

Transfer Analysis of Provenance Trials Reveals Macroclimatic Adaptedness of European Beech (*Fagus sylvatica* L.)¹

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Abstract – The aim of the study was to analyse provenance tests of beech situated close to the Southeastern-continental limits of the species, in order to develop a response model of adaptation and plasticity of populations on evolutionary-ecological basis, following sudden climatic changes as a result of transplanting. Modelling of juvenile height was performed with the help of ecodistance variables. The concept of transfer analysis and ecodistance is based on the hypothesis that phenotypic response to macroclimatic changes depends on the inherited adaptive potential of the population and on the magnitude and direction of experienced environmental change. In common garden experiments, the transfer to the planting site is interpreted as simulation of environmental change. The application of ecodistance of transfer for evaluating common garden experiments provides much needed quantitative information about response of tree populations to predicted climatic changes.

The analysis of three field experiments of European beech in SE Europe invalidate earlier doubts about the existence of macroclimatic adaptation patterns in juvenile growth and justify restrictions of use of reproductive material on the basis of evolutionary ecology. The presented model illustrates that response to climatic change is regionally divergent, depending on testing conditions and on hereditary traits. In particular, climatic warming in the central-northern part of the range may lead to production increase. However, under the stressful and uncertain conditions at the lower (xeric) limit of the species, growth depression and vitality loss are predicted. The deviating behaviour of higher elevation provenances support their separate treatment.

The results may be utilised in climate change adaptation and mitigation policy in forestry and nature conservation, to revise rules for use of reproductive material and also for validating evolutionary and ecological hypotheses related to climate change effects.

genetic adaptation / common gardens / climate change / phenotypic stability / ecodistance

Kivonat – Származási kísérletek áttelepítési elemzése igazolta a bükk makroklímatis adaptáltságát. A délkelet-európai, alsó (szárazsági) határhoz közeli származási kísérletek elemzésének célja az alkalmazkodás és plaszticitás által meghatározott válaszreakciók modellezése volt. Az evolúció-ökológiai alapon felépített modell az áttelepítés következtében fellépett hirtelen

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klímaváltozás leírásához az ún. ökológiai távolság elvét alkalmazza. Az áttelepítési elemzés azon a hipotézisen alapszik, hogy a populáció makroklimatikus változásra adott (fenotipikus) válaszreakciója – minden más tényező állandósága mellett – az öröklött adaptív potenciáltól, és az érzékelt klimatikus változás mértékétől függ. A közös tenyészkerti kísérletekbe való áttelepítést a környezet szimulált változásaként értelmezzük. Az áttelepítés ökológiai távolsága a származási kísérletek újszerű értékelését teszi lehetővé, és régóta hiányzó kvantitatív információkat szolgáltat a fás populációk klímaváltozással kapcsolatban várható válaszárol.

Az elemzésbe vont három DK-európai bükk kísérlet eredményei a fiatalkori növekedés tekintetében igazolják a fajon belüli, makroklimatikus alkalmazkodási mintázat eddig kétségbevonat létezését, amely indokoltá teszi a szaporítóanyag-használat evolúciós ökológiai alapú szabályozását. A bemutatott modelltől látható, hogy a klímaváltozásra adott válaszokban regionális különbségek léteznek, amelyeket a kísérleti környezet és az öröklött tulajdonságok határoznak meg. A faji área közép-északi részén a melegedés produkció-növekedést eredményezhet. Ugyanakkor a szárazsági (alsó) határ szélsőséges és bizonytalan viszonyai növekedés-csökkenést és vitalitás-vesztést prognosztizálnak. A magasabb tszf. magasságú helyszínek származásai eltérően viselkednek, és ez indokolja külön kezelésüket.

Az eredmények felhasználhatók a klímaváltozáshoz alkalmazkodás stratégiájának megfogalmazásához mind az erdőszetben, mind a természetvédelemben. Segítségükkel pontosíthatók a szaporítóanyag felhasználási szabályok, és értékelhetők a klímaváltozási hatásokkal kapcsolatos különböző evolúciós és ökológiai hipotézisek is.

genetikai adaptáció / közös tenyészkert / klímaváltozás / fenotípusos stabilitás / ökológiai távolság

1 INTRODUCTION: CLIMATIC SELECTION AND ADAPTATION STRATEGY

Different hypotheses on the adaptation strategy of trees are co-existing in contemporary genetics and ecology. With regard to predicted climate scenarios, scarcity of reliable information on responses to macroclimatic changes is a central problem and obstacle. In order to formulate realistic predictions, both the nature of genetic adaptation to past and current climate, and the level of sensitivity to sudden environmental changes have to be understood and properly interpreted. In the context of large-scale climatic changes, *macroclimatic adaptation* is an important component to study and evaluate. It is *the fraction of within-species adaptive genetic diversity which is attributable to adaptation to macroclimatic factors*.

Although climatic selection might act more reliably on local, microclimatic level, macroclimate is exclusively considered here mainly for three reasons: climatic scenarios utilized for forecasting describe changes on macro-level only, and on the other hand, data on micro- and meso-level climate is in most cases not sufficient for proper analysis. Finally, the extensive sampling pattern of the studied set of populations prohibits a finer-scale approach.

Under selection pressure, genetic resources of populations are adjusted to maintain competitive growth, adapted phenology, reproductivity and tolerance to diseases and pests, i.e. stability and adaptability. Differing direction and intensity of selection pressure within the species' range exert a disruptive selection effect, which may lead to characteristic, stabilised patterns of adaptive genetic variability. Counting on the strong and lasting effects of local selection, a close ("ecotypic") adaptation is implicitly assumed for K-strategist tree species such as beech. This assumption has been generally accepted in practical silviculture; a view which has been nourished by classic field experiments with perennials, starting with Clausen et al. (1940).

