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Seed Transfers of Silver Birch (*Betula pendula*) from the Baltic to Finland – Effect on Growth and Stem Quality

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Silver birch (*Betula pendula* Roth) seed origins from the Baltic countries, Finland and Russia were compared for survival, growth and stem quality, and the effect of latitudinal seed transfer distance examined in two provenance trials. The trials were located on moist upland forest soils at Tuusula (60°21'N) in southern Finland and at Viitasaari (63°11'N) in central Finland. The material consisted of 21 stand and single tree origins ranging from latitudes 54° to 63°N. Survival, height, dbh, relative stem taper, stem volume/ha and the proportion of trees with a stem defect (vertical branch or forked stem), were assessed when the trees were 22 years old. Significant differences were detected among the origins regarding all the measured traits in both trials. Southern Finnish origins produced the highest volume per unit area in central Finland, whereas Estonian and north Latvian stand seed origins, as well as the southern Finnish plus tree origins, were the most productive ones in southern Finland. The more southern the origin, the higher was the proportion of trees with a stem defect in both trials. The latitudinal seed transfer distance had a significant but relatively small effect on survival, stem volume/ha and proportion of trees with a stem defect. The proportion of trees with a stem defect increased linearly in relation to the seed transfer distance from the south. The relationship of both survival and stem volume/ha to the seed transfer distance was curvilinear. Volume/ha was increased by transferring seed from ca. 2 degrees of latitude from the south. A longer transfer from the south, as well as transfer from the north, decreased the yield.

Keywords *Betula pendula*, climatic adaptation, provenance, stem defect, yield
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1 Introduction

Silver birch (*Betula pendula* Roth) has an important role in Finnish forestry both as a widespread hardwood species in the forest landscape and as a raw material in the mechanical and chemical forest industry. Cultivation of silver birch has been practiced since the 1960's (Raulo 1978), reaching its peak in the beginning of the 1990's, when more than 20 million birch seedlings from nurseries were delivered yearly for planting, but since then planting of birch has steadily decreased (Finnish Statistical... 2007). However, as a deciduous species able to benefit more than conifers from predicted climate warming the significance of birch is expected to increase in the future (Kellomäki et al. 1996, Talkkari 1998).

The cultivation of birch in Finland has been based on seeds of native origin collected from stands of high quality, or nowadays produced in polythene greenhouse seed orchards (Hagqvist 1991, Viherä-Aarnio 1994). Genetically improved Finnish seed is available in abundance (Hagqvist and Hahl 1998, Finnish Statistical... 2007), and practically no imported seed origins have been used. However, transferring seed from south to north may offer an opportunity to improve yield, as shown with Norway spruce of Baltic seed origin in Finland (Hagman 1980). As a part of Finland's National Strategy for Adaptation to Climate Change it has also been suggested that seed of slightly more southern origin should be used to maximize carbon fixation and storage (Marttila et al. 2005). The free trade of forest cultivation material within EU may also give rise to efforts to introduce birch seeds or seedlings to Finland from the Baltic countries. Thus, there is an increased need to improve our knowledge about more southern seed origins. In general, seed transfer studies are a valuable tool to improve our understanding of adaptation of trees to changing climatic conditions.

The few existing studies concerning the performance of birch of Baltic origin in Finnish conditions have been carried out with small seedlings or young saplings. Velling (1979) reported results on the early survival, phenology and growth of silver birch of Baltic origin in nursery and field trials. Some Baltic origins were also included in studies of annual physiological rhythm of silver birch by Koski and Sievänen (1985), Li et al. (2002, 2003) and Viherä-Aarnio et al. (2005). Due to their later growth cessation and consequently longer growth period, the Baltic origins were faster growing than the native Finnish ones (Velling 1979, Viherä-Aarnio et al. 2005). On the other hand, due to poor climatic adaptation, they were more prone to abiotic and biotic damage leading to lower survival and quality defects (Velling 1979, Viherä-Aarnio and Heikkilä 2006). So far, studies of mature trees have not been made.

The first progeny trials of birch in the Nordic countries were established in Sweden in the 1940's and thus, Johnsson (1951, 1967) was the first to compare birch families of geographically distant origin. Johnsson also pioneered birch provenance research by establishing extensive trials in 1973–74 (Johnsson 1976). Based on these trials, Stener (1997) studied the differences in yield, stem quality and wood density among seed origins, and developed seed transfer rules for birch in Sweden. Erkén's (1972) study based on progeny trials established in northern Sweden in 1947–51 also dealt with seed transfers. In Finland, extensive progeny trials of silver birch were established in the 1960's in southern and central part of the country. Principles for seed transfers were based on the results from these trials (Raulo and Koski 1977, Raulo 1979). Long distance seed transfers from south to north and differences between southern and central Finnish birch families in adaptation were studied by Raulo (1976). In Norway, Langhammer (1982) compared single tree progenies of birch from open pollination covering a wide number of origins from Norway, Sweden, Finland and Latvia. In Germany, combined progeny and provenance trials, including origins from central Europe, Finland and Sweden, were established in 1976 (Kleinschmit and Otto 1980) and analyzed some 20 years later (Kleinschmit 1998, 2002).

The aim of this study is to compare commercial sized silver birch of Baltic and native Finnish seed origin grown in Finland, and to examine the effect of latitudinal seed transfer on the growth and stem quality.

2 Material and methods

2.1 Field Trials

The study material consisted of two silver birch provenance trials situated at Tuusula, southern Finland (60º21'N, 25º02'E, 50 m asl) and at Viitasaari, central Finland (63°11'N, 26º07'E, 180 m asl) (Fig. 1).

The trials included stand seed origins from Latvia (7), Estonia (2), Russia (2) and Finland (6) (Table 1, Fig. 1). In addition, half-sib progeny from two open-pollinated and full-sib progeny from two controlled crosses of south Finnish plus trees and progeny from open pollination from one Lithuanian plus tree were included.

The trials were established with two-year-old seedlings in spring 1981. A randomized complete block design with four blocks of 22 plots each was used. Within each block the 22 seed origins were randomized to the plots. At Tuusula and Viitasaari 25 and 49 seedlings per plot were planted, respectively. The spacing was 2 × 2 m in both trials, and the plot size 10 × 10 m and 14 × 14 m at Tuusula and Viitasaari, respectively. The trials were established on moist, upland forest sites, classified as a *Myrtillus* site type (MT) at Tuusula, and as *Oxalis-Myrtillus* site type (OMT) at Viitasaari according to the Finnish site type classification (Cajander 1949). Before planting, the sites were prepared by ploughing. Sprouts of competitive broad-leaved species were removed mechanically according to normal forestry practice during the early development of the trials.

