Genetic background of response of tree populations to aridification at the xeric forest limit; consequences for climatic modelling

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Introduction: xeric limits and genetics

Trees, as dominant components of forest ecosystems, are of high ecological importance in the temperate belt and receive much attention with regard to adaptation potential and future risks of diversity loss and extinction. Much of the literature however is based on simulations and models, the genetic background of which are often deduced from results with annuals or other fast reproducing organisms. It should be remembered that lifespan plays a decisive role in the adaptation process and mechanisms functional in annuals or even shorter generation organisms might be irrelevant for trees when considering the timeframes of present climate change scenarios. Analyses of the genetic structure of forest trees show that their genetic system and diversity parameters are *diametrically different* from annual plants or animals (Hamrick *et al.* 1992).

The crucial problem of realistic interpretation of adaptation processes in trees is however the missing of field observations, first of all in common garden tests. In forestry, these tests have a very long tradition ("provenance tests"). Tests with trees are difficult to establish, laborious and time consuming to maintain and measure. Provenance testing of forest trees may be one of the most important contributions of forestry to biological sciences. They are unique because they have been established with natural-state populations, adapted to specific conditions. They are unique also because these tests have been established across continents, at many sites and maintained over decades. Important insights in evolutionary ecology, e.g. on processes and patterns of adaptation, have been collected and utilized very early (Langlet 1971). It is all the more surprising that much of the very extensive work of forest geneticists failed to capture the attention of ecologists (e.g. Morgenstern 1996, Geburek and Turok 2005, Eriksson and Ekberg 2001, Mátyás 1997, 2000, Müller-Starck and Schubert 2001).

Another important field often missed when modelling and predicting responses to changes, is the production biology of forest trees (forest yield science). Large-scale assessments deal with response of forest stands to extant climate change effects and weather extremes (e.g. Briceno-Elizondo *et al.* 2006, Lapenis *et al.* 2005, Kramer and Mohren 2001). For instance, data show for large parts of Western Europe an unprecedented acceleration of forest growth in the recent warming decades, exceeding in some cases 50% (Spiecker *et al.* 1996). Interpreting these data might alleviate prediction difficulties of adaptive behaviour of tree populations. These shortcomings emphasise the importance of cross-disciplinary research (Mátyás 2006b).

Climatic modelling of xeric limits needs genetic considerations

The determination of "climatic envelopes" of forest tree species has been a long-time topic, in principle already since Alexander von Humboldt's observation of links between climates and vegetation physiognomy. Climatic demands of tree species and of forest ecosystems have however attained a sudden actuality in the context of adaptation to predicted climatic changes. Recent publications on bioclimatic modelling and predicted climate change-triggered vegetation shifts are abundant and have been considered also in the fourth report of IPCC (chapter on Europe, 2007).

Models and analyses deal however mostly with the shift of the thermic ("upper" or "front") limits of distribution (e.g. for Europe: Savolainen *et al.* 2004, for North America: Wang *et al.* 2006, for North Asia: Lapenis *et al.* 2005, Rehfeldt *et al.* 2003). Migration at the front, i.e. the shift of vegetation is the most visible and illustrative response to climate change. "Forward" colonisation more sensitive to climatic changes than loss of vitality and retreat at the xeric limits which is buffered by persistence and plasticity as explained later. No surprise that investigations at the xeric limits are seldom, mostly dealing with montane-Mediterranean conditions (e.g. Pigott and Pigott 1993, Penuelas *et al.* 2001, Westphal and Millar 2004, Piovesan and DiFilippo 2005, Jump *et al.* 2006, Fournier *et al.* 2006) and often lack a clear climatological foundation necessary for more general conclusions. The report of IPCC (2007) also misses to deal with the retreating rear limits according to their importance.

