Growth response of European larch (*Larix decidua* Mill.) populations to climatic transfer

By V. FOFF[1], F. WEISER[2], E. FOFFOVÁ[3] and D. GÖMÖRY[4,*]

Abstract

The study focuses on growth responses of *Larix decidua* provenances to climatic transfer based on a regional provenance experiment. This comprises a series of 5 trial plots situated in Germany and Slovakia, where 12 indigenous Sudetic and West-Carpathian larch provenances are planted. Transfer rates were defined as differences in altitudes or climatic variables between the site of plantation and the site of origin. 1st and 2nd-order polynomial regressions were used for the identification of overall trends of growth performance and responses to transfer.

Sudetic provenances clearly outperformed the Carpathian ones on all test sites. When all provenances were considered jointly, height and breast-height diameter mostly showed significant monotonous geographical and climatic trends: the performance generally decreased with increasing altitude and precipitations and decreasing temperatures. The relationships between growth response and transfer rates (ecodistances) were mostly linear. However, when Sudetic and Carpathian provenances were considered separately, most significant response curves were unimodal. There is a very good correspondence between the responses in height and diameter growth within geographic groups, but the responses are not consistent between groups. Joint regression analysis showed that most provenances exhibited average stability. Stability indices are quite consistent between the response traits and did not show any association with the geographical position, climate of origin, or growth performance.

The results indicate that populations in different climates remain adapted to a common optimum, the extent of local adaptation is quite limited. Possible explanations of this observation are briefly discussed.

Key words: Larix decidua, local adaptation, phenotypic plasticity, provenance research, climatic transfer.

Introduction

Forest tree species as long-lived perennials are exposed both to spatially heterogeneous environments and environmental fluctuations during their lifetimes. Recently, human-induced global climatic processes have not only changed spatial patterns of temperatures, precipitation and other biologically relevant climatic parameters, but also generated more frequent occurrence of hardly predictable extreme events such as long-term droughts, extremely snowy winters, black frosts etc. (IPCC, 2007). Biological systems, including tree populations, have not many options under such situation: if they cannot accommodate to the new situation at the original location or migrate, they are endangered by becoming extinct (AITKEN et al., 2008). In order to persist at the location of origin without migration, trees may rely on phenotypic plasticity or change their genetic structures through natural selection (KAWECKI and EBERT, 2004; LEIMU and FISCHER, 2008). These two strategies are mutually exclusive, at least partially: the capability of a genotype to be expressed in different phenotypes under different environments (relying on environment- dependent modification of gene expression levels) helps it in escaping the selection pressure (GIMENO et al., 2009).

In forest science, phenotypic responses of genotypes to environmental changes have traditionally been studied by provenance experiments. Transferring populations of different origin into the common conditions of each experimental site, aimed to eliminate environmental effects on phenotypic traits of interest, may be regarded as a sort of space-for-time substitution: trees are grown under climates which may occur in the future in their sites of origin. Modern provenance experiments often comprise numerous provenances (sometimes covering the whole range of a species) repeatedly planted on series of trial plots under a wide range of environments (cf. KRUTZSCH, 1992; WEISGERBER and ŠINDELÁŘ, 1992; ALIA et al., 2011). Such experimental setups allow testing of the reactions of provenances to transfer, helping to determine both the environment where a particular provenance performs best, and the optimum provenance for a particular site. If data from such broadly designed provenance trials are available, climate-related responses of tree populations may be assessed by general transfer functions and population response functions (REHFELDT et al., 1999; AITKEN et al., 2008). Both approaches rely on the relationship between survival, growth or other fitness-related traits of the planted trees and geographic or climatic distances between provenances and trial site locations. The simplest way for defining ecological distance is taking the difference of geographic coordinates or climatic characteristics between the site of origin and the site of plantation (MÁTYÁS, 1994). Transfer functions can be used both

[1] Forest Information Agency, ČSA 396/13, 033 01 Liptovský Hrádok, Slovakia.

[2] Institut für Forstgenetik, J.H. von Thünen Institut, Eberswalder Chaussee 3a, D-15377 Waldsieversdorf, Germany.

[3] National Forestry Centre, TG Masaryka 22, 96092 Zvolen, Slovakia.

[4] Technical University in Zvolen, Faculty of Forestry, TG Masaryka 24, 96053 Zvolen, Slovakia.

