Future of Beech in Southeast Europe from the Perspective of Evolutionary Ecology

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Abstract – The aim of this study is to provide quantitative information on the effect of climatic change on the growth and vitality of European beech: although the species is considered in its optimum highly plastic and adaptable, it becomes climate-sensitive closer to its xeric (lower) distribution limits. The future of beech in Southeast Europe requires special attention because this region harbours significant populations living at or near their xeric distribution boundary. Even though the low elevation occurrences are uniquely vulnerable to climatic shifts, observations and modelling studies pertaining to this region are particularly scarce.

Out of climatic factors determining the xeric distributional limits for beech, Ellenberg's drought index (*EQ*) appeared as the most influential. Growth response analyses in comparative tests have confirmed the existence of macroclimatic adaptation of beech and have proven that warming and more arid conditions lead to decline of growth and vitality, while no decline was observed if *EQ* changed in the opposite direction. The response to weather extremes was investigated in field plots. Recurrent summer droughts of 3 to 4 consecutive years, above mean *EQ* value 40-42 resulted in pest and disease attacks and mass mortality.

The discussed approaches indicate consistently a high level of uncertainty regarding the future of beech at the xeric limit in Southeast Europe. According to field observations and bioclimatic data in Hungary, a large part of low-elevation beech forests presently in the zone of *EQ* index ≥20 might be threatened by the warming in the second half of the century, while higher-elevation occurrences may remain stable.

The interpretation of the results bears some stipulations, such as the consequence of ecological and human interactions in influencing present distribution patterns, the unclear role of persistence, natural selection and plasticity and uncertainties of climate projections. Grim projections may probably be partly overwritten by the mentioned stipulations and by careful and prudent human support.

genetic adaptation / climate change / drought tolerance / range retraction / xeric limits

1 INTRODUCTION

Adaptation strategy of forest trees is receiving growing attention in view of expected climatic changes. Scarcity of reliable information on responses to macroclimatic changes is a central problem and obstacle of planning for the future. In order to formulate realistic predictions, both

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the nature of adaptation to past and current climate, and the level of sensitivity to sudden environmental changes have to be understood and properly interpreted.

Conflicting approaches and unclear role of different factors determining adaptability keep adaptation to macroclimate still unresolved, in spite of its importance for practical forest management, for response prediction and risk management. Species-level (genetic) adaptation pattern is the basis for setting the rules of reproductive material use, for concepts to conserve genetic resources and for strategies to adapt to expected effects of environmental changes (Mátyás et al. 2009a).

The distribution of European beech extends across ecologically and climatically variable regions. Compared to other wide-spread tree species of Europe, it is still the one which was left in a relatively natural condition as – although in a distributional range reduced by man – it was seldom regenerated artificially and its reproductive material was not subject to large-scale commercial relocations such as oaks or Scots pine. Thus, present populations of European beech are still close to a "wild state". Therefore beech is a well suited model species to study adaptation strategy of long-living, deciduous climax species to climate and to changes of climate. The species is considered climate-sensitive and vulnerable to changes. Therefore its response to predicted large-scale changes of climate is a critical issue.

In this study an attempt is presented to trace, quantify and project the impacts of macroclimatic change on the distribution and vitality of beech, with results interpretable for the practice, as such information is urgently needed to develop adaptation strategies for both forestry and conservation. Investigations were concentrated to the xeric limits in SE Europe. This region, where the retreat of the species is imminent, has been largely neglected by European studies (Jump et al. 2009, Mátyás 2010, Lindner et al. 2010). The authors consider the detailed, practice-oriented investigation of climate impacts at the xeric limits of primary importance because especially the low elevation occurrences of beech in the region are uniquely vulnerable to climatic shifts.

Although climatic selection acts on the local, microclimatic level, macroclimate is generally considered as an appropriate surrogate. We also follow this convention in this study mainly for two reasons: available climatic scenarios define changes on macro-level only, and on the other hand, in forestry, local data on micro- and meso-climate are in most cases lacking or unreliable.

1.1 Hypotheses of adaptation strategy and pattern of beech – ecotypes, random effects vs. macroclimatic clines

Hypotheses in contemporary silviculture on the adaptation strategy of K-strategist or climax tree species are originating from ecology. Considering the strong and lasting effects of local selection, a close ("ecotypic") adaptation has been implicitly assumed for K-strategist tree species' such as beech. This view has been further supported by numerous field experiments with perennials, starting with Clausen et al. (1940). Studies on intraspecific genetic variation patterns of beech also explain spatial differentiation mostly as ecotypic (e.g. Wühlisch et al. 1995, Kleinschmidt – Svolba 1995, Jazbec et al. 2007), i.e. as result of close adaptation to local ecological conditions. As a corollary, beech is generally considered to be a climate-sensitive species throughout its entire European distribution area.

Recent developments of phylogeography and molecular genetics provide arguments pointing towards the role of random effects in counteracting close adaptation. First, the postglacial return of beech from various refugia to Central, and especially to Northern Europe is relatively recent, and its migration speed to follow climatic shifts is low (Davis 1981). Its genetic structure seems to have been impacted by random separations and mergers of lineages (Magri et al. 2006, Gömöry – Paule 2010). This renders a very close adaptation to local conditions less probable. Long-range gene flow and genetic interaction

between distant populations, although less intense than in the case of widespread conifers, is also acting against well differentiated ecotypes. For example, a recent study identified beech pollen transport – depending on wind trajectories – as distant as from NE France to Catalonia (Belmonte et al. 2008). There are a number of other biotic reasons why the genetic system of tree species may robustly counteract strict local adaptation (Mátyás 2007).

Annual growth and development cycle of beech 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, it may be assumed that diverging direction and intensity of climatic selection leaves also traces in the adaptive genetic variation pattern within the species. Proofs of macroclimatic selection are however surprisingly seldom found in beech. For instance, the range-wide analysis of metabolic allozyme gene loci has established correlations of allelic frequencies with climate-dependent factors such as altitude and continentality (Comps – Mátyás et al. 1998). Traces of genetic similarity among geographically distant populations growing on climatically similar sites point in the same direction (A. Borovics pers. comm.). The patterns of phenological behaviour observed in early phase of beech provenance trials also suggest a clear effect of macroclimate on genetic differentiation within the species. For example, bud break of beech shows a clinal East-West pattern: Atlantic coast provenances[1] are late, while Alpine and SE-European continental ones are early flushing (Wühlisch et al. 1995, Führer et al. 2009, Gömöry 2009).

Considering the pace of expected changes as compared to the generation length of beech, it is obvious that adaptation to rapid changes and to extreme events can function only if a strong component of plasticity (and, possibly, not yet identified epigenetic effects) is augmenting the inefficiency of selection and gene flow to adjust genetically set responses (Mátyás et al. 2010a, Finkeldey – Hattemer 2010). Surprisingly this aspect is largely missing from the agenda of ecological and genetic research in beech, but also generally in forest tree species.

1.2 The threat to xeric limits in SE Europe

Xeric (or rear, trailing) limits at the low latitude and low altitude end of distribution ranges are determined by climatic aridity (Mátyás et al. 2009b). Xeric limits of beech are apparent along lower elevations of Mediterranean mountain ranges, however on the temperate-continental plains and hills of SE Europe they are more difficult to follow due to more complex ecology and human disturbance. These limits are handled by contemporary statistic and process-oriented models with considerable uncertainty (Kramer et al. 2010).

At the xeric limit ecosystems are dependent on a volatile minimum of rainfall and are therefore sensitive to prolonged droughts. What makes this zone especially vulnerable to climatic shifts is the magnitude of the *latitudinal lapse rate* in flat terrain. It is generally known that the altitudinal lapse rate (gradient) for temperature (i.e. the rate of change with increasing elevation) amounts to 5.0–6.5 ºC/1000 m. At the same time, the latitudinal lapse rate is less recognized: in the temperate zone its mean value is around 6.9 ºC/1000 km – a difference of three magnitudes (Jump et al. 2009). One degree of temperature increase causes a shift upwards along a mountain slope of approximately 170 m: the same change on a plain triggers a shift of close to 150 km northward. A consequence is that obviously even minor changes of temperature *affect disproportionately larger tracts on plains* as compared to mountainous regions. Presuming a spontaneous migration speed for beech of approx. 20 km/century (Davis 1981, Mátyás 2007) an increase of temperature of just 1ºC would imply for beech a horizontal migration time of 750 years to follow the change. This fact explains the much larger vulnerability of low elevation occurrences in Southeast Europe.

[1] The term "provenance" is used in the paper synonymously for "transferred population of known origin".

According to calculations of the IPCC (Christensen et al. 2007), predicted temperature changes of the critical summer climate at the end of the century are much milder in North Europe between latitude 50º and 70º N, as compared to South Europe between 50º and 30º N. *Table 1* shows that changes are more extreme in summer than those of annual averages. Drought projections for Southern Europe are also serious, while none are predicted for North Europe.