However, molecular genetic studies have revealed the effect of strong counteracting forces such as genetic drift and isolation, but first of all the effect of postglacial migration which produced for woody species such as beech characteristic geographic patterns. These patterns follow rather routes of colonisation than ecological conditions (Comps et al. 1998, Comps et al. 2001, Magri et al. 2006). There are a number of other biotic reasons why the genetic system of tree species may robustly counteract climatic selection (Mátyás 2007).

Conflicting approaches and unclear role of different factors determining adaptability keep macroclimatic selection still as an open question, in spite of its importance for practical forest management. Adaptation to macroclimate is the basis for setting the rules of reproductive material use, for concepts to conserve genetic resources of species, and for strategies to adapt to and to mitigate expected effects of environmental changes. This raises the following questions:

- what kind of phenotypic response is expected if macroclimatic environment changes,
- how much of observed response is attributable to macroclimatic adaptation,
- what is the role of phenotypical stability,
- what is the relation of macroclimatic to micro-scale (local) adaptation?

In the present study only a part of these problems are addressed.

2 TRACING MACRO-CLIMATIC SELECTION ON QUANTITATIVE TRAITS

Annual growth and development cycle of beech – as for any other temperate species – is governed besides the photoperiod by the amount of physiologically effective heat sum (Kramer 1994, Chuine et al. 2003) and of course precipitation. As the latter two are unevenly distributed across the range of the species, diverging direction and intensity of climatic selection may be assumed. The consequence of climatic selection, differentiation in phenological behaviour is well reflected by field test results. For example, budbreak of beech shows a clinal East-West pattern: Atlantic coast provenances are late, while Alpine and SE-European continental sources are early flushing (Wühlisch et al. 1995, Führer et al. 2009, Gömöry 2009).

Reports on similar patterns are expectable also for growth traits. However, studies on growth of beech provenances in field tests describe instead of climate-related patterns rather an ecotypic (i.e. unexplained random) type of variation (e.g. Wühlisch et al. 1995, Kleinschmidt – Svolba 1995, Jazbec et al. 2007), or explain spatial differentiation in response by the phylogenetic past (e.g. Gömöry 2009). (The term "provenance" is used synonymously in the paper for "transferred population of known origin".)

2.1 The ecodistance approach of modelling macroclimatic adaptation

For the investigation of macroclimatic adaptation, the concept of ecodistance has been applied. The ecodistance (ecological distance) concept is based on the idea that if populations adapted to certain ecological (climatic) conditions are transferred to a new environment, and all other site factors are kept equal or disregarded, their *phenotypic response to climate depends not only on the climatic conditions where the population is actually grown or tested, but also on the ecodistance of transfer, i.e. on the magnitude and direction of environmental change experienced due to the transplanting to the test site, related to the macroclimate they had been adapted to originally*. Accordingly, the ecodistance value of a locally adapted population in a test takes the value 0. The concept of transfer analysis and ecodistance (Mátyás & Yeatman 1992, Mátyás 1994, 1996, Mátyás et al. 2008b) has been used for the analysis and modelling of data of common garden (provenance) tests. This approach enables a pooled comparison of various test sites and thus increases statistical reliability. Applying ecodistance instead of simple geographic or ecological parameters allows the detection of general patterns of adaptation. An important advantage of the concept is that *responses to transfer into new environments may be interpreted as simulations of future climatic changes*: a realistic validation of prediction models.

In the transfer analysis, the climatic variable (E) selected to best describe macroclimatic adaptation serves as independent variable, expressed as difference between test site (X_t) and location of origin (X_o). It may be a simple or complex variable such as drought or continentality index, or a principal component etc.

The ecodistance (ΔE) is then calculated as

$$\Delta E = X_t - X_o$$

For example, if the variable is mean annual temperature, and $X_t > X_o$, the positive value of ΔE expresses a simulated warming of the environment through transfer to the site.

2.2 Modeling response of populations to transfer

According to the classical additive model of Fisher (1958) and Wright (1950), the phenotypic response of an individual or population (P_i) may be described as the sum of the estimated genetic (γ_i) and the environmental (ε_i) deviations from the experimental mean (μ):

$$P_i = \mu + \gamma_i + \varepsilon_i$$

Both the genetic and the environmental component may be partitioned for our purposes. Regarding the effect of the environment, response strongly depends on the site potential of the test. The site conditions have a powerful influence on differentiation between populations and on interaction effects. It is therefore advisable to separate the test site potential (T), expressed usually as the local mean of tested populations, and the interaction effect (see further below).

There are two types of genetic response to transfer which may be calculated from a dataset containing data of numerous populations from a set of experimental sites:

a) General or “species-specific” response (G) to macroclimatic change, calculated from pooled data of the observed trait Y from all (t) test sites, and all (p) provenances, providing the function

$$Y_G = f(\Delta E_{tp})$$

The function supplies quantitative information on the pooled response to changing environment, triggered by the transfer of locally adapted populations into a new ambient. (Needless to say that ΔE values for the same provenance are different at every test location.)

b) As the various populations investigated may have a different microevolutionary background and have been exposed to selection effects of different nature and intensity, the general response will conceal much of the between-provenance genetic differentiation. Individual, population-specific response (P) of population “ p ” across test sites, defined as response function *per se* in recent literature (e.g. Thomson - Parker 2008). It is indicating individual sensitivity or phenotypic plasticity of the population to changes, in interaction with local site conditions. It is identical with the term “reaction norm” of ecology:

$$Y_p = f(\Delta E_p)$$

In case of sufficient data, the function may define the physiological (genetic) optimum for the population in the climatic niche.

The residual of the recorded population mean at a test site, which is left unexplained by the other additive components, is regarded as interaction (I) and error. *Interaction* in genetic sense is the part of response which appears as deviation from the average response regressions established across the test sites, *causing a change in ranking* of populations (see Figure 3). Strong interaction effects indicate narrower plasticity, and responsiveness to certain (usually extreme) conditions.