[*] Corresponding author: DUŠAN GÖMÖRY. Technical University in Zvolen, Faculty of Forestry, TG Masaryka 24, SK-96053 Zvolen, Slovakia. Phone +421-45-5206226, Fax: +421-45-5332654. E-Mail: dusan.gomory@tuzvo.sk

directly for provenance recommendation and indirectly for improving the delineation of provenance regions or other transfer rules for forest reproductive material (UKRAINETZ et al., 2011).

European larch (*Larix decidua* Mill.), as a species with fragmented distribution range, is expected to exhibit a strong genetic differentiation among local and regional subpopulations and thus a strong geographic variation in silvicultural traits (MATRAS and PÂQUES, 2008). This is why it has been the object of provenance research from the very beginning of large provenance experiments coordinated by the International Union of Forestry Research Organizations (IUFRO). The first international experiment with this species was even organized by R. Schober during the wartime in 1944, and was succeeded by a later experiment in 1958 (GIER-TYCH, 1979; WEISER, 1992; WEISGERBER and ŠINDELÁŘ, 1992). In 1994, a regional experiment with indigenous populations from Czecho-Slovakia and domesticated populations from Germany was organized. The aim of our study was assessing the patterns of reaction of indigenous larch populations from the Sudetes and Western Carpathians to transfer in the latter experiment.

Materials and Methods

Experimental material

The combined provenance/progeny experiment under study was initiated by F. Weiser in the late 1980s. Seeds were collected between 1987 and 1992, from 14 indige-nous stands, 8 plantations, 5 seed orchards and the experiment also comprises 3 hybrid progenies *Larix decidua* × *L. kaempferi*. Seeds were sown in the spring 1994 in Waldsieversdorf, and plants were distributed in 1996 to trial sites in Germany, Czech republic and Slo-vakia and planted. Randomized block design with three replicates was used, whereas 50 plants per plot in the German trials and 25 plants per plot in the Slovak and Czech trials were planted at 2×2 m spacing.

In 2004, coordinated measurements were undertaken. Height and breast-height diameter (BHD) data are available for trial sites GE1 Müncheberg, GE2 Templin, GE3 Lindau, SK1 Antol and SK2 Hnilčík. Twelve provenances representing indigenous populations are planted in all these sites and were included into the study. The overview of provenances and trial sites is given in *Table 1*.

Climatic variables for provenances and trial sites were obtained from the WorldClim database (HIJMANS et al., 2005) using the grid with 30 arc-seconds resolution. The following bioclimatic variables were considered: mean annual temperature (tempY), temperature seasonality (standard deviation of monthly temperatures; tempSEA), maximum average temperature of the warmest month (tempMAX), minimum average temper-ature of the coldest month (tempMIN), annual precipita-tion (precY), precipitation of the driest month (precDRY), precipitation seasonality (coefficient of variation of monthly precipitations; precSEA). In addition, geograph-ic coordinates were considered in the evaluation: longi-tude (long), latitude (lat) and altitude (alt) (*Table 1*).

Table 1. – Geographical coordinates and climatic variables of European larch provenances and trial sites.

	Name	Code	Longitude	Latitude	Altitude (m)
Country	**Trial sites**				
Germany	Müncheberg	GE1	13° 48'	52° 42'	90
Germany	Templin	GE2	13° 36'	53° 24'	80
Germany	Lindau	GE3	12° 12'	51° 54'	70
Slovakia	Antol	SK1	18° 54'	48° 24'	620
Slovakia	Hnilčík	SK2	20° 33'	48° 52'	650
Region	**Provenances**				
Sudetes	Brníčko	P9	16° 58'	49° 54'	370
Sudetes	Radim	P10	17° 36'	50° 06'	520
Sudetes	Ruda nad Moravou	P11	16° 51'	50° 01'	480
Sudetes	Horní Benešov	P12	17° 36'	49° 58'	530
Carpathians	Staré Hory	P13	19° 06'	48° 51'	850
Carpathians	Biely Váh	P14	19° 54'	49° 02'	900
Carpathians	Štrbské Pleso	P15	20° 04'	49° 08'	1500
Carpathians	Smokovec	P16	20° 12'	49° 09'	1320
Carpathians	Vyšné Hágy	P17	20° 06'	49° 06'	1300
Carpathians	Muráň	P18	20° 00'	48° 40'	1050
Carpathians	Smižany	P19	20° 27'	48° 54'	850
Carpathians	Chminianska Nová Ves	P22	20° 59'	49° 00'	650

Table 1. – Continued.