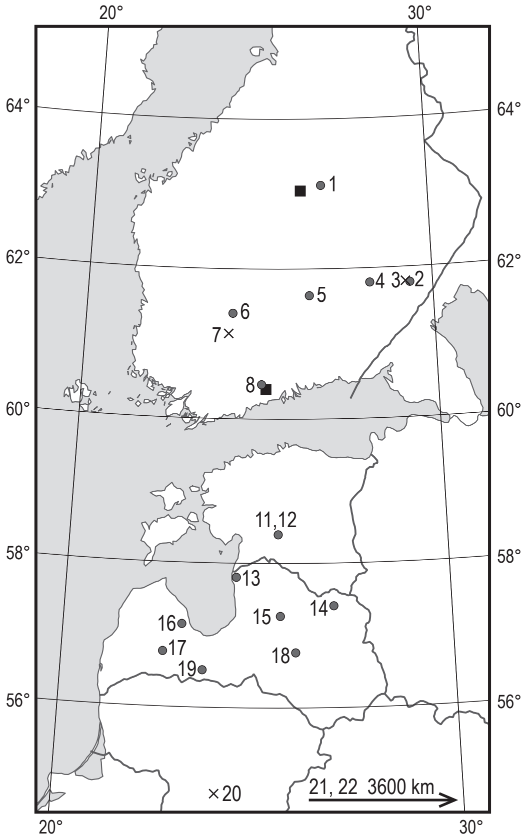

Fig. 1. Silver birch seed origins and location of the two field trials included in this study. ● = stand seed origin, × = single tree origin, ■ = field trial. Numbering of origins refers to Table 1.

2.2 Measurements

The trials were measured in November 2000 and April 2001, when the trees were 22 years old. Tree height (dm) and diameters (mm) over bark at 1.3 (dbh) and at 6.0 m height were measured. The number of vertical branches and the number of forks per stem were counted. A strong upright branch, which develops from a damaged leader after being replaced by a lateral shoot was defined as a vertical branch. In the case of forked stem, the leader is divided into two (or more) leaders of equal size. All living trees were measured. Survival (%) was assessed. Stem taper was calculated as the difference between $d_{1.3}$ and $d_{6.0}$ and the relative taper (%) calculated as a percent of the $d_{1.3}$ value. Individual stem volumes were calculated using tree height and the two diameters and the regression models for birch developed by Laasasenaho (1982), and the respective volumes/ha were computed. There was no removal due to thinning, because the trials had not been thinned before the measurements. Thus, the stem volume/ha corresponds to total yield less natural mortality. The volume of natural mortality was not recorded. Relative frequencies (%) of trees with stem defect, i.e. a vertical branch or a forked stem, were calculated as a percentage (%) of all measured trees.

Table 1. Silver birch seed origins included in this study. FIN = Finland, EST = Estonia, LV = Latvia, LT = Lithuania, RUS = Russia. Numbering of origins refers to Fig. 1.

	Origin	Latitude, N	Longitude, E	Altitude, m
1	FIN, Pielavesi	63°18'	26°49'	165
2	FIN, Punkaharju	61°48'	29°18'	92
3[a]	FIN, E1987 Punkaharju	61°48'	29°18'	80
4	FIN, Sulkava	61°48'	28°10'	110
5	FIN, Joutsa	61°40'	26°15'	110
6	FIN, Kangasala	61°25'	24°09'	50
7[a]	FIN, E2812 Valkeakoski	61°12'	24°00'	90
8	FIN, Tuusula	60°27'	24°58'	50
9[a]	FIN, E3012 Tuusula × E2378 Punkaharju	60°22' / 61°48'	25°03' / 29°19'	60 / 80
10[a]	FIN, E3013 Tuusula × E2812 Valkeakoski	60°22' / 61°12'	25°03' / 24°00'	60 / 90
11	EST, Viljandi	58°20'	25°30'	
12	EST, Viljandi	58°20'	25°30'	
13[b]	LV, Salacgrīva	57°49'	24°21'	10
14	LV, Alūksne	57°28'	26°59'	180
15	LV, Liepa	57°22'	25°30'	100
16	LV, Dursupe	57°11'	22°58'	20
17	LV, Saldus	56°42'	22°27'	120
18	LV, Jaunkalsnava	56°41'	25°55'	100
19	LV, Zaļenicki	56°31'	23°29'	30
20[a]	LT, U8863 Girionys	54°50'	24°	72–100
21	RUS, Novosibirskaya obl., Maslyanino	54°30'	84°	
22	RUS, Novosibirskaya obl., Maslyanino	54°30'	84°	

[a] single tree progeny
[b] mixture of *B. pendula* and *B. pubescens*; excluded from the analysis

2.3 Statistical Methods

The statistical analyses were performed on the plot means and proportions. Percentages of survival, relative stem taper and trees with stem defect were *arcsin* √p transformed before analysis. The transformation had practically no effect on the test results and, thus, original values of the variables were used in the final analyses.

An analysis of variance was used to test the significance of differences among the seed origins in survival, tree height, diameter at breast height (dbh), relative stem taper, volume/ha and proportion of trees with a stem defect. Tukey test was used to identify which means were significantly ($p = 0.05$) different.

A linear mixed model analysis was used separately for the two trials to examine the effects of the latitude of seed origin on survival, growth and stem quality,

$$y = \mu + \alpha L + \beta L^2 + \gamma_i + \varepsilon \quad (1)$$

where y is the response variable, μ general mean, L latitude of seed origin, γ_i random block effects ($i = 1,...,4$) and ε error term.

The response variables analyzed were survival, tree height, dbh, relative stem taper, volume/ha and proportion of trees with stem defect. Latitude (L) and the square of latitude (L^2) were used as covariates.

A linear mixed model analysis was used for the combined data containing both trials to determine the seed transfer distance models for survival, growth and stem quality,

$$y = \mu + \tau_i + \alpha_i D + \beta_i D^2 + \gamma_{ij} + \varepsilon \quad (2)$$

where y is the response variable, μ general mean, τ_i fixed trial effects ($i = 1,2$), D seed transfer distance, γ_{ij} random block effects ($j = 1,...,4$) and ε error term.

