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Climatic Stress Test of Scots Pine Provenances in Northeastern Europe Reveals High Phenotypic Plasticity and Quasi-Linear Response to Warming

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Abstract: *Research Highlights*: Scots pine (*Pinus sylvestris* L.) phenotypic plasticity will buffer and even benefit from temperature increases in Northeast Europe this century, except for the southern peripheries of the range. *Objectives*: The "stress test" aimed to assess the inherent potential of existing populations to withstand projected changes in their lifetimes at their original location. *Materials and Methods:* This study applied an alternative analytic approach to calculate response and transfer equations from historic height growth data from provenance tests in the former USSR and Hungary. *Results:* Contrary to earlier analyses, the populations displayed quasi-linear responses to mimicked warming without clear ecological optima, forecasting a general growth acceleration north of Lat. 53° N. Climate-triggered mortality is predicted for the near future in the southern peripheries. Locally adapted populations at the distribution confines of the northern and southern limits deserve special attention. *Conclusions*: The observed adaptability to warming moderates the necessity of genetic management interventions such as assisted migration. The support of natural processes of adaptation and acclimation will be sufficient in boreal and central Northeast Europe this century. Evacuating heat and drought-tolerant populations should be envisaged in the endangered zone to conserve valuable genetic resources.

Keywords: provenance test; climate change; response modelling; reaction norm; transfer equation; heat and drought stress; adaptation; phenotypic plasticity; assisted transfer; ecological genetics

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1. Introduction

A rapid climate shift threatens circumpolar boreal forests, which cover ca. 16% of the global landmass. Scots pine (*Pinus sylvestris* L.) is a dominant species in that biome. Due to its enormous Eurasian range, the species has been a preferred object of provenance studies for two centuries [1–3]. In recent decades, provenance experiments have been rediscovered as important data sources to investigate the effects of climatic change on forest trees and to plan adaptive forest management for an uncertain future [4–7]. The speed of ongoing changes means that the survival and growth of presently existing populations will depend on their standing genetic adaptability to respond to climatic changes during their lifetimes. Within-population natural selection may occur [8], but long-term evolutionary processes are ineffective because the available time frame is too short.

European provenance research on Scots pine is extensive, yet the accessible literature on Northeast Europe is scarce. The present study focused on this vast region, which marks the continental–boreal part of the European range of the species. Some studies have investigated the response of these populations to rapid climatic changes, but mostly on a restricted scale. Research results and publications are sparse due to political transformations and research priority changes in the post-Soviet states, including Hungary (for a literature background, see Section 4.1).

The present study reanalyzes historic height data from the VNIILM Scots pine provenance test [9] established in the former USSR and Hungary. The "climatic stress test" aims to determine the expectable survival and growth of the *extant generation* of the species under current and future climates, i.e., their phenotypical plasticity. While projections from field inventory data or ecophysiological analyses assess phenotypical plasticity indirectly, provenance test data may provide the information straightforwardly, justifying the recovery of information hidden in historic provenance trial datasets [10–12].

Consequently, the aims of the analysis were:

- to identify the trend in growth responses across the investigated climate range based on reaction norms of populations;
- to compare transfer functions calculated for selected test locations to analyze their configuration under different climatic conditions;
- to place the responses into the context of climate projections; and
- to assess the inherent potential of Scots pine in the study region to withstand projected changes *in their original location*.

2. Materials and Methods

2.1. The VNIILM Provenance Test Network

E.P. Prokazin—the former head of the Forest Seed Laboratory of the Federal Research Institute of Forest Melioration (VNIILM) in Pushkino, Russia—established the VNIILM transcontinental provenance test for Scots pine between 1974 and 1976 with 126 provenances from across the former USSR [9,13]. The majority of the 33 test sites were concentrated in the European part of the country (Figure 1). Nearly complete sets of provenances were outplanted at only two central locations (16. Kovrov, Vladimir, RU, and 17. Davydovka, Voronezh, RU). At all other sites, the set of provenances was adjusted to the regional climatic conditions. The present study analyzed only mean heights of provenances per test at the age of 15–17 years published in the source paper [9]. Tables A1 and A2 list the revised basic data of the test sites and of the provenances mentioned in this study.

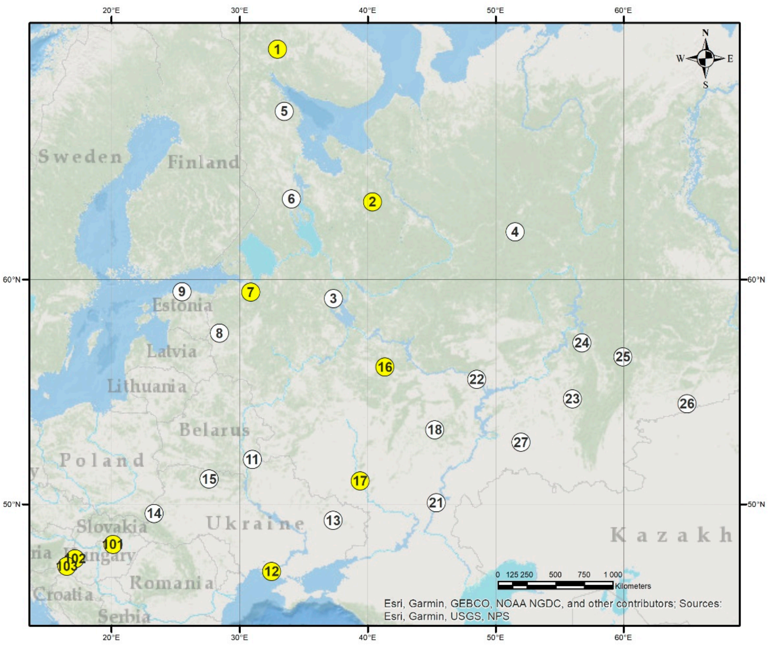


Figure 1. Test sites of the VNIILM Scots pine provenance experiment network established in Northeastern Europe and Hungary. The gray shading shows the approximate contiguous range of the species. Table 1 and Table 4 contain details of the tests marked in yellow in this figure. Table A1 lists the basic data of all numbered sites.

2.2. The Hungarian Tests

The first author introduced 66 seed lots from the VNIILM experiment that originated predominantly in the European part of the USSR to Hungary to test with other provenances from Central and Western Europe [14]. The populations were outplanted in 1978/79 at four field locations (one perished). Two-year-old seedlings were planted in plots of 40 plants in four repetitions and in randomized order. Spacing varied among tests between 1.4–2.0 m × 1.0–1.6 m. The height growth of provenances was measured until age 17; in one case (Recsk), it was measured until age 23 (Table 1).

Table 1. Test sites of the VNIILM experimental set in Hungary.

Code, Location, and County Name	N. Latitude Decim.	E. Longitude Decim.	Elevation (m a.s.l.)	Growing Degree Days * 1981–2010 (CHELSA)	Annual Precipitation (mm) 1981–2010 (CHELSA)	Mean Annual Height Increment ** (cm)
101. Recsk, Heves	47.930	20.120	179	24.311	607	43.5
102. Egyházashetye, Vas	47.170	17.120	134	25.896	668	38.2
103. Kerkafalva, Zala	46.770	16.490	196	25.355	752	42.7

* heat sum above 5 °C. ** calculated for age 17.

The original aim of establishing this experimental series of Russian provenances, unique in Central Europe, was the selection of potentially drought-tolerant populations for conifer plantations in Hungary. The measurements in the experiments continued until 1997, but the results were only published on a restricted level [14–17] due to the changes in research priorities. These remained internationally unnoticed until now.

2.3. The Selected Study Region within the Range of Scots Pine

The plains of Northeast Europe (in this study, the term Northeast Europe also encompasses parts of Southeast Europe such as Ukraine, Hungary) are devoid of isolating topography, have rather regular climatic gradients, and are covered by a fairly contiguous range of the species. The region is less affected by human intervention than Central Europe. The selected area includes the central and northern parts of European Russia, Ukraine, Belarus, and partly the Baltic states (the country and location names with respect to states, formerly parts of the USSR, are valid as of 1 January 2022), excluding the Baltic coast, which is under stronger maritime influence. It covers the whole climatic tolerance range of the species (Table A2).

The study region is represented by 26 VNIILM test locations. Only one site, 12. Oleshky, UA, lies outside the natural distribution range of Scots pine. Three Hungarian sites also outside the species range were included to consolidate the responses at the southern limits (Figure 1, Table 1). An *important and unique* feature of this study is the existence and inclusion of four test sites outside the species range.

2.4. Selection of Climate Variables and the Climate Data Source

The East European Plain provides 400 to 800 mm of precipitation, which is sufficient for the species, and the projections of CHELSA models forecast only insignificant changes until the end of the century. This is most conspicuous at the southern limits receiving the least rainfall (e.g., provenances 60, 62, and 72). An exception is the outlier Hungarian population nr. 999. In the absence of significant anomalies and future moisture deficit, growth and survival will likely be determined by temperature changes. Other analyses support the secondary role of precipitation (Section 4.1). Therefore, it was excluded from the model even though it is undoubtedly a determining climate factor.