Code	tempY (°C)	tempMAX (°C)	tempMIN (°C)	tempSEA (°C)	precY (mm)	precDRY (mm)	precSEA (mm)
trial sites							
GE1	8.8	22.0	-3.9	69.8	567	32	22
GE2	8.1	23.2	-3.6	67.4	578	31	21
GE3	8.6	22.3	-2.4	66.1	530	30	24
SK1	7.2	23.0	-7.6	73.6	775	46	25
SK2	5.2	20.1	-8.8	73.0	787	32	39
Provenances							
P9	7.0	22.0	-5.8	68.9	620	26	45
P10	7.0	21.6	-6.0	68.5	692	33	41
P11	7.2	21.9	-5.9	68.6	618	27	45
P12	6.9	21.6	-6.1	68.5	700	34	41
P13	6.6	22.4	-8.4	73.8	862	48	29
P14	5.2	20.1	-9.3	71.3	940	52	38
P15	4.0	18.2	-10.3	69.3	1064	50	41
P16	5.3	20.3	-9.4	71.6	825	35	44
P17	4.9	19.4	-9.1	69.3	924	43	41
P18	5.9	21.1	-8.9	73.2	759	38	37
P19	6.1	21.6	-9.4	73.0	787	37	39
P22	6.4	22.8	-8.2	75.2	731	35	38

Abbreviations of variables: long – longitude, lat – latitude, alt – altitude, tempY – mean annual temperature, tempSEA – temperature seasonality, tempMAX – maximum temperature of the warmest month, tempMIN – minimum temperature of the coldest month, precY – annual precipitation, precDRY – precipitation of the driest month, precSEA – precipitation seasonality.

Data analysis

Differences in height and BHD between trial sites and provenances were tested by a two-way analysis of variance using the GLM procedure of the statistical system SAS v. 9.1 (SAS 2010). Both provenance and trial site were considered fixed-effect factors.

For the identification of general origin-related trends of growth performance, overall height and BHD means of provenances were correlated with climatic and geographic variables. As the data distributions are not bivariate normal (this is especially true for geographic coordinates, as the Sudetic and Carpathian provenances are separated by a large gap), Spearman's rank correlation coefficients were calculated.

Responses to transfer were assessed using the methodology of general transfer functions (REHFELDT et al., 1999). Ecological distance (ecodistance), i.e. the difference in geographical coordinates or environmental variables between the trial site and the location of origin (MÁTYÁS, 1994), was used as a measure of environmental change for the transferred provenances. As experiments were unbalanced, least-square means of tree height and BHD calculated using the procedure GLM (SAS, 2010) were used to measure the performance of provenances, and were regressed against ecodistances. Because the distributions of responses along a geographic or environmental gradient may be unimodal, data were fitted to both linear and quadratic regression models:

$$y_{ij} = \beta_0 + \beta_1 E_{ij} + \varepsilon_{ij}$$
and
$$y_{ij} = \beta_0 + \beta_1 E_{ij} + \beta_2 E_{ij}^2 + \varepsilon_{ij}$$

Table 2. – Two-way analysis of variance of heights and breast-height diameters.

Source of variation	DF	Height		BHD	
		F-test	*P*	*F*-test	*P*
Trial site	4	521.55	<0.0001	245.97	<0.0001
Provenance	11	26.48	<0.0001	17.24	<0.0001
Trial site × Provenance	44	6.21	<0.0001	5.43	<0.0001

where y_{ij} is the response variable (performance of the j-th provenance at the i-th trial site), E_{ij} is the ecodistance (difference of geographic/climatic variables between the i-th trial location and the j-th provenance location) and ε_{ij} is the experimental error. The appropriate regression model was chosen based on the significance of the quadratic regression term, goodness of fit (adjusted R^2) and the Akaike Information Criterion.
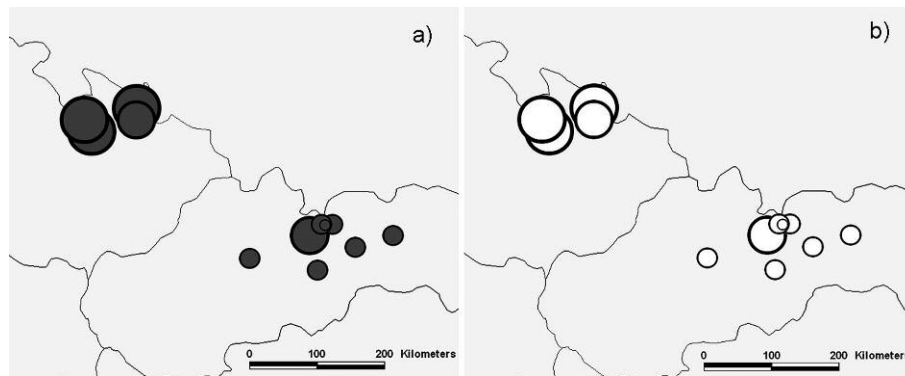