Table 1. Predicted annual and summer climate changes for the period 2080-2099 vs. the reference period of 1980-1999, according to the A1B scenario (data from the IPCC, Christensen et al. 2007)

	mean annual temperature dT (°C)	mean summer temperature dT (°C)	Change of mean annual precipitation dP (%)	mean summer precipitation dP (%)	percentage of dry summers (%)
South Europe, Mediterranean	+3.5	**+4.1**	- 12	**- 24**	**42**
North Europe	+3.2	**+2.7**	+ 9	**+ 2**	**0**

The expected drought frequency was separately modelled by us for the Carpathian Basin due to the importance of this climate factor (Gálos et al. 2007). The results of the projection, using the regional climate model REMO developed by the Max Planck Institute for Meteorology (Hamburg) indicate a very similar outcome: in the second half of the 21st century every second year could bring major summer drought events *(Table 2).* Projected summer precipitation change is of special significance at the xeric limits which may affect profoundly the available climatic niche of dominant forest species, such as beech. This justifies the separate treatment of the Southeast European region.

Table 2. Frequency of recent and projected drought events for Hungary, according to scenario A1B, calculated with MPI's REMO regional climate model. Reference period: 1961-1990 (Gálos et al. 2007)

Period	Drought summers		
	number of years (out of 50 years)	mean of precipitation anomalies (%)	mean of temperature anomalies (°C)
1951–2000	15	–28.0	+0.9
2001–2050	17	–19.8	+1.5
2051–2100	26	–37.6	+4.2

1.3 Climatic factors of the xeric distributional limits for beech in SE Europe

The actual climatic envelope (niche) of beech has been repeatedly modelled (e.g. Kölling 2007, Fang – Lechowitz 2006, Bolte et al. 2007, Kramer et al. 2010). However, the studies focus on continental-scale effects of climate change, using low resolution climatic and species distribution data.

To identify the limiting macroclimatic factors at the xeric distributional limits of beech forests a regional modelling analysis was carried out in Hungary (Czúcz et al. 2010). Only data of occurrences were analysed which fulfilled the criteria of zonality (i.e. primarily determined by macroclimate). The stands have been grouped by the inventory grid system of the Forest Service (~1.5×1.9 km cells). The response variable was the percentage of presence of beech in the respective cell.

The probability of presence of beech was modelled by the variables seasonal and monthly temperature and precipitation means, interpolated for the grid cells. In addition Ellenberg's climate quotient (*EQ*, Ellenberg, 1988) was also applied, defined as the mean temperature of the warmest month (July, T_{07}) divided by annual precipitation (P_a):

$$EQ = 1000\ (T_{07} / P_a)$$

Ellenberg's climate quotient is a simple index expressing the joint effect of temperature and precipitation, and it has been generally used to express humidity conditions in Central Europe.

As the main modelling tool we used conditional inference-based regression trees (Hothorn et al. 2006). This technique identifies at every branching only the most influential variable. We fitted several regression tree models to subsets of the data in a bootstrap-like framework, using different calibration and evaluation data sets each time (for details see Czúcz et al. 2010). Examples of regression tree models are presented in *Figure 1*.

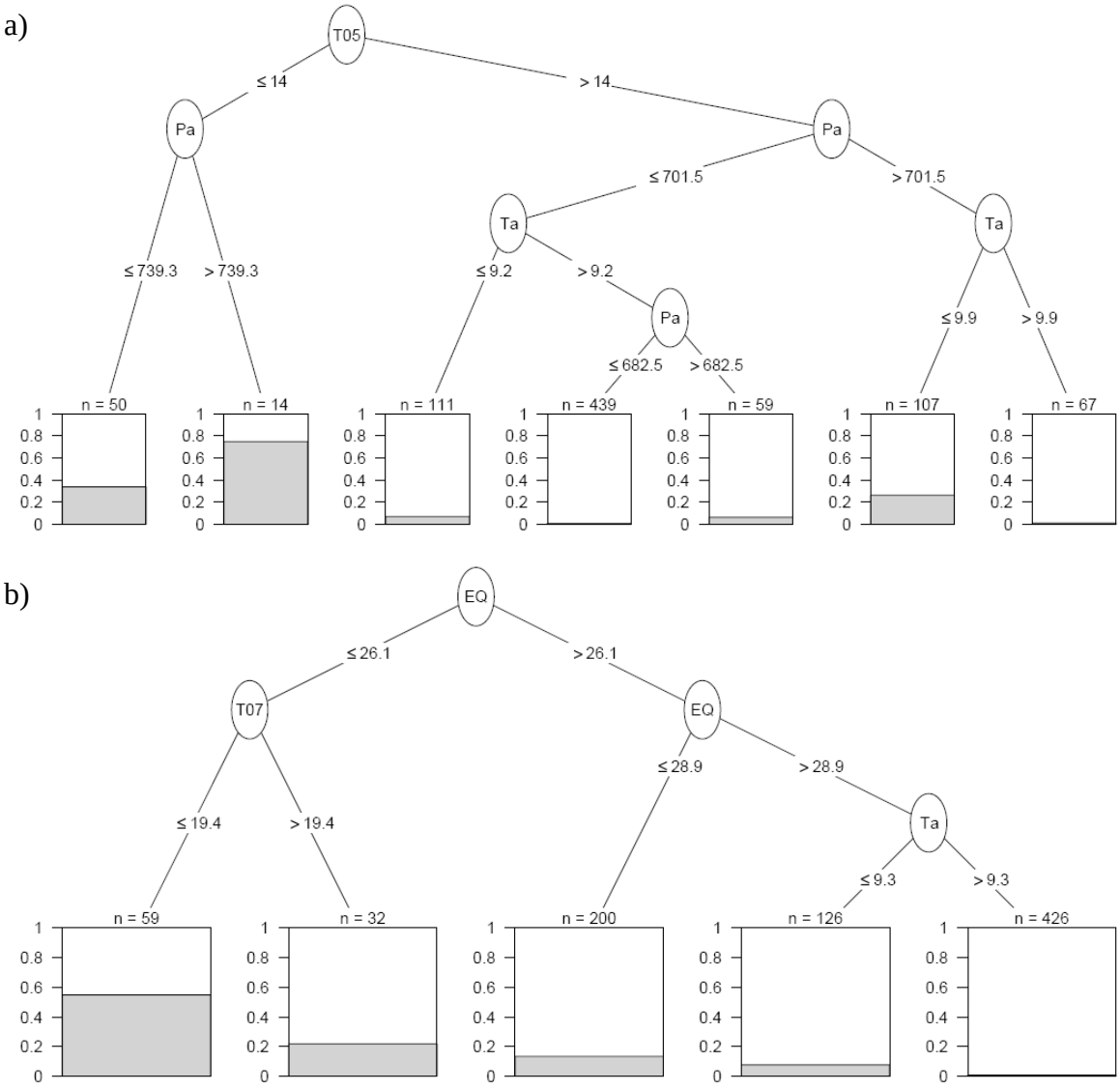

Figure 1. Examples of regression tree models for the xeric limits of zonal beech forests, determined by (a) basic climatic predictors only; and (b) with EQ included. In the terminal nodes bar diagrams visualize the probability of presence. (n: number of cells in the node). See text for variable names (Czúcz et al. 2010)

Out of the basic set of climatic variables late spring (May) temperature (T_{05}) appeared as the most influential predictor. In addition, annual precipitation (P_a) also played a significant role in determining the presence of beech near its xeric limit *(Figure 1a).* Grid cells with high late spring temperatures (T_{05} > 13.5–14 °C) contained relatively few beech stands. Alternatively, cells with the highest probability of presence had relatively cool May temperatures (T_{05} <14 °C), and received a higher amount of rainfall (>740 mm) per year.