The unified additive model to comprise all components is then:

$$Y = \mu + G + P + T + I + \varepsilon$$

where the residual error (ε) may include also genetic components unrelated to macroclimatic adaptation.

3 A CASE STUDY: ANALYSIS OF THREE SE-EUROPEAN TRIALS

In the case study the construction of an additive response model is presented, based on the ecodistance concept. The selected variable for ecodistance calculations is one of multiple options. Environmental effects other than macroclimate (e.g. soil characteristics) are not discussed here because these are beyond the interests of this study.

The transfer analysis had been applied since its first formulation (Mátyás - Yeatman 1992) for numerous conifer species. For beech, growth response predictions have not been validated thus far by field tests, rather backed by climatic envelopes (Fang - Lechowicz 2006, Czúcz et al. 2009). The beech provenance test series (Wühlisch 2007) offers an opportunity to obtain results similar to conifers with a "recalcitrant" broadleaved species.

3.1 Selected ecodistance variable

For ecodistance calculation, Ellenberg's climate quotient (*EQ*) has been selected. It is a simple index to express humidity, respectively continentality of climate and has been developed by Ellenberg (1988) first of all for beech. Recent analyses have proven its high distinctive power to predict presence of beech under Central European conditions (Czúcz et al. 2009). Ellenberg's climate quotient is defined as the mean temperature of the warmest month (July, T_{07}) divided by the annual precipitation (P_{ann}):

$$EQ = 1000 \cdot T_{07} \cdot P_{ann}^{-1}$$

The quotient indicates favourable climatic conditions for beech if the *EQ* value lies below approximately 26 for Central Europe. In Hungary, zonal sites with *EQ* values above 28 represent the xeric (lower) limits of the distribution of species (Czúcz et al. 2009). *EQ* values of provenances² and test sites are given in *Tables 1 and 2*.

Table 1. Data of analysed beech provenance trials (for geographic locations see Figure 1)

a. Geographic, climatic data						
Reg. Nr.	Country	Location	Altitude a.s.l. (m)	July mean temperature (°C)	Annual mean precipitation (mm)	Ellenberg index (<i>EQ</i>)
2012	Slovenia	Straza	545	19.3	1260	15.3
2015	Hungary	Bucsuta	200	19.7	747	26.3
2020	Slovakia	Mlacik - Tále	850	16.8	779	21.5
mean						21.0
b. Statistical data						
Reg. Nr.	Aver. height (H)	Site effect (<i>T</i>) (cm)	Std. deviation of prov. means	Linear regression slope H' vs. ΔEQ of provenances		F value between prov.
2012	228.3	+17.5	17.9	+0.628		14.00***
2015	218.9	+8.1	25.3	-0.690		3.36**
2020	185.2	-25.6	11.3	-1.572		3.40**
210.8		0				

3.2 Analysed experiments and provenances

On the basis of an unpublished preliminary surveying study (Mátyás et al. 2008a), three experiments of the 1998 series of the all-European beech provenance trials (Wühlisch 2007) have been selected for analysis (*Table 1a and 1b*). The tests have been chosen within a region of restricted size, to grant a relatively uniform synergy of climatic factors.

² The term "provenance" is used synonymously for "transferred population of known origin"

The test sites are located in the Carpathian basin, in Hungary, Slovenia and Slovakia, at different elevations (*Figure 1*). All three are under the influence of the more or less humid-continental climate of SE Europe. The mid-elevation site in Slovenia provides climatically optimal conditions, while the two other sites are more continental as shown by their Ellenberg indices (*Table 1a*).

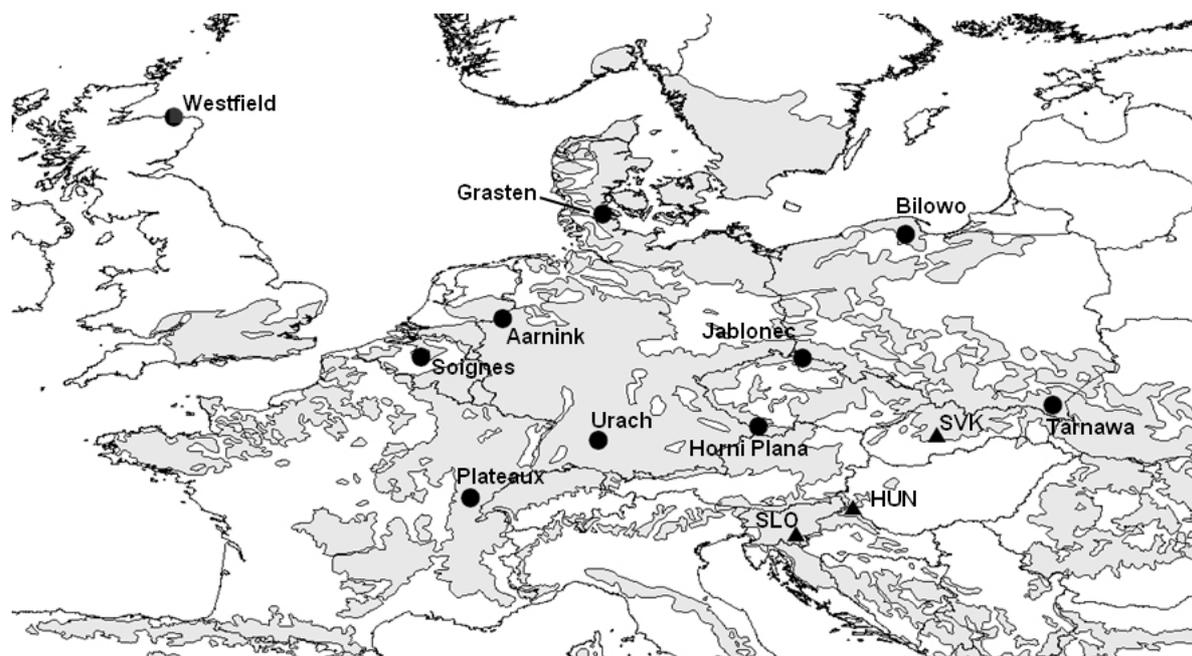


Figure 1. Location of 10 beech populations selected for statistical analysis and of the 3 test sites. The distribution range of beech (grey shade) has been provided by EUFORGEN