Figure 1. – Geographical distribution of the average performance of provenances over all trial sites: a) heights, b) breast-height diameters. Range of circle sizes corresponds to $4 \times$ standard deviation.

Appendix 1. – Sample sizes (n) and means (least-square estimates ± standard errors) of height and BHD at different sites.

		Trial plot				
		GE1	GE2	GE3	SK1	SK2
Sudetic provenances						
P09	n	98	75	71	44	56
	H	574.2 ± 11.7	384.7 ± 13.3	426.0 ± 13.7	575.7 ± 17.4	526.4 ± 15.4
	BHD	53.8 ± 1.7	34.4 ± 2.0	40.3 ± 2.0	56.2 ± 2.6	56.4 ± 2.3
P10	n	75	75	75	45	59
	H	559.3 ± 13.3	373.8 ± 13.3	474.9 ± 13.3	533.1 ± 17.2	516.9 ± 15.0
	BHD	51.9 ± 2.0	35.5 ± 2.0	48.6 ± 2.0	46.1 ± 2.6	55.5 ± 2.2
P11	n	97	75	69	42	63
	H	601.4 ± 11.7	404.4 ± 13.3	321.4 ± 13.9	577.4 ± 17.8	534.6 ± 14.5
	BHD	58.3 ± 1.7	40.9 ± 2.0	28.1 ± 2.1	55.5 ± 2.7	57.1 ± 2.2
P12	n	94	73	57	50	64
	H	580.3 ± 11.9	384.9 ± 13.5	267.1 ± 15.3	618.0 ± 16.3	479.8 ± 14.4
	BHD	51.4 ± 1.8	35.4 ± 2.0	19.3 ± 2.3	58.3 ± 2.4	51.5 ± 2.2
Carpathian provenances						
P13	n	95	73	71	54	49
	H	509.7 ± 11.8	352.4 ± 13.5	307.7 ± 13.7	531.5 ± 15.7	435.1 ± 16.5
	BHD	47.1 ± 1.8	32.2 ± 2.0	25.7 ± 2.0	47.1 ± 2.3	45.3 ± 2.5
P14	n	75	74	71	52	62
	H	558.8 ± 13.3	370.8 ± 13.4	387.0 ± 13.7	536.3 ± 16.0	512.9 ± 14.7
	BHD	53.9 ± 2.0	35.7 ± 2.0	36.6 ± 2.0	49.7 ± 2.4	55.3 ± 2.2
P15	n	75	72	59	43	48
	H	450.1 ± 13.3	314.2 ± 13.6	311.0 ± 15.0	476.5 ± 17.6	370.6 ± 16.7
	BHD	38.3 ± 2.0	27.9 ± 2.0	26.5 ± 2.2	45.3 ± 2.6	36.7 ± 2.5
P16	n	93	75	68	47	58
	H	552.4 ± 12.0	402.3 ± 13.3	263.3 ± 14.0	521.3 ± 16.8	441.4 ± 15.2
	BHD	51.7 ± 1.8	39.3 ± 2.0	18.9 ± 2.1	55.2 ± 2.5	46.1 ± 2.3
P17	n	88	75	71	34	44
	H	539.7 ± 12.3	386.0 ± 13.3	302.7 ± 13.7	484.8 ± 19.8	413.0 ± 17.4
	BHD	48.7 ± 1.8	35.4 ± 2.0	25.3 ± 2.0	44.8 ± 3.0	41.7 ± 2.6
P18	n	88	75	72	34	47
	H	515.8 ± 12.3	370.5 ± 13.3	349.0 ± 13.6	534.1 ± 19.8	442.6 ± 16.8
	BHD	45.6 ± 1.8	34.0 ± 2.0	33.2 ± 2.0	49.6 ± 3.0	46.8 ± 2.5
P19	N	75	75	62	46	47
	H	494.1 ± 13.3	375.4 ± 13.3	349.5 ± 14.7	512.8 ± 17.0	454.7 ± 16.8
	BHD	44.1 ± 2.0	35.9 ± 2.0	32.5 ± 2.2	46.7 ± 2.5	47.7 ± 2.5
P22	n	83	70	66	33	55
	H	530.7 ± 12.7	350.9 ± 13.8	269.0 ± 14.2	540.3 ± 20.1	416.9 ± 15.6
	BHD	50.0 ± 1.9	33.1 ± 2.1	21.2 ± 2.1	54.5 ± 3.0	42.8 ± 2.3