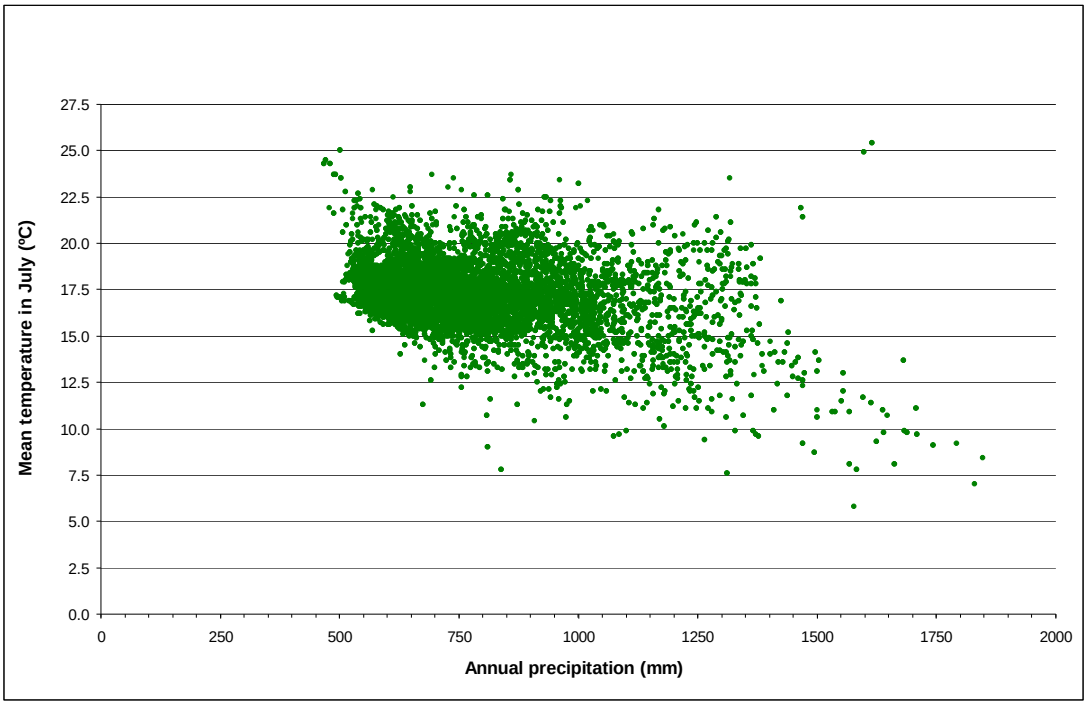

Figure 2. The climate envelope of beech in Europe using long term (1950-2000) climatic average of annual precipitation and mean July temperature. Climate data were extracted from the WoldClim high resolution interpolated climate database. (Compiled for EUFORGEN beech distribution data by E. Rasztovits)

If Ellenberg's climate quotient (*EQ*) was included among the predictor variables, it almost always appeared as the most distinguishing predictor. In the example of *Figure 1b* its maximum (limiting) value was 28.9. Apart from *EQ*, May temperature and annual temperature appeared again in other runs of bootstrapped decision tree models (Czúcz et al. 2010). The obtained results for limiting climate conditions for beech at low latitude/low altitude were compared with other, published ones *(Table 3).*

Table 3. Comparison of results of the present analysis with literature data on xeric limits of beech occurrence (Czúcz et al. 2010)

Source	Temperature limit (°C)	Precipitation limit (mm)	*EQ* index limit (°C/mm)
Fang and Lechowicz 2006	ann. mean < 13.5, July mean < 23.0	ann. mean > 900	29.0
Kölling 2007, cool-dry limit	ann. mean < 9.5	ann. mean > 500	–
Kölling 2007, warm-humid limit	ann. mean < 13.5	ann. mean > 850	–
Goetz in: Bolte et al. 2007	–	ann. mean > 500	–
Hoffman in: Bolte et al. 2007	July mean <19.0	–	–
Czúcz et al. 2010, "xeric limit"	ann. mean < 9.3	ann. mean > 680	28.9

* warmest month: 23.0 °C

The climate envelope of beech *(Figure 2)* indicates practically no presence below 500 mm annual precipitation and the bulk of occurrences stay below 20°C July mean. Most of the marginal points around the "main cloud" may be presumed to be non-zonal occurrences utilising surplus humidity (e.g. seeping water on slopes etc.). Data of *Table 3* show that the precipitation conditions at the continental xeric limit in Hungary are much drier than at the warm-humid limit in SW Europe, where the higher annual mean temperature requires significantly more rainfall. The study of Fang and Lechowicz (2006) analysed a large number of climate factors and indices, among them Ellenberg's index. Their "xeric limit" values refer to the hottest sites beech might tolerate. Despite the limited scope of their dataset, the closeness of the estimated *EQ* limit of 29.0 to ours is surprising.

It is obvious that when modelling the probability of presence of beech, neither temperature nor precipitation can be considered as a single factor. This is illustrated also on the example of the two climate factors determining *EQ (Figure 2). EQ* index seems to characterise the climate conditions for beech in the region reliably and will be used for analysing responses to changing conditions in the followings.

2 GROWTH RESPONSE TO CHANGING CLIMATIC CONDITIONS (TRANSFER ANALYSIS)

The response of populations to changed climatic environment is analysed on the basis of the genetic tolerance limit hypothesis. According to the hypothesis, the fitness of a population adapted to a certain environment declines rapidly with worsening conditions. Natural selection intensifies simultaneously and adjusts the genetic makeup to the changed environment, depending on available genetic variability. At the genetic tolerance limit climatic selection ends up in mass mortality, where the genetic and ecological possibilities of adaptation are exhausted (Mátyás 2010a, *Figure 3*). Due to competitive or trophic interactions in the ecosystem, fitness is usually sooner lost than the genetically set critical tolerance, through pest and disease attacks or competition by other tree species. In ecology, this is expressed as the difference between "physiological" (in reality: genetic) and ecological tolerance.

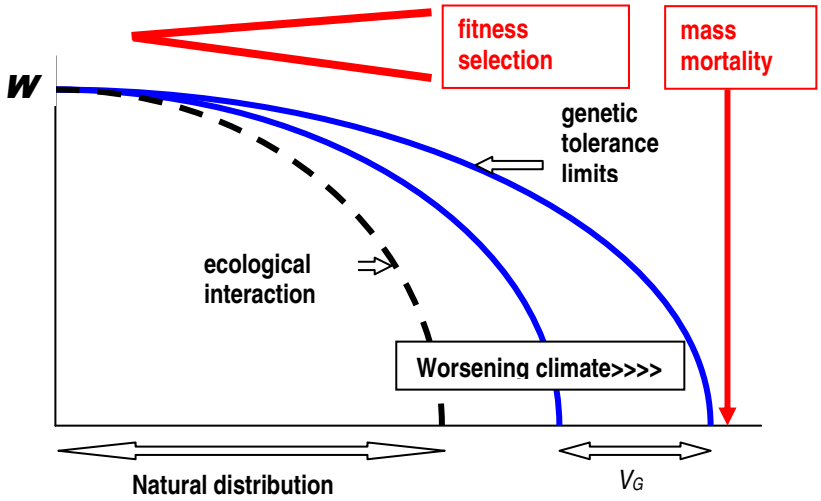

Figure 3. Ecological-genetic hypothesis of fitness loss along a climatic cline: tolerance decline and mortality triggered by worsening of climatic conditions. The genotypic variance of limits of tolerance (V_G) represents the basis of natural selection. The dashed line marks the ecological limitations of the species (Mátyás et al. 2010a)

Quantitative, adaptive genetic differentiation among provenances (in growth, phenology, and health) measured in common garden tests may be utilized to model the result of climatic selection and to forecast the effects of climatic change, as the response of populations at the test site can be interpreted as a simulation of environmental changes. Climate change as experienced by tested populations in the common garden is expressed as *ecodistance* ("space for time substitution" Mátyás et al. 2009a, 2010a).

For beech, growth response projections have not been validated thus far by field tests. The all-European beech provenance trials initiated by Muhs and collaborators (Muhs – Wühlisch 1993, Wühlisch 2007) are likewise suitable for modelling growth response to climatic changes through transfer analysis. For this purpose, experiments of the 1998 test series have been selected in SE Europe (Mátyás et al. 2009a). In this study results of two sites are introduced. For ecodistance calculation, Ellenberg's climate quotient (*EQ*) was applied. 10th year heights, measured in winter 2005/2006, have been used for the analysis.

The mid-elevation site in Straža, Slovenia provides climatically optimal conditions, while the Hungarian one (Bucsuta) is continental and relatively close to the xeric (trailing) limits of the distribution of beech, as shown by the Ellenberg indices *(Table 4).*

Table 4. Geographic, climatic data of two beech provenance trials (from Mátyás et al. 2009a)

Reg. Nr.	Country	Location	Altitude a.s.l. (m)	July mean temperature (^{o}C)	Annual mean precipitation (mm)	Ellenberg index (*EQ*)
2012	Slovenia	Straža	545	19.3	1260	15.3
2015	Hungary	Bucsuta	200	19.7	747	26.3

In *Figure 4*, data of 10 populations are shown which are represented in both tests. The ecodistance between the *EQ* at origin and *EQ* at the test site (*ΔEQ*) expresses the change of climate, where positive values indicate transfer to warmer/drier, and negative ones transfer to cooler/more humid conditions.

At the warm-continental site in Hungary (*EQ* = 26.3), all the 10 provenances have been transferred into an environment with increased continentality, higher mean 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 (i.e. less stressful) than their original climate.

Response regressions were calculated between mean heights of provenances and ecodistances expressed in *EQ* values. The polynomials *(Figure 4)* express that response of provenances depends on the difference of climatic conditions at the origin and the test sites, i.e. ecological distance is a valid concept for explaining responses and substantiate the existence of macroclimatic adaptation. At the warm site in Bucsuta, Hungary, the calculated polynomial shows a clear decline of height growth beginning from *ΔEQ* value 4. Such a clear effect of changed climate is not visible at the cool, humid site in Slovenia. In this case most provenances were brought into a cooler, wetter environment than they were adapted to (*ΔEQ* reached nearly the same values as in Hungary, however in opposite direction); therefore no growth depression was detectable with growing ecodistance. This illustrates that negative response to changing environment is triggered only if the shift happens toward warmer/drier climate. The presented results for beech are supported by data of other species such as pine, larch and spruce species (for review, see Mátyás et al. 2010a) where very similar trends have been found.