International literature on Scots pine corroborates that temperature factors, particularly the length of the vegetation period, are dominant in determining growth in the largest part of the range. This is also valid for the study region. An exploratory analysis of the data from the VNIILM provenance test [18] indicated that thermal variables yielded the highest correlations (compared to precipitation and drought indices) out of 90 climate factors and that degree day variables of various kinds were among the best predictors of 15-year height. In detail, the temperature sum of the vegetation period has shown the highest correlation with the inherent growth of provenances [17,19] (see also Section 4.1).

Warming in the vegetation period is the most critical with respect to climate change; therefore, selecting the variable annual growing degree days above 5 °C (GDD) appeared reasonable. As the correlation of climatic variables with growth may differ for provenances from different climate zones [17], choosing a single major variable was vital to attain general comparability. The effect of rainfall has been introduced only in the final analysis step (Section 3.4).

The CHELSA global climate database [20] was selected for the analysis because of available growing degree day and precipitation data for recent and projected climate scenarios. The climate period of 1981–2010 was applied for recent conditions, i.e., for the test period.

A new generation of projections—the shared socioeconomic pathway (SSP) scenarios—was applied to the projection of future climates [21]. From the SSP scenarios, the authors selected SSP3-7.0 and SSP5-8.5. Both scenarios represent pessimistic pathways. Pathway SSP3-7.0 counts high greenhouse gas emissions, with doubled emissions by 2100, leading to an estimated global increase of 2.1 °C. This scenario was applied to the period 2041–2070. Pathway SSP5-8.5 counts very high CO_2 emissions, which triple until 2075. This scenario was applied to 2071–2100, leading to an estimated temperature increase of 4.4 °C, which is more extreme than scenario RCP8.5. The present study chose these selections because it did not consider other factors, such as unforeseen ecological and biological changes affecting Scots pine growth and survival (e.g., more severe droughts, new insect pests) in the analysis.

2.5. Analysis of Provenance Data

The mean height of provenances aged 15–17 years [9] has been used as a proxy for growth potential and vitality. Height is the quantitative trait with the highest heritability, less affected by environmental factors, and it characterizes the potential of a given site. No intervention was performed up to the age of the measurement. Due to minor age differences at measurement, mean height at a given site was converted into an annual rate of growth, i.e., into a mean annual height increment (Z).

The lack of detailed plot data warranted the application of regression analysis instead of more sophisticated modelling (e.g., [11,22]). Thus, reaction norms and transfer equations were calculated. To obtain *reaction norms* (*response equations*), increments of individual populations in different trials were regressed vs. temperature sums. Functions describing the phenotypic growth response of different populations transferred to a single test site are termed *transfer equations*. Thus, while reaction norms (response functions) describe an array of phenotypes of the same population in a range of environments, transfer functions describe the phenotypic response of an array of populations in a single environment (Figure A2). Linear and quadratic regressions were calculated, but only significant or sensible ones are shown. Data from reaction norms and transfer equations are presented only for selected provenances and trials. Table A2 includes data from all provenances in the study area (Figure 7). Exploratory analyses indicated that the careful design of the experiments (Table A1) provided acceptable estimations of site potential via the test means [18].

Following exploratory analyses [17,18], the growth response was modelled with *unilateral* equations. The equations predict growth in warming temperature scenarios at the *original location* of the populations. The responses to future warming are mimicked by the space-for-time substitution in provenance tests [6,7]—an approach that found a worldwide application in ecological genetic research.

For stylistic reasons, the present study uses the term provenance to describe "population" and origin as a synonym for geographic provenance. Following the source publication [9], the provenances and test sites are coded by their original two- or three-digit numbers, which are partly identic. The test site and provenance codes are distinguished in every case when mentioned to avoid misinterpretations.

2.6. Estimating the Climatic Limits of Survival

For obvious reasons, provenance experiments have not been planned for sites that facilitate the assessment of critical climatic conditions for survival. The xeric (trailing) limit is a critical boundary for the functioning of the manifold services the forest cover provides [23]. Although it marks significant changes in land cover and landmass carbon balance [24–27], its importance in research and forest and land management remains underestimated [10]. Local site conditions may influence the presence and survival of populations in this border zone [28]. The dispersed distribution pattern renders the climatic determination of critical limits very elusive. Therefore, two approaches were foreseen for its estimation: (a) identifying trends of growth decline based on provenance test data, and (b) the indirect determination of the critical limit applying forest health information, using field inventory data (details in Section 3.4).

The provenances were analyzed in two groups to trace the survival limits:

(1) the north–central provenances, to investigate the change in responses along the north–south climate gradient; and
(2) the southern provenances, from sites under heat and drought stress (precipitation < 550 mm), where the identification of selective effects of the warmer and drier climate was expected (Tables 2 and 3).

3. Results

3.1. Reaction Norm (Response Equation) of North–Central Provenances

Eight populations were selected to represent the climate gradient from the boreal northwest of European Russia southward to latitude 56° N (Table 2). They represent the gradient from the front (thermal) limit of the species at 02. Kandalaksha, RU, to the continental mixed (nemoral) forests zone at 25. Jelgava, Latvia. Table 2 shows equation parameters for linear and quadratic reaction norms of the populations. Table A2 presents the geographic data of the provenances.

Table 2. Linear and quadratic parameters and R^2 values of reaction norm equations of the mean annual increment of north–central populations vs. the heat sum of test sites. Provenances are ranked by GDD at their origin. Insignificant values ($p > 0.05$) are in italics.

Provenance		Linear Equation		Quadratic Equation	
Name	**GDD ***	**Slope**	**R^2**	**Parameters of x**	**R^2**
02. Kandalaksha, RU	667	1.081	0.453	insignificant **	-
04. Plesetsk, RU	1096	1.474	0.546	$-0.083x^2 + 4.327x$	0.597
15. Pryazha, RU	1153	1.202	0.487	$-0.110x^2 + 4.895x$	0.623
09. Totma, RU	1296	1.543	0.489	$-0.1635x^2 + 7.160x$	0.678
19. Lisino, RU	1351	1.667	0.512	$-0.208x^2 + 9.380x$	0.628
28. Rasony, BY	1582	1.319	*0.344*	insignificant	-
23. Kresttsy, RU	1550	1.569	0.507	$-0.137x^2 + 6.659x$	0.557
25. Jelgava, LAT	1589	1.338	*0.274*	insignificant	-

* growing degree days at the origin of the population. ** at $p > 0.05$.

The reaction norms (response equations) of four boreal (nr. 2, 4, 9, 15) and four central (nr. 19, 23, 25, 28) provenances show no clear trend regarding linear statistical parameters. All display a consistent increase in growth with the rise in growing degree days (see slope data in Table 2). Only a few provenances improve the fit (R^2) when quadratic equations are applied. The northernmost population, 02. Kandalaksha, RU, outplanted across the whole climatic range of field tests from 1. Monchegorsk, Murmansk, RU, to Hungary (tests 102, 103), also shows a linear response regression (Figure 2). Provenance 09., Totma, Vologda, RU, shows the strongest quadratic effect (Figure 3), displaying a clear "adaptation lag" of the maximum. A moderate decline in performance appeared in the extreme Hungarian tests (nr. 101, 102, 103).

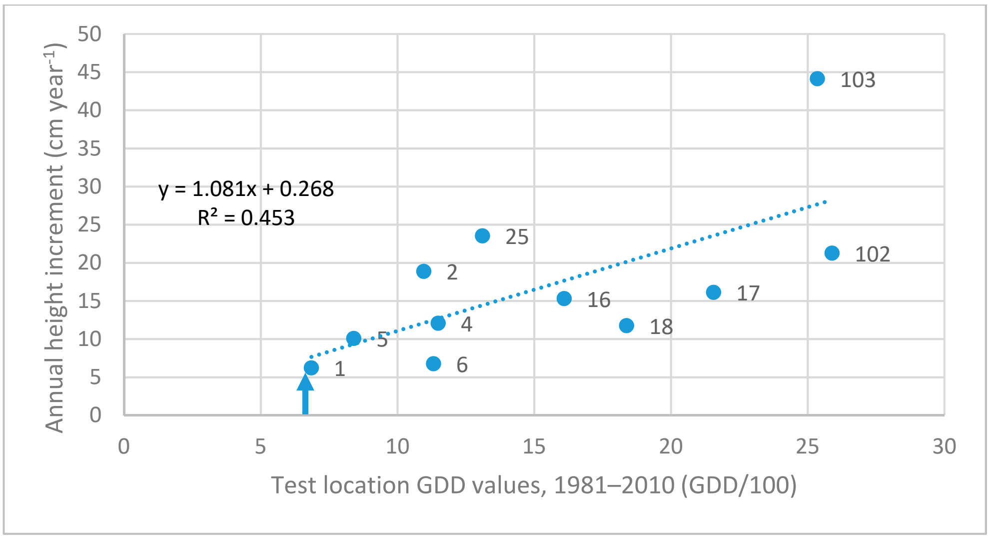


Figure 2. Linear reaction norm of the annual mean increment (cm) vs. the test location degree days (GDD/100) of provenance 02., Kandalaksha, Murmansk, RU, north of the polar circle. The arrow marks the heat sum at its origin (GDD: 667). Numbers show codes of test locations (see Table A1; Figure 1).