Table 3. – Spearman rank correlation coefficients of height and BHD vs. geographic and climatic variables of provenances and summary of quadratic regression models.

| Variable | Rank correlations | | | | Quadratic regressions[1] | | | | | |
| | Height | | BHD | | Height | | | BHD | | |
	r_S	P	r_S	P	Max[2]	Adj-R^2	P	Max[2]	Adj-R^2	P
lat	0.477	ns	0.537	ns	NA	NA	ns	NA	NA	ns
long	-0.768	0.0035	-0.698	0.0116	NA	NA	ns	NA	NA	ns
alt	-0.721	0.0081	-0.729	0.0072	1007	0.6068	0.0418	NA	NA	ns
tempY	0.683	0.0144	0.701	0.0122	5.55	0.6127	0.0403	5.54	0.6061	0.0420
tempMAX	0.246	ns	0.310	ns	20.86	0.6387	0.0338	20.88	0.5607	0.0552
tempMIN	0.662	0.0190	0.673	0.0166	-9.05	0.5515	0.0581	NA	NA	ns
tempSEA	-0.595	0.0411	-0.550	ns	NA	NA	ns	NA	NA	ns
precY	-0.678	0.0153	-0.734	0.0065	NA	NA	ns	NA	NA	ns
precDRY	-0.613	0.0341	-0.704	0.0106	NA	NA	ns	NA	NA	ns
precSEA	0.393	ns	0.504	ns	NA	NA	ns	NA	NA	ns

[1] Carpathian provenances only; [2] maximum of the regression function; for measurement units, see *Table 1*; NA – not applicable; ns – non-significant.

Regression models were calculated using the REG procedure (SAS, 2010).

Ecodistance, at which the quadratic regression function attains the maximum (optimum rate of provenance transfer), was derived by setting the first derivative of the regression function equal zero and solving for *E*:

$$\mathrm{d}y/\mathrm{d}E = \beta_1 + 2\beta_2 E = 0 \Rightarrow E(\max) = -\beta_1/2\beta_2$$

Joint regression analysis (FINLAY and WILKINSON, 1963) was used to assess the stability of individual provenances. Performances of individual provenances were regressed against the mean performance of all provenances for each site, whereas the slopes of the linear regression describe the stability.

Results

Overall trends across trial sites

Both trial sites and provenances exhibited a significant effect on height and diameter growth of European larch (*Table 2*). In general, Sudetic provenances clearly outperformed the Carpathian ones on most sites (*Fig. 1, Appendix 1*). Nevertheless, the provenance × trial site interaction was also significant both for height and BHD, meaning that the provenances differ in their reactions to the environments of the trial sites.

When all provenances were considered, height and breast-height diameter mostly showed significant monotonous geographical and climatic trends, as indicated by significant Spearman's rank correlations with altitude and climatic variables (*Table 3*). The performance of larch provenances generally decreased with increasing altitude and precipitations and decreasing temperatures at the site of origin. Climatic seasonality showed a significant effect only in the negative height growth response to temperature variation during the year. However, as mentioned above, groups of provenances originating from different biogeographic regions (the Sudetes and the Carpathians) behaved differently. When only the Slovak (Carpathian) provenances were considered, the overall performance (average over test sites) was unimodally related to altitude and temperatures, no significant linear trend was observed. The optimum climates (as indicated by the maximum of the response function) were absolutely consistent for height and BHD growth (*Table 3*).

Responses to transfer

For most geographic and climatic variables, highly significant regression models were found in the whole provenance set. Nevertheless, the general transfer functions were mostly linear, and explained between 6.9% and 45.0% of the total variance (*Table 4*). Growth performance of larch provenances improves with the transfer to higher elevations, sites with lower annual and minimum temperatures and higher precipitation. Unimodal response was found only in few cases. Transfer towards the West by approx. 3° of longitude improves both average height and diameter of larch provenances. Height growth also improves when a provenance is transferred ~1° southwards.