Table 2. Data of the 12 maritime (M), continental (C) and Alpine (A) beech provenances common in the 3 tests, ranked by their EQ index (for geographic locations see Figure 1)

Type	Nr.	Location name, country	Altitude a.s.l. (m)	July mean <i>T</i> (°C)	Annual mean <i>P</i> (mm)	EQ of origin	Corrected mean <i>H'</i> (cm)	Additive height response (cm)	Average ecodistance (EQ index)	Regression <i>H'</i> vs. EQ across tests
A	35	Hinterstoder AUT	1250	11.8	1380	8.6	216.4	+6.54	12.46	+2.660
A	53	Postojna M. SLO	1000	17.0	1718	9.9	222.5	+12.58	11.20	-1.432
C	51	Horni Plana CZE	990	13.4	1014	13.2	194.8	-15.07	7.73	-3.313
C	6	Plateaux FRA	600	17.5	1223	14.3	197.5	-12.37	6.69	-4.239
C	48	Jablonec CZE	760	13.5	944	14.3	203.0	-6.87	6.56	-1.014
C	31	Urach GER	760	16.4	887	18.5	211.7	+1.83	2.43	+2.251
M	17	Westfield GBR	10	14.0	741	18.9	214.1	+4.23	2.03	+2.746
M	21	Grasten DEN	45	16.3	810	20.1	189.3	-20.57	0.96	+1.458
M	14	Aarnink NED	45	17.5	794	22.0	229.3	+19.43	-0.94	+1.258
M	13	Soignes BEL	110	17.9	796	22.5	214.4	+4.53	-1.38	+0.524
C	40	Tarnawa POL	540	17.6	762	23.1	228.1	+18.23	-2.03	-1.440
M	67	Bilowo POL	250	15.5	643	24.1	216.5	+6.63	-2.93	+1.740

The experiments contain 36 provenances, however not exactly the same ones. 12 populations have been selected from the 36 which are represented in all three tests and where available climatic data seemed to be reliable (*Table 2, Figure 1*). Out of the 12 provenances, 5 originate from low elevation sites in maritime climate, with *EQ* indices between 19 and 24. Another 5 populations have been transferred from inland, continental regions where beech is occupying sites at medium elevations. The original sites have generally *EQ* values below 20, except for Tarnawa, Poland (23.1) and are situated in medium mountains (540 to 990 m). Two Alpine populations originate from altitudes at or above 1000 m with *EQ* values below 10.

At the warm-continental site in Hungary (*EQ* = 26.3), all the 12 provenances have been transferred into an environment with increased continentality, higher average temperatures and higher drought stress. On the other hand, in the Slovenian test (*EQ* = 15.3) the majority of the selected populations has been brought into an environment cooler/wetter than their original climate.

For the analysis, 8th year heights measured in winter 2005/2006 have been used. Between-provenance *F* values from variance analysis of the 3 test sites (Mátyás et al. 2008a) are presented in *Table 1b*. In the following analyses only average heights of tests have been used. Obviously damaged or crippled trees have been omitted from the calculation.

3.3 Separating components of the additive model

Effect of test site potential differences

The additive *test site effect* (*T*) is the difference of test averages from the grand mean of all experiments (210.8 cm, *Table 1b*). Measured average heights of provenances at the three tests were corrected with the test site effect, to make them directly comparable (corrected heights are denoted further as *H'*). A correction for standard deviation differences between tests was omitted because the range of variation of provenance means indicates the differentiating power of the site (*Table 1b*).

The Slovak site has the lowest site potential, first of all due to its relatively harsh conditions. It shows also the lowest standard deviation of means. At the Hungarian site, differentiation between populations is the strongest, presumably also because of higher climatic stress, close to the climatic limit for beech (i.e. the xeric limit, Mátyás et al. 2008b, Jump et al. 2009).

General (“species-specific”) response

Response to transfer has been analysed by two types of regressions: calculating the individual response of provenances to respective ecodistances across sites, and by using means of all three tests for both provenances and ecodistances.

“Mean ecodistance” expresses the general effect of climatic conditions of the tests as experienced by differently adapted provenances. It is calculated from the difference between the average of *EQ* value of tests (21.0, *Table 1a*) and the *EQ* of origin of populations (*Table 2*).

The limited number of observations allowed only the calculation of a linear function instead of the theoretically expected curvilinear one. The data and regression shown in *Figure 2* display a significant decline of height towards increasing warming ($R^2 = 0.486^{**}$)³. The Alpine provenances appear as outliers, maybe partly caused by inaccurate climate interpolation at higher elevations, but more probably due to truly different adaptation, as the context of precipitation vs. temperature is modulated by altitude. The analysis by

³ Throughout the paper, star signs stand for level of significance: * = 0.05, ** = 0.01 and *** = 0.001 probability

Gömöry (2009) also points out the divergent behaviour of populations from higher elevations. Therefore these were excluded from further calculations.