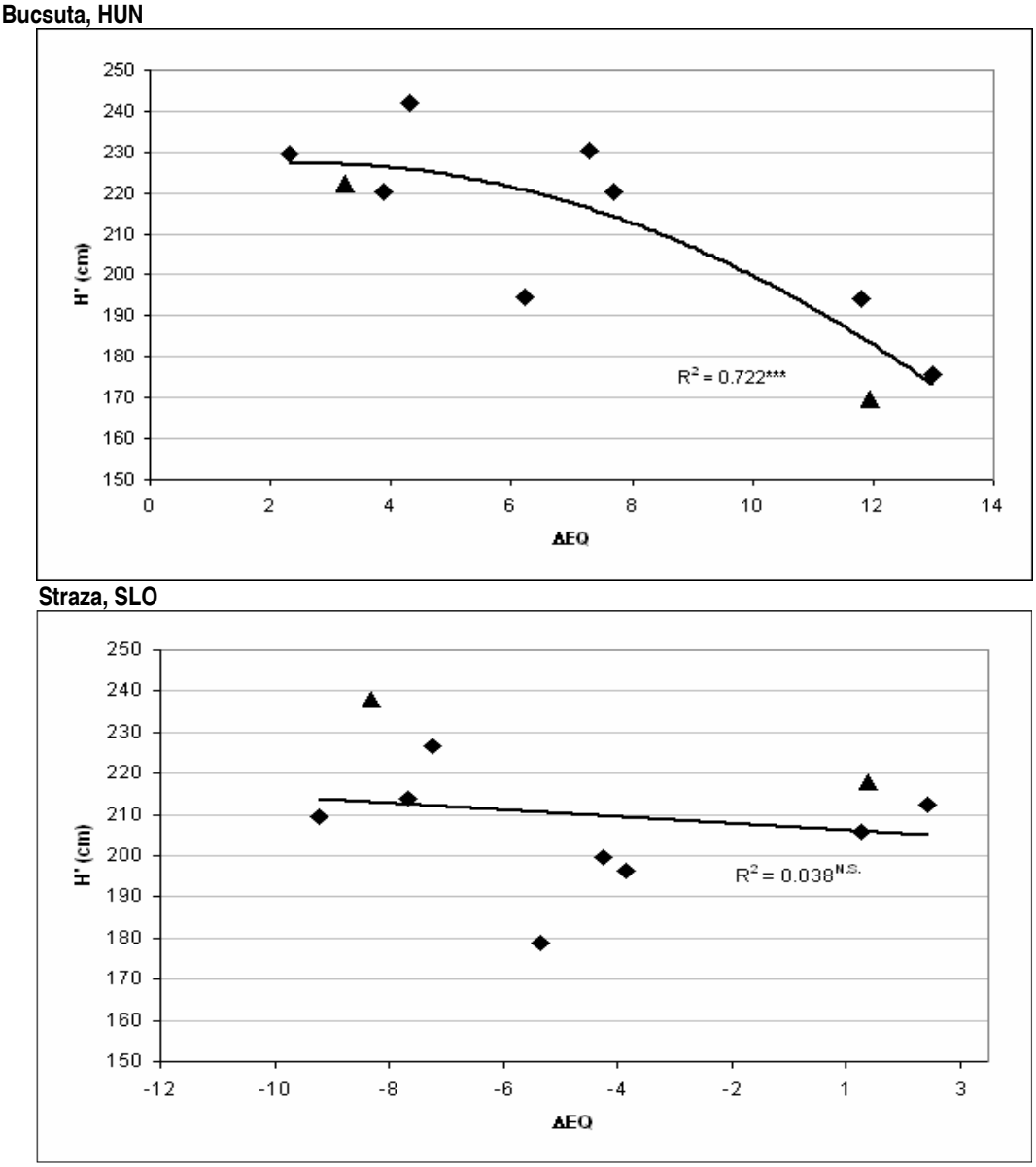

Figure 4. Regression of 1o-year height (H') of 10 identical provenances with ecodistance, at two sites with strongly differing EQ values. The sequence of provenances is the same. Compare the two provenances marked with ▲ for interaction: Tarnawa (POL, left) and Plateaux (FRA, right). Both mountain populations perform much better at higher elevation in Slovenia than in Hungary (Mátyás et al. 2009a)

The individual response of a population to changing environmental conditions along an ecological gradient is described by the term *phenotypic plasticity*. In general, plasticity has been found much more significant than expected from a "closely adapted" species. This is illustrated by the data of the Slovenian test site *(Figure 4*). Even relatively distant transfers (with high *EQ* values) do not show growth depression. Similar effects could be observed in other trials across Europe. However, close to the xeric limit, in Hungary, the buffering of plasticity does not function, as described before. Distinct interactions could be identified only in individual cases *(Figure 4).*

The growth response (or transfer) analysis of the SE European beech trials yielded the following main conclusions:

- a climate-dependent component of adaptive genetic response could be identified across populations of different origin, i.e. adaptation to (and consequently, selection effect of) macroclimate exists in beech in spite of counteracting evolutionary and ecological effects;
- the change of climatic conditions toward warming and more arid conditions lead to decreasing height growth and vitality, while vitality is not affected if changes happen in the opposite direction.
- phenotypic plasticity of all populations is considerable, but near the xeric limit its effect ceases.

2.1 Response to weather extremes

Effects of climatic change are described as shifts of vegetation zones, realised through "migration" of species. In case of forest trees, "migration" means loss of competitive potential and subsequent decline of vitality followed by pest and disease attack. However, the response of forests to drought – contrary to grass or crop vegetation – is not immediate. Forest stands, even drought-sensitive beech, survive single extreme summers and recover merely with yield loss. This is the result of deep rooting of trees, utilizing deeper soil water resources. The situation is different if drought years happen consecutively.

In the literature "mortality syndrome" (Worrall et al. 2008) cases have mostly been treated as isolated, transient problems related to extreme events, rather than as a consequence of a long-term climate shift. This is because the gradual, relatively slow change of climatic means does not express the current effect of extremes at the xeric limits. Spontaneous climatic selection is driven by recurrent drought events and the symptoms of change appear usually quite abruptly. Climatic means in models should be regarded therefore rather as surrogates for extreme events. The long-term, gradual shift of climatic factors has merely a *predisposing* role. Besides climate, the site conditions, age and structure of stand play also a predisposing role. *Inciting* factors are mainly connected to climatic anomalies especially at the xeric limits. Pests or diseases attacking populations of weakened vitality are then the *direct or proximate causes* of mortality.

Health and vitality loss due to climatic extremes: case study of beech in SW Hungary

The gradually growing moisture deficit in Hungary has led to health problems in Hungarian beech forests since the 1990s, first of all in the Southwest of the country where climatic changes were the strongest, and where the stands are at low elevation and close to the xeric limits. The weakened trees became more sensitive to secondary pests and pathogens and showed symptoms of health deterioration (early leaf abscission, sparser crowns, etc.).

The extent of climate damages of the drought years 2000–2004 has been investigated in two West Hungarian state forest companies. In 460 damaged forest compartments (total area: 3900 ha) 87.7 thousand cu.m. of damaged timber was harvested. The damaged stands were mostly above 60 years (T. Szép, unpubl. data).

The area most damaged was the Zalaegerszeg forest district (Zala county), where mass mortality was triggered in mature beech stands after regeneration cuts, when the canopy closure was opened up. This led to the outbreak of the otherwise harmless beech buprestid (*Agrilus viridis*). Damage of *Biscogniauxia nummularia* disease and of the beech bark beetle (*Taphrorychus bicolor)* occurred together with the buprestid damage. As a consequence close to 70,000 cu.m. of sanitary felling had to be executed in 2005 in that forestry district alone (*Figure 5*, Lakatos – Molnár 2009). The type of damage supports the observation of forest protection experts that disturbance of the closed canopy increases the risk of climate damage.