When Sudetic and Carpathian provenances are analysed separately, significant response curves are frequently unimodal. There is a very good correspondence between the responses in height and diameter growth within geographic groups, but the responses are not consistent between groups. For example, Sudetic provenances prefer transfer to climates with lower winter temperatures than at their sites of origin (as indicated by negative optimum transfer rates for the variable tempMIN), whereas Carpathian provenances behave in the opposite way (*Table 4*).

Norms of reaction

In spite of a relatively low number of tested provenances, both the set of trial sites and the set of prove-

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Table 4. – Regression models summary for general transfer functions in relation to geographic and climatic variables.

Predictor variable	Response variable							
	Height				Breast-height diameter			
	slope[1]	max[2]	Adj-R^2	P	slope[1]	max[2]	Adj-R^2	P
	All provenances							
long	NA	-3.06	0.2167	0.0004	NA	-3.39	0.2976	<0.0001
lat	NA	-1.12	0.3125	<0.0001	1.93	NA	0.4222	<0.0001
alt	0.10	NA	0.2235	<0.0001	0.01	NA	0.3070	<0.0001
tempY	-16.92	NA	0.0691	0.0239	-2.94	NA	0.1959	0.0002
tempMAX	NA	NA	NA	ns	-1.97	NA	0.0858	0.0132
tempMIN	-18.27	NA	0.3116	<0.0001	-2.40	NA	0.4454	<0.0001
tempSEA	16.33	NA	0.4075	<0.0001	1.89	NA	0.4499	<0.0001
precY	0.28	NA	0.2370	<0.0001	0.04	NA	0.3347	<0.0001
precDRY	NA	-21.9	0.2432	0.0001	0.48	NA	0.2014	0.0002
precSEA	NA	NA	NA	ns	NA	NA	NA	ns
	Sudetic provenances							
long	23.0	NA	0.1816	0.0347	-2.92	NA	0.2504	0.0143
lat	NA	-0.228	0.3943	0.0055	NA	-1.41	0.4243	0.0036
alt	0.179	NA	0.0229	0.0113	0.024	NA	0.3315	0.0047
tempY	NA	NA	NA	ns	-3.81	NA	0.1641	0.0432
tempMAX	NA	NA	NA	ns	NA	NA	NA	ns
tempMIN	NA	-0.50	0.4844	0.0014	NA	-1.21	0.4801	0.0015
tempSEA	NA	3.32	0.6201	0.0001	NA	3.66	0.6325	<0.0001
precY	0.434	NA	0.2236	0.0204	0.059	NA	0.3543	0.0033
precDRY	7.24	NA	0.2163	0.0224	NA	NA	NA	ns
precSEA	NA	NA	NA	ns	NA	NA	NA	ns
	Carpathian provenances							
long	NA	-2.54	0.1781	0.0100	NA	-2.65	0.2845	0.0008
lat	NA	2.85	0.4565	<0.0001	NA	2.32	0.5114	<0.0001
alt	0.089	NA	0.1352	0.0113	0.012	NA	0.2353	0.0009
tempY	NA	NA	NA	ns	-2.27	NA	0.1119	0.0199
tempMAX	NA	NA	NA	ns	NA	NA	NA	ns
tempMIN	NA	2.42	0.4009	<0.0001	NA	1.75	0.4907	<0.0001
tempSEA	NA	1.40	0.3673	<0.0001	NA	1.95	0.4075	<0.0001
precY	0.236	NA	0.1467	0.0085	0.033	NA	0.2585	0.0005
precDRY	NA	-18.0	0.1474	0.0197	NA	-15.7	0.1504	0.0185
precSEA	NA	NA	NA	ns	NA	NA	NA	ns

[1] slope of the linear regression model (if appropriate); [2] maximum of the quadratic regression model (if appropriate); for measurement units, see *Table 1*; NA – not applicable; ns – non-significant; Abbreviations of variables: see *Table 1*.

Table 5. – Stability coefficient of European larch provenances as assessed by joint regression analysis.

