showed growth performance below average, likely being delayed by damage of spring frosts at juvenile age (Balut and Sabor 1993, Gailis 1993, Beuker 1994, Danusevicius and Persson 1998). Although reported as well performing at juvenile age (Rone 1984) and showing good results in other provenance studies (Giertych 2007), Western Russian seedlots did not have any advantages in Western Latvia three decades after planting.

In contrast to earlier conclusions that provenance transfer eastwards is undesirable in Latvia due to frost damage risks (Gailis 1993), seedlot from Remte had the highest mean DBH combined with the lowest probability of trees with spike knots (42.7%) in Kalsnava (Table 1). However, Remte is a seed sample from the first-generation seed orchard, which comprises plus trees from forest stand in the locality, thus indicating possible positive effect of selected clonal material with sufficient adaptability even in less desirable growing conditions. Nevertheless, BA for Remte was not among the highest ones and close to the trial mean, indicating possible lower early survival in more continental conditions. Still, we could not draw further conclusions – data from trees thinned to adequate density and with known budburst time would be needed.

In Kalsnava, differences in stem straightness between provenances were pronounced, though not having any regional trends. In earlier studies, no provenance effect on stem straightness has been reported (Giertych 2007, Ulbrichová et al. 2015). However, we did not observe any

extremes on the provenance level (Table 1), most of trees having one or more bends.

Not only the above-mentioned spike knots and double leaders, but also thick branches reduce the monetary value of tree (Makinen et al. 2003). Moderate positive correlation between provenance mean DBH and branch diameter (Table 4) corresponded to conclusions that trees of fast-growing provenances tend to form thicker branches (Zobel and Jett 1995), though the ratio between branch diameter and DBH stays low with increasing growth (Persson and Persson 1997).

In conclusion, under the milder coastal climate in Western Latvia, the provenances from the Ukrainian Carpathian Mountains (Bohdan, Myslivka, Torun) and Lithuania (Panevėžys) show overall superior growth performance 34 years after planting, suggesting positive effect of northward transfer of late flushing seedlots to sites which are not prone to frequent frost events, thus possible utilization for assisted migration. Regarding productivity and stem quality, the Latvian provenances show variable performance, indicating to importance of careful selection even within commonly suggested local provenance regions. The early flushing Western Russian provenances do not have any advantages in Western Latvia.

In the harsher climate of Eastern Latvia, a high proportion of trees with spike knots were observed, and differences in percentage of corresponding stem defect were determined by provenance region. Hence, we suggest selection of appropriate well-adapted seedlots with the low presence of stem defects within Central and Eastern Latvian provenances regions in order not to reduce the monetary value of stemwood at mature age.

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