Table 2. Average survival, height, dbh, stem taper, stem volume/ha and proportion of trees with a stem defect and their variation at the Viitasaari (63º11'N) and Tuusula (60º21'N) trials. The local origin at Viitasaari is Pielavesi (63º18'N) and that at the Tuusula trial is the Tuusula origin (60º27'N).

	Viitasaari Average (*S.D.*)	Viitasaari Lowest origin mean	Viitasaari Highest origin mean	Viitasaari Local origin mean	Tuusula Average (*S.D.*)	Tuusula Lowest origin mean	Tuusula Highest origin mean	Tuusula Local origin mean
Survival (%)	54.0 (*13.3*)	30.1	64.7	64.3	73.1 (*13.1*)	58.0	86.8	67.8
Height (m)	13.9 (*1.1*)	12.1	15.4	14.0	15.0 (*1.3*)	12.6	16.5	14.7
Dbh (cm)	11.9 (*0.9*)	10.3	13.2	11.4	11.6 (*1.1*)	9.8	13.1	11.8
Relative stem taper (%)	30.2 (*3.9*)	24.8	37.3	27.8	26.2 (*3.9*)	22.2	32.8	27.3
Stem volume (m^3/ha)	104.8 (*34.1*)	47.0	139.7	116.3	141.5 (*40.3*)	74.4	194.0	130.0
Trees with a stem defect (%)	50.9 (*18.0*)	26.9	79.0	38.6	55.5 (*14.9*)	34.0	77.8	41.7

The response variables analyzed were survival, volume/ha and proportion of trees with stem defect. Seed transfer distance was defined as the latitudinal difference of the seed origin and location of the field trial (lat. of origin – lat. of trial site). The seed transfer distance (D) and the square of seed transfer distance (D^2) were used as covariates. Linear mixed model was used to test which covariates and interactions of covariates and trials were included in the model (Table 3) from which the parameter values of Eq. (2) were calculated (Table 4).

Coefficient of determination for seed transfer distance was computed as

$$R^2 = \frac{s_0^2 - s_d^2}{s_0^2} \qquad (3)$$

where s_d^2 is the residual variance of the model (2) and s_0^2 is the residual variance of the reduced model in which seed transfer variables are not included.

The linear mixed model analyses for testing the effect of seed origin latitude and seed transfer distance were performed only on the Finnish and Baltic stand seed origins. The two entries from Novosibirsk, Russia were excluded from the analysis because they originate from a climatically very different, continental area in Siberia (Table 1, Fig. 1). The single tree progenies were also excluded. The Finnish ones could not be regarded as representatives of southern Finnish natural populations since their parent trees had been selected as plus trees on the grounds of good growth (Raulo and Koski 1977).

Analyses were performed with the SPSS 15.0 statistical package (SPSS, Chicago, IL).

3 Results

3.1 Survival, Growth and Stem Quality of Different Seed Origins

3.1.1 Survival

At Viitasaari, where the origins had been transferred from the south to the north, the average survival of different seed origins varied from 30 to 65% (Fig. 2a, Table 2). Significant differences were detected among the seed origins ($p<0.001$). Girionys (Lithuania), as well as Saldus and Zaļenicki (southern Latvia) origins had the lowest survival, whereas the southern and central Finnish origins had the highest survival. Survival increased linearly and statistically significantly ($p < 0.001$) with increasing seed origin latitude.

At Tuusula the average survival of different origins varied from 58 to 87% (Fig. 2b, Table 2). Significant differences were detected among the origins ($p<0.001$), but the pattern of variation among origins was not as clear as at Viitasaari. While origins from Girionys, Novosibirsk (Russia) and Zaļenicki (southern Latvia), had low survival, the Finnish stand seed origins from Pielavesi and Joutsa, as well as the local Tuusula origin, were also among the weakest. Origins from Alūksne (northern Latvia), Viljandi (southern Estonia) and Kangasala (southern Finland) had the highest survival. The pattern of variation in survival was curvilinear in relation to the seed origin latitude ($p=0.042$).

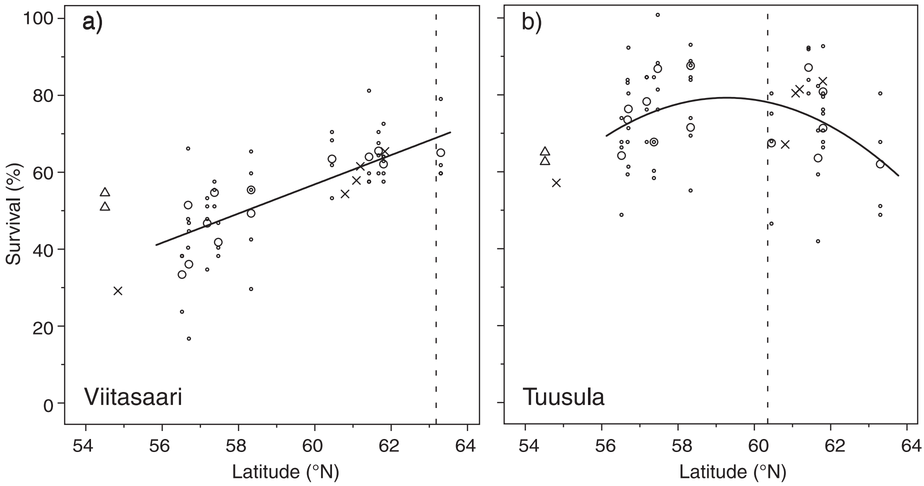

Fig. 2. Average survival of the silver birch seed origins in relation to the seed origin latitude for the Viitasaari (a) and Tuusula (b) trials. The first order line (Viitasaari) and second order curve (Tuusula) are based on the plot means of stand seed origins excluding Novosibirsk. ○ = mean of a stand seed origin, · = plot mean of a stand seed origin, Δ = mean of Novosibirsk origin, × = mean of a single tree origin. Latitude of the field trial is indicated by the dashed line.

3.1.2 Height, Diameter and Stem Taper

Significant differences were detected in height, dbh and relative stem taper among the seed origins at both trials (all $p<0.001$).