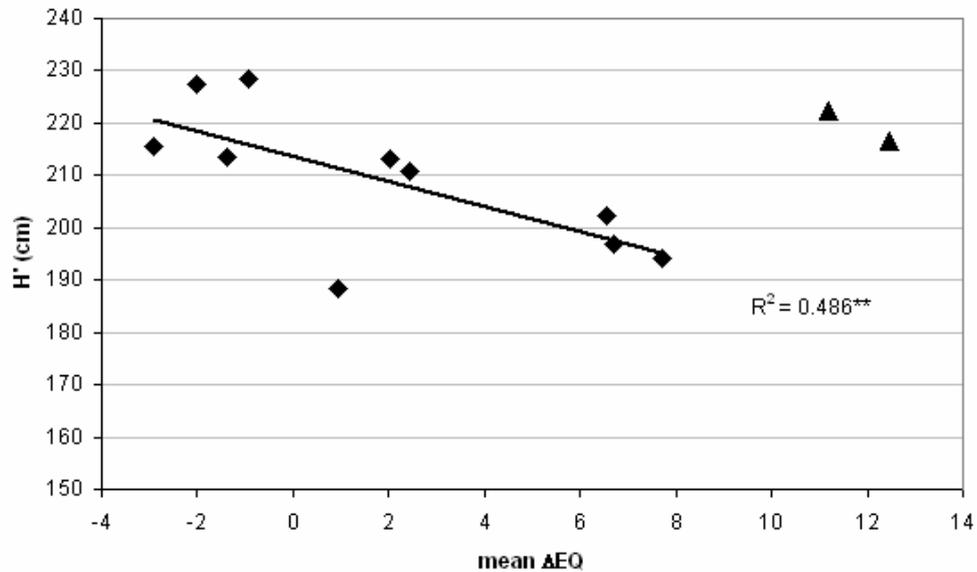


Figure 2. General response regression for corrected mean height (H') vs. mean ecodistance of provenances. Means are averages of all 3 tests. Equation is calculated for 10 maritime and continental provenances only, \blacktriangle indicates the two Alpine outliers

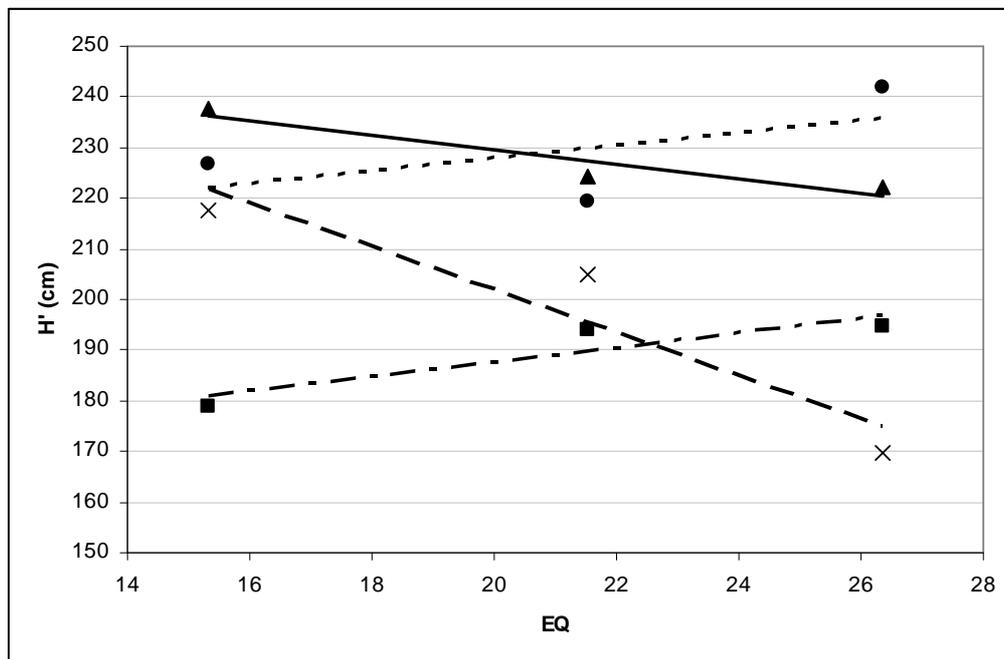


Figure 3. Reaction norm of corrected heights (H') of two maritime provenances Aarnink (\bullet), Grasten (\blacksquare), and of two continental ones Tarnawa (\blacktriangle) and Plateaux (\times), displaying individual differences in response against EQ values of test sites

Comparing response regressions of different provenances across test sites, the calculated slopes show a marked differentiation. A group of mostly maritime provenances show improving performance with warming and dryer conditions (positive slopes), while continental populations display an opposite trend (*Table 2, Figure 3*). The results propose a relationship between the (climatic) origin and the character of response to changing climate. The connection, expressed by the slope values of the regressions, is significant ($R^2 = 0.383^*$). This indicates that a *general or "species-specific" response (G)* may be predicted by using ecodistance and site conditions as independent variables (see later for details).

Table 3. Results of analysis of variance of mean heights of 10 provenances at 3 locations (uncorrected height data in cm units)

Effect	SS	DF	MS	F	p
Provenances	4946.00	9	549.6	2.620	0.039
Sites	7110.30	2	3555.1	16.949	0.001
Interaction and error	3775.66	18	209.8		

Individual response of populations

Deviation of the population mean from the grand mean represents the *individual, population-level additive response (P)*. Population-specific differences of response across sites suggest also divergent sensitivity to climatic change, thus regression statistics characterise phenotypic plasticity. Low regression slope values indicate stable performance across sites (*Table 2, Figure 3*).

Table 3 shows the results of the analysis of variance of (uncorrected) means of 10 provenances at 3 sites. No surprise that the effect of sites is clearly more significant compared to the effect of provenances.

Interactions

In *Figure 4*, response of populations is comparable at two locations, as the horizontal sequence of populations is identical in the graphs. (The sequence is the same as in *Table 2*, as populations are ranked by their original EQ values; at the extreme left: Bilowo, Poland.) A closer observation leaves no doubt that interactions with local climatic conditions exist. Two provenances are marked for interaction: Tarnawa (PL) and Plateaux (FR). Both originate from medium elevations and perform at low elevation in Hungary below average, and the opposite is true for Slovenia.

Interaction was found confounded with microsite inhomogeneity: in the variance analysis by test locations (Mátyás et al. 2008a) replication \times provenance interactions were significant ($P = 0.01$, not shown) in the Slovak and Hungarian trials, but not in Slovenia. Therefore the *interaction component (I)* was not separated from the residual (error) component.

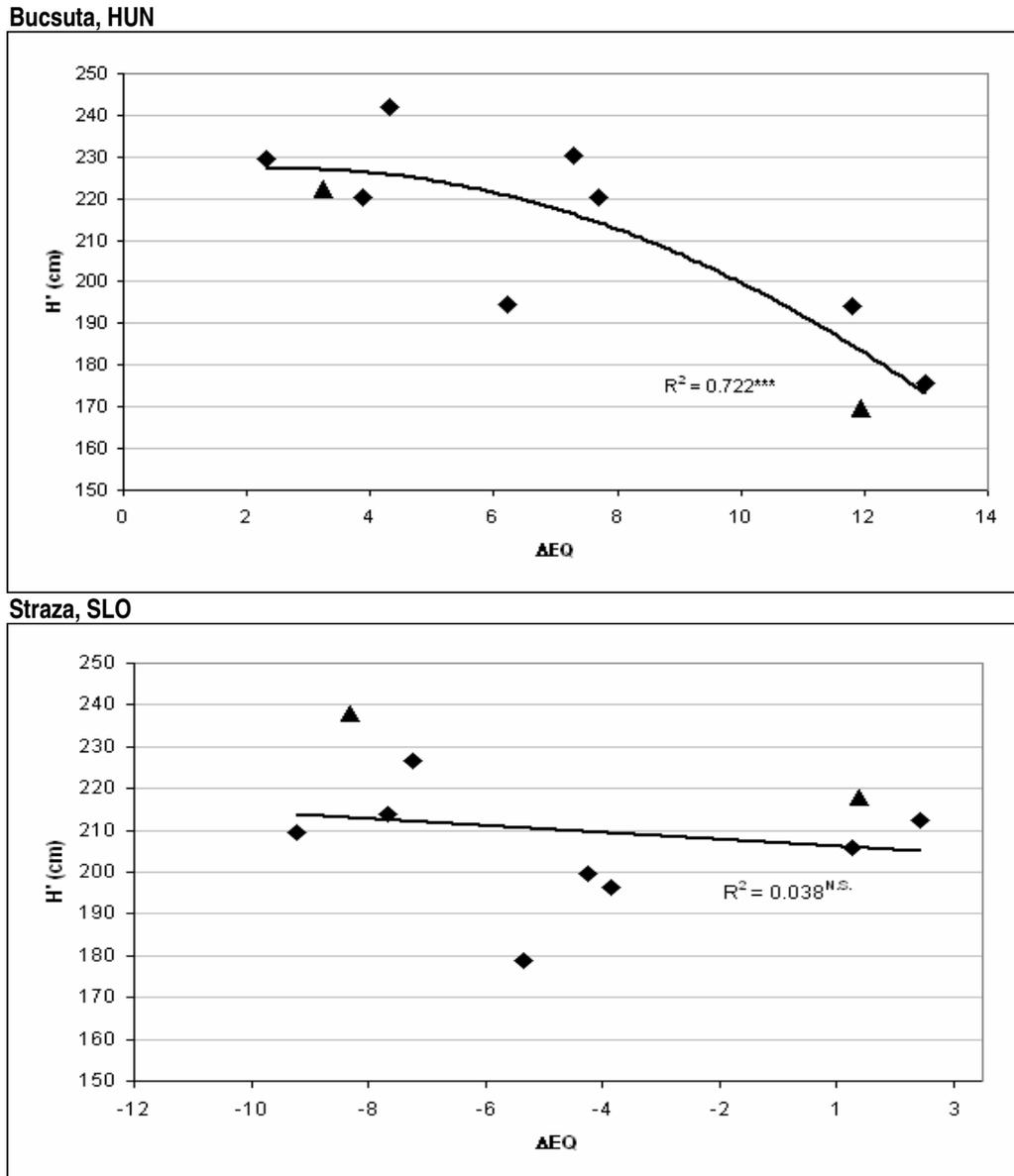


Figure 4. Regression of corrected height (H') of 10 identical provenances with ecodistance, at two sites with strongly differing EQ values (top: Bucsuta, HUN: 26.3, bottom: Straza, SLO: 15.3). The sequence of provenances is the same. Compare the two provenances marked with \blacktriangle for interaction: Tarnawa (POL, left) and Plateaux (FRA, right). Both mountain populations perform much better at higher elevation in Slovenia than in Hungary

Construction of a 3-D response surface model

Based on the previous results, a three-dimensional model is presented which expresses that height growth response to macroclimatic change depends on the climatic distance by which the adapted populations were moved (ΔEQ), and on the climatic environment where they are tested ($siteEQ$). Corrected height (H') serves as dependent variable. Although the regression is theoretically exponential, due to the low number of tested sites, only a linear response surface has been fitted on the data (Figure 5). Calculated for 10 provenances, the equation of general height response is:

$$H' = 162,63 + 2,288 * \Delta EQ + 2,674 * siteEQ - 0,223 * \Delta EQ * siteEQ$$

The proportion of variance accounted for is 35.78%, the coefficient $R = 0,598^{***}$, the individual differences between provenances left unconsidered. The distribution of residuals is even, indicating a balanced regression. Certain parts of the response surface are not supported by data and are separated by lines in *Figure 5*. The regression surface illustrates and summarises some important conclusions:

- increasing, positive EQ values, i.e. warming and more arid conditions lead to decreasing height growth and vitality;
- the effect of worsening of climatic conditions increases toward the lower (xeric) limit of distribution (EQ = 28)
- the interaction of site and macroclimatic adaptation is significant, an equation excluding the interaction component explains only 27.5% of the variation.

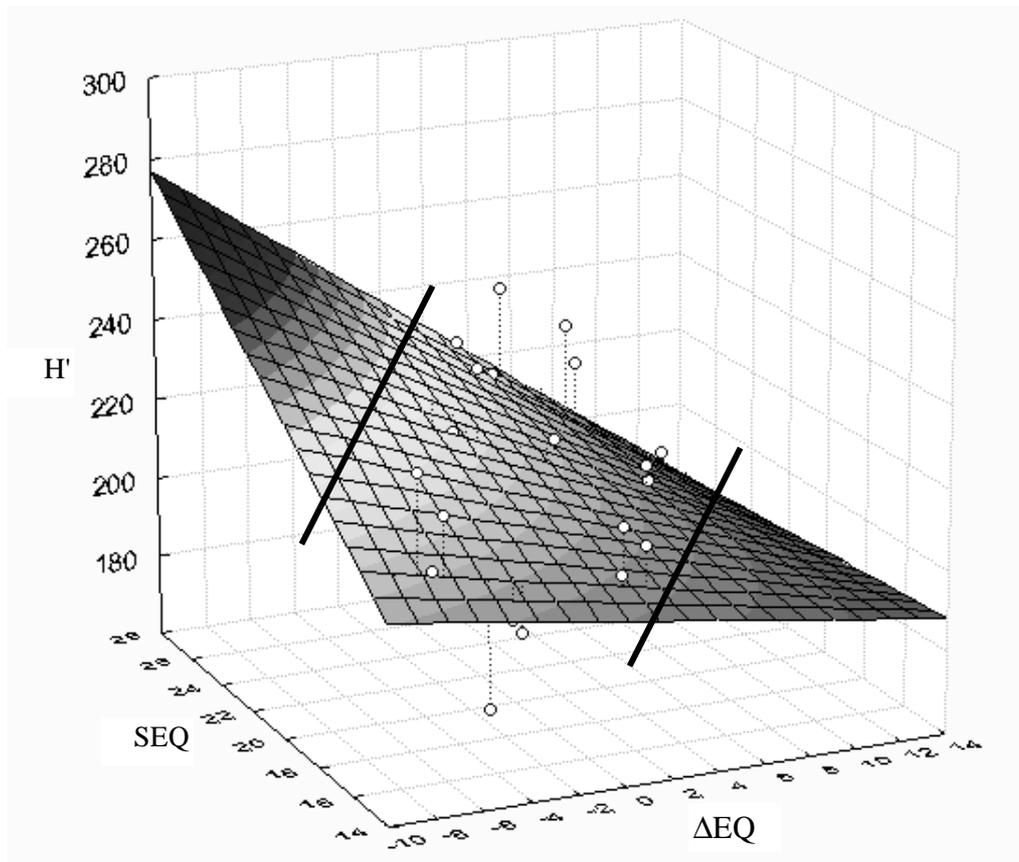


Figure 5. Linear model of height response of tested provenances, with corrected height (H') as dependent, and ecodistance of provenances (ΔEQ), respectively EQ value of sites (SEQ) as independent variables. Positive EQ values of ecodistance (to the right on the X axis) stand for simulated warming effect. Lines separate the part of the surface not supported by data

4 DISCUSSION

4.1 Modelling adaptive response to macroclimatic change

Modelling of expected response has to express that adaptation is an evolutionary-genetic issue. Present ecological models of phenotypic behaviour usually treat temperate tree species, including beech as monolithic, genetically uniform entities (e.g. Kramer 1994, Chuine et al. 2003, Czúcz et al. 2009). Another approach is the application of process-based genetic simulations which describe genetic processes on local level (Kramer et al. 2008). Both approaches

necessarily disregard within-species adaptive differentiation: ecological models assume functional properties of species uniform across space. This is a general problem of bioclimatic models (Mátyás et al. 2009, Jeschke – Strayer 2008).

The special feature of the selected set of experiments is, that due to the specific climatic relations between test locations and provenances, it provides a unique opportunity to study adaptive differentiation and responses to climatic warming. Detecting adaptive responses for a species exhibiting a strongly developed plasticity (Wühlisch et al. 1995, Kleinschmidt – Svolba 1995, Gömöry 2009) did not promise easy results. The selected variable EQ applied for the ecodistance approach seems to describe, however, macroclimatic conditions sufficiently well, at least for Central Europe and low to medium elevations.

The study was successful in detecting that

- adaptation (and consequently, selection effect) to macroclimate exists in spite of counteracting genetic and evolutionary forces;
- response of provenances strongly depends on the climatic conditions at origin and at the test, i.e. ecological distance is a valid concept for explaining responses;
- site potential and the local climatic conditions decide not only height response and its differentiation, but also interactions;
- a general, species-specific component of genetic response could be identified beside the individual differences of populations;
- interaction was noticeable mainly in relation to altitudinal changes.

The regression surface shown in *Figure 5* summarises the general trend of response to macroclimatic change. At the warm-continental site in Hungary, all provenances had been moved into warmer and drier conditions and the calculated polynomial shows a clear decline of height growth beginning from ΔEQ value 4 (*Figure 5*). Such a strong effect is not visible at the site with lowest EQ value, in Slovenia, where most populations came into a cooler and wetter (i.e. less stressful) environment than original. In this case growth depression with growing ecodistance was not detectable.

Regarding the mean performance of individual populations in the average of sites, the Dutch provenance Aarnink was the best, and Grasten from Denmark the worst (*Table 2*, *Figure 3*). This had little or nothing to do with the (macroclimatic) distance from the test sites.

The individual response of a population to changing environmental conditions is described by the term *phenotypic plasticity*. Between-provenance differences in plasticity are detected by testing growth response along an ecological gradient, in our case by calculating regression of height vs. EQ values of the test sites (*Figure 3*).

4.2 Caveats and limitations to the analysis

In the case study an attempt was made to quantify and model the genetic effect of macroclimatic selection on juvenile height growth of beech. A trait important for early-stage competition, height is integrating effects of numerous growing seasons, which makes it logically related to climate which represents also an average of annual fluctuations. Climate means hide however year-to-year and local deviations from long term averages, although irregular extreme events may have a decisive selection effect (Berki et al. 2007). Climate means should be therefore regarded rather as surrogates for extremes.

For analysis of climatic adaptation, large-scale international trials seem to be ideal, as they are established with natural populations of known origin, sampled across a large area. It is a pity and a serious fault of international provenance research that sufficiently reliable, detailed climate data are missing in most cases. Ecological characterisation was traditionally confined to description of geographic parameters (coordinates, altitude). The selective role of concrete

climatic parameters has been analysed in detail only in recent literature, as interpolated, digital databases are increasingly accessible (e.g. Rehfeldt et al. 2003, 2008, Mátyás et al. 2008b). Interpolations may, however, carry considerable bias especially for higher elevations and regions with complex topography. The relatively low number of test sites and of populations, certainly limit the general validity of results. However, it is suspected, that synergy of climatic components might change across larger regions and therefore an evaluation in an ecologically restricted area might bring better results as pooling all available data without preliminary screening.

The analysed data were measured in juvenile stage. Switches in ranking may be expected up to higher ages in beech, and early age–age correlations are unreliable (Kleinschmidt – Svolba 1995). Also, results refer to the investigated populations and sites and may not be fully applicable in other environments. Therefore the application of the method on extended datasets is absolutely necessary.

Also, modelling the evolutionary-genetic background of adaptive response is still not precise enough for predictions as it fails to regard biotic interactions and migration limitations (Jeschke - Strayer 2008, Jump et al. 2009) or human interference such as planned forest management (Mátyás et al. 2009).

Finally an additional factor causing estimation errors should be mentioned. This lies in the unavoidable contradiction between the conditions of natural regeneration and selection populations are adapted to, and the necessarily different, artificial character of nursery raising and outplanting in comparative tests. In common gardens, populations experience transfer into rather artificial environments. This has little to do with natural conditions of regeneration, but one should remember that the aim of these studies is a) to derive information on use of reproductive material, and b) to forecast effects of man-made climatic changes. Neither of them are typically natural processes.

Understandably, a simulation of the natural ecological demands of a tree species in the field tests would cause a further loss of precision of response identification. Thus, the planned experimentation itself compromises the exact determination of genetic response: an unsolvable contradiction and an unexpected parallel to Heisenberg's uncertainty principle in quantum physics (Mátyás et al. 2008b).

5 CONCLUSIONS

5.1 Implications for the management and conservation of beech

The existence of macroclimatic adaptation patterns in juvenile growth justifies genetically based regulations for use of reproductive material. Regarding the sensitivity of beech to macroclimatic changes, the results show that adaptive pattern and plasticity of the species is fairly comparable to better explored conifer species such as pines, spruces (Mátyás – Yeatman 1992, Rehfeldt et al. 2003, 2008, Mátyás et al. 2008b, Thomson – Parker 2008).

Main conclusions for reproductive material use are:

- it would be more appropriate to use ecologically-based criteria instead of geographic-based ones to define recommended directions and limits of transfer;
- transfer effects are not similar in different part of the distribution area, in particular:
- in the range of the climatic optimum, in the area centre, and towards the thermal limit (northward) transfers are less critical;
- proposed separate treatment of higher elevation populations is supported by the deviating behaviour of provenances from above 1000 m;
- stressful and uncertain conditions at the lower (xeric) limit of the species demand there more rigorous rules for use and conservation.

Observations of mortality events close to the lower (xeric) limit of the species indicate that stability and vitality of populations depends not only on growth rate modelled from test results. Extreme weather events (droughts) may weaken physiological condition of populations relatively fast and may lead to insect and disease outbreaks in regions generally suitable for the species (Berki et al. 2007, Lakatos – Molnár 2009). Therefore, when defining maxima of allowable (ecological) distance of transfer, the principle of precaution should be observed, i.e. limits should be drawn stricter than the results of response regressions suggest.

Regarding climate change, the most important question is how populations react to warming, i.e. to positive ΔEQ values. The test in Hungary did detect sensitivity to EQ differences above the value of 4 (Figure 4).

Closer to the xeric/continental limit, already smaller changes are limiting presence (Czúcz et al. 2009). The results support the opinion that predicted climatic changes will not have serious consequences and even lead to production increase in the central-northern part of the range and at higher elevations as shown for conifers (Mátyás et al. 2008b). It is strongly cautioned from overestimating the plasticity potential found in this experiment, for regions close to the lower (xeric) limit of the range, furthermore also because the results obtained at juvenile age may not be maintained in later age.

Differences in growth performance and plasticity of provenances left unexplained by macroclimatic factors sustain earlier assumptions that local genetic adaptation also exists (“ecotypes”) and maybe also epigenetic effects; neither of them have been investigated in detail in this analysis. It seems that in beech, a population- (stand-) level differentiation co-exist with large-scale adaptedness and with significant plasticity. This supports the maintenance of selection of stands for reproductive material procurement (seed stands).

5.2 Application and advantages of the proposed approach

The proposed approach provides otherwise inaccessible information on the real-world effects of expected climatic changes. The success of evaluation depends of course on the characteristics of the dataset: number and quality of test sites, number and differentiation of populations and last not least, the reliability of recorded data.

The obtained results may be applied in adaptation and mitigation policy in forestry and related fields such as nature and gene conservation, e.g. for planning human-aided migration (Marris 2009). Typical uses are rules of forest reproductive material use, assessment of local, adapted populations or conservation strategy of marginal populations (Mátyás 2007).

The results may be useful also for testing or validating ecological models, evolutionary and ecological concepts and hypotheses related to climate change effects (see review of Jump – Peñuelas 2005, Mátyás et al. 2008b, Jump et al. 2009). The design and concept of presently existing tests are however unsuitable to elucidate problems such as micro-scale adaptation, ongoing selection in extant populations, or the importance of genetic carryover (epigenetic) effects. These questions need further, very carefully planned experimentation.

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