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Adaptation Capacity of Norway Spruce Provenances in Western Latvia

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Received: 19 June 2019; Accepted: 23 September 2019; Published: 25 September 2019

Abstract: In Europe, numerous Norway spruce (*Picea abies* L. Karst.) provenance trials have been established and evaluated at a juvenile age. Still, information about the adaptation potential and long-term fitness of transferred seedlots in the Baltic Sea region is lacking. The aim of the study was to evaluate the adaptation capacity of provenances and assess the patterns of their long-term reaction to environmental transfer. We examined a 32-year-old provenance trial in the mild Baltic Sea coastal climate of Western Latvia. Significant differences in height and stem volume were observed among provenances. Growth superiority for certain local and Carpathian provenances was maintained over more than one-third of the rotation period. The best predictor of climate transfer functions was minimum temperature of the coldest month at the place of origin, explaining 28% variation in tree height. Populations from sites with more frost days and a colder mean annual temperature, minimum temperature, and lower annual heat-moisture index than the planting site were generally taller.

Keywords: provenance transfer; environmental transfer models; forest regeneration

1. Introduction

High and increasing productivity of Norway spruce (*Picea abies*) has been observed in Europe, partly determined by climate change [1]. According to projections, until the end of the twenty-first century, the Northern Europe and Baltic Sea region may face an increase in mean annual temperature by ca. 3° C, longer drought periods in summers, and rarer, yet more intensive precipitation [2]. Norway spruce is a plastic coniferous species, differentiated in different environments [3]. However, the plasticity has limits, thus, the effect of further climate change is uncertain [4]. Therefore, it is important to test adaptation capacity of transferred seedlots, which can be a tool to supplement local seed sources in the future [5]. Identification of both productive and robust provenances for utilisation in different climatic environments is in the focus of genetic adaptation to climate change [6]. The regeneration of Norway spruce almost exclusively by planting implies the importance of the adaptation of selected populations to their target planting locations through breeding and selection, thus reducing the potential risks for initial investments in stand establishment [7,8]. In general, a gain of ca. 10% in volume production by selecting a non-local seed source can be obtained [9].

Originally aiming to determine seed transfer zones and maximise the productivity of planted forests with the most appropriate reproductive material, provenance trials now may give valuable information about the long-term adaptation (climate-response) of tree populations [10–13]. Similar to other Baltic Sea region countries [14], in Latvia, studies about genetic differences among Norway spruce populations from geographically distant regions of its natural distribution were in the focus of breeding activities during the 1970s, when provenance testing was expanded [15]. The most extensive provenance trials were established in 1972–1974, covering different environmental conditions and including a comprehensive set of foreign reproductive material from collections of the International Union of Forest Research Organizations (IUFRO) [16]. One trial from the experimental series remained suitable for analysis at the age of 32 years, also covering seed source regions with present climate similar to the future one projected in Latvia [2]. The overall results at early evaluations have shown that Norway spruce from foreign regions did not have any advantages, except material from Eastern Europe, which formed larger stems and ensured greater total yield in Western Latvia. Poor growth performance was found for provenances from Northern Europe and most of the Western European material [17]. On an international scale, numerous provenance trials have been established [5]. In particular, the IUFRO international experiment series has provided valuable information about population differentiation for growth and stem quality traits [18,19]. However, most of the studies have been conducted at young age [20], but the growth performance of provenances relative to each other can change over time [21–23], when affected by variable meteorological conditions and extreme events [24]. The evaluation of provenance experiments decades after establishment is rather rare. Only a few studies, mainly carried out in Central Europe, focusing on specific seedlots with short transfer distances, have been described [20–22,25–29]. Still, long-term evaluation of provenance trials is lacking in the Baltic Sea region.

Studies have shown rather efficient adaptation after a transfer to different environment at species level, where the transferred material exhibits notably better growth and lower sensitivity to meteorological factors (shifts in limiting meteorological factors) already at the second generation after transfer [30]. Most likely this is the effect of such processes as natural selection at the first generation that would take place at younger age and be enhanced by increasing competition [30,31], as well as climatic conditions affecting gene expression of adaptive traits during seed production [32–34]. Although lack of various site conditions prohibits one from simultaneously determining optimal provenances and the most appropriate environments for them [35], the trial may give valuable information about, first, the long-term fitness of seedlots with origins in different environmental conditions and, second, any trends associated with environmental transfer distance. Therefore, the aim of the study was: 1) to evaluate the adaptation potential of Norway spruce provenances three decades after planting, and 2) to assess the patterns of long-term reaction of those provenances to environmental transfer.