The average height of the origins varied from 12.1 to 15.4 m at Viitasaari (Fig. 3a, Table 2). Origins from Girionys and Novosibirsk were the shortest and southern Finnish plus tree progenies and Sulkava stand seed origin the tallest. At Tuusula, the average height of the origins varied from 12.6 to 16.5 m (Fig. 3b, Table 2). Origins from Novosibirsk, Girionys, Kangasala and Pielavesi were the shortest while those from Alūksne and Liepa (northern Latvia) and Viljandi, as well as the controlled crossings of southern Finnish plus trees, were the tallest. The pattern of variation in height in relation to seed origin latitude was curvilinear in both trials (Viitasaari $p=0.020$, Tuusula $p=0.019$).

The average diameter of the origins varied from 10.3 to 13.2 cm at Viitasaari (Fig. 3c, Table 2). Origins from Novosibirsk, Girionys, Zaļenicki and Alūksne, as well as the local Pielavesi origin, had the smallest average diameter whereas the southern Finnish plus tree origins and Sulkava stand seed origin had the largest average diameter. At Tuusula, the average diameter of the seed origins varied from 9.8 to 13.1 cm (Fig. 3d, Table 2). Origins from Novosibirsk and Pielavesi had the smallest average diameter while those from Alūksne, Liepa, Viljandi and the controlled crossing of southern Finnish plus trees had the largest average diameters. At Viitasaari the seed origin latitude did not have a significant effect on dbh, but had a curvilinear effect at Tuusula ($p = 0.001$).

The average relative stem taper of the different seed origins varied from 25 to 37% at Viitasaari (Fig. 3e, Table 2). Origins from Girionys and Novosibirsk had the highest and that from Sulkava had the lowest relative stem taper. At Tuusula, the average relative stem taper for the different seed origins varied from 22 to 33% (Fig. 3f, Table 2). Origins from Novosibirsk and Pielavesi had the highest relative stem taper, and origins from Alūksne and Viljandi the lowest. At Viitasaari, the relative stem taper decreased linearly, significantly although slightly, with increasing seed origin latitude ($p=0.001$). At Tuusula, the relative stem taper increased in relation to increasing seed origin latitude ($p<0.001$).

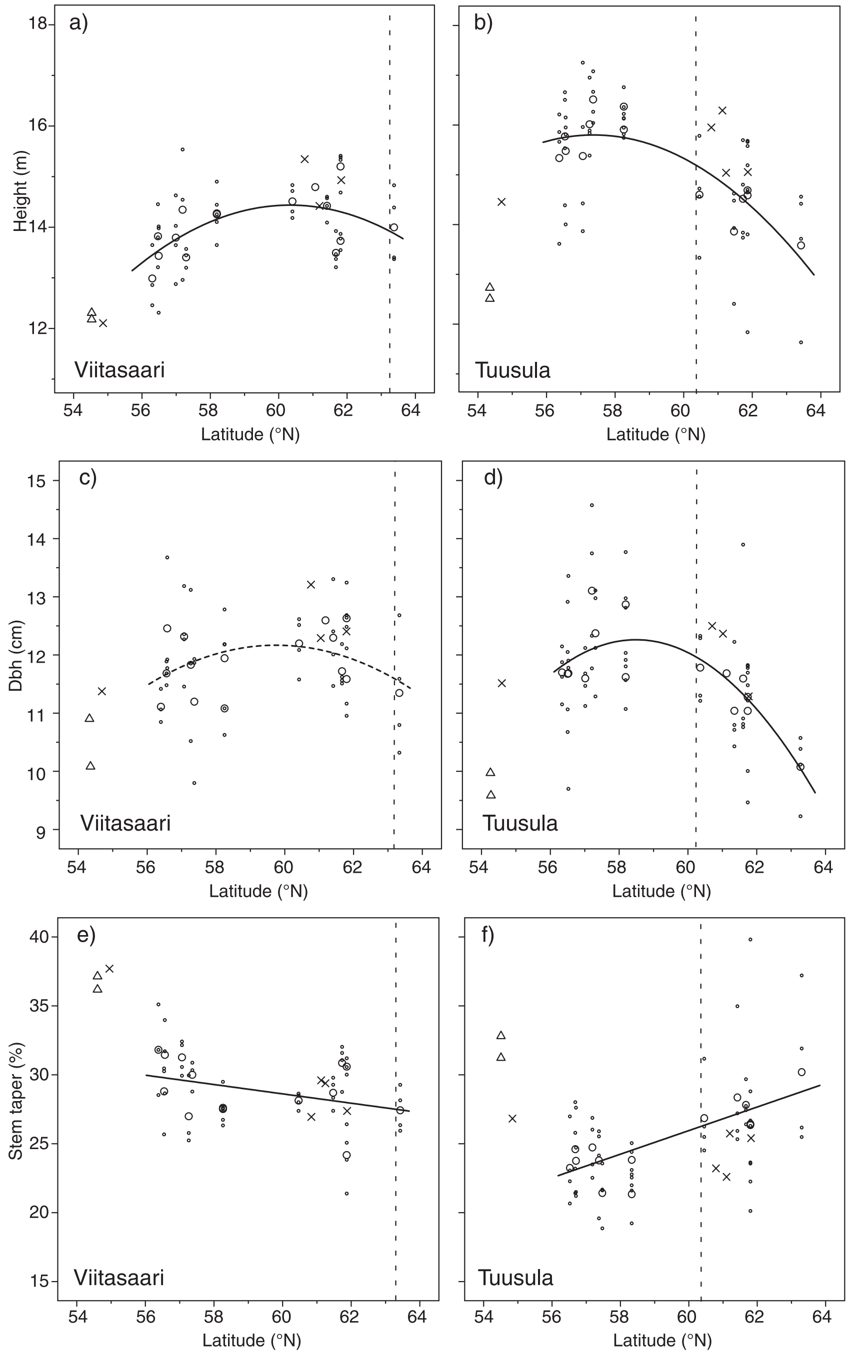

Fig. 3. Average height (ab), dbh (cd) and relative stem taper (ef) of the silver birch seed origins in relation to seed origin latitude for the Viitasaari (ace) and Tuusula (bdf) trials. The first order (stem taper) line and second order (height, dbh) curves are based on the plot means of stand seed origins excluding Novosibirsk. ○ = mean of a stand seed origin, · = plot mean of a stand seed origin, Δ = mean of Novosibirsk origin, × = mean of a single tree origin. Latitude of the field trial is indicated by the dashed line.