Figure 5. Symptoms of beech decline in 2004 in Zala county, following the damage of Taphrorychus bicolor on the trunk (Molnár – Lakatos 2009)

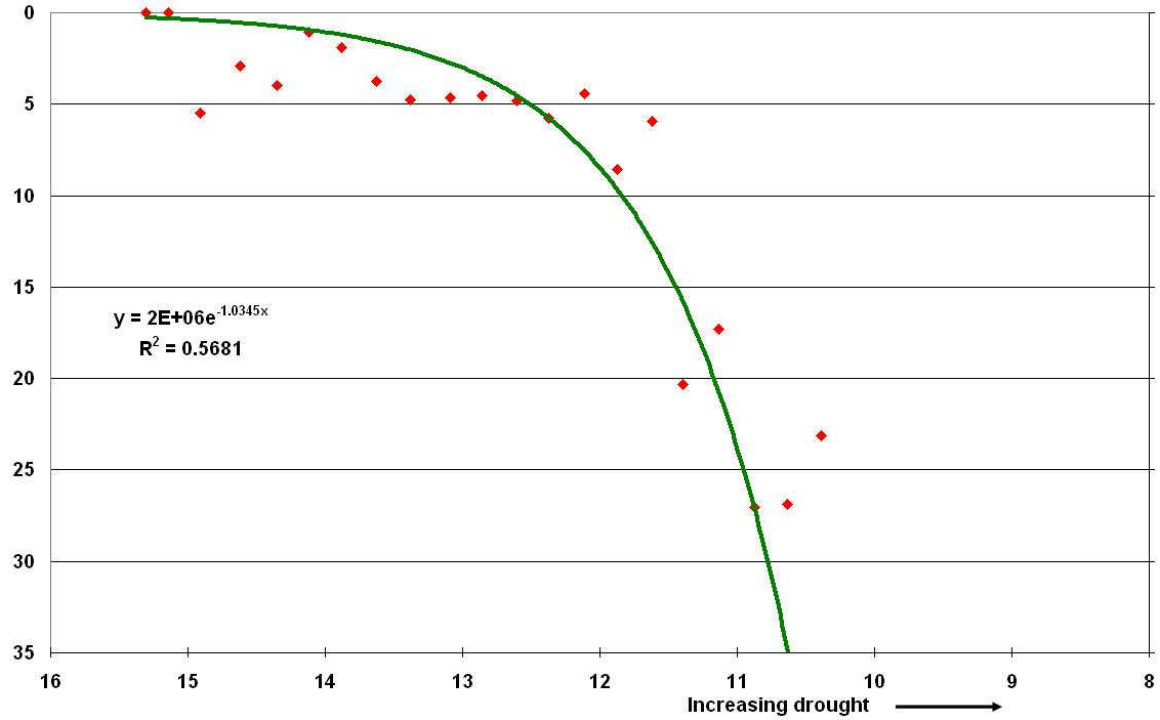

Figure 6. Percentage of compartments in West Hungarian forest companies damaged by drought events 2000-2004 (vertical axis) in relation to their climatic position (climate worsens toward lower tolerance index values, horizontal axis). Compare with hypothetic graph in Figure 3. Explanation in the text (T. Szép, unpublished data)

A close correlation was found between the climate classes and the percentage of stands damaged to various degrees *(Figure 6).* Berki's tolerance index was used for climate classification which considers in addition to summer temperature and precipitation also spring rainfall (Berki et al. 2009).

Extrapolating the correlation onto the national forest area, 23% of the 104 thousand ha of beech forests may be assumed as threatened with 9 million cu.m. of total standing volume. For 2065, a tripling of these figures was extrapolated (76%, 29 million cu.m.). To avoid further increase of damages, a faster rotation (lowering of rotation age) is proposed by silviculturists (T. Szép, unpubl. data).

Analysis of drought events

For the closer definition of extreme weather effects leading to the "mortality syndrome" in beech, threatened stands have been selected in different parts of the country. Criteria of selection were: at least medium-age, zonal site (primarily climate dependent site, at least medium deep soil with no defects, no hydrological influence) and position as close to the xeric limit as possible. Weather conditions and mortality events in the stand in the recent past were reconstructed.

For the analysis on annual basis, *EQ* had to be modified to be suitable to characterise individual years' weather. Mean temperature of the 3 summer months was used for the annual *EQ* index instead of just July's, to avoid random effects of individual months (in case of 30-year climate averages, this is not a problem). Investigation of mortality frequency has shown that single drought events did not threaten the stability of populations. The recurrent drought period lasting up to five years in some areas, has however resulted in very serious mortality in the investigated beech stands, in one case the population went extinct *(Figure 7)*. As an example, effects of consecutive drought events are shown for a South Hungarian beech forest at the xeric limits of distribution. The stand has been selected at the edge of the xeric limit which is indicated by the frequency of droughty years. Years with EQ indices significantly above 30 have been considered as drought events. Mass mortality started in 2003, in the fourth year of consecutive drought, after an extremely dry summer *(Figure 8)*.

Observations at other locations have confirmed that in case of beech, recurrent drought events of 3 to 4 consecutive years (depending on severity) lead in general to irreversible mass mortality and local extinction (Berki et al. 2009). It was also found that not only the number of consecutive years, but the severity of drought period has an influence on the decline. Data of selected observation plots near the xeric limit *(Figure 7)* confirm a direct, causal link between health and drought. Mean summer drought severity above *EQ* value 40–42 seem to trigger a mass mortality syndrome.

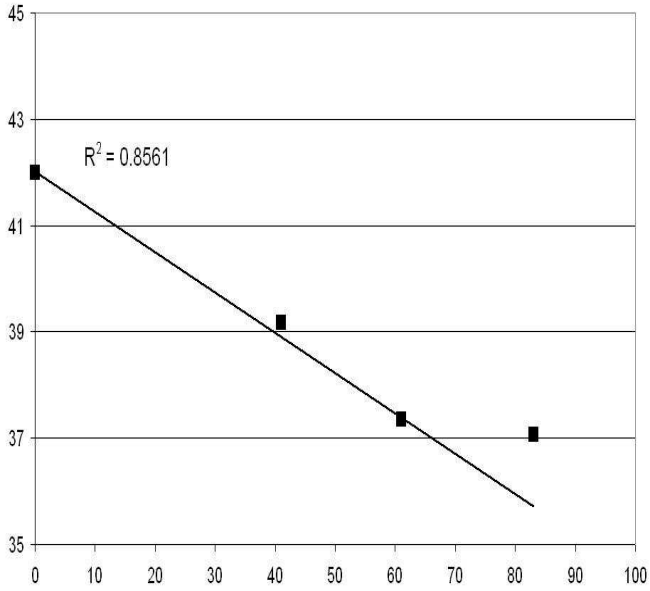

Figure 7. Average EQ value of the drought years 2000-2004 (vertical axis) and the health condition of selected mature beech plots at the xeric limit, at the end of the period (percentage of healthy individuals, horizontal axis) (unpublished data of Berki and Móricz)

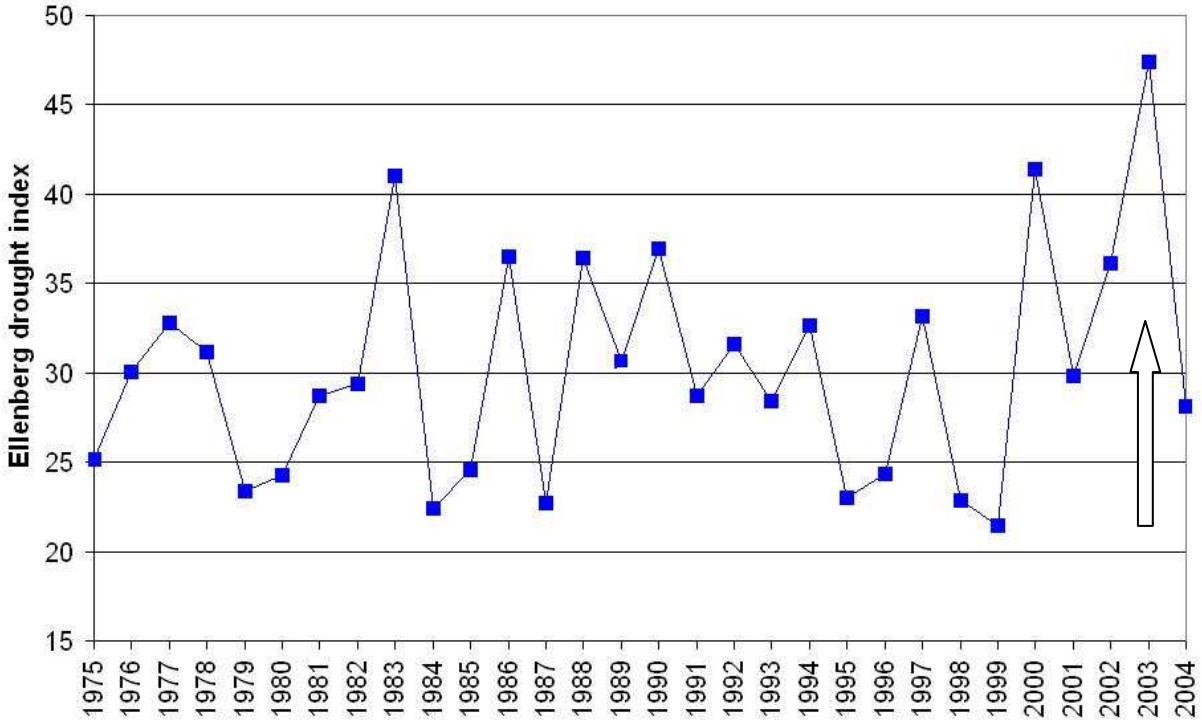

Figure 8. Drought frequency and the initiation of mass mortality of beech at the location Fiad (South Transdanubia). Years with EQ indices (vertical axis) significantly above 30 have been drought events. Mass mortality started in Fiad in 2003, in the fourth year of consecutive drought (arrow) (after Berki et al. 2009)

3 PROJECTIONS INTO THE FUTURE

How exactly xeric limits of beech will shift in the future is poorly explained by currently available models. Predictions about the role of selection and adaptation are ambiguous, as judgements of genetic adaptive potential rely first of all on model results with neutral traits, and neither statistical nor process oriented models handle conditions at the xeric limits properly (Kramer et al. 2010). Although the possibility of selection sweep as a consequence of adaptation is acknowledged but no studies exist at the trailing limits of distribution, where extreme selection for fitness comes into effect. The reliability of existing models is first of all hampered by not considering the main limiting factor at the xeric limit, i.e. the occurrence of droughts. In addition, human effects (forestry, land use) have to be considered not only for the past, but also for the future. It is also important to reiterate that present projections and models practically ignore the region, and this is supported by a detailed European study by Lindner et al. (2010). In the followings, projections for SE Europe are discussed according to the three approaches presented before.