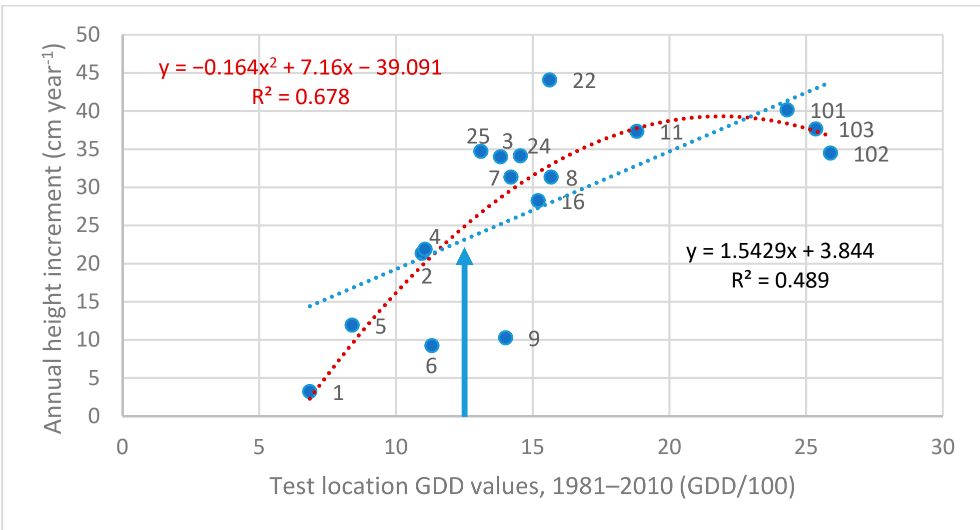


Figure 3. Linear and quadratic reaction norms of the mean annual increment (cm) vs. the test location degree days (GDD/100) of provenance 09., Totma, Vologda, RU. The arrow marks the heat sum at the origin of the population (GDD: 1296). Numbers show codes of test locations (see Table A1).

The generally moderate difference between linear and quadratic fits (R^2) indicates that the quadratic effect added to the R^2 value is not overriding and, in three cases, is insignificant. However, three provenances (nr. 09, 15, 19) show considerable quadratic effects, shaped first by extreme conditions in the northernmost and the hottest test sites. The decline of the mean annual increment due to extreme warming visible in the example of Totma (Figure 3) is caused by an increase in GDD from 1302 at the origin to over 2500 in

Hungary (nr. 101, 102, 103), which is an improbable warming in this century at the original location (see details on projections in Section 3.4).

The northern provenances beyond latitude 60° N. display a declining relative increment in a southerly direction. Their performance falls increasingly below the level of more southern provenances at the warmer sites. The relative increment of the northernmost population, 02. Kandalaksha, RU, attains roughly 50% of the "local" population (999) at Hungarian site 102. Egyházashetye (Figure 5D).

3.2. Reaction Norm (Response Equation) of Southern Provenances

The group contains ten populations from the east–west strip at the dispersed southern distribution limits, south of latitude 56° N. (Table 3), and tested at locations with a high heat sum above 1500 GDD. Provenance 29., Lenino, Homel, BY, originates from the mixed forest zone. The other nine provenances were selected along the Ukrainian–Russian forest–steppe limit of the species (Tables 3 and A2; Figure 7).

Table 3. Linear and quadratic parameters and R^2 values of reaction norm (response) equations of the mean annual increment of populations south of latitude 56° N. vs. the heat sum at test sites. Provenances are ranked by GDD at their origin. Insignificant values ($p > 0.05$) are in italics.

Provenance		**Linear Equation**		**Quadratic Equation**	
Code, Name, Country	**GDD ***	**Slope**	**R^2**	**Parameters of x**	**R^2**
29. Lenino, BY	1874	1.626	0.466	insignificant **	-
38. Svessa, UA	1884	*0.974*	*0.153*	$-0.238x^2 + 11.112x$	*0.230*
35. Olevsk, UA	1909	1.170	0.326	insignificant	-
56. Voron./Khrenovoe, RU	2022	*0.644*	*0.082*	insignificant	-
55. Voron./Grafskaya, RU	2033	*0.890*	*0.191*	insignificant	-
37. Borispol, UA	2136	1.581	0.426	insignificant	-
40. Slovyansk, UA	2392	1.812	0.581	insignificant	-
60. Veshenskaya, RU	2393	1.774	0.719	$-0.0984x^2 + 5.9472x$	0.735
39. Cherkasy, UA	2259	1.370	0.399	insignificant	-
62. Kamyshin, RU	2274	1.413	0.404	insignificant	-

* growing degree days at the origin of the population. ** at $p > 0.05$.

The growth of populations that inhabit the mixed forest (nemoral) zone, mostly in Belarus, has been tested repeatedly in Western Europe. There, they stand out for excellent inherent growth potential and plasticity. Provenance 29., Lenino, Homel, BY, represents this metapopulation. The population displays a steep, linear reaction norm (Table 3) and a strongly increasing relative increment with the growing heat sum of the tests. Both indicate high resilience toward increasing heat stress and support the positive results in Western Europe.

The populations south of latitude 53° N are primarily endangered by projected warming in their lifetimes (Figure 7). The tests belong mostly to the southern part of the test network; thus, the regression equations cover a narrower thermal range (Figure 4).

The nearly identic presence of populations in the investigated test sites permits a realistic comparison of reaction norms of provenances from the East European xeric limit of Scots pine. The response parameters (Table 3) display predominantly linear equations. All populations increase their growth linearly toward warmer sites, especially at the warmest test sites, where they show no major vitality loss. For example, the southernmost provenance, 40. Slovyansk, Donetsk, UA, displays a typical steep and linear reaction norm, tolerating even the warmest sites outside the range (nr. 102, 12; Figure 4). At Hungarian site nr. 102, the performance of South Ukrainian populations corresponds to that of the "local" Hungarian provenance (nr. 37, 39, 40 vs. 999; Figure 5D).

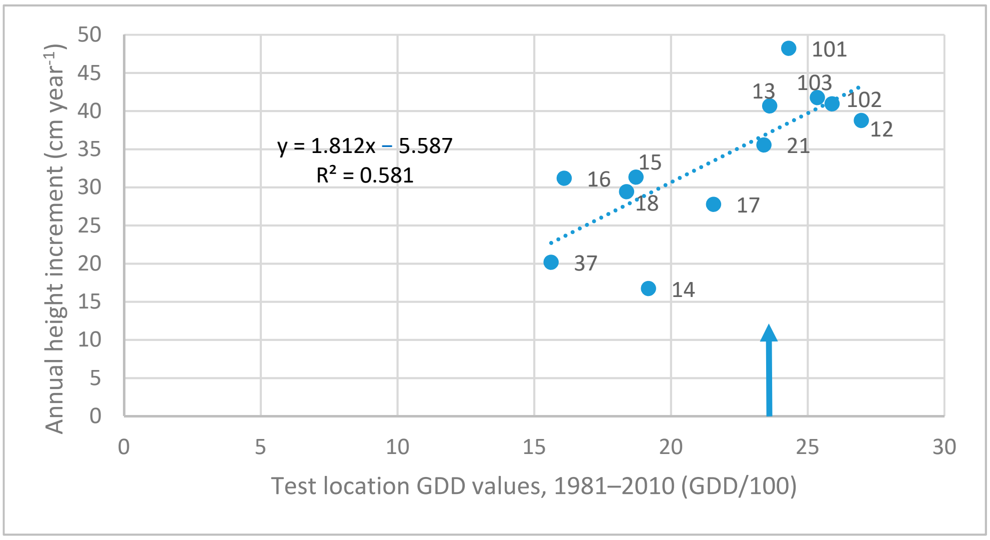


Figure 4. Linear reaction norm of the mean annual increment (cm) vs. test location degree days (GDD/100) of the southernmost Ukrainian provenance 40. Slovyansk, Donetsk, UA (latitude 48.83° N). The arrow marks the degree days at the origin (2392 GDD). Numbers show codes of test locations (see Table A1).

Compared to the equations of the northern sources, few southern provenances display significant quadratic responses. The reason is the broader climatic range of tests for the northern group, which covers a difference of over 2000 GDD (see also Section 3.4). Regarding phenotypic plasticity, there is no basic difference between the responses of northern and southern provenances.

The relationship between *inherent growth potential* and the heat sum at origin was investigated in all populations. "Virtual mean increments" (see explanation, Figure A1) of populations were regressed against the heat sum at their origin. Figure A1 shows a significant, quasi-linear correlation between heat sum and growth potential at the origin. Only the populations on the southern xeric limits (nr. 39, 40, 60, 62) display a slight decrease in inherent growth potential, which is possibly the trade-off effect of a higher heat and drought tolerance at the cost of reduced growth [29]. A similar linear relation between aridity at the origin and the inherent growth potential of provenances was detected in sessile oak [30].

3.3. Investigation of Transfer Functions

Data from transfer equations are presented for nine VNIILM and Hungarian test locations (Table 4). The first five tests containing boreal and central sources cover the cooler part of the investigated climate space, and their results are of lesser interest. The hottest test sites, 12. Oleshky, UA, and the three Hungarian tests (nr. 101, 102, and 103), beyond the natural distribution limits of Scots pine, are the most valuable "anchor point" locations to investigate the climate stress tolerance of populations.

Contrary to the usual bell-shaped quadratic equations in provenance test analyses, the transfer equations in this study show alternate forms and an obvious dependence on the climatic position of the test sites (Figure 5A–D).