3.1.3 Volume / ha

Significant differences were detected in stem volume/ha among the seed origins at both trials ($p<0.001$).The average stem volume/ha of the seed origins varied from 47 m^3/ha to 140 m^3/ha at Viitasaari (Fig. 4a, Table 2). Origins from Girionys, Novosibirsk, Zaļenicki, Saldus and Alūksne had the lowest average stem volume/ha values, whereas the southern Finnish stand and plus tree origins had the highest average stem volume/ha values. At Tuusula, the average stem volume/ha values among the different seed origins varied from 74 to 194 m^3/ha (Fig 4b, Table 2). Origins from Novosibirsk and Girionys as well as stand seed origins from Joutsa and Pielavesi had the lowest average stem volume/ha values while origins from Alūksne, Liepa and Viljandi and some of the southern Finnish plus tree origins had the highest values. The relationship between stem volume/ha and seed origin latitude was curvilinear at both trials (Viitasaari $p=0.011$, Tuusula $p<0.001$).

3.1.4 Stem Defects

Significant differences in the proportion of trees with stem defect among the seed origins were detected at both trials ($p=0.001$). The average proportion of trees with a stem defect at Viitasaari varied among the seed origins from 27 to 79% (Fig. 5a, Table 2). The origins from Lithuania and Latvia had the highest proportion of trees with a stem defect, whereas stand seed origins from Sulkava, Joutsa and Pielavesi, as well as one of the controlled crosses of southern Finnish plus trees had the lowest proportion of trees with a stem defect. At Tuusula, the average proportion of trees with a stem defect varied from 34 to 78% (Fig. 5b, Table 2). Origins from Novosibirsk and Girionys had the highest proportion and seed origins from Sulkava and Tuusula (local) had the lowest proportion. At both trials, the proportion of trees with a stem defect decreased linearly and significantly (Viitasaari $p<0.001$, Tuusula $p=0.002$) with increasing seed origin latitude.

Table 3. p-values for the fixed factors and interactions included in the linear mixed model from which the parameter values of seed transfer models (Eq. 2) are determined (Table 4).

	Trial	Transfer	Transfer^2	Trial x transfer^2
Survival	< 0.001	0.014	< 0.001	
Stem volume / ha	< 0.001	< 0.001	< 0.001	0.048
Trees with stem defect	0.068	< 0.001		

Table 4. The parameter values of seed transfer models (Eq. 2) for survival (%), stem volume (m^3/ha) and trees with a stem defect (%) for the Tuusula and Viitasaari trials and the coefficients of determination R^2 (%) for latitudinal seed transfer distance (degrees).

	Trial	Intercept	Coefficient		R^2
			Transfer	Transfer^2	
		$\mu + \tau_i$	α_i	β_i	
Survival	Viitasaari	63.020	–1.879	–0.8049	28
	Tuusula	77.294	–1.879	–0.8049	
Stem volume / ha	Viitasaari	113.054	–13.977	–3.0609	46
	Tuusula	160.861	–13.977	–4.6486	
Trees with stem defect	Viitasaari	36.931	–2.954		22
	Tuusula	49.497	–2.954		

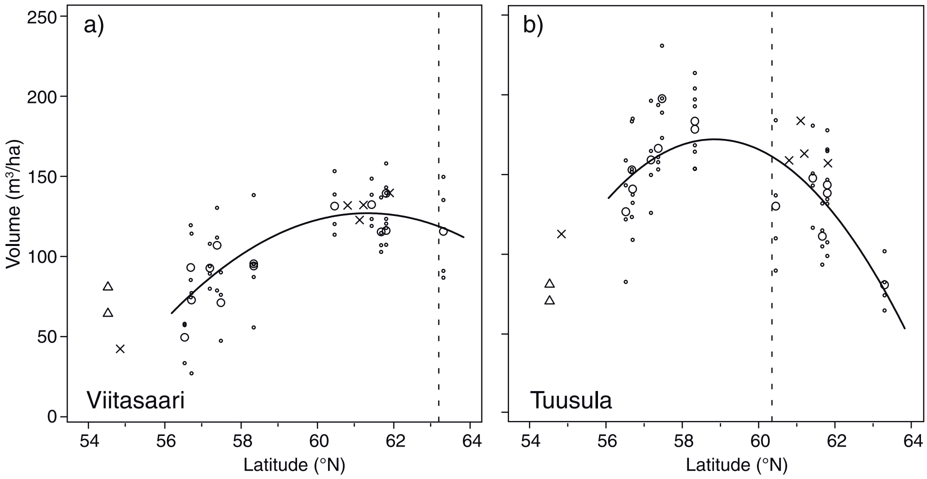

Fig. 4. Average stem volume/ha of the silver birch seed origins in relation to the seed origin latitude for the Viitasaari (a) and Tuusula (b) trials. The second order curves are based on the plot means of stand seed origins excluding Novosibirsk. ○ = mean of a stand seed origin, · = plot mean of a stand seed origin, Δ = mean of Novosibirsk origin, × = mean of a single tree origin. Latitude of the field trial is indicated by the dashed line.

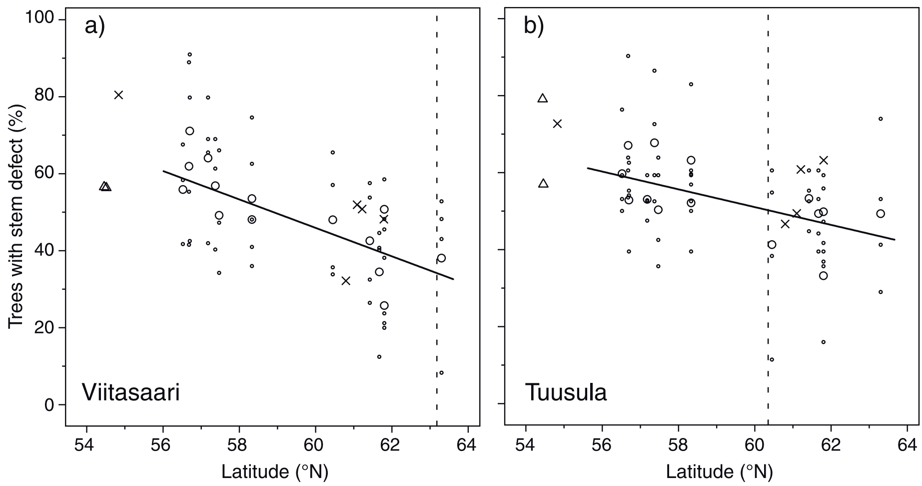

Fig. 5. Average proportion of trees with a stem defect for each silver birch seed origin in relation to seed origin latitude for the Viitasaari (a) and Tuusula (b) trials. The first order lines are based on the plot means of stand seed origins excluding Novosibirsk. ○ = mean of a stand seed origin, · = plot mean of a stand seed origin, Δ = mean of Novosibirsk origin, × = mean of a single tree origin. Latitude of the field trial is indicated by the dashed line.