2. Materials and Methods

2.1. Experimental Material

The study site was located in the Western part of Latvia (56°51′ N; 22°31′ E) and situated in a flat terrain at 100 m above sea level (a.s.l.). The mean annual temperature was 6.2 °C. The mean monthly temperature ranged from −9 °C to + 16.8 °C in February and July, respectively. The annual precipitation sum was ca. 700 mm. The planting site could be characterized by weak climate continentality, typical along the western and southern Baltic Sea coast and the Riga Gulf [36]. Similar conditions can be found in Southern Sweden [37].

The trial was established on former agricultural land with 2-year-old bare-rooted planting stock and an initial density of 5000 stems ha^{-1} (2 × 1 m) using the recommended standard IUFRO methodology [16]. Provenances were planted in 15-tree block-plots in eight replications. At the age of 19 years, systematic thinning had been done, retaining 50% of the stems. At the age of 32 years, selective thinning had been done, retaining approximately 950 stems ha^{-1}, or ca. 20 of the largest trees for each provenance evenly distributed among replications. The trial was destroyed by a storm shortly after the selective thinning; therefore, the study relies on the most recent measurements available before the destruction (age 32 years).

The trial consisted of 14 provenances from the IUFRO collection (3 from Tatra Mountains in Slovakia, 3 from Carpathian Mountains in Romania, 2 from Germany, 2 from Denmark, and one from Latvia, Finland, Sweden and Norway), 14 Latvian provenances, seven provenances from the Carpathian Mountains in Ukraine, nine provenances from the former German Democratic republic, and one provenance from Lithuania (Figures 1 and 2, Table S1). In the present study, the regional grouping of provenances in seed zones was done according to Dietrichson (1979) and Fottland and Skrøppa (1989) [38,39] (Table S1).

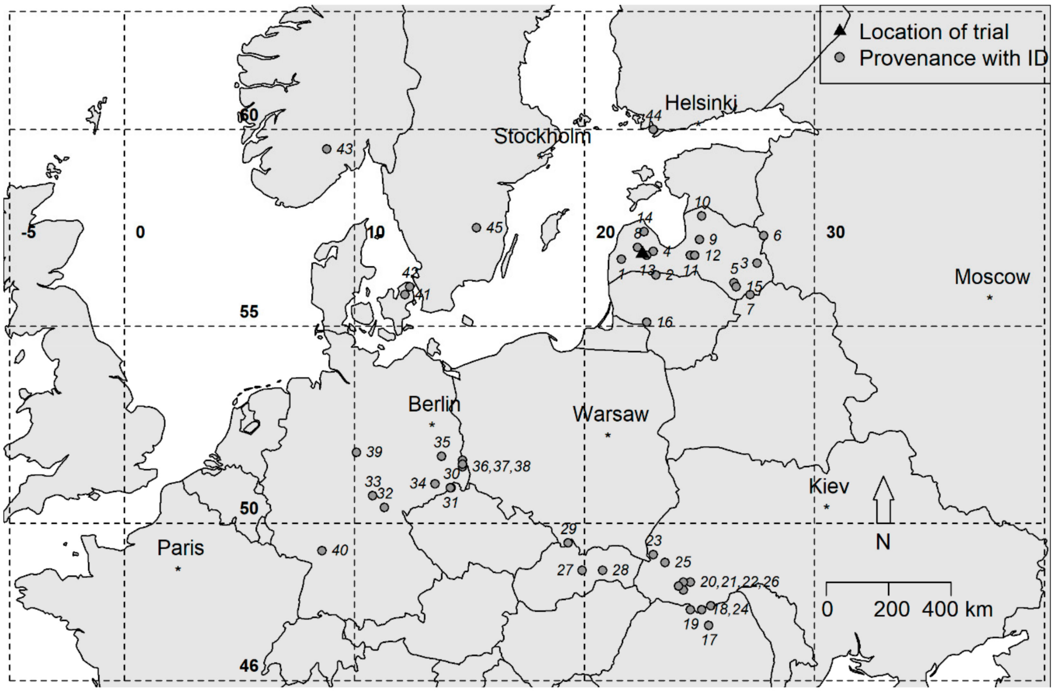


Figure 1. Provenance collection sites and location of studied trial.