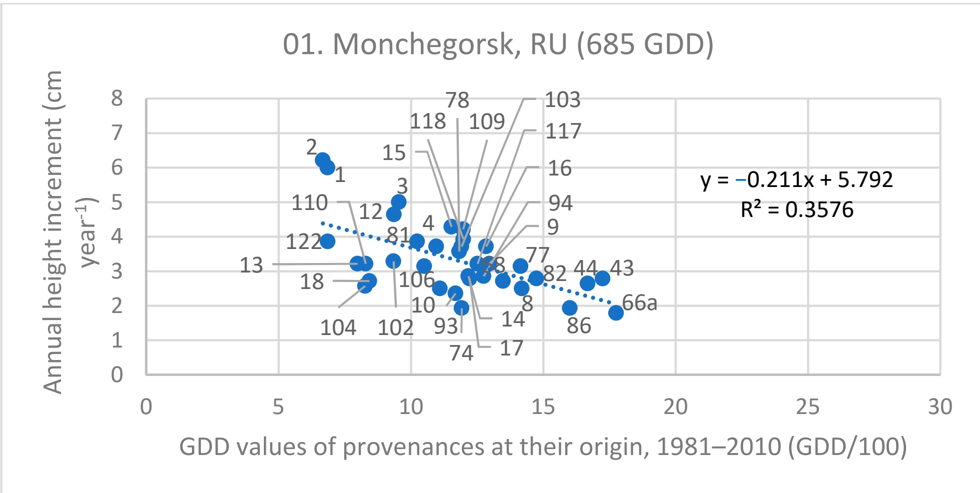
The coldest boreal site, 01. Monchegorsk, RU (Figure 5A), located at the thermal (front) limit, shows the only linear transfer equation with an (insignificant) negative slope; i.e., the best adapted, geographically and climatically closest ("local") populations 1 and 2 performed best. All other populations were transferred to a site *colder* than the original, except for 122. Ayan, Khabarovsk, RU. This geographically most distant but climatically close East Siberian provenance from the Pacific coast has also shown a relatively "good" mean increment (3.8 cm year^{-1}).

Table 4. Transfer equations of the mean annual height increment (Z) of a set of populations at individual test sites vs. annual degree days at their origin (GDD). The test sites are ranked by their GDD values. Insignificant values ($p > 0.05$) are marked in italics (see also Figure 5).

Test Sites and Their GDD Value		Z cm year^{-1}	Linear Equation		Quadratic Equation	
Code, Name, and Country	**GDD**		**Slope**	**R^2**	**Parameters of x**	**R^2**
01. Monchegorsk, RU	685	3.34	*−0.211*	0.358	insignificant	-
02. Plesetsk, RU	1095	19.00	insign.	-	$-0.133x^2 + 3.034x$	*0.222*
07. Lisino, RU	1420	33.12	insign.	-	$-0.284x^2 + 9.231x$	*0.281*
16. Kovrov/Vladimir, RU	1609	30.30	0.369	*0.137*	$-0.075x^2 + 2.685x$	*0.293*
17. Davydovka/Voronezh, RU	2156	25.78	0.612	0.475	$-0.030x^2 + 1.556x$	0.507
101. Recsk, HU	2431	45.66	0.773	0.382	$-0.069x^2 + 3.2375x$	0.423
103. Kerkafalva, HU	2535	43.81	0.733	0.294	insignificant	-
102. Egyházashetye, HU	2589	40.02	1.082	0.545	$-0.067x^2 + 3.2696x$	0.608
12. Oleshky, UA	2696	33.45	1.290	0.311	insignificant	-

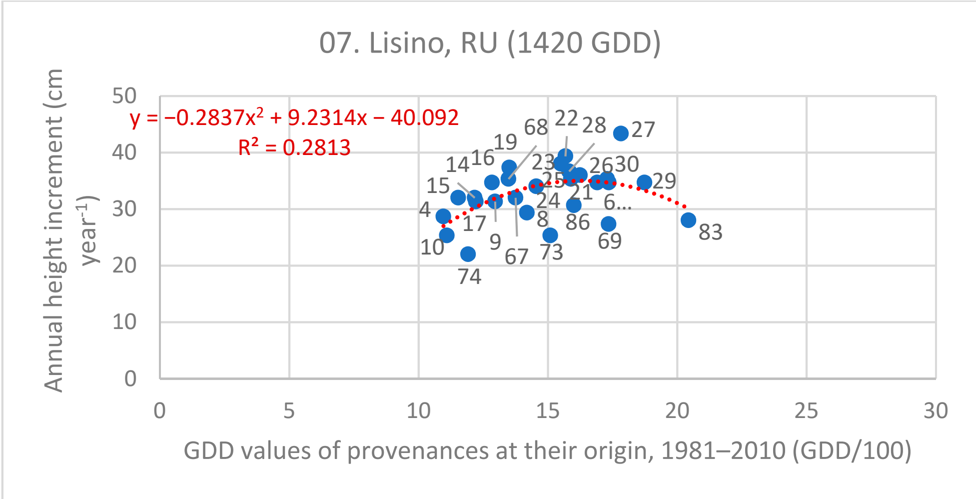
The milder test sites (02 and 07) display quadratic transfer equations, although of low significance. In test 07., Lisino, RU (Figure 5B), the local provenance (19) shows an "adaptation lag" vs. more southern provenances. The other investigated Russian experiments (nr. 16, 17) show similar linear equations where the quadratic versions contribute only modestly to the regression fit (Figure 5C).

The equations of the Hungarian trials and Oleshky (12) also display a minor or insignificant quadratic component. Hungarian test 102. Egyházashetye displays the most remarkable transfer equation (Figure 5D), illustrating the vitality of populations close to the critical limit. It shows the poor growth of boreal provenance 02., Kandalaksha, RU, which is, nonetheless, still surviving in the hot climate, but also the superior performance of the southernmost Ukrainian populations (nr. 36 to 40) and of "local" provenance 999. Pornóapáti, HU. The mentioned provenances cause the minor quadratic effect. The transfer equations reveal that their configuration and orientation are not necessarily bell-shaped but *depend on the set of populations present in the test and the site position* in the climatic space of the species range. *None of the tests* displayed clear limits of survival.



(**A**)

Figure 5. *Cont.*



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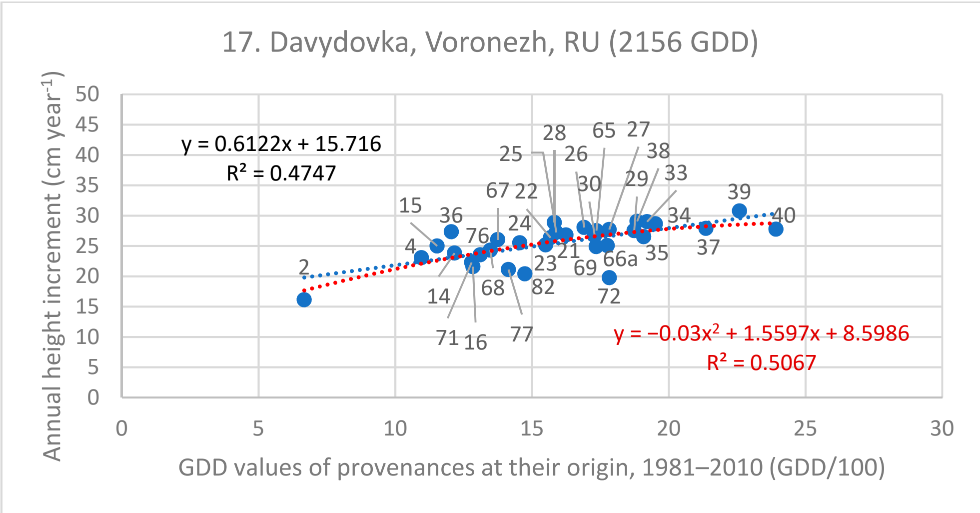

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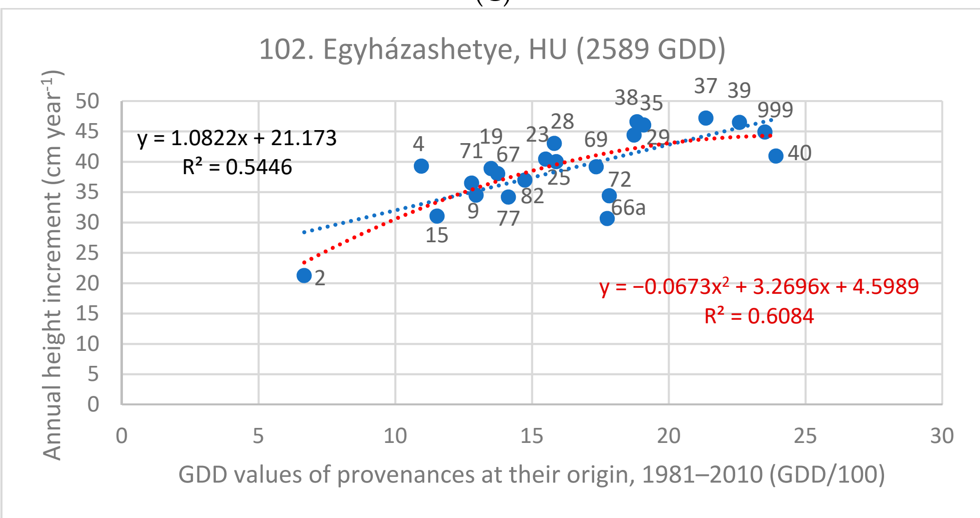

(**D**)

Figure 5. (**A–D**) The shift of transfer equation shapes from quasi-linear to quadratic, depending on the position of the trials in the climatic space of the species range. The figures show regressions of the annual height increment of populations (cm) at four trial sites vs. the degree days at their origin (GDD/100). Numbers show provenance codes (see Table A1).