3.2 Effects of Seed Transfer Distance on Survival, Growth and Stem Quality

3.2.1 Survival

A mixed model analysis of covariance with seed transfer distance as a covariate, was carried out for the combined data from both trials, but from which the single tree progenies and Novosibirsk origins were excluded. According to the model, the variation of survival of the seed origins was curvilinear in relation to the latitudinal seed transfer distance ($p<0.001$) (Table 4, Fig. 6). Also the trial had a significant effect on the survival (Table 3). According to the model, the highest survival could be attained by using the local origin or transferring seed from no more than 2 degrees of latitude (ca. 220 km) from the south, whereas longer transfers from the south will decrease the survival. A long transfer from the north will also decrease the survival.

3.2.2 Volume/ha

Stem volume/ha of the seed origins was also curvilinearly related to latitudinal seed transfer distance (Table 4, Fig. 7). The trial ($p<0.001$), the transfer distance ($p<0.001$) and the square of transfer distance ($p<0.001$) had a significant effect on the volume (Table 3). In addition, there was a weak but significant interaction ($p=0.048$) between the trial and the square of seed transfer distance, i.e. the effect of seed transfer is different depending on the trial (Table 4). According to the model, highest stem volume would be attained by transfer of ca. 2 degrees of latitude from the south, whereas longer transfers from the south as well as transfers from the north would decrease the yield.

3.2.3 Stem Defects

The proportion of trees with a stem defect increased linearly ($p<0.001$) with increasing seed transfer distance from the south (Table 4, Fig. 8). According to the model, the proportion of trees with a stem defect would increase by ca. 3% for every increase in seed transfer distance from the south by 1 degree of latitude.

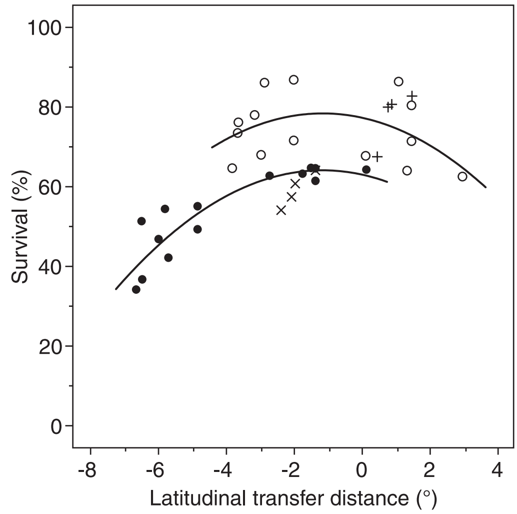

Fig. 6. Average survival of the silver birch seed origins in relation to latitudinal seed transfer distance for the Tuusula (upper line) and Viitasaari (lower line) trials. The second order curves are based on the plot means of Finnish and Baltic stand seed origins. ○ = mean of a stand seed origin at Tuusula trial, ● = mean of a stand seed origin at Viitasaari trial, + = mean of a single tree origin at Tuusula trial, × = mean of a single tree origin at Viitasaari trial.

4 Discussion

Our study is the first one in Finland in which the effect of seed transfers on the performance of silver birch was examined in provenance trials established with population seed samples. Results on the yield and stem quality of Baltic seed origins of silver birch at commercial size grown in Finland are also reported for the first time. Velling (1979) examined the phenology and height growth of Baltic silver birch provenances in the nursery and their success during the first few years in field trials, and our study included exactly the same Latvian, Estonian and Finnish origins.

Survival was found to show wide variation among the origins (Table 2, Fig. 2). The survival of Baltic origins was much higher in our study than that reported for seedlings by Velling (1979). At Tuusula, the survival of the Latvian origins was 65–86% and that of the Estonian origins

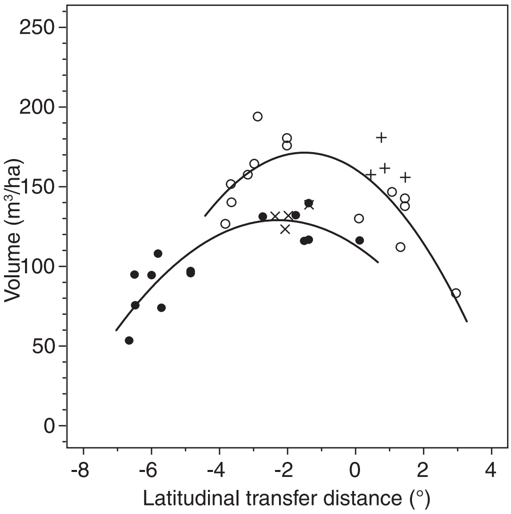

Fig. 7. Average stem volume/ha of the silver birch seed origins in relation to latitudinal seed transfer distance for the Tuusula (upper line) and Viitasaari (lower line) trials. The second order curves are based on the plot means of Finnish and Baltic stand seed origins. ○ = mean of a stand seed origin at Tuusula trial, ● = mean of a stand seed origin at Viitasaari trial, + = mean of a single tree origin at Tuusula trial, × = mean of a single tree origin at Viitasaari trial.

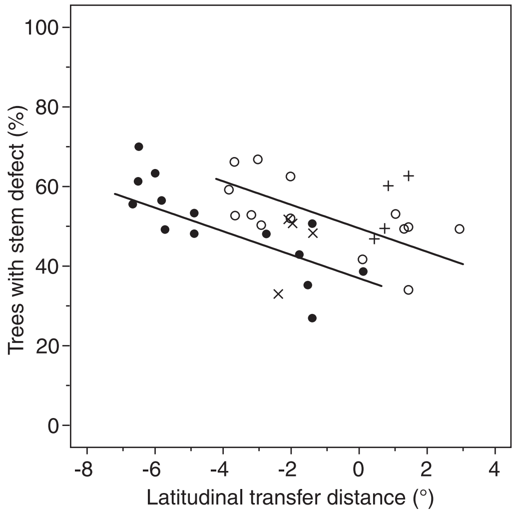

Fig. 8. Average proportion of trees with a stem defect of the silver birch seed origins in relation to latitudinal seed transfer distance for the Tuusula (upper line) and Viitasaari (lower line) trials. The first order lines are based on the plot means of Finnish and Baltic stand seed origins. ○ = mean of a stand seed origin at Tuusula trial, ● = mean of a stand seed origin at Viitasaari trial, + = mean of a single tree origin at Tuusula trial, × = mean of a single tree origin at Viitasaari trial.