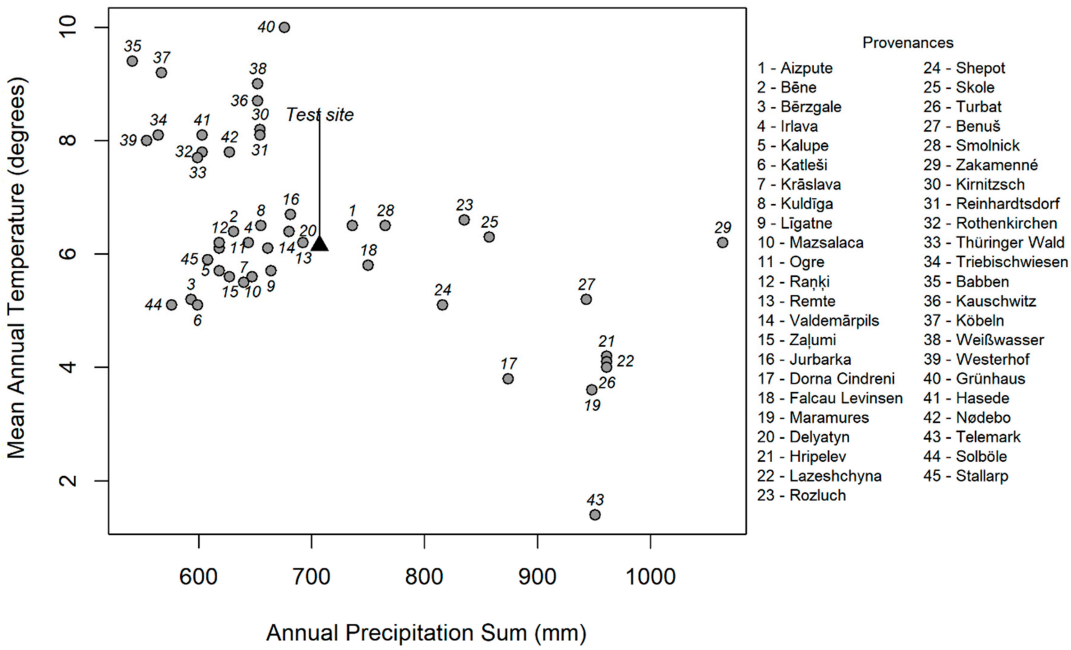


Figure 2. The climate position of the provenances and the test site across mean annual temperature and annual precipitation sum.

At the age of 32 years, the height and diameter at breast height (DBH) for all living trees was measured. Stem volume (StVol) was determined [40] and used in further analysis instead of DBH. Climatic variables for provenances and the test site were obtained from a gridded (0.5° latitude/longitude grid cells) climate dataset CRU TS4.01 [41]. The variables from the nearest grid points used were the mean annual temperature (MAT), annual precipitation sum (APS), number of frost days (FROST), and maximum (MAX) and minimum (MIN) temperatures of the warmest and coldest months, respectively. In addition, we calculated the annual heat-moisture index (AHM) as a parameter integrating both MAT and APS [42] to better reflect evapotranspiration and soil moisture content [26]. The values represented time period of years 1901–2016.

2.2. Data Analysis

All data analysis was conducted in R, v. 3.3.1 [43]. We performed a linear mixed effects analysis of the relationship between the studied growth parameters (height and stem volume) and provenance:

$$y_{ijk} = \mu + P_i + r_j + p_k + \varepsilon_{ijk}, \tag{1}$$

where y_{ijk} is the tree level response variable of the kth tree from the ith provenance in the kth plot, nested within the jth replication, P_i is the fixed effect of the ith provenance, r_j is the random effect of the jth replication, p_k is the random effect of the kth plot, and ε_{ijk} is the experimental error. We performed the analysis using the package lme4 [44]. Scott-Knott test was applied for multiple comparisons of the provenance means using R package ScottKnott [45].

We assessed the response to the provenance transfer with general transfer functions [46]. The distribution of response along an environmental gradient may be unimodal [35]; thus, the growth of provenances was related to the climate transfer distance using both linear and quadratic regression models:

$$Y_i = \beta_0 + \beta_1 D_{ij} + e_{ij}, \tag{2}$$

and

$$Y_i = \beta_0 + \beta_1 D_{ij} + \beta_2 D_{ij}^2 + e_{ij}, \tag{3}$$

where Y_i is the response variable (height of stem volume) of the ith provenance, D_{ij} is the climate transfer distance of the ith provenance for climate variable j, and e_{ij} is the residual. The climate transfer distance was calculated as the difference in climatic variables between the planting site and provenance origin [13] (Figure 2). If both regressions were significant, the selection of the model was based on the significance and goodness of fit. Pearson correlation analyses was used to quantify the association between the climatic variables at the seed origins.

3. Results

3.1. Provenance Effect

At the age of 32 years, the proportion of remaining trees after the second thinning was 17%. The mean height ± standard deviation (SD) and the mean stem volume ± SD were 15.5 ± 1.6 m and 0.22 ± 0.08 m^3, respectively. The provenance was a significant factor ($p < 0.01$) (Table 1) affecting growth of the trees (Figure 3).

Table 1. Analysis of Variance Table for mixed effect models used to test provenance effect on studied traits.