3.1 Bioclimatic models

For predicting future distribution of beech on the basis of bioclimatic models, climatic projections of the Intergovernmental Panel on Climate Change (IPCC, Christensen et al. 2007) were applied *(Table 5).*

Table 5. Expected changes of climatic conditions by 2050 and estimated climatic space of zonal beech (Δbeech) forest stands in Hungary. Projected changes in summer half year temperature (ΔTs °C) and precipitation (ΔPs, percents) are shown for six IPCC AR4 climatic scenarios (extracted from Czúcz et al. 2010)

	HADCM3 A2	HADCM3 A1B	HADCM3 B1	CNCM3 A2	CSMK3 A2	GFCM21 A2
ΔTs	+2.9	+3.3	+2.6	+2.4	+1.8	+2.1
ΔPs (%)	–13.4	–10.9	–12.4	–9.6	+ 0.4	–11.4
Δbeech (%)	97–99	94–99	97–99	97–99	56–96	92–99

Table 5 reveals surprisingly high levels of range reduction, relatively independently from applied scenario projections. The projected potential distributions indicate a drastic reduction in macroclimatically suitable sites for beech, as 56–99% of present-day zonal beech forests might be outside their optimal bioclimatic niche by 2050. However, the projections of analysis only pertain to zonal beech forests in plachor position and other uncertainties of the projections are also high (Czúcz et al. 2010).

3.2 Responses predicted from transfer analysis

Predictions in the literature based on the hypothesis of close local adaptation envisage a general decline across the whole range of the species ("decoupling": Jump, Penuelas 2005). As it was shown in *Figure 4*, plasticity of populations is significant, and it may be anticipated that except for regions in the vicinity of xeric limits, productivity of beech will not decline (in sufficiently humid areas, even increase) until *EQ* values do not reach the critical maximum.

With worsening climatic conditions, vitality decline reaches 20% of height loss according to *Figure 4a*, around +13 *ΔEQ* in the Bucsuta test site. Based on field experience this amount of decline may be judged as a limit for competitive survival and a vitality decline where attack of pests and diseases may lead to mass mortality.

For the sake of a simple exploratory calculation let us assume that climatic changes will result in relatively homogeneous shifts in EQ values throughout the SE European distributional range of beech. Using the projected statistics of IPCC for Southern Europe (partly presented in *Table 1*), the climatic shift until 2080 was calculated as +11 *ΔEQ*. This suggests that – using the distribution limit value of 29 *EQ* – at locations with present *EQ* values below 29 – 11 ≈ 18~20 *EQ*, beech may survive, even if under stress. The larger part of the distributional range, especially Atlantic NW Europe as well as the higher elevation occurrences of the continental mountains (e.g. the Carpathians or the Balkan Range), fall into this group.

On the contrary, at the low-elevation xeric limits *EQ* would rise in 2080 from 29 to 40 *EQ*. Theoretically, part of these populations could survive as well, assuming that mass mortality starts only if the difference from the originally adapted climate surpasses +13 *ΔEQ* as stated above – if no extreme events and subsequent pests, epidemics occur in this time period. This assumption seems rather unrealistic. It has to be emphasized that all modelled responses were measured within the present distribution range of beech; there is no test site *outside* the xeric limits (which is a deplorable, but understandable drawback of the provenance test series). It is therefore impossible to formulate a more realistic estimate based on transfer analysis for the locations close to the limits.

3.3 Responses validated by field observations

The future frequency of drought events has been analysed for the territory of Hungary. The projected frequency of drought summers (precipitation decline exceeding 15% of the seasonal

mean) were calculated with MPI's REMO regional climate model *(Figure 9).* It is highly remarkable that from 2050 onward, the model projects at least one occasion per decade when 3 or more consecutive years with drought summers will happen, while only three such periods are projected for the first half of the century. Although droughts hit usually regionally, the predicted drought frequency may have an impact on the most part of the investigated beech area at least once during the century. The close link between extreme events and pest outbreaks exacerbate the expected damages *(Figures 6-8).* Drought will have its effect also on natural regeneration of stands as well (Czajkowski et al. 2005). These results support the grim outcome of the bioclimatic forecast for the second half of the century.

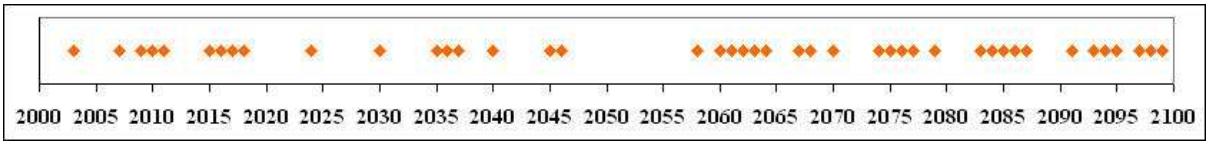

Figure 9. Frequency of consecutive drought events for Hungary, according to scenario A1B, based on results of the REMO model. Symbols depict years of droughty summers (Gálos et al. 2007)

Concluding, the outcome of the projections indicates a high level of uncertainty regarding the future of beech in Southeast Europe. According to the bioclimate approach 56–99% of present-day zonal beech forests might be outside their optimal climatic niche by 2050. The extrapolations of field observations on "drought plots" at the xeric limit also point toward a nearly complete loss of all beech stands in course of the century. Both analyses were carried out predominantly in mature, grown-up stands. For the transfer analysis performed on common garden populations only juvenile, 10 year old saplings were available. This approach confirmed the stability of mountain populations of SE Europe but provided no clues for the low-elevation zone close to the xeric limit. Although plasticity may support adaptation potential to a certain limit, *the part of the SE European continental range of beech where EQ values are currently above 20, has to be considered as a potential mass mortality zone* and respective precautionary measures should be taken.

4 CAVEATS OF INTERPRETATION OF THE RESULTS

Numerous studies (Gessler et al. 2007, Hlásny – Turčáni 2009, Kremer et al. 2010, Lindner et al. 2010) and also IPCC's 2007 report forecast a decline in growth and production of forest stands for East Europe. This projection is not measurable yet as a general trend (e.g. Somogyi 2008) although significant warming of the climate was already taking place. It should be noted that one reason for the missing evidence for gradually worsening vitality of beech in Southeast Europe has to be sought probably in the improper contents of datasets. Analyses are usually based on large-scale forest inventory data or wide-mesh monitoring points which are not precise enough to trace complex effects of opposing trends of environmental effects acting simultaneously across climatic gradients. For example, an international monitoring program (ICP Forests[2]) has gathered in Europe an immense body of information about the decline of tree health, including beech. The data have been of limited use for modelling trends because of low representation of threatened regions; there are too few sample points and insufficient ecological and genetic background data (Mátyás 2010).

[2] International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests

A general bias of both statistical and process-based modelling is caused by assuming actual limits of beech being in equilibrium with the ecological niche. This may imply an instant breakdown if climate conditions change ("decoupling") which is obviously not the case. For example, the xeric limit described by *EQ* 29 follows fairly exactly the distribution of beech at the beginning of the last century in Hungary. If limits would have been in ecological equilibrium, the present area of beech should have shrunk to its half during the 20th century, following the observed climate shift, a mean temperature increase of approx. 0.6°C *(Figure 10).* This extent of area contraction did not happen, although the mass mortality events in the SW part of the range were located in this zone.