72–87%, but survival of these origins at Viitasaari was considerably lower, 34–54% and 49–54%, respectively. Thus, the longer the transfer from the south, the lower the survival. On the other hand, the low survival of Pielavesi origin transferred south to Tuusula by ca 3 degrees of latitude, is probably due to its weaker growth, smaller size and consequently poorer ability to compete with weeds. The same reason was suggested also by Johnsson (1976) and Stener (1995) in Sweden.

Wide variation in stem volume/ha was detected among the different origins at both trials in our study. At Viitasaari, the highest stem volume/ha was achieved by the southern Finnish stand and plus tree origins, but a long transfer from the Baltic resulted in low yield. At Tuusula, the north Latvian Alūksne and Estonian origins produced the highest volume/ha, which was at maximum nearly 80 m^3/ha more than that reported by Niemistö (1997) at similar age and sites. This is an indication of the higher growth potential of more southern origins. Single tree progenies of Latvian origin (Zaļenicki, Alūksne, Liepa, Jaunkalsnava and Dursupe) also performed well at Ås (lat. 59°40'N), south-eastern Norway (Langhammer 1982).

The better yield of the more southern birch origins from Estonia and north Latvia is probably due to their longer growth period compared to native ones (Velling 1979, Viherä-Aarnio et al. 2005). Velling (1979) found that the height growth of Baltic origin seedlings continued longer in the autumn and these origins were significantly taller than the Finnish origin seedlings after two years. Timing of autumn coloration of the Baltic origins was also much later than that of the Finnish ones (Velling 1979). A negative correlation between latitude and the timing of growth cessation, autumn coloration as well as defoliation has been reported in earlier nursery and common garden experiments of birch species (Clausen 1968, Johnsson 1976, Sharik and Barnes 1976). The later cessation of height growth of southern birch origins is due to their longer critical night length compared to the northern ones (Håbjørg 1972, 1978, Viherä-Aarnio et al. 2006). The photoperiodic control of vegetative growth is strong in juvenile silver birches, because they have a free growth pattern (Pollard and Logan 1976, Junttila and Nilsen 1993), and lengthening night at the end of summer induces cessation of height growth, terminal bud set and development of dormancy (Wareing 1956, Nitsch 1957).

Since cessation of height growth is necessary for the frost hardening process (Weiser 1970), delayed growth cessation also delays frost hardening and makes the southern origins susceptible to frost damage. Long transfer from Baltic countries up to Viitasaari, as well as from southern Latvia to Tuusula, resulted in higher mortality and, consequently, low yield. Long transfer from southern and central Finland to northern Lapland also resulted in low survival as well as reduced height growth and bushy-like growth form (Raulo 1976).

As increasing stand density decreases stem taper (Niemistö 1995), the differences we observed in relative stem taper among the origins are probably related to different spacings within the plots due to mortality. The most southern origins with low survival were growing in less dense stands than the more northern origins with higher survival (Fig. 3). On the other hand, the higher stem taper of the northern Pielavesi origin at Tuusula may be due to its slower growth rate, and lesser within plot competition and later self-pruning.

Producing high-quality timber for the plywood and joinery industry is an important goal of growing silver birch in Finland, and there are great differences in price between saw and plywood logs and pulpwood, and between logs of different quality (e.g. Heräjärvi and Verkasalo 2002, Velling et al. 2002). The value of birch as a raw material for veneer is determined first of all by the size of the logs, but stem taper and incidence of defects also affect the amount and quality of the veneer obtained (Heiskanen 1966, Kärkkäinen 1986). Forks and vertical branches are generally caused by a developmental disorder or damage of the leader shoot and thus indicate poor adaptation to the physical or biotic environment.

In this study, trees of more southern origin were more likely to have a stem defect. The longer growth period and delayed hardening of the southern origins makes them susceptible to frost damage causing forking, vertical branches and bushy-like growth (Raulo 1976). Stem defects can also be caused by moose browsing when young. Silver birch transferred from more southern latitudes (southern Estonia, southern Sweden, Scotland, Russia) to Finland have been shown to be more heavily browsed by moose than the more northern, native ones (Viherä-Aarnio and Heikkilä 2006).

Our results showed that stem volume/ha was greater for origins that had been transferred northwards by ca. 2 degrees of latitude, whereas longer transfers resulted in decreased yield. According to the model, a transfer of 2 degrees of latitude from the south increased the volume/ha by about 10 m^3 compared to the local origin at Tuusula (Table 4, Fig. 7). Thus, in the most southern part of Finland some improvement in yield could be achieved by using Estonian or northern Latvian origins. However, this might come at the expense of reduced stem quality and risk of moose damage (Viherä-Aarnio and Heikkilä 2006). The use of the Baltic material is clearly not suitable for central Finland (latitude 63°).

The studies by Raulo and Koski (1977) and Raulo (1979), based on extensive progeny trials, indicated that transfer distances of ca. 200 km from the north to the south, or from south to the north in southern and central Finland are possible without any systematic effect on mortality, growth or stem quality. Erkén (1972) observed increased mortality in birch progenies when transferred ca. 3 degrees of latitude northwards in northern Sweden while Johnsson (1976) and Stener (1997) found a weak response to seed transfers within a few degrees of latitude in Sweden in either a northwards or southwards direction. Thus, in the southern and middle parts of Sweden (south of latitude 61°N) it is recommended that transfer to the north can be made within 2 degrees of latitude and in northern Sweden (north of latitude 61°N) within 1.5 degrees, without any noteworthy effect on growth, quality and mortality (Stener 1997).