3.4. Stress Test of Populations in Future Climates

The last step to estimate the future performance of provenances is their climatic positioning in the context of projected climatic changes. The recent climate of provenances at their origin and their projected climates in the same geographic position were placed into the two-dimensional climatic space of annual precipitation and growing degree days. Figure 6 illustrates the climatic positions of populations in the three time periods. Accordingly, three positions appear for every selected population.

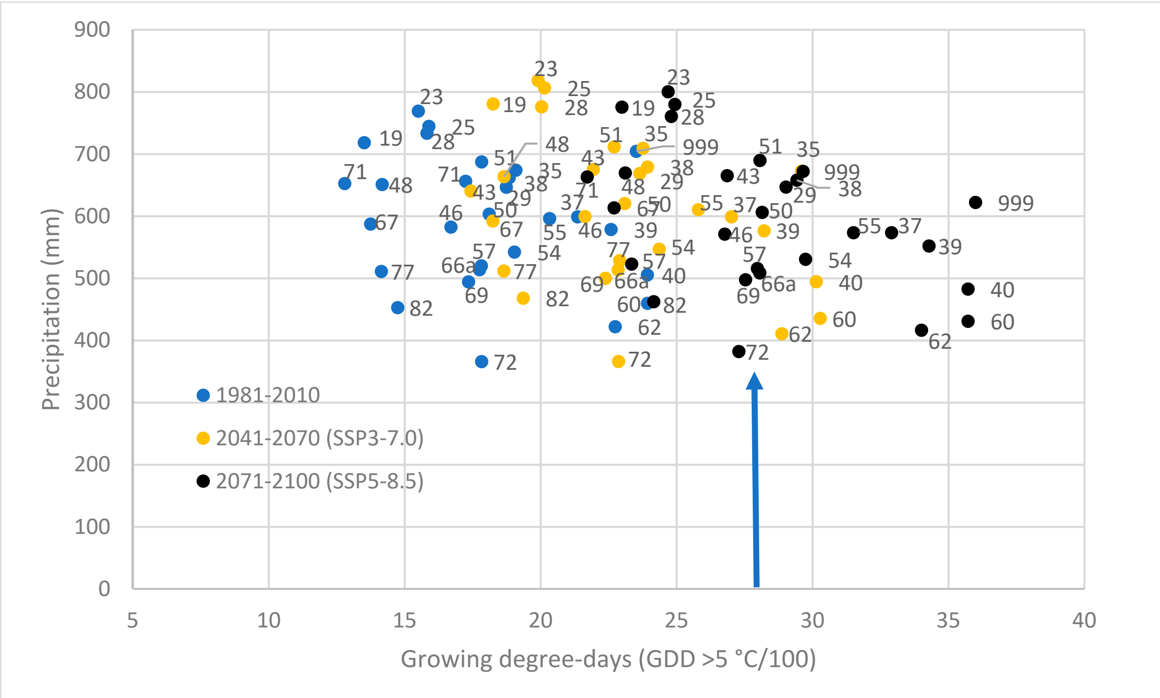

Figure 6. Past and future climates of selected populations at their original location in the climate space of annual precipitation vs. growing degree days (GDD >5 °C/100) for the recent climate period 1981–2010 (blue) and two CHELSA scenarios, SSP3-7.0 for 2041–2070 (orange) and SSP5-8.5 for 2071–2100 (black). All climate data were calculated for the respective period at the original location of the population. Numbers show provenance codes (see Table A2). The arrow points to the critical limit of 2800 GDD. Only a selection of the analyzed populations is shown in the figure.

In the absence of climate-related mortality results, an estimate was required to predict the critical limit of survival of the populations (see the explanation in Section 2.6). The drawing of the survival limit was based on field inventory data for afforestation of Scots pine in Hungary. The species was introduced across practically all actual climate zones as part of a national afforestation program. A forest habitat subzone, virtually devoid of successful plantations and situated at the limit of the forest–steppe climate zone, was identified in the south of the country, in the Körös-Maros interfluvial plateau, which is covered by chernozem soils on loess bedrock, with adequate water-holding capacity, i.e., representing climate-zonal conditions. Its recent climate served for setting the limit at 2800 GDD in terms of annual heat sum (CHELSA data for 1981–2010) and was used as an "anchor value" for the critical survival limit (Figure 6).

The projected climatic conditions of most central and northern populations are below the critical limit of 2800 GDD, even in the worst-case scenario for the 2071–2100 period. Consequently, the provenances mostly north of latitude 53° N or from higher elevations (36. Rakhiv, Lviv, UA) will respond to warming with unbroken growth until the end of the century (marked green in Figure 7).

A few southern provenances appear in predicted climatic positions that exceed the limit during scenario SSP3-7.0 for 2041–2070 (marked red in Figure 7). Although they display mostly linear reaction norms, provenances 39, 40, 60, 62, and 999 will be endangered at their original location around the middle of the century (Table 3). Transcaucasian provenance 126., Tovuz, Azerbaijan (elev. 730 m, Table A1), also belongs to this group. The rest (marked yellow in Figure 7) may suffer from decline and mortality at their original sites but only by the end of the century, in the 2071–2100 period. The pattern indicates a clear zonation of critical climatic position by GDD value and latitude, respectively. In general, vulnerable populations are found south of latitude 53° N and the most endangered are isolated occurrences in the forest–steppe zone, south of 50° N, including Hungarian provenance 999 (Figure 7).

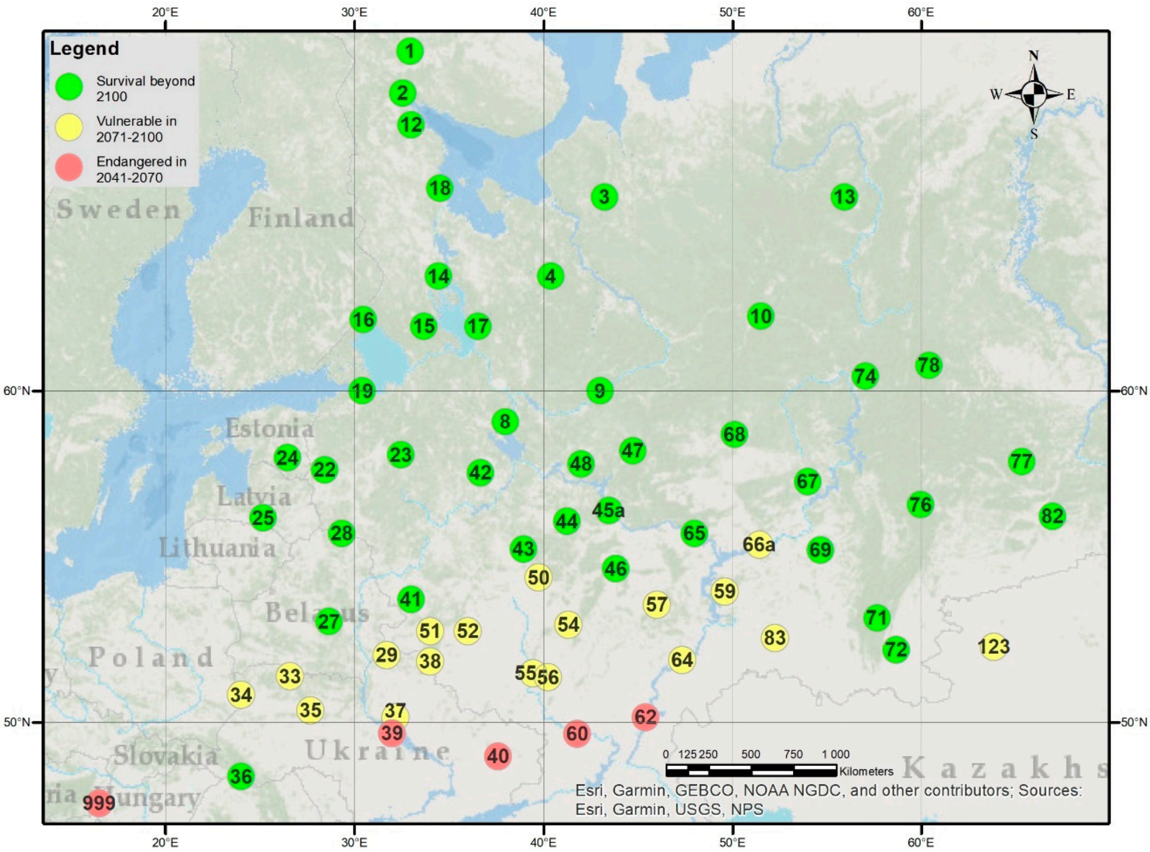

Figure 7. Map of Northeast European Scots pine provenances analyzed in the study (see Table A2). The colors represent their projected status in the 21st century at their original location: survival and accelerated growth beyond 2100 (green), vulnerable in the 2071–2100 (yellow) period, and endangered in the 2041–2070 (red) period. The gray shading roughly depicts the contiguous range of the species.