Provenance		Height				BHD			
		b[1]	Adj-R^2	t[2]	P	b[1]	Adj-R^2	t[2]	P
Brníčko	P9	0.891	0.862	-0.624	ns	0.959	0.776	-0.164	ns
Radim	P10	0.605	0.468	-1.386	ns	0.385	-0.011	-1.564	0.0964
Ruda nad Moravou	P11	1.268	0.952	1.889	0.0660	1.329	0.943	2.023	0.0566
Horní Benešov	P12	1.517	0.954	3.135	0.0175	1.592	0.941	3.002	0.0199
Staré Hory	P13	1.037	0.988	0.649	ns	1.019	0.995	0.558	ns
Biely Váh	P14	0.905	0.895	-0.621	ns	0.908	0.822	-0.448	ns
Štrbské Pleso	P15	0.794	0.915	-1.729	0.0794	0.747	0.821	-1.492	ns
Smokovec	P16	1.159	0.865	0.710	ns	1.382	0.823	1.223	ns
Vyšné Hágy	P17	0.931	0.866	-0.385	ns	0.892	0.853	-0.596	ns
Muráň	P18	0.887	0.979	-1.759	0.0767	0.772	0.943	-2.411	0.0367
Smižany	P19	0.769	0.982	-4.453	0.0056	0.685	0.932	-3.427	0.0133
Chmínianska Nová Ves	P22	1.237	0.969	2.146	0.0492	1.328	0.900	1.506	ns

[1] stability coefficient (slope of the regression $y = a + b\bar{y}$); [2] test of H_0: $\beta = 1$; ns – non-significant.

nances cover a relatively broad span of altitudes, aspects and temperature and precipitation regimes within the larch distribution range in Central Europe. Consequently, average performance of provenances within a trial site is a sufficiently reliable index of the quality of the environment at the site.

Joint regression analysis yielded only few regression coefficients, showing at least marginally significant difference ($P<0.10$) from one, which means that most provenances exhibited average stability *sensu* FINLAY and WILKINSON (1963). Stability indices are quite consistent between the response traits (*Table 5*). Nevertheless, they did not show any association with the geographical position or climate of origin, nor they were associated with growth performance (data not shown).

Discussion

Geographical patterns of phenotypic traits, as reflected in common garden experiments, are frequently considered to result solely from local adaptation by natural selection, whereas climate is usually regarded as the main driver of selection. Actually, this logic underlies the delineation of provenance regions as the basic framework for the use and transfer of forest reproductive material under the current European legislation (Directive 105/1999/EC). Nevertheless, non-random large-scale trends and patterns of genetic and, consequently, phenotypic variation may arise from non-adaptive processes as well, such as migration from different glacial refugia or isolation by distance (GÖMÖRY et al., 1999; MIMURA and AITKEN, 2007). Such patterns have very commonly been identified in rangewide international provenance experiments (GIERTYCH and OLEKSYN, 1992; KRUTZSCH, 1992; WEISGERBER and ŠINDELÁŘ, 1992), but their interpretation is not straightforward, because separating the effects of neutral processes from those of selection is not an easy task. Therefore, our study focused on a small-scale experiment.

The tested populations were collected within a relatively small territory. No detailed study of the Holocene history of larch in Europe, such as available for the other commercially and ecologically important tree species, has been conducted. However, apparent genetic similarity and absence of any clear geographical trends or patterns of genetic differentiation within the Sudetic-West-Carpathian area (LEWANDOWSKI and MEJNARTO-WICZ, 1991; LEWANDOWSKI, 1997), and a clear differentiation from western Alps and Scandinavia (MAIER, 1992; SEMERIKOV et al., 1999; SEMERIKOV and LASCOUX, 2003), let us suggest that all populations included in our study have probably originated from the same glacial refugium. *Larix*-type pollen percentages at several C[14]-dated Slovak sites (Hozelec, Liptovský Ján) at the beginning of the Holocene are relatively high (EPD database; http://pollen.cerege.fr/fpd-epd/), indicating that initial population sizes were high and gene pools of larch populations were not significantly affected by genetic drift. Even today, larch belongs to the main constituents of forest stands in the regions where provenances were collected. All this suggests that for all the populations tested in this series of trials adaptation through natural selection started from identical or very similar basic gene pools. On the other hand, larch distribution range has become strongly fragmented later in the Holocene, and at present there is a large gap between the Carpathian and Sudetic distribution range. The extent of local adaptation is given by the balance between gene flow and natural selection (SAVOLAINEN et al., 2007; KRUTOVSKY et al., 2012). European larch is a wind-pollinated species, and the low differentiation levels in Central Europe mentioned above are indicative of extensive gene flow. However, considering the relatively low motility of *Larix* pollen (KRIŽO and SLOBODNÍK, 1996), range fragmentation may have created efficient isolation barriers and has contributed to the observed differentiation in growth performance between the Carpathian and Sudetic provenances. Therefore, the observed overall trends as presented in *Table 3* may be misleading and need not result from local adaptation. A general growth superiority of Sudetic provenances has been stated in many previous studies based on older experiments (the Austrian 1890 experiment, IUFRO experiments 1908, 1944, 1958/59: CIESLAR, 1914; GIER-TYCH, 1979; ŠŤASTNÝ, 1960; SCHOBER, 1985; WEISGERBER and ŠINDELÁŘ, 1992). It is thus possible that pooling Sudetic provenances with Carpathian populations located eastwards and generally at higher elevations produced false geographic trends, even though these trends are fully concordant with what has generally been observed in provenance experiments of conifers (decreasing growth performance with the elevation of origin and harsher climatic regime; cf. WRIGHT, 1976). Unimodal trends, although identified in a limited subset of Carpathian provenances and thus valid only for this region, seem to be more reliable.