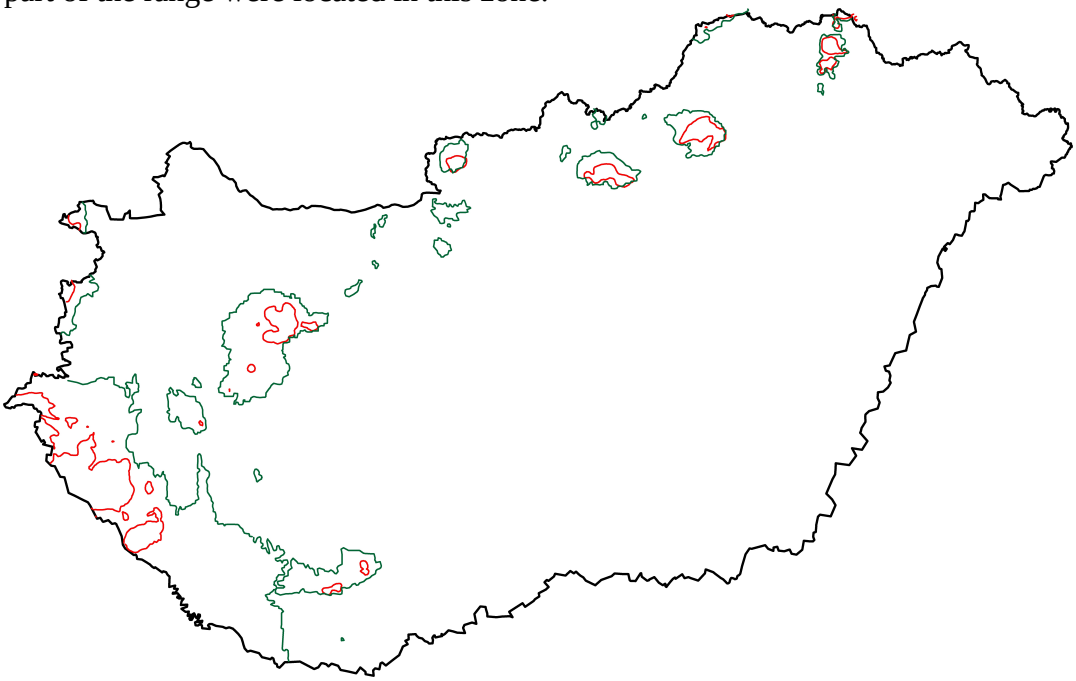

Figure 10. Shrinking of the climatic xeric limit of beech (EQ = 29) in Hungary between the beginning of the 20th century (1900-1930, green) and for the period 1975-2004 (red). (design: E. Rasztovits)

Projection of limits of genetically and ecologically set climatic tolerance has numerous additional constraints. For better interpretation of the results of this study the following four are highlighted: the consequence of ecological and human interactions in determining distribution patterns, the role of persistence, plasticity and natural selection, and uncertainties of climate projections, especially of precipitation conditions.

Genetically set (potential) tolerance limits are *per definitionem* wider than realized actual ones. It is a well known ecological rule that actual distributions of species are regulated by complex, often hidden interactions between host, competitors and consumers which may modify tolerance limits. The change of climatic environment affects also consuming and pathogenic organisms; the selection pressure by consumers may be rearranged. Forecasts are unreliable in this respect, because previously unknown pests and diseases may appear or harmless ones may change their virulence any time.

Modelling of adaptive response fails to regard not only biotic interactions and migration limitations (Jeschke – Strayer 2008, Jump et al. 2009) but especially human interference such as planned forest management. Planned forestry means that the structure, species composition and demography conditions of forests are determined by current management concepts, strategies and laws. Spontaneous processes are suppressed or tolerated only as far as they fit into the accepted strategies (Mátyás et al. 2010a). Therefore the predictive power of bioclimatic models has its limitations; nevertheless it is still the common projection method.

Accordingly, models based on bioclimate data do not consider the intrinsic persistence of tree species, which is mostly linked to longevity. The actual absence of seeding and reproduction may also mislead locally, as reproduction may happen anytime during the century-long lifetime of a tree, if suitable weather conditions favour it. In addition the extent of plasticity forest trees can rely on is still insufficiently known (see in detail in: Mátyás et al 2010a).

At the same time the results of the common garden tests support the opinion that predicted climatic changes may lead to production increase in the central-northern part of the range and at higher elevations due to the plasticity of the species (Mátyás et al. 2010a). It is strongly cautioned however from overestimating the plasticity potential in regions close to the lower (xeric) limit of the range.

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. 2010) and necessarily disregard within-species adaptive genetic differentiation. It is a general problem of bioclimatic models that consequences of genetic selection and adaptation is still not properly handled (Jeschke – Strayer 2008, Mátyás 2010, Lindner et al. 2010). The expectation that populations under extreme climatic stress may acclimate and genetically adapt infinitely is deceptive, as resources for adaptation and plasticity cannot be extended beyond the limitations set by the genetic system of species *(see Figure 3 and 6)*, and this is valid for beech as well.

Bioclimatic models usually do not count with the effects of extreme weather events, which have shaped also the past distribution ranges. Also, the limited precision of predicted precipitation changes are not stressed enough. This is of special significance in particular at low elevation plains and hills which are extremely sensitive to relatively minor humidity variations. For example, Hungary lies very close to the climatic division line separating areas of increasing (N. Europe) and decreasing (S. Europe) precipitation both in summer and winter (Christensen et al. 2007). Close to the xeric limits, relatively slight deviations in the climate pattern may seriously affect summer precipitation dependent beech. This is illustrated by the projections calculated from the different climatic scenarios *(Table 5).* The CSMK3 scenario predicts no decrease in summer rainfall, which affects the projection significantly. The effect of relatively minor changes visualises the uncertainty of projections generated by potential reversion of precipitation trends (Czúcz et al. 2010). Further details on uncertainties of projections may be found in Mátyás (2009), Czúcz et al. (2010), and Mátyás et al. (2010a).

5 FINAL CONCLUSIONS

Summing it up, projections into the far future may be biased by a number of uncertainties, first of all by the uncertainty of climate projections themselves. This part lies however beyond the expertise of a forester. Taking the ensemble of deductions of current, fairly deviating projections for granted, the comparison of very different approaches confirm the probability of serious climate impacts on distribution, health and productivity of beech. These effects will appear nonetheless differentiated, according to the ecological and genetic status of local beech occurrences. It is also important to note that contrary to mortality events and health decline along the xeric limits of the species, “compensatory” colonisation at the thermic (or front) limits, as projected by ecological models, will not happen spontaneously because of human obstacles to colonisation and due to the fairly low migration speed of beech compared to other deciduous species (Davis 1981, Mátyás 2009, Jump et al. 2009).

The verification of the existence of macroclimatic adaptation patterns 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. Observations of mortality events close to the lower (xeric) limit of the species indicate that stability and vitality of populations depend not only on shifts in climatic means. Extreme weather events (droughts) may weaken physiological condition of populations relatively fast and may lead to insect and disease outbreaks also in regions generally suitable for the species. 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 (Mátyás et al. 2010a). It seems that in beech, local differentiation co-exists with macroclimatic adaptation and with well developed plasticity.

The shrinking of future distribution of beech as suggested by various bioclimatic models (e.g. Thuiller et al. 2005, Czúcz et al. 2010) represent probably pessimistic scenarios which may be alleviated not only by the mentioned features but also by prudent human support (e.g. artificial regeneration and other silvicultural measures, see Mátyás 2010a). In the major part of the range the predicted changes will not trigger any decline due to the plasticity of the species: the predicted "decoupling" is improbable (Jump, Penuelas 2005). It would be however misleading to expect the same level of persistence and plasticity at the threatened xeric limits as across the rest of the range.

Therefore the forecasts have to be taken serious close to the xeric limits, and especially at low elevations. Field observations near the retracting distributional limits confirm that the decline process is ongoing in many locations (Penuelas et al. 2007, Berki et al. 2009). Considering the rapid shrinking of suitable bioclimatic space and the increasing selection pressure of abiotic and biotic stressors at the xeric limits, the results underline the importance of adaptive strategies both for management and conservation of forest resources. This calls also for relevant, well designed field studies and further development of prediction methods and modelling (Mátyás 2010).

The results of this study may contribute to the adjustment of adaptation and mitigation policy in forestry and nature conservation, to the revision of rules for deployment of reproductive material and also to validating evolutionary and ecological hypotheses related to climate change effects.

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REFERENCES

BERKI, I. – RASZTOVITS, E. – MÓRICZ, N. – MÁTYÁS, CS. (2009): Determination of the drought tolerance limit of beech forests and forecasting their future distribution in Hungary. Cereal Research Communications, 37: 613–616.

BELMONTE, J. – ALARCÓN, M. – AVILA, A. – SCIALABBA, E. – PINO, D. (2008): Long-range transport of beech (*Fagus sylvatica* L.) pollen to Catalonia (north-eastern Spain) Int. J. Biometeorol. 52: 675–687.

BOLTE, A. – CZAJKOWSKI, T. – KOMPA, T. (2007): The north-eastern distribution range of European beech – a review. Forestry, 80 (4): 413–429.

CHRISTENSEN, J.H. – HEWITSON, B. – BUSUIOC, A. – CHEN, A. – GAO, X. – HELD, I. et al. (2007): Regional Climate Projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. & Miller, H.L. (eds) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK. 747–845.

CHUINE, I. – KRAMER, K. – HÄNNINEN, H. (2003): Plant development models. In: Schwartz, M.D.(ed.): Phenology: an integrative environmental science. Kluwer Ac. Publ. 217–235.