4. Discussion

4.1. Literature Background of Growth and Survival Projections in Northeast Europe

Future performance estimations for Northeast European Scots pine populations in a warming world are controversial. It has been predicted that climate warming may threaten survival [31] and cause premature growth onset in the species [32]. Physiological research has proven that this will not occur [33]. Populations at the geographical limits of distribution were generally considered more susceptible to climatic changes [34]. Recent Scandinavian investigations [35,36] remarked upon the high plasticity of Scots pine, predicting increased survival and growth in the north. Earlier analyses of the VNIILM experiment [19] have also documented that warming does not automatically trigger a decline in vitality; however, the models indicated bell-shaped responses. In a nursery test, seedlings from stands at the extreme northern limits of the species responded with faster growth to higher temperatures, but higher precipitation had no effect. At the same time, seedlings of extreme southern provenance were best adapted to survival in drier conditions [37], but at their original sites, the improvement of resilience through assisted migration is not applicable due to the lack of climate-matching populations [38].

Recent Russian sources formulate no unanimous opinion on the adaptive response of the species to climatic changes. Although new concepts in provenance research were presented in time in that country [16], the VNIILM provenance research [9,19,39] was not pursued further. While the necessity of defining new seed zones based on results from provenance tests was proposed [40], others [41] maintained the principle of "local is the best". A clear increase in future growth rate has been predicted [42] based on local provenance tests north of latitude 59° N. The issue of growth decline was raised at the xeric limits of the distribution in the south of Ukraine [43], but without relying on data from provenance tests. A dramatic loss of forest cover was predicted [24,44] for the climatically analogous forest–steppe zone of South Siberia; however, a newer physiological analysis yielded ambiguous results for Scots pine [45].

4.2. Discussion of Results

4.2.1. Linearity of Growth Response to Warming

Linear reaction norms (response equations) seem to contradict the conceptual model of phenotypical response along an ecological gradient, which describes the response with rather symmetric, bell-shaped quadratic equations and clear maxima. Undoubtedly, the obtained linear equations are statistical simplifications and depict quasi-linear sections of a quadratic response function, the clearly nonlinear part of which remained mainly undetected. Obviously, the test conditions were not extreme enough, although four test sites of the study are situated far outside the range of the species. This indicates considerable reserves for adaptation.

The quasi-linear growth acceleration effect of warming is also supported by the finding that the onset of growth of Scots pine in spring is triggered mainly by accumulated heat. The cessation of growth is less fixed and is related to the joint effect of photoperiod and temperature [36]. Similar phenomena have been found not only in conifers, such as the Norway spruce [46] and silver fir [47], but also in broadleaved species, such as beech [48,49] or sessile oak [30,50].

The combination of quasi-linear reaction norms and quadratic transfer functions adds up to an adaptive response surface for the climate space covered by the tests. The transfer equations represent "crosscuts" of the quasi-linear reaction norms. *Their configuration and orientation depend on the sampled set of populations in the test and on the position of the test site in the climatic space of the species range*. Similarly, individual reaction norms depend on the ecological/climatic alignment of the populations within the species range and the involved tests that determine the equation (Figure A2). Thus, the origin and range of the data must be considered in interpretations.

This phenomenon was described first for jack pine [4] (Figure A2) and has led to the rediscovery of provenance tests as valuable sources of field-based information on phenotypic plasticity and to the interpretation of the results as responses to mimicked climate change [4,5,7,51].

4.2.2. Effective Phenotypic Plasticity Supported by Epigenetics?

The phenotypic variation pattern, adapted to climates at origin, is routinely attributed to Mendelian genetic processes [52]. The surprisingly linear pattern of growth responses, but also the remarkably close correlation of the recent heat sum at the origin with inherent ("virtual") growth (see Section 3.2 and Figure A1), raises the question of whether the phenotypic pattern of growth traits is generated exclusively by Mendelian heredity or is complemented by epigenetic effects.

Forest genetic research has confirmed traces of epigenetic effects in adaptive traits [53], first in Norway spruce [54,55] but also in Scots pine [56–58]. These findings indicate that epigenetics may play a role through "shortcutting" adaptation to the rapidly changing environment for Scots pine, although the magnitude of contribution to Mendelian genetic processes is still unclear. Most probably, the disregarding of epigenetic effects may exaggerate estimations of time needed for adaptation and lead to inflated inferences of generation numbers. An earlier analysis of the VNIILM test estimated a "generic lag" of up to 1500 years to match global warming in Northern Eurasia [19].

4.2.3. Limitations of the Study

Several compromises had to be accepted when dealing with historical data from an experiment designed and built on other concepts nearly 50 years ago. A shortcoming of all climate-based analyses of provenance tests is the missing site data (soil, hydrology). Unexplained site factor differences contribute to a huge random variation in all provenance tests, making the genetic contribution to growth appear small [11].

Regarding climate, only periodic averages were investigated, and temporal and spatial anomalies [59], including the effect of changing photoperiod due to transfers, were ignored. Predictions about the future performance of the species are based on currently valid scenarios. The critical tolerance limit had to be estimated indirectly. Further, the responses of provenances measured in the early adult stage do not fully represent the entire life cycle; thus, projections may be over-optimistic [60]. Survival records could have improved the predictive power of the provenance test, but the source paper [39] contains data unsuitable for analysis. The analysis of plotwise survival data at age 22 in Hungarian test 102. Egyházashetye did not provide noteworthy results either.

The present study concedes statistical limitations but considered the analysis reasonable because the results emerged from data from many populations tested in numerous field tests that have shown coherent results. Related to predictive models that use polynomial quadratic functions [11,19,22], the results of this study, which applied a simpler univariate approach, are statistically comparable.

5. Conclusions for the Future of Scots Pine in Northeast Europe

The study provides general information for a large ecologically and economically vital part of the vast range of the species. It confirms the distinct role of phenotypic plasticity in future adaptation. The selected analysis variable, heat sum (annual growing degree days above 5 °C, GDD), has shown a strong correlation with vitality (height growth) of populations tested under different climate conditions. The correlation of recent heat sum at the site of origin with the inherent growth potential of populations is also highly significant (Figure A1). The results substantiate the noteworthy effect of the test site conditions on the configuration of response and transfer equations (Figure 5A–D).

The alternative analytic approach revealed that the quasi-linear reaction norms (response equations) of the investigated populations display no ecological optima in the studied climate space. Contrary to earlier analyses of the species, adaptation to fluctuating environments does not lead to clear optima in a lock-and-key fashion [61,62]. The response patterns are the result of a complex process of tracking temporal and spatial variations in the physical and biotic environment of the past.

The responses confirm a general growth acceleration north of Lat. 53° N, according to the climatic projections for this century (Figure 7). Phenotypic plasticity (including assumed epigenetic effects) may also grant proper acclimation for the offspring generation. This is especially valid for the boreal and superboreal populations and indicates considerable reserves for adaptation (Figures 2 and 3).

However, these optimistic predictions are invalid in the southern part of the range. Climate-triggered mortality may appear along the xeric (trailing) limits of the species in the coming decades. The provenances marked vulnerable (yellow) and endangered (red) in Figure 7 delineate the approximate borders of critical zones. Except for ecologically sheltered sites, the long-term maintenance of Scots pine stands will not be practicable in the endangered zone due to the lack of climate-matching populations.

The significance of local adaptation at both limits of the distribution range has been documented (Figure 5A,D) and should be considered for management decisions. In the milder boreal and central zone, the growth of local provenances shows an "adaptation lag" compared to the performance of more southern provenances (Figure 5B). The steep slopes of reaction norms of some isolated southern occurrences (nr. 39, 40, 60; Table 3) indicate their high heat and drought tolerance and plasticity, which are also apparent far beyond the distribution limits of the species (Figure 4).

The study findings indicate that the phenotypic plasticity of Scots pine populations may buffer and even benefit from temperature increases in a large part of the range, despite rapid climate changes, as long as a sufficient amount of precipitation is available. Excluding other threats such as wildfires, methane, and carbon dioxide seeping from the soil, this phenomenon could nurture expectations of increasing carbon sequestration. Considering the logistic and financial hurdles of the large-scale application of assisted migration, the management supporting spontaneous adaptation processes seems sufficient in the northern part of the studied region until the end of the century. Evacuating valuable resilient populations should be envisaged in regions where the species is vulnerable to or endangered by declining growth and rising mortality in the coming decades.

Outside the study area examined, in the western and southern part of the European range of Scots pine, geographical diversity and legislative fragmentation are significantly greater (thirty states share the species' range). This hinders the implementation of systematic sampling and large-scale field analysis on a scale similar to the present study. The methodologically diverse studies focus mainly on expected range shifts and the persistence of specific populations on a regional level, and most apply growth models to project future conditions. The models predict an overall increase in growth and carbon stock in the northern part of the range [35,37,63,64] and at altitudinal treelines, indicating the dominant effect of temperature. Compared to other boreal species, Scots pine displays greater adaptability and responsiveness to silvicultural management [65]. In contrast, growth models of low-elevation Mediterranean populations signal a decline due to warming [66]. There, effects of climatic stress may be reduced by management, e.g., by stand density regulation [67]. In summary, growth models and other data from different sources substantiate the results of the present study.

Research results also indicate the existence of similar climatic response phenomena in many other species [12]. These experiences may significantly contribute to shaping the climate change strategy in silviculture and nature conservation [68,69] to ensure the long-term resilience of forests in a rapidly changing world [10,70].