According to the seed transfer rules outlined by Heikinheimo (1949) for Norway spruce and Scots pine in Finland, in both conifer species higher yield can be obtained by using seed of more southern origin, as was the result also for birch in our study. In Norway spruce transfers over a distance of 200–300 kilometers (ca. 2–3 latitudes) northwards in South and Central Finland seemed to be safe and even advantageous with respect to growth (Heikinheimo 1949, Hagman 1980). Regarding the seed transfer distance, Norway spruce is, thus, more flexible than birch was shown to be in our study. For Scots pine, transfer distances exceeding 200 kilometres were not advisable according to Heikinheimo (1949) and nowadays even more strict recommendations are applied (Hyvän metsänhoidon... 2006).

Transfers from north to south could only be examined at the Tuusula trial where origins from southern and central Finland had been transferred southwards distances of up to 3 degrees of latitude. A long transfer (3 degrees) from central Finland to the southernmost part of the country considerably reduced the volume/ha (by 84 m^3/ha, more than 50% of the value predicted by the model for the local origin) (Fig. 7). Simultaneously the proportion of trees with stem defect decreased by about 10% (Fig. 8). However, even a shorter transfer distance (1–2 degrees) from the north had a negative effect on volume (Fig. 7), which contradicts the results reported by Raulo and Koski (1977), Raulo (1979) in Finland and by Stener (1997) in Sweden. According to Stener (1997), in the southern and middle parts of Sweden transfer to the south can be made within 3 degrees of latitude and in northern Sweden within 2 degrees.

In Erkén's (1972) study, silver birch origins that had their origin within ± 1 latitude from the site of the trial were the best with regards to growth, whereas a long transfer from the north (3 degrees of latitude) resulted in reduced growth. According to Stener (1995) a transfer of Finnish birch origins 400–600 km southwards to southern Sweden had negative effects on survival and growth of the trees, and use of Finnish origins is not recommended in southern Sweden south of latitude 59°N (Stener and Werner 1997). Even longer transfers southwards were carried out in Germany in the 1970's, where southern Finnish birch origins proved to be very slow growing compared to central European ones (Kleinschmit and Otto 1980, Kleinschmit 1998, 2002).

A long distance transfer southwards of the central Finnish origin resulted in lower yield compared to the local southern origins, but also compared to the performance of the origin on its home site (Fig. 7). In conifers the southward transfer increased the yield of northern origins (Beuker 1996). The transfer southwards means a transfer to warmer climate, but at the same time, a transfer to short day conditions. Cessation of height growth of birch, a species with free growth (Pollard and Logan 1976, Junttila and Nilsen 1993), is regulated in the first hand by photoperiod (Wareing 1956, Nitsch 1957), the northern birch origins having shorter critical night length for growth cessation than the southern ones (Håbjørg 1972, 1978, Viherä-Aarnio et al. 2006). This in turn induces earlier growth cessation of the northern origins (Viherä-Aarnio et al. 2005). The length of the growing season in northern areas after climate warming is, thus, underestimated by the geographical transfer southwards (Beuker 1996). In Scots pine and Norway spruce the shoot elongation is a predetermined process and cessation of height growth will take place regardless of the photoperiod (Lanner 1976, Beuker 1996). Due to the differing regulation of growth cessation, the response of birch to climate warming cannot probably be deduced from southward transfers equally with the conifers. It has, however, been predicted that birch in the future will benefit from warming up of climate and lengthening growing season (Kellomäki et al. 1996, Talkkari 1998).

A weak but significant interaction was detected between the transfer distance and the trial, i.e. the transfer distance had a different effect depending on the trial. The model would, thus, allow slightly longer transfers for the more northern trial at Viitasaari. From an ecological point of view, it is difficult to explain this, and the result must be regarded with suspicion. As a rule, shorter transfers from the south are recommended for the northern areas than for the southern ones (e.g. Stener 1997). One explanation for the interaction between the trial and transfer distance, i.e. the different shape of curves in Fig. 7 could be that transfers from the north are only included at Tuusula, but missing from Viitasaari trial, which may have given the curves a slightly different shape. It must also be kept in mind that the latitudinal location and the site quality of the trials, poorer at Tuusula (MT) than at Viitasaari (OMT), are confounding effects which could not be separated in the analysis. Thus, it is not clear whether the interaction is due to differences in site quality or latitudinal location of the trials.

The Finnish single tree progenies were, in most cases, above the average height, dbh and stem volume/ha predicted by the model (Fig. 3 and 4) although not significantly (Tukey, $p<0.05$) better than the stand seed origins from same geographical areas. The volume/ha of the plus tree progenies was also considerably greater than the volume of planted, unthinned stands of silver birch of similar age and site in southern and central Finland (Niemistö 1997). The parent trees of these progenies were originally selected as plus trees on the basis of their good growth, and our results may be regarded as an indication of selection advantage. Indeed, the southern Finnish plus tree origins achieved practically as high yields as the imported Baltic stand seed origins (Fig. 4 and 7).

The latitudinal seed transfer distance had a significant effect on survival, stem volume/ha and stem quality of the silver birch origins. However, the coefficients of determination for transfer distance in model (2) remained rather low (Table 4), i.e. the unexplained variation was high. Thus, factors other than latitude must be involved in explaining the variation among the origins. In Latvia, the coastal areas of the Baltic sea are climatically more maritime than the eastern parts of the country (Laivinš and Melecis 2003), and differences in climatic adaptation among the Latvian birch populations might exist even at the same latitude.

There was wide variation within the origins among the different blocks in the trials (Figs. 2–5). This probably indicates varying site factors between and within the blocks. Silver birch is sensitive to soil factors e.g. nutrition, moisture and physical structure. In northern Finland, silver birch prefers similar sites as Scots pine, dry soils with low solute concentration (Sutinen et al. 2002), and it is generally known that silver birch does not thrive well on wet, cool, fine textured and poorly aerated soils. The models could possibly be improved by including the soil variables of the trial sites as well as more variables describing the seed origins, e.g. temperature and continentality of their home sites.

In conclusion, latitudinal seed transfer distance had a significant effect on survival, yield and stem quality of silver birch. The coefficients of determination for seed transfer distance were rather low, because, there are, besides the seed transfer distance, other factors that explain the performance of birch origins in the field conditions. In the most southern part of Finland, slightly higher volume growth could be obtained by using silver birch origins from Estonia or northern Latvia, ca. 2 degrees further south, but the stem quality would be lowered. Yields as high as those from Baltic stand seed origins were obtained using southern Finnish plus tree origins, and nowadays even better, improved, material of native origin is available from seed orchards.

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