Bioclimatic modelling of distribution ranges is based on the concept that distributional patterns depend – among other factors – on the physiological tolerance limits to climatic effects. This generally recognised rule has to be extended by the statement that physiological tolerance is unquestionably determined by genetics. Tolerance can be defined as the ability of a genotype to maintain its fitness despite damage. It is also presumably genetically correlated with phenotypic plasticity, i.e. with growth vigour across environments (Weis *et al.* 2000; Mátyás and Nagy 2005). Limits of tolerance are therefore genetically set and will determine the presence or absence of species (Figure 1).

Thus, adaptive response to environmental stress is ultimately a genetic issue, and *bioclimatic modelling is basically dealing with the search for the genetically set tolerance limitations.*
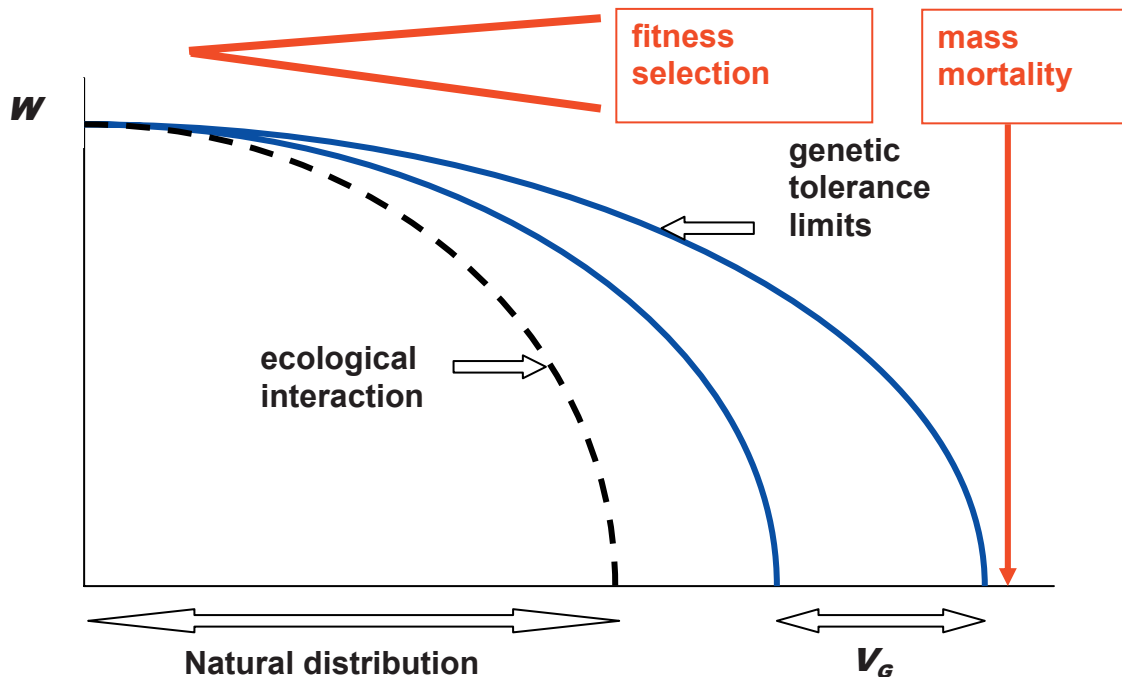

Figure 1. Ecological-genetic model of fitness decline and mortality triggered by worsening of climatic (site) conditions. The phenotypic variance of limits of tolerance (V_{PT}) represents the basis of natural selection. Due to interactions in the ecosystem, the natural distribution is usually stronger limited, than the genetically set critical tolerance(Mátyás 2006a)

Quantitative genetic approach to interpretation of adaptive behaviour of forest trees

The basic concept may be summed up as follows:

- importance and effects of climate factors may be effectively studied on zonal tree species, especially at the distributional limits;
- much of the intraspecific genetic differentiation among populations of dominant tree species with large distributional ranges is linked to climatic adaptation and illustrates the functioning of climatic selection;
- given climatic conditions (at test sites) trigger differentiated responses depending on the adaptedness of populations of different origin;
- limits of tolerance are genetically determined; the fitness of a population experiencing worsening environmