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UDK 630*I

ASSESSMENT AND PROJECTION OF CLIMATE CHANGE IMPACTS IN SOUTHEAST EUROPEAN FORESTS: A CASE STUDY OF COMMON BEECH (*FAGUS SYLVATICA* L.)*

Ocena in napoved vplivov podnebnih sprememb v gozdovih jugovzhodne Evrope na primeru bukve *(Fagus sylvatica* L.)

Abstract: In view of expected climatic changes, the future of common 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 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 climate quotient (EQ) appeared as the most indicative. 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 towards cooler or moister conditions. 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 common 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. Grim projections may however be partly overwritten by uncertainties of modelling and by careful and prudent human support.

Keywords: genetic adaptation, climate change, drought tolerance, range retraction, xeric limits, trailing limits, Fagus

Ključne besede: : genetska prilagoditev, podnebne spremembe, toleranca na sušo, zmanjševanje habitata, meja sušnosti, robna območja razširjenosti, Fagus

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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 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 (Matyas et al., 2009a).

The distribution of European or common beech *(Fagus sylvatica* L.) 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 it was seldom regenerated artificially and its reproductive material was not subject to large-scale commercial relocations such as oaks or Norway spruce. Therefore beech is a well suited model species to study adaptation strategy of long-living climax species to climate and to changes of climate.

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. Xeric (or rear, trailing) limits at the low latitude and low altitude end of distribution ranges are determined by climatic aridity (Matyas et al., 2009b). These limits are handled by contemporary statistic and process-oriented models with considerable uncertainty (Kramer et al., 2010). Xeric limits of common 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. This region, where the retreat of the species is forecasted, has been largely neglected by European studies (Jump et al., 2009; Matyas, 2010; Lindner et al., 2010).

Although climatic effects act on the local, microclimate level, macroclimate has been analysed 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.

ADAPTIVE STRATEGY AND PATTERN OF COMMON BEECH

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 common beech also explain spatial differentiation mostly as ecotypic (e.g. Wühlisch et al., 1995; Kleinschmidt, Svolba, 1995; Jazbec et al., 2007).

It may be assumed that diverging direction and intensity of macroclimatic selection leaves also traces in the adaptive genetic variation pattern within the species. Proofs are however surprisingly seldom found in beech. The rangewide analysis of metabolic allozyme gene loci has established correlations of allelic frequencies with climate-dependent factors such as altitude and continentality (Comps 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 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).

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 common 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). 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 common 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 (Matyas, 2007).

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 (Mâtyâs et al., 2010a; Finkeldey, Hattemer, 2010).

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

CLIMATIC FACTORS OF THE XERIC DISTRIBUTIONAL LIMITS FOR COMMON 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). The studies have focused on continental-scale climate patterns, using low resolution climatic and species distribution data.

To identify the limiting microclimatic factors at the xeric distributional limits of common beech forests a regional modelling analysis was carried out in Hungary (Czúcz et al., 2011). 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 (~1.5x1.9 km cells). The response variable was the percentage of presence of beech in the respective cell.

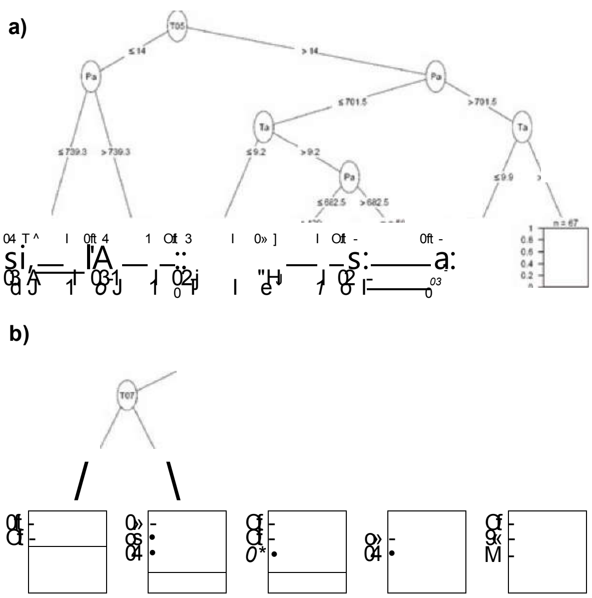

Figure 1. Examples of regression tree models for the xeric limits of zonal beech forests, determined by (a) basic climatic predictors only; and (b) with EQ included. In the terminal nodes bar diagrams visualize the probability of presence. (n: number of cells in the node). See text for variable names (Czúcz et al., 2011)

Slika 1. Primer modela regresijskega drevesa za primer sušnostne meje zonalnih bukovih gozdov glede na (a) osnovne klimatske parametre in (b) osnovne klimatske parameter in EQ indeks. Diagrami končnih vej prikazujejo verjetnost pojavljanja bukovih gozdov. N - število celic v končni veji. Imena spremenljivk so razložena v besedilu (Czúcz in sod., 2011)

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_{g7}) divided by annual precipitation *(P)*

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

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 conditional inference-based regression trees were used (Hothorn et al., 2006). This technique identifies at every branching only the most influential variable (for details see Czúcz et al., 2011). Examples of regression tree models are presented in Figure 1.

Out of the basic set of climatic variables late spring (May) temperature (T_{g5}) 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 (Fig. 1a). Grid 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.

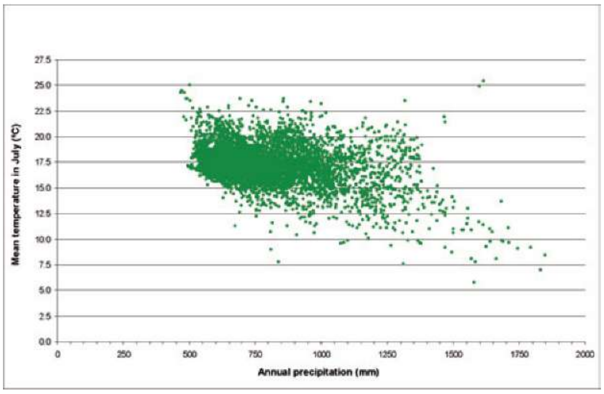

Figure 2. The climate envelope of common beech in Europe using long term (1950-2000) climatic average of annual precipitation and mean July temperature. Climate data were extracted from the WorldClim high resolution interpolated climate database. (Designed from EUFORGEN beech distribution data by E.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

Slika 2. Klimatski pogoji uspevanja bukve v Evropi na osnovi dolgoletnega (1950-2000) povprečja letnih padavin in povprečne julijske temperature. Podatke smo pridobili iz WorldClim visokoločljive baze podatkov. (Povzeto po EUFORGEN bazi distribucije bukve; E. Rasztovits)

If Ellenberg's climate quotient (EQ) was included among the predictor variables, it appeared as the most distinguishing predictor, according to Figure 1b its maximum (limiting) value was 28.9. The obtained results for limiting climate conditions for beech at low latitude/low altitude were compared with other, published ones (Table 1).

The climate envelope of common 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 1 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. EQ index seems to characterise the climate conditions for beech reliably and will be used for analysing responses to changing conditions in the followings.

GROWTH RESPONSE TO CHANGING CLIMATIC CONDITIONS

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 (Mâtyâs et al., 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

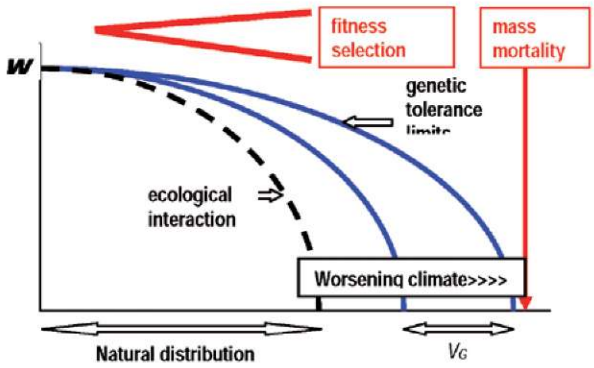

Figure 3. Ecological-genetic hypothesis of fitness loss along a climatic cline: tolerance decline and mortality triggered by worsening of climatic conditions. The genotypic variance of limits of tolerance (VG) represents the basis of natural selection. the dashed line marks the ecological limitations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

Slika 3. Ekološko-genetska hipoteza izgube fitnesa vzdolž klimatksega gradienta: zmanjševanje tolerance in večanje smrtnosti kot posledica zmanjševanja ustreznosti klimatskih razmer. Genotipska variance tolerančne omejitve (VG) predstavlja osnovo za naravno selekcijo. Prekinjena črta označuje ekološke meje vrste (Matyas in sod., 2010a)

Table 1. Comparison of results of the present analysis with literature data on xeric limits of common beech occurrence (Czücz et al., 2011)

Preglednica 1. Primerjava podatkov sušnih omejitev bukve glede na podatke v literaturi

Source	Temperature limit (°C)	Precipitation limit (mm)	EQ index limit (°C/mm)
Fang, 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 in sod., 2007	-	ann. mean > 500	-
Hoffman in: Bolte in sod., 2007	July mean <19.0	-	-
Czücz in sod., 2011, "xeric limit"	ann. mean < 9.3	ann. mean > 680	28.9

is expressed as the difference between "physiological" (in reality: genetic) and ecological tolerance.

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 (Matyas, 1994; 1996). Climate change as experienced by tested populations in the common garden is expressed as ecodistance ("space for time substitution" Matyas et al., 2009a; 2010a).

The all-European beech provenance trials initiated by Muhs and collaborators (Muhs, Wühlisch, 1993; Wühlisch, 2007) have been selected for modelling growth response to climatic changes through transfer analysis. Experiments of the 1998 test series have been analysed in SE Europe (Matyas 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 2).

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 *(AEQ)* expresses the change of climate, where positive values indicate transfer to warmer/drier, and negative ones transfer to cooler/moister 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/moister (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 *AEQ* 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, moister environment than they were adapted to *(AEQs* reached nearly the same values as in Hungary, however in opposite direction); therefore no growth depression was detectable with growing ecodistance. This illustrates that a negative response to changing environment is triggered only by shifts toward warmer/drier climate. The presented results for beech are supported by data of other species such as Scots pine, European larch and Norway spruce (for review, see Matyas et al., 2010a) where very similar trends have been found.

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:

- 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

Table 2. Geographic, climatic data of two common beech provenance trials (from Matyas et al., 2009a)

Preglednica 2. geografski in klimatski podatki dveh provenienčnih poskusov z bukvijo (slovenija in Madžarska) (povzeto po Matyas in sod., 2009a)

Reg. Nr.	Country	Location	Altitude a.s.l. (m)	July mean temperature (°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

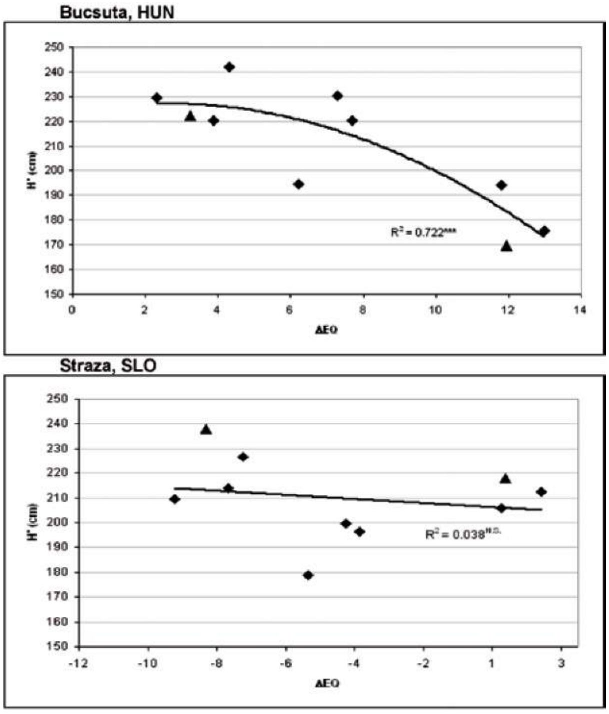

Figure 4. Regression of 10-year height (H') of 10 identical provenances with ecodistance, at two sites with strongly differing EQ values. The sequence of provenances is the same. compare the two provenances marked with • for interaction: Tarnawa (poL, left) and plateaux (Fra, right). Both mountain populations perform much better at higher elevation in Slovenia than in Hungary (Matyas et al., 2009a)

Slika 4. Regresijska krivulja višine desetletnih sadik (H'), desetih identičnih provenienc in njihovih ekodistančnih vrednosti s prikazom na dveh rastiščih , ki se značilno razlikujeta glede na EQ vrednosti. Provenienčno zaporedje je v obeh poskusih enako. Za interakcijo primerjaj obe provenience, označeni z • Tarnawa (POL, levo) in Plateaux (FRA, desno). Obe gorski populaciji mnogo bolje uspevata na rastišču na večji nadmorski višinini v Sloveniji glede na Madžarski poskus (Matyas in sod., 2009a)

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.

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 common 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. Spontaneous climatic selection is driven by recurrent drought events and the symptoms 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 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 (towards Slovenia) 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, Molnar 2009). The type of damage supports the observation of forest protection experts that disturbance of the closed canopy increases the risk of climate damage.

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 the summer temperature and precipitation also spring rainfall (Berki et al., 2009).

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 climatic position as close to the xeric limit as possible. Weather conditions and mortality events in the stand in the recent past were reconstructed.

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 one case the population went extinct (Figure 7). Observations 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 mature stands of similar

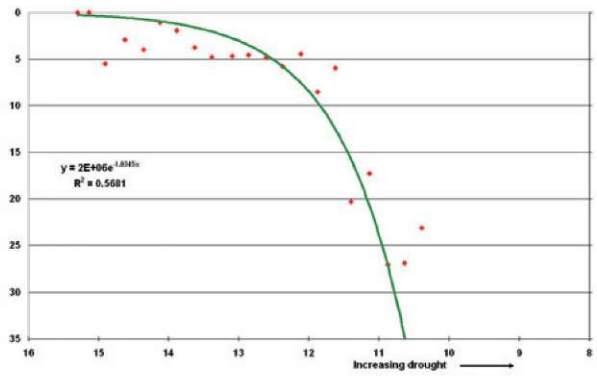

Figure 6. Percentage of compartments in West Hungarian forest companies damaged by drought events 2000-2004 (vertical axis) in relation to their climatic position (climate worsens toward lower climatic tolerance index values, horizontal axis). Compare with hypothetic graph in Figure 3. Explanation in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

Slika 6. Delež oddelkov v zahodni Madžarski z zabeležbo posledice suš v letih 2000-2004 (y os) v odnosu z njihovim klimatskim položajem (x os), pri čemer se klimatske razmere za bukev slabšajo v smeri zniževanja indeksa tolerance. Primerjaj s hipotetičnim grafikonom na Sliki 3 in glej razlago v besedilu (T. Szép, neobjavljeni podatki)

age near the xeric limit (Figure 7) indicate a direct, causal link between health and drought. Mean summer drought severity above EQ value 40-42 seems to trigger a mass mortality syndrome.

PROJECTIONS INTO THE FUTURE

How exactly xeric limits of common 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,

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

Slika 5. Simptomi propadanja bukve na območju Zala (leto 2004), kot posledica napada bukovega kosmatega lubadarja *(Taphrorychus bicolor)* (Molnar, Lakatos, 2009)

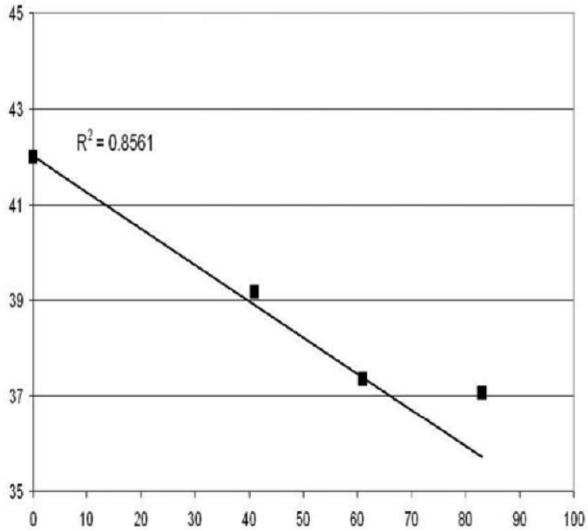

Figure 7. Average *EQ* value of the drought years 2000-2004 (vertical axis) and the health condition (percentage of healthy individuals, horizontal axis) of selected mature beech stands at the xeric limit, at the end of the period (unpublished data of Berki and Moricz)

Slika 7. Prikaz povprečne *EQ* vrednosti v sušnih letih 2000-2004 (y os) in zdravstvenega stanja dreves izraženega v deležu zdravih posamenikov (x os) v izbranih odraslih sestojih bukve z območja sušne omejitve vrste pri zaključku opazovalnega obdobja (neobjavljeni podatki Berkija in Moricza)

where extreme selection for fitness comes into effect. In the followings, projections for SE Europe are discussed according to the three approaches presented before.

BIOCLIMATIC MODELS

For predicting future distribution of common beech on the basis of bioclimatic models, climatic projections of the Intergovernmental Panel on Climate Change (IPCC, Christensen et al., 2007) were applied (Table 3).

Table 3 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 (Czucz et al., 2011).

RESPONSES PREDICTED FROM TRANSFER ANALYSIS

Plasticity of common beech 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 case of warming, in sufficiently humid areas, it may even increase, until *EQ* values do not approach the critical maximum.

With worsening climatic conditions, vitality decline reaches 20 % of height loss around +13 *AEQ* according to the Bucsuta site data (Figure 4a). Based on field experience this amount of decline may be judged as a limit for competitive survival and a vitality condition 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 region. Using the projected statistics of IPCC for Southern Europe, the climatic shift until 2080 was calculated as +11 *AEQ*. Subtracting this shift from the distribution limit value of *29 EQ* (Table 1) it is suggested that at locations with current *EQ* values below 29 - 11 = 18 ~ 20 *EQ,* beech may survive, even if under stress. The larger part of the distributional range at higher elevations falls into this group.

Table 3. Expected changes of climatic conditions by 2050 and estimated climatic niche change of zonal beech stands (Abeech) in Hungary. Projected changes in summer half year temperature (ATs °C) and precipitation (APs, percents) are shown for six IPCC AR4 climatic scenarios (extracted from Czücz et al., 2011)

Preglednica 3. Pričakovane spremembe podnebnih značilnosti do leta 2050 z oceno spremembe kimatske niše zonalnih bukovih gozdov (Abeech) na Madžarskem. Projekcije sprememb polletnih temperatur v poletnem obdobju (ATs °C) in padavin (APs,v odstotkih) s prikazom šestih IPCC AR4 scenarev spreminanja podnebnih razmer (povzeto po Czücz in sod., 2011)

	HADCM3 A2	HADCM3 A1B	HADCM3 B1	CNCM3 A2	CSMK3 A2	GFCM21 A2
ATs	+ 2.9	+ 3.3	+ 2.6	+ 2.4	+ 1.8	+ 2.1
APs	-13.4%	-10.9%	-12.4%	-9.6%	+ 0.4%	-11.4%
Abeech	97 - 99 %	94 - 99 %	97 - 99 %	97 - 99 %	56 - 96 %	92 - 99 %

On the contrary, at the low-elevation xeric limits *EQ* would rise in 2080 from 29 to 40 *EQ*. Theoretically, a part of these populations could survive as well, if experiencing less than +13 *AEQ* change as indicated above, assuming that no extreme events and subsequent pests, epidemics occur. This assumption seems however rather unrealistic.

It has to be emphasized that 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.

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 8). It is highly remarkable that from 2060 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 low-elevation beech area at least once during the century. The close link between extreme events and pest outbreaks exacerbate the expected damages (Figures 6, 7). 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.

Concluding, the outcome of the projections indicates a high level of uncertainty regarding the future of common 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 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 in the future 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 climatically threatened zone and respective precautionary measures should be taken.

CAVEATS OF INTERPRETATION OF THE RESULTS

Numerous studies (Gessler et al., 2007; Hlasny, Turčani, 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 common 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 (Matyas, 2010).

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

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

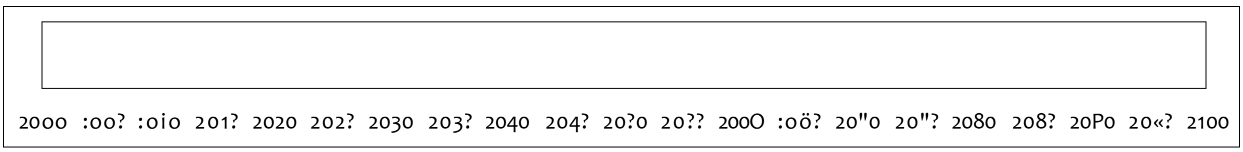

Figure 8. Frequency of consecutive drought events for Hungary, according to scenario A1B, based on results of the REMO model. symbols depict years of droughty summers (Galos et al., 2007)

Slika 8. Pogostost pojavljanja zaporednih sušnih dogodkov za Madžarsko, glede na scenarij klimatskih sprememb A1B, pridobljen z modelom RESO. Simboli predstavljajo predvidena leta v katerih predvidevamo sušna poletja (Galos in sod., 2007)

an instant breakdown if climate conditions change ("decoupling") which is obviously not the case. For example, if distribution of beech in Hungary would have been in ecological equilibrium, the present area of beech should have shrunk to its half during the 20th century, following a mean temperature increase of approx. 0.6°C. 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 (Matyas et al., 2010b).

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 ones are highlighted: the hidden effects of ecological interactions, the consequence of 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 (Matyas et al., 2010a).

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: Matyas 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 (Matyas 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 common beech as monolithic, genetically uniform entities (e.g. Kramer, 1994; Chuine et al., 2003; Czucz et al., 2011) 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; Matyas, 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 3). 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. Further details on uncertainties of projections may be found in Matyas (2009), Czucz et al. (2011), and Matyas et al. (2010a).

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 common 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; Mâtyâs, 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 differentiations also exist ("ecotypes?") and maybe also epigenetic effects (Mâtyâs et al., 2010a). It seems that in common beech, local differentiation co-exists with macroclimatic adaptation and with well developed plasticity.

The shrinking of future distribution of common beech as suggested by various bioclimatic models (e.g. Thuiller et al., 2005; Czücz et al., 2011) represent probably pessimistic scenarios which may be somewhat alleviated not only by the mentioned features but also by prudent human support (e.g. artificial regeneration and other silvicultural measures). 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" (Jump, Penuelas, 2005) is improbable. 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 (Mâtyâs, 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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