Model Response Variable	Sum of Squares	Degrees of Freedom	Mean Square	F	*p*-Value
Height	193.630	44	4.007	4.017	<0.001
Stem volume	0.539	44	0.012	2.990	<0.001

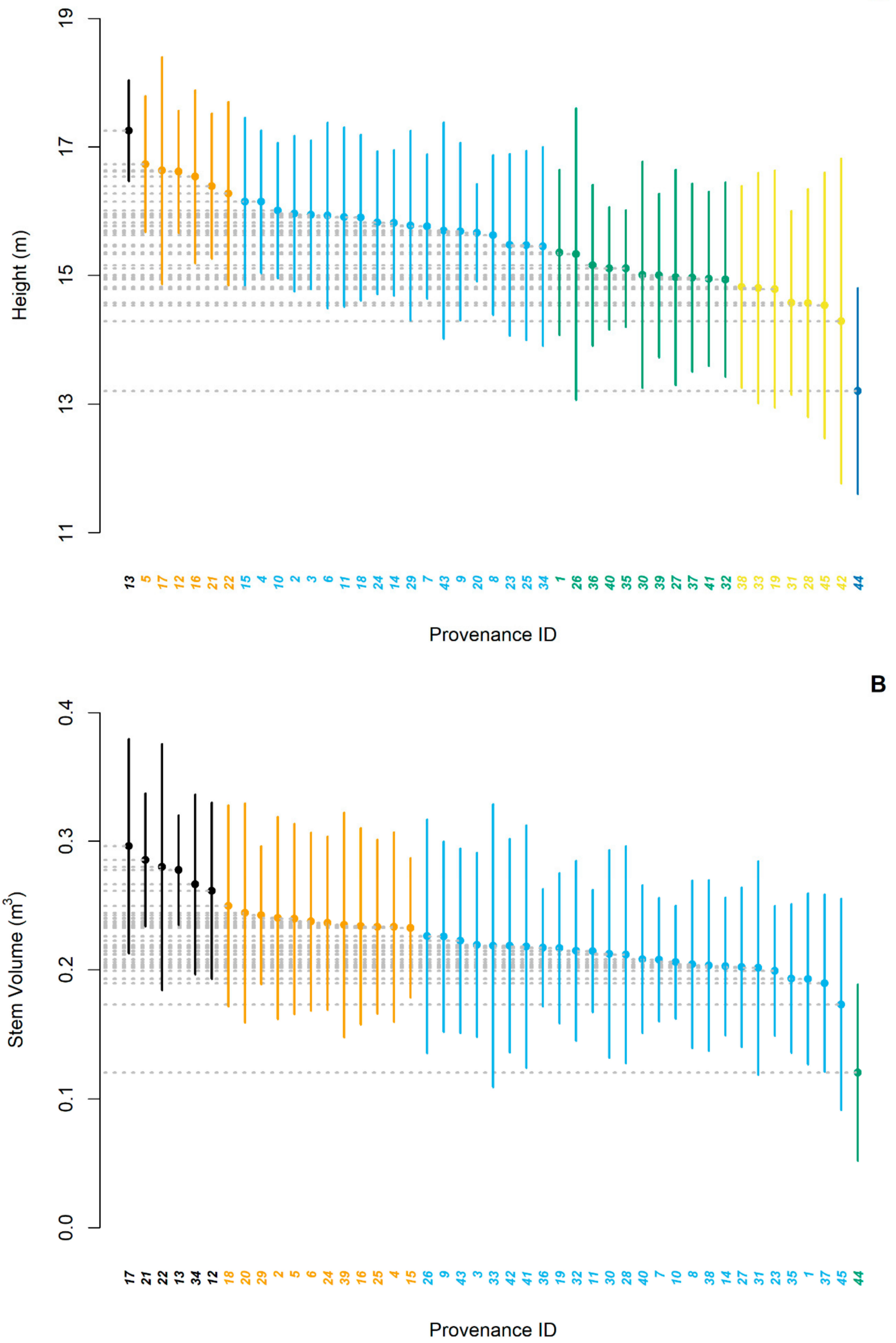


Figure 3. Provenance mean height (**A**) and stem volume (**B**) with standard deviations using Scott–Knott algorithm (α = 0.05, distinct homogenous groups denoted by different colours).