The analysis of general transfer functions indicates that environments occupied by larch populations in Central Europe are generally suboptimal: the relationship between growth performance and ecodistance is linear in most cases, meaning that unidirectional transfer results in better growth. The general pattern is a better height and diameter growth achieved when populations are transferred into higher elevations, i.e. into climates with lower temperatures and more precipitations. This contradicts the findings of REHFELDT et al. (1999a, 2003), who observed in the Siberian *Larix* species either local optimality or improved growth and survival associated with the transfer to warmer climates. However, discordances between the response patterns of different provenance sets indicate that Sudetic and Carpathian provenances are genetically differentiated and a joint analysis of both groups produces false monotonous trends. In fact, when groups are treated separately, trends of responses to transfer are again generally unimodal, which means that there is a certain optimum transfer rate for each group, which is reflected in the best growth performance; both not-reaching and exceeding of this transfer rate results in decreased fitness. In the light of the ongoing climate change, Carpathian provenances generally supporting warmer winters and drier summers than they experience at their sites of origin may have an advantage compared to Sudetic populations with opposite preferences.

Responses may even be population-specific rather than group-specific, as demonstrated in other conifers (REHFELDT et al., 2002; ANDALO et al., 2005; GÖMÖRY et al., 2012). A highly significant trial site × provenance interaction for both height and diameter growth gives a support for this assumption. However, the experimental setup of our study did not allow assessing population response functions, first because of a low number of test sites, second because test sites did not cover the whole width of the climatic gradient, as the test sites were located generally at lower elevations and more to the West of the sites of origin. The linear shape of the growth response to geographic or climatic transfer, whenever we observed it, may simply result from the fact that the optimum for most provenances is situated outside the geographic or climatic range of the test sites. This is especially true for the altitudinal transfer: behaviour of larch provenances at high elevations (where larch commonly occurs in the Carpathians) could not be assessed.

Phenotypic plasticity may be an alternative strategy used by a tree species to cope with spatial heterogeneity and temporal fluctuations of climate (VITASSE et al., 2009). However, as it is based on the capacity of an organism to modify gene expression patterns depending from the environmental context, it counteracts selection pressure and may hamper the evolutionary response (GIMENO et al., 2009; MIMURA and AITKEN, 2010). An unexpected homogeneity of reaction norms in both studied growth traits supports this assumption. Our study did not confirm earlier observation of stability of larch provenances decreasing with increasing performance (KULEJ, 2004), nor the stability-environment relationship observed in other conifers (cf. MÁTYÁS, 1996). Moreover, incongruences of optimum transfer rates between geographical groups (e.g., related to latitudinal transfer, minimum temperatures or temperature seasonality) may be due to the fact that all populations have similar climatic optima (related to the geographical position) placed between both groups, again indicating limited extent of local adaptation, as observed in other conifers (REHFELDT et al., 1999; GÖMÖRY et al., 2012). However, a detailed population-level analysis of responses to transfer and a broader variety of response traits are necessary to provide a reliable support for this hypothesis.

Studies of responses of tree populations to climate change are accomplished on different scales, rely on different experimental setups and different materials. It is thus not surprising that their outcomes are different, frequently even controversial. Understanding of the mechanisms underlying climatic adaptation in trees and a reliable prediction of their future behaviour under climate change require inclusion of physiological traits into provenance research and, ultimately, identification of genes with adaptive significance and mapping their variation patterns within species' ranges.

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