CLAUSEN, J. – KECK, D.D. – HIESEY, W.W. (1940): Experimental studies on the nature of species. Vol I and II-IV (the additional volumes published in 1945, 1948, 1958) Carnegie Inst. Publ. Nr 520, Washington D.C.

COMPS, B. – MÁTYÁS, CS. – GEBUREK, T. – LETOUZEY, J. (1998): Genetic variation in beech populations along the Alp chain and in the Hungarian basin. Forest Genetics 5: (1) 1–9.

CZAJKOWSKI, T. – KUHLING M. – BOLTE A. (2005): Einfluss der Sommertrockenheit im Jahre 2003 auf das Wachstum von Naturverjüngungen der Buche (*Fagus sylvatica* L.) im nordöstlichen Mitteleuropa, Allg. Forst- u. Jagdztg. 176: 133–143.

CZÚCZ, B. – GÁLHIDY, L. – MÁTYÁS, CS. (2010): Present and forecasted xeric climatic limits of beech and sessile oak distribution at low altitudes in Central Europe. Ann. of Forest Sci., (accepted, in press)

DAVIS, M. (1981): Quaternary history and stability of forest communities. In: West, D.C., et al. (ed.): Forest succession: concept and application. Springer, New York, 132–153

ELLENBERG, H. (1988): Vegetation ecology of Central Europe, 4th ed., Cambridge University Press

FANG, J. – LECHOVICZ, M.J. (2006): Climatic limits for the present distribution of beech (*Fagus* L.) species in the world, J. Biogeogr., 33: 1804-1819.

FINKELDEY, R. – HATTEMER, H.H. (2010): Genetische variation in Waeldern – Wo stehen wir? (Genetic variation in forests – state of the art) Forstarchiv, 81: 123–129

FÜHRER, E. – RASZTOVITS, E. – CSÓKA, GY. – LAKATOS, F. – BORDÁCS, S. – NAGY, L. – MÁTYÁS CS. (2009): Current status of European beech (*Fagus sylvatica* L.) genetic resources in Hungary. Comm. Inst. Forestalis Bohemicae, Praha (in print)

GÁLOS, B. – LORENZ, PH. – JACOB, D. (2007): Will dry events occur more often in Hungary in the future? Env. Res. Letters, 2: 034006 (9pp) doi: 10.1088/1748-9326/2/3/034006

GESSLER, A. – KEITEL, C. – KREUZWIESER, J. – MATYSSEK, R. – SEILER, W. – RENNENBERG, H. (2007): Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. Trees – Structure and Function, 21: 1–11.

GÖMÖRY, D. (2009): Geographic patterns in the reactions of beech provenances to transfer. Report for COST E52 meeting, Thessaloniki, Greece (manuscript) 8 p.

GÖMÖRY, D. – PAULE, L. (2010): Reticulate evolution patterns in western-Eurasian beeches. Botanica Helv. 120: 63-74

HLÁSNY, T. – TURČÁNI, M. (2009): Insect pests as climate change driven disturbances in forest ecosystems. In: STRELCOVÁ, K. – MÁTYÁS, C. – KLEIDON, A. et al. eds. (2009): Bioclimatology and natural hazards. Springer, Berlin

HOTHORN, T. – HORNIK, K. – ZEILEIS A., (2006): Unbiased recursive partitioning: a conditional inference framework, J. Comput. Graph. Stat. 15 651-674.

JAZBEC, A. – SEGOTIĆ, K. – IVANKOVIĆ, M. – MARJANOVIĆ, H. – PERIĆ, S. (2007): Ranking of European beech provenances in Croatia using statistical analysis and analytical hierarchy process. Forestry, 80, (2): 151–162

JESCHKE, J.M. – STRAYER, D.L. (2008): Usefulness of bioclimatic models for studying climate change and invasive species. In: OSTFIELD, R.S. - SCHLESINGER, W.H. (eds.): The year in Ecology and conservation, 2008. Ann. New York Ac. Sci., Boston 1134: 1–24

JUMP, A.S. – PEÑUELAS, J. (2005): Running to stand still: adaptation and the response of plants to rapid climate change. Ecology Lett. 8: 1010–1020

JUMP, A. – MÁTYÁS, CS. – PEÑUELAS, J. (2009): The paradox of altitude for latitude comparisons in species range retractions. (Review) Trends in Ecology and Evolution, 24: 12, 694–700, doi: 10.1016/j.tree.2009.06.007

KLEINSCHMIDT, J. – SVOLBA, J. (1995): Results of the Krahl-Urban beech provenance experiments 1951, 1954, and 1959 in Northern Germany. In: MADSEN, S. (ed.): Genetics and silviculture of beech. Proc. 5th IUFRO Beech Symp., Danish Forest and Landscape Res. Inst., Forskningsserien 11/1995, 15–34

KÖLLING, C. (2007): Klimahüllen von 27 Waldbaumarten. AFZ - der Wald, 23: 1242–1244

KRAMER, K. (1994): Selecting a model to predict the onset of growth of *Fagus sylvatica*. J. of Appl. Ecology, 31: 172–181.

KRAMER, K. – DEGEN, B. – BUSCHBOM, J. – HICKLER, T. – THUILLER, W. – SYKES, M. – DE WINTER, W. (2010): Modelling exploration of the future of European beech (*Fagus sylvatica L.*) under climate change – Range, abundance, genetic diversity and adaptive response. For. Ecol. Managem., 259: 2213–2222.

LAKATOS, F. – MOLNÁR, M. (2009): Mass mortality of beech on Southwest Hungary. Acta Silvatica & Ligniaria Hung., 5: 75-–82

LINDNER, M. and 11 further authors (2010): Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Managem., 259 (4): 698–709

MAGRI, D. – VENDRAMIN, G.G. – COMPS, B. and 11 further authors (2006): A new scenario for the Quaternary history of European beech populations: paleobotanical evidence and genetic consequences. New Phytologist 171: 199–222

MÁTYÁS, CS. (2007): What do field trials tell about the future use of forest reproductive material? In: KOSKELA, J., BUCK, A., TEISSIER DU CROS, E. (eds.): Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, 53–69

MÁTYÁS, CS. (2009): Ecological challenges of climate change in Europe's continental, drought-threatened Southeast. In: Groisman, P.Y. –Ivanov S.V. (eds.): Regional aspects of climate-terrestrial-hydrologic interactions in non-boreal Eastern Europe. NATO Science Series, Springer Verl., 35–46

MÁTYÁS CS. (2010): Forecasts needed for retreating forests (Opinion) Nature, 464: Apr. 29, 1271

MÁTYÁS, Cs., BOŽIČ, G., GÖMÖRY, D., IVANKOVIĆ, M., RASZTOVITS, E. (2009a): Juvenile growth response of European Beech (*Fagus sylvatica* L.) to sudden change of climatic environment in SE European trials. iForests, Florence, 2: 213–220 doi: 10.3832/ifor0519-002

MÁTYÁS, CS. – VENDRAMIN, G.G. – FADY, B. (2009b): Forests at the limit: evolutionary-genetic consequences of environmental changes at the receding (xeric) edge of distribution. Ann. of Forest Sci., 66: 800–803

MÁTYÁS, CS. – BOROVICS, A. – NAGY, L. – UJVÁRI-JÁRMAY, É. (2010a): Genetically set response of trees to climatic change, with special regard to the xeric (retreating) limits. Forstarchiv, Hannover, 81: 130–141 (2010) doi 10.2376/0300

MUHS, H.-J. – WUEHLISCH, G. VON (1993): Research on the evaluation of forest genetic resources of beech - a proposal for a long-range experiment. In: MUHS, H.-J. – WUEHLISCH, G. VON (eds.): The scientific basis for the evaluation of forest genetic resources of beech. Proc. of an EC workshop, Ahrensburg, W. doc. for the EC, DG VI, Brussels 257–261

PEÑUELAS, J. – OGAYA, R. – BOADA, M. – JUMP, A.S. (2007): Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). Ecography 30 829–837.

SOMOGYI, Z. (2008): Recent trends of tree growth in relation to climate change in Hungary. Acta Silv. et Lign. Hung. 4: 17–27

THUILLER, W. – RICHARDSON, D.M. – PYŠEK, P. – MIDGLEY, G.F. – HUGHES, G.O. – ROUGET, M. (2005): Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biol. 11: 2234–2250

WORRAL, J.J. – EGELAND, L. – EAGER, T. – MASK, R.A. – JOHNSON, E.W. – KEMP, P.A. – SHEPPERD, W.D. (2008): Rapid mortality of *Populus tremuloides* in Southwestern Colorado, USA. For. Ecol. Managem., 255: 686–696

WÜHLISCH, G. VON – KRUSCHE, D. – MUHS, H.J. (1995): Variation in temperature sum requirement for flushing of beech provenances. Silvae Genet. 44: 343–346

WÜHLISCH, G. VON (2007): Series of international provenance trials of European beech. In: Improvement and Silviculture of Beech, Proc. the 7th Intern. Beech Symp. IUFRO Res. Gr. 1.10.00, RIFR, Teheran, Iran 135–144