The seedlots from the Carpathian Mountains (Dorna Cindreni, Hripelev, Lazeshcyyna), Triebischwiesen from Germany and local provenances from Western Latvia—Remte and Raņķi (Figure 1)—had the highest stem volume that was up to 35% higher than that of the trial mean, and were significantly more productive than other seedlots, forming homogenous group (Figure 3). Regarding tree height, Remte was significantly ($p \leq 0.05$) better than other seedlots, as well as a cluster formed by Latvian provenances—Kalupe and Raņķi, and Dorna Cindreni, Jurbarka, Hripelev and Lazeshchyna from Carpathians was superior (Figure 3). However, the local Baltic provenances showed variable performance: Although Remte and Raņķi were among the most productive seedlots regarding StVol, such provenances as Kuldīga, Valdemārpils, and Aizpute had poor performance, the latter having significantly lower StVol than Raņķi. (Figure 3).

The worst growing provenance (−45% in StVol comparing to the trial mean) was Solböle from Finland, being significantly less productive than the other seedlots. The mean H for the corresponding provenance was 14.4% smaller compared to the trial mean. In addition, Stallarp from Central Sweden showed poor results regarding growth traits, yet not significantly different from most of the other seedlots. Two Danish provenances had average values for the studied traits. From the Tatra Mountains, only Zákamenné performed above average in terms of StVol (Figure 3).

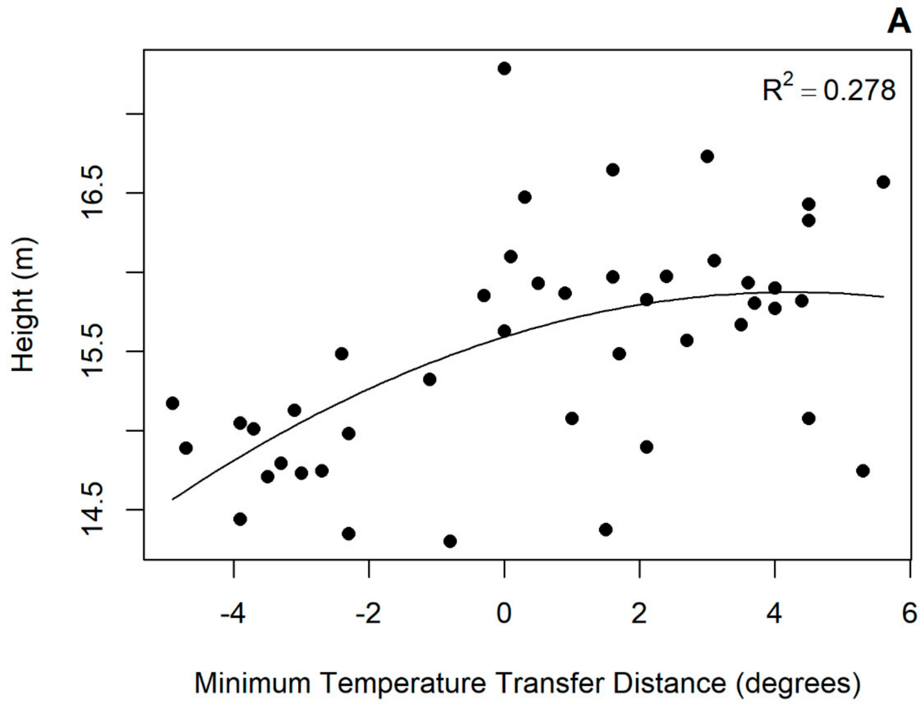
3.2. Transfer Functions

We found significant regression models for all predictor variables except MAX (Table 2, Figure 4). The general transfer functions explained between 7.8% and 27.8% of the total variance (Table 2). The best predictor was MIN, which explained 27.8% and 17.7% of variance in H and stem volume, respectively. Among best predictors were also MAT and FROST, which explained 21.5% and 18.8% of the variance in H, respectively. Linear transfer functions were stronger for StVol, while quadratic trait-response models were better for describing H response to climate transfer. The quadratic regression model appeared to be better than linear functions for describing the relation between tree height and MIN, MAT, FROST and AHM. Height at the test site was greater for populations transferred from provenances with up to approximately 3 °C colder MAT, 4 °C colder MIN, 40 days longer frost period and 4 units lower AHM (Figure 4, Table 2). Such transfer was predicted to improve height by ca. 0.3 m comparing to the local provenances (Figure 4). Transfer from origins with warmer and dryer climate with less frost days than planting site tended to result in relatively slow height growth.

Table 2. Summary of significant ($p < 0.05$) regression models for general transfer functions. Abbreviations of variables: APS—annual precipitation sum (mm), MAT—mean annual temperature (°C), MAX—maximum temperature of warmest month (°C), MIN—minimum temperature of coldest month (°C), AHM—annual heat-moisture index, FROST—annual sum of frost days.