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Data Availability Statement: Original data from the VNIILM experiment are accessible in the source publications [9,39]. The English transliteration of Cyrillic location names differs from the spelling used in the original papers. To facilitate comparisons with the original sources, the number codes of test sites and provenances were not changed.

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

Appendix A. Tables of Revised Data and Figures on Growth Response

Original geographic coordinates of test sites and provenances have been revised and digitalized. The country and location names with respect to states that were formerly part of the USSR are valid as of 1 January 2022. Test locations and provenances outside the study region are listed only if explicitly mentioned in the text or appearing with code numbers in figures.

Original data from the VNIILM experiment are accessible in the source publications [9,39]. The English transliteration of Cyrillic location names differs from the spelling used in the original papers. To facilitate comparisons with the original sources, the number codes of test sites and provenances were not changed.

Table A1. Revised data from analyzed test sites (not all appear in the study).

Nr., Location and District, Country Code	N. Latitude Decim.	E. Longitude Decim.	Elevation (m a.s.l.)	GDD 1981–2010 (CHELSA)	P_{ann} (mm) 1981–2010 (CHELSA)	Z * (cm year^{-1})
1. Monchegorsk, Murmansk, RU	67.850	32.950	126	685.1	681	3.3
2. Plesetsk, Arkhangelsk, RU	62.900	40.400	108	1095.9	716	19.0
3. Cherepovets, Vologda, RU	59.250	37.333	114	1382.7	653	32.6
4. Kortkeros, Komi, RU	61.812	51.532	95	1149	691	16.3
5. Chupa, Karelia, RU	65.950	33.500	114	840.3	681	12.5
6. Medvezhyegorsk, Karelia, RU	63.000	34.050	119	1132	762	9.3
7. Lisino, Saint Petersburg, RU	59.500	30.867	53	1420.8	704	33.5
8. Pskov, Pskov, RU	57.833	28.433	54	1567.6	720	31.8
9. Järva, Järva, EST	59.517	25.500	32	1401.3	696	9.1
11. Lenino, Homiel, BY	52.194	31.000	124	1910.8	635	39.7
12. Oleshky, Kherson, UA	46.500	32.500	7	2696.6	437	33.6
13. Izyum, Kharkiv, UA	49.168	37.312	73	2361.2	536	36.1
14. Sambir, Lviv, UA	49.523	23.327	317	1918.2	788	25.9
15. Olevsk, Zhytomyr, UA	51.235	27.624	195	1872	710	32.6
16. Kovrov, Vladimir, RU	56.396	41.357	121	1609.4	629	28.8
17. Davydovka, Voronezh, RU	51.152	39.421	90	2156	556	24.4
18. Lunino, Penza, RU	53.592	45.246	128	1838	553	34.9
21. Kamyshin, Volgograd, RU	50.072	45.363	113	2340.4	419	32.4
22. Zelenodolsk, Tatarstan, RU	55.865	48.520	106	1684.8	545	45.8
23. Ufa, Bashkortostan, RU	55.000	56.000	80	1810.5	667	24.4
24. Kungur, Perm, RU	57.433	56.750	145	1455.2	589	33.8
25. Revda, Yekaterinburg, RU	56.833	59.967	298	1310.8	552	35.6
26. Zverinogolovskoye, Kurgan, RU	54.783	64.967	80	1783.1	374	39.2
27. Buzuluk, Samara, RU	53.000	52.000	81	1991.1	559	39.0
29. Suzun, Novosibirsk, RU	53.767	82.333	154	1614.7	436	40.7
30. Boguchany, Krasnoyarsk, RU	58.350	97.500	421	1129.1	473	21.1
31. Turukhansk, Krasnoyarsk, RU	66.000	89.000	46	831.3	972	16.4
32. Zaudinsk, Buryatiya, RU	51.833	107.667	507	1521.3	253	11.0
34. Svobodny, Amur, RU	51.398	128.077	199	1696.8	591	11.7
35. Urumkai, Kokshetau, KZ	52.500	69.833	412	1538.4	378	20.3
36. Dolon, Semey, KZ	50.667	79.333	163	2176.5	259	26.9
37. Shaki, Shaki, AZ	41.283	47.200	1369	1561.9	1033	20.4
101. Recsk, Heves, HU	47.930	20.120	179	2431.1	607	43.5
102. Egyházashetye, Vas, HU	47.170	17.120	134	2589.6	668	38.2
103. Kerkafalva, Zala, HU	46.770	16.490	196	2535.5	752	42.7

* mean annual height increment of populations represented in the test. It represents an estimation of site potential.

Table A2. Revised data from analyzed provenances (not all appear in the study).

Nr., Location and District, Country Code	N. Latitude Decim.	E. Longitude Decim.	Elevation (m a.s.l.) (WC2.1)	GDD 1981–2010 (CHELSA)	P_{ann} (mm) 1981–2010 (CHELSA))	Z_{ann} * (cm year^{-1})
1. Monchegorsk, Murmansk, RU	67.850	32.950	126	685.1	681	9.0
2. Kandalaksha, Murmansk, RU	67.000	32.550	0	667.1	825	7.5
3. Pinega, Arkhangelsk, RU	64.750	43.233	66	954.7	765	12.6
4. Plesetsk, Arkhangelsk, RU	62.900	40.400	108	1095.9	716	18.1
8. Cherepovets, Vologda, RU	59.167	38.000	103	1419	663	25.0
9. Totma, Vologda, RU	60.000	43.000	126	1296	632	23.8
10. Kortkeros, Komi, RU	61.917	51.500	124	1109.4	709	10.1
12. Chupa, Karelia, RU	66.333	33.000	4	936	722	10.9
13. Kadzherom, Komi, RU	64.750	55.917	128	798.2	875	
14. Medvezhyegorsk, Karelia, RU	62.900	34.450	23	1216.9	763	18.6
15. Pryazha, Karelia, RU	61.667	33.667	166	1153	798	18.3
16. Sortavala, Karelia, RU	61.833	30.467	61	1283.8	715	19.4
17. Pudozh, Karelia, RU	61.667	36.550	87	1221.5	871	19.6
18. Kem, Karelia, RU	64.950	34.517	21	843.3	588	7.8
19. Lisino, St. Petersburg, RU	60.000	30.417	31	1350.9	718	23.9
21. Velikie Luki, Pskov, RU	56.383	30.500	91	1624.2	651	
22. Strugi Krasnye, Pskov, RU	57.833	28.433	54	1567.6	720	
23. Kresttsy, Novgorod, RU	58.250	32.467	67	1549.9	769	26.3
24. Elva, Tartu, EST	58.167	26.467	98	1455.3	695	
25. Jelgava, Jelgava, LAT	56.450	25.167	79	1588.7	745	31.2
26. Prienai, Kaunas, LIT	54.700	23.967	100	1690.8	698	
27. Asipovichi, Mahiljov, BY	53.300	28.667	144	1782.4	631	
28. Rasony, Vitsebsk, BY	56.000	29.333	157	1582	734	30.8
29. Lenino, Homel, BY	52.233	31.717	154	1873.7	647	33.7
30. Sionim, Hrodna, BY	53.417	25.250	156	1729.1	695	
33. Dubrovitsya, Rivne, UA	51.533	26.600	146	1920.8	645	
34. Sambir, Lviv, UA	50.917	24.000	178	1951.3	646	
35. Olevsk, Zhitomir, UA	50.400	27.667	226	1908.8	674	33.3
36. Rakhiv, Lviv, UA	48.117	24.000	965	1205.1	1361	
37. Borispil, Kyiv, UA	50.167	32.167	116	2136.2	599	38.5
38. Svesa, Sumi, UA	52.017	34.000	163	1884.4	662	35.5
39. Cherkasi, Cherkasi, UA	49.617	32.000	96	2259.1	579	38.4
40. Slovyansk, Donetsk, UA	48.833	37.600	64	2392.2	506	37.8
42. Bezhetsk, Tver, RU	57.750	36.667	128	1470.9	634	
43. Orekhovo-Zuyevo, Moskva, RU	55.533	38.950	124	1724.3	656	34.2
44. Kovrov, Vladimir, RU	56.350	41.250	83	1667.4	616	
46. Pervomaysk, Nizh. Novgorod, RU	54.933	43.833	181	1670	583	33.9
47. Manturovo, Kostroma, RU	58.367	44.733	132	1424.1	647	
48. Kostroma, Kostroma, RU	58.000	42.000	156	1417	651	
49. Kaluga, Kaluga, RU	54.417	36.267	194	1640.2	712	
50. Solotcha, Ryazan, RU	54.667	39.750	101	1810.3	603	33.7
51. Gavan-Kukuyevka, Bryansk, RU	53.000	34.000	160	1783.1	687	34.0
52. Orel, Orel, RU	53.000	36.000	200	1761.8	674	32.6
54. Sosnovka, Tambov, RU	53.200	41.333	137	1903.8	542	35.8
55. Grafskaya, Voronezh, RU	51.633	39.467	112	2033.1	596	36.9
56. Khrenovoye, Voronezh, RU	51.500	40.250	165	2022.3	572	34.2
57. Nikolsk, Penza, RU	53.833	46.000	154	1782	520	34.1
59. Melekess, Ulyanovsk, RU	54.233	49.583	83	1861.9	577	
60. Veshenskaya, Rostov, RU	49.600	41.800	56	2393	460	41.5
62. Kamyshin, Volgograd, RU	50.167	45.400	154	2274.2	422	38.4
64. Volsk, Saratov, RU	52.067	47.350	174	1975.1	628	
65. Vasilyevo, Tatarstan, RU	56.000	48.000	58	1735.6	504	
66a. Kamskie Polyani, Tatarstan, RU	55.667	51.433	52	1775.4	514	
67. Votkinsk, Udmurtia, RU	57.500	54.000	244	1374.9	588	
68. Slobodskoy, Kirov, RU	58.817	50.100	148	1347.6	719	

Table A2. *Cont.*

Nr., Location and District, Country Code	N. Latitude Decim.	E. Longitude Decim.	Elevation (m a.s.l.) (WC2.1)	GDD 1981–2010 (CHELSA)	P_{ann} (mm) 1981–2010 (CHELSA))	Z_{ann} * (cm year^{-1})
69. Dyurtyuli, Bashkortostan, RU	55.500	54.667	125	1734.8	494	
69a. Dyurtyuli, Bashkortostan, RU	55.500	54.667	125	1734.8	494	
70. Duvan, Bashkortostan, RU	55.700	57.900	312	1451.2	516	
71. Beloretsk, Bashkortostan, RU	53.417	57.667	605	1279.2	653	
71a. Beloretsk, Bashkortostan, RU	53.950	58.400	537	1317.5	537	
72. Zilair, Bashkortostan, RU	52.400	58.667	360	1782.8	366	
73. Okhansk, Perm, RU	57.700	55.417	92	1509.4	549	
74. Krasnovishersk, Perm, RU	60.383	57.050	128	1191.7	948	
76. Revda, Yekatyerinburg, RU	56.833	59.967	298	1310.8	552	
77. Tavda, Yekaterinburg, RU	58.067	65.300	52	1414.1	511	
78. Ivdel, Yekaterinburg, RU	60.667	60.400	86	1182.5	551	
79. Kurgan, Kurgan, RU	55.467	65.333	79	1699.8	396	
81. Surgut, Tyumen, RU	61.417	73.333	70	1023.7	671	
82. Zavodoukovsk, Tyumen, RU	56.500	66.950	129	1474	453	
83. Buzuluk, Orenburg, RU	52.783	52.250	72	2043.5	503	
123. Novonezhinka, Kostanay, KZ	52.500	63.833	205	1938.7	323	
126. Tovuz, Tovuz, AZ	41.000	45.500	881	2779.6	495	
999. Pornóapáti, Vas, HU	47.170	16.500	273	2351.9	704	

* mean annual height increment ("virtual mean increment") was calculated for the location of origin to characterize the inherent growth potential of provenances (see Section 3.2). Not all provenances had sufficient data to estimate the increment.

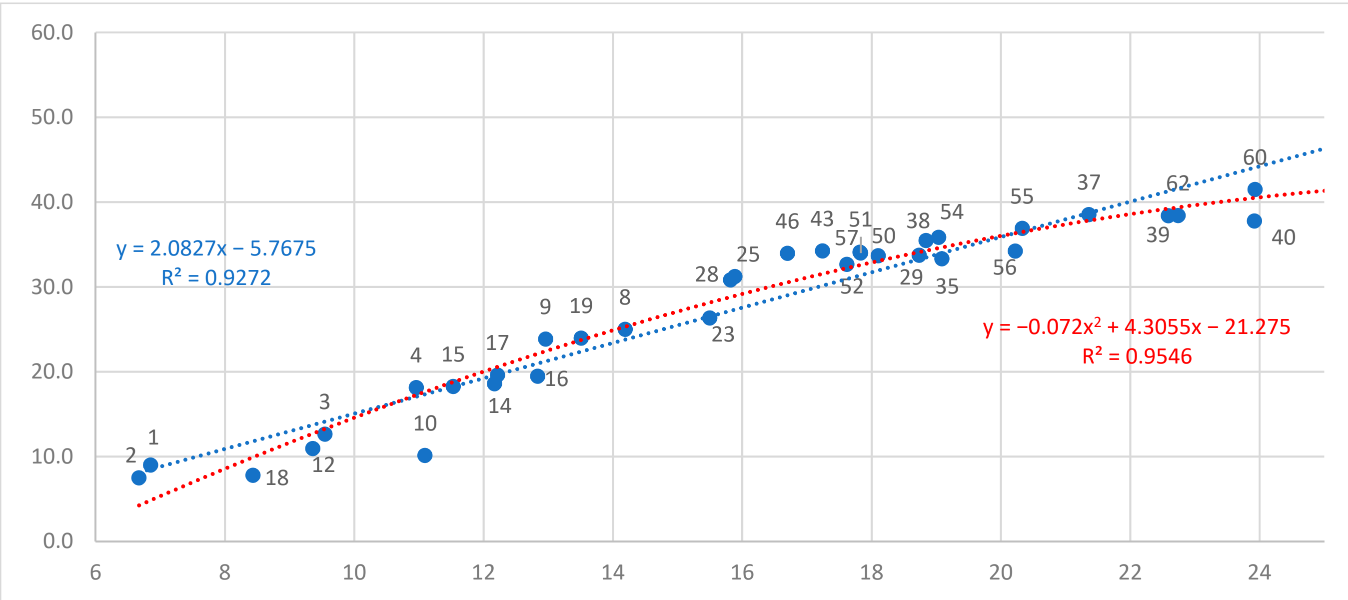

Figure A1. The pattern of inherent growth potential in the study area. Linear and quadratic regressions of the heat sum (GDD/100, x-axis) of provenances versus the inherent mean annual increment (cm year^{-1}, y-axis) are calculated for the location of their origin. The numbers indicate the code nr. of populations (see Table A2).

Inherent Growth Potential of Populations (Explanation for Figure A1)

The relation of inherent growth potential to the heat sum at origin was investigated for all analyzed populations. Linear reaction norm (response) equations were used for the calculation of "virtual mean increments". The virtual increment (i.e., the growth potential at the point of origin) was calculated using the respective response equation for the point of origin. For example, the GDD value of provenance 9., Totma, Vologda, RU, in Figure 3 is 1296 and the virtual mean increment is 23.8 cm year^{-1}, calculated from the linear equation.

Figure A2 shows that the transfer equations represent "crosscuts" of the quasi-linear reaction norms. Their configuration and orientation depend on the sampled set of populations in the test and on the position of the test site in the climatic space. Similarly, individual reaction norms also depend on the ecological/climatic alignment of the populations within the species range and the involved tests that determine the equation.

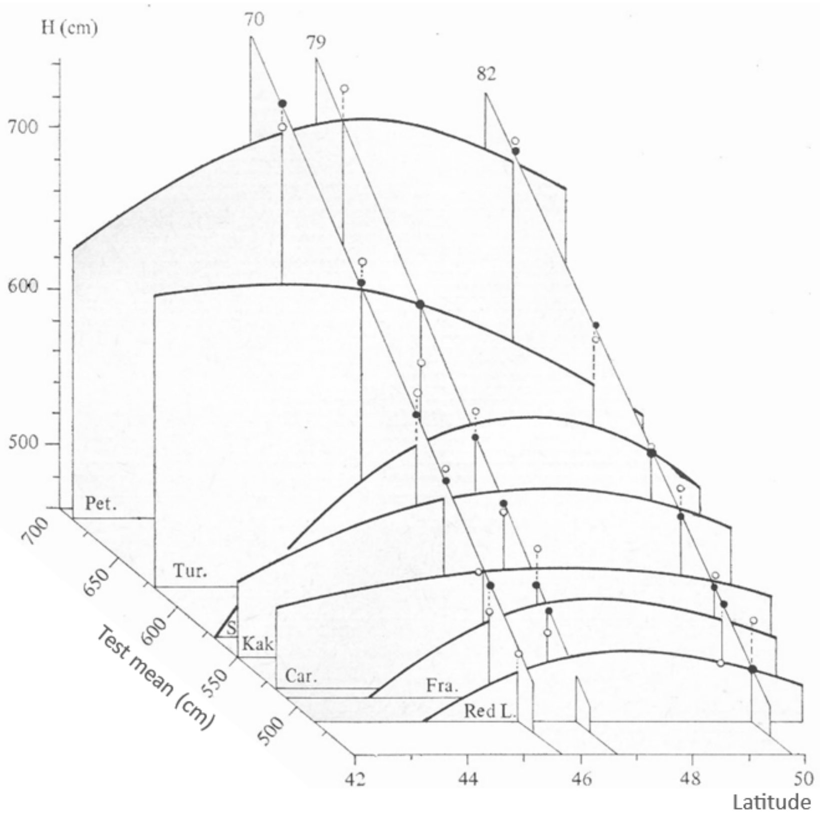

Figure A2. Axonometric image of a response surface, formed by quadratic and linear equations of 15-year height vs. latitude and site potential, measured in seven provenance experiments for jack pine (*Pinus banksiana* Lamb.) in Ontario, Canada. Quadratic transfer equations show the transfer equations of provenance heights (H; z-axis, in cm) vs. N. latitude (x-axis) and are arranged by site potential, i.e., by the mean heights (y-axis, in cm) of the seven tests (their abbreviated names appear in the respective left corner). Linear reaction norms with measured and predicted heights in the tests (empty and filled circles, respectively) are shown for three selected provenances (nr. 70, 79, 82). Reproduction from [4], with permission of the publisher.

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