Transfer Distance	Response Variable									
	Tree Height					Stem Volume				
	β0	β1	β2	Adj-R^2	F Statistic	β0	β1	β2	Adj-R^2	F Statistic
APS	na [1]	na	na	na	na	0.223	−0.0001	na	0.078	4.644
MAT	15.523	2.145	−0.9747	0.215	6.884	0.227	0.006	na	0.127	7.254
MAX	na	na	na	na	na	na	na	na	na	na
MIN	15.523	2.487	−0.833	0.278	9.276	0.223	0.004	na	0.177	10.250
AHM	15.523	1.4793	−1.1611	0.119	3.909	0.228	0.002	na	0.115	6.598
FROST	15.523	−1.852	−1.245	0.188	5.970	0.222	−0.001	na	0.151	8.673

[1] not applicable.



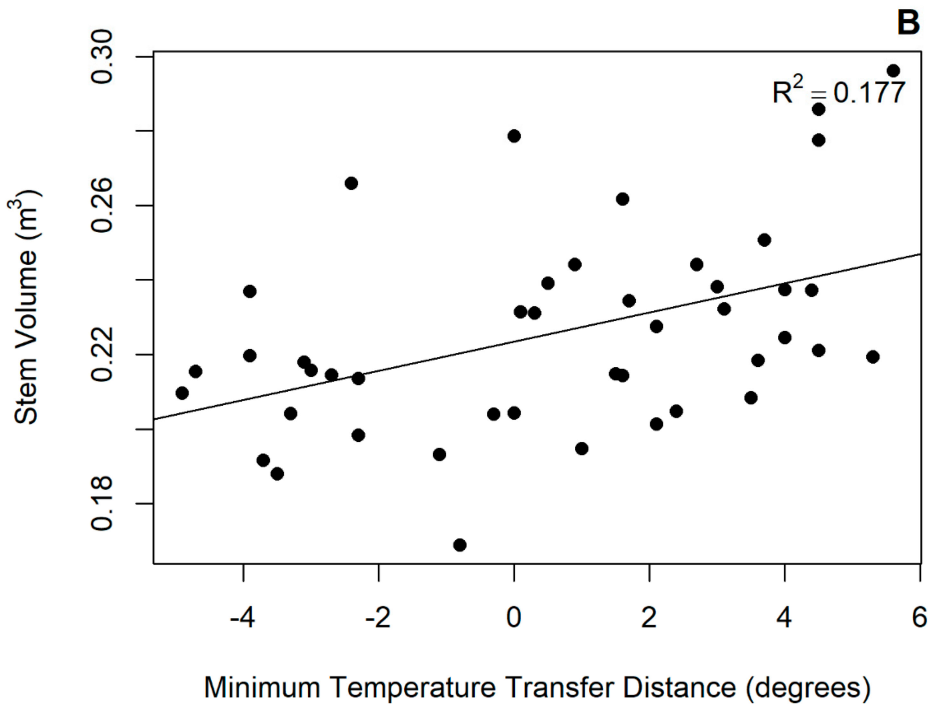


Figure 4. The best fitted linear and quadratic climate transfer functions for height (**A**) and stem volume (**B**).

Stem volume was greater for populations transferred from provenances with colder MIN and MAT, longer period of FROST, lower AHM and higher APS. Within represented climatic range of provenances, such transfer was predicted to improve stem volume by up to 14% compared to the local seedlots. Still, climate transfer functions were weaker for stem volume comparing to H, and explained 7.8%–17.7% of total variance.

The climatic variables had significant ($p \leq 0.05$) correlations among themselves (Table 3). Strong positive correlations ($r \geq 0.79$) were estimated among MAT, MIN and AHM. Both APS and FROST had negative, moderate to strong correlations ($-0.56 \leq |r| \leq -0.96$) with other climatic variables, yet being strongly correlated ($r = 0.69$) with each other (Table 3).

Table 3. Estimated correlations between climatic variables in the upper diagonal part and their *p*-values in the lower diagonal part. Abbreviations of variables: APS—annual precipitation sum, MAT—mean annual temperature, MAX—maximum temperature of warmest month, MIN—minimum temperature of coldest month, AHM—annual heat-moisture index, FROST—annual sum of frost days.

	APS	**MAT**	**MIN**	**MAX**	**AHM**	**FROST**
APS		−0.61	−0.56	−0.57	−0.92	0.69
MAT	<0.01		0.90	0.82	0.84	−0.96
MIN	<0.01	<0.01		0.51	0.79	−0.94
MAX	<0.01	<0.01	<0.01		0.71	−0.71
AHM	<0.01	<0.01	<0.01	<0.01		−0.89
FROST	<0.01	<0.01	<0.01	<0.01	<0.01	

4. Discussion

4.1. Provenance Effect on Growth Performance

Significant differences between provenances were observed for both H and StVol. Our results confirmed the general finding at younger provenance trials that certain populations having the greatest H and StVol were from the Baltic States and Carpathians [10,18,47–49], indicating the importance of both phenotypic plasticity and local adaptation [50]. However, other Carpathian and local seedlots showed poor performance (Figure 3), confirming previously noticed possible variation within one region as wide as between distant origins [14] due to high genetic variation [12]. Good adaptation of transferred provenances might depend on sufficient genetic diversity, which, for the Norway spruce populations in the Carpathian Mountains in Ukraine and Romania, were reported to be moderate to high, with no significant differences regarding altitude [51,52]. Similar to our results, both the most productive transferred Central European seedlots and the best performing local provenances were reported to show similar growth in long-term trials in Southeast Norway [53]. In Southern Sweden at similar latitude and climatic conditions as our study site, the highest ranks of H and StVol had provenances from the Baltic States and Carpathian Mountains [37], exceeding the trial mean by 23% and 65% in H and StVol, respectively, at the age of 22 years. The mild climate in the study site may have favoured the superior performance of the Carpathian provenances. Similarly, relatively frost-free sites in Southern Sweden were suitable for any fast growing provenances transferred northward, though seedlots with origins as far south as Romania are not generally recommended for sites with a high frost risk due to late growth cessation and subsequent autumn frost damage [37,54]. Applying long transfer distances, the southernmost origins showed poor growth in Finland [55].

The relative difference in tree height between certain provenances and the trial mean tends to reduce with increasing age and that a levelling of tree height could be expected [16]. Nevertheless, at the age of 32 years, the provenance deviation from the trial mean was still pronounced, reaching +11% and −14% for the best and worst seedlots, respectively. Besides, the best and worst performing provenances had remained stable, when comparing to early evaluations of the study site at the age of 8–17 years [16,17]. In Austria, 10% differences between provenances were reported [26], while Czech study found −15%–20% variation from the trial means at the 36-year-old experiment [20].

4.2. Provenance Response to Tranfer

From a statistical point of view, different transfer models could be chosen to identify any trends of provenance reaction to transfer [56,57]. Due to the use of limited number of populations and relatively short climate transfer distances, an individual transfer function relating climatic variables in individual provenances was fitted to the linear and quadratic regressions instead of more complicated models (e.g. Weibull) [26]. Transfer functions explained the growth response to the climate transfer distance of certain climatic variables fairly accurately: The effect of predictor variables was rather strong for H, explaining up to 28% of the total variance with the climate transfer distance between the planting side and place of origin (Figure 4). Growth response for H to changes in a certain environmental factor followed unimodal curve, reaching maximum and thus indicating when factors were optimum (Figure 4, Table 2) [35,58]. As indicated also by our results for H, trees are adapted to local conditions and similar or better growth could be expected at small transfer distances, while seedlots originating from long ecological distances lag behind [13,46,57,59]. However, climate transfer distance was weaker predictor for stem volume implying possible stronger effect of other random environmental factors [46]. The dominating linear trend for StVol most likely indicated the limited climate range of analysed provenances, not covering the full range of the Norway spruce distribution and the subsequent gradient of environmental variables, and the climate of the optimum seed source for the test site might be outside the climate range of the tested populations [35]. Nevertheless, the scope of our study was limited to the seed source regions with present climate similar to the predicted future climate in the Baltic Sea region [2].

Generally, for both response variables, the results might be affected by selective thinning retaining the best trees from each provenance and thus mitigating the differences. However, retention of best growing trees after the thinning was in compliance with our aim to evaluate adaptation capacity. Therefore, response of the top performing trees from each provenance after thinning could better describe potential of the best possible reproductive material, meanwhile excluding potentially maladapted sources.

4.3. Relation between Provenances and the Significant Climate Variables

The most important climatic variables for predicting growth were MIN, MAT and FROST, which also had the strongest correlations among each other ($|r| \geq 0.90$) (Table 3). Thus, plantations established with seed sources having a climate to a certain level colder than the plantation may be more productive than plantations established with local seed sources (Figure 4). The places of origin with MIN and MAT ca. 3–4 °C lower and FROST by up to 40 days longer than the planting site were in the Carpathian Mountains and Eastern Latvia. The latter one indicated a better performance with increasing seed source continentality [20], as noticed in earlier studies [10,29]. Also in Estonia, more continental Belorussian provenances were found to be appropriate for use in practical forestry [60]. Photoperiodic adaptation of Carpathian provenances, causing their longer growing season in more northern light regime at the test site [61], is the most likely cause of their superior productivity, meanwhile adaptation to harsher mountainous environment in higher elevations had ensured their resistance against any potential late spring or early autumn frosts [62]. This may indicate that continental and mountainous populations are growing in suboptimal climate, and their growth potential can be fully expressed with transfer to milder conditions [59,63]. Similarly, for Douglas fir, tree height growth was greater for provenances with lower mean temperature of the coldest month (MTCM) than the planting site, when they were moved to warmer winters with MTCM up to ca. 5°C higher [64]. Optimal climate transfer distance of ca. 1 °C for MAT was reported in Slovakia [24].

Meanwhile pronounced eastward transfer was unfavourable, as also noticed earlier [65]. Despite some exceptions, German provenances with the most notable transfer eastwards primarily showed a growth performance below average, while the provenances from the eastern parts of Latvia were generally performing well (despite the short longitudinal transfer distance westwards) as noticed before [10,19,37,49].

Our study site could be described with a favourable, rather mild coastal climate without frequent extreme climatic events, where the differences among provenances may not have fully manifested themselves as in sites with harsh climatic conditions [12,16,37,66]. The steepness of obtained transfer functions (Figure 4) might change with harsher climatic conditions. For Scots pine (*Pinus sylvestris* L.) in Sweden, continued increase of height growth was observed with environmental transfer on mild site, while optimal transfer distance was negligible at the harsh sites, reaching optimum peak [67]. In a study with multiple provenance tests of *Quercus petraea* L., survival and growth was noticed to decrease for all provenances with transfer to much harsher (namely dryer) sites, yet considerable plasticity to planting site conditions, including extreme climatic events was indicated [68]. Norway spruce is drought-sensitive [3], so this aspect also needs to be considered while recommending enrichment of the selection population with transferred material. However, positive growth response in H and StVol with transfer to dryer environment was indicated by AHM and APS climate transfer functions (Table 2), suggesting good adaptation capacity of the best performing provenances after thinning. A study with Douglas fir (*Pseudotsuga menziesii*) has shown negligible growth reduction induced by soil-water deficit after severe drought period for provenances from wetter environments comparing to large reduction for drier origins [69].

Although climatic variables suggested to be overall weak predictors for genotype × environment interaction, study in Sweden indicates that well-performing *P. abies* genotypes at sites with harsh conditions might not be the same as seedlots being superior at milder sites [70]. Still, multiple site analysis indicates that same populations could be deployed over large areas in southern Sweden when frost-prone genotypes are excluded [70], similar to removal of potentially maladapted genetic material during thinnings in our study site. We stress that our results describe tendencies when seedlots are transferred to sites with similar mild Baltic Sea coastal climate as in the studied trial, and further studies should address provenances response in harsher conditions.

To summarize, most of the countries in the Baltic Sea region have strict regulations in use of reproductive material in forest regeneration (transfer). Our study indicates that these restrictions might be modified to allow or even favour certain transferred Norway spruce provenances demonstrating high productivity and robustness, which could supplement currently used seed orchard material and thus encourage the migration of genes and adaptation to ongoing climatic changes. Also creation of new control crosses involving transferred superior clones from identified climatic regions/provenances with local material to widen the genetic variation and probability finding well adapted material for future seed orchards should be considered.

5. Conclusions

Significant and large differences in productivity among provenances were pronounced three decades after planting. In the rather mild climate of Western Latvia, certain Carpathian and local provenances showed long-term superiority in growth, justifying use of selected well growing and robust transferred provenances to boost the diversity and adaptation capacity in breeding population. The use of superior provenances from the Carpathian Mountains with the highest observed adaptation capacity may provide by ca. 14% higher stem volume than local origins from the Baltic region.

Overall, superior growth is expected with transfer from more continental climates. The present factors indicating potential improvement in growth in future climate are mean annual temperature, minimum temperature of the coldest month and annual heat-moisture index lower, and number of frost days higher than that of the projected future site conditions. Nevertheless, the scope of the present study is limited to the climate range of analyzed provenances, and the observed trends may be restricted to planting sites with mild climate without frequent extreme climatic events. Considering potentially various response to transfer in test sites with different climate characteristics, verification of the results in harsher, more continental conditions is required.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/10/10/840/s1, Table S1: Overview of provenances included in the studied trial.

Author Contributions: Conceptualization, A.G. and P.Z.; methodology, Ā.J.; data collection, J.K.; data analysis, P.Z. and J.K.; writing—original draft preparation, P.Z., I.D.; writing—review and editing, A.G., Ā.J. and T.M.; supervision, A.G.

Funding: This research received no external funding.

Acknowledgments: Material was collected and analysed in the projects "Forest tree breeding for establishment of high genetic quality stands" and the state research programme ResProd No 2014.10-4/VPP-6/6.

Conflicts of Interest: The authors declare no conflict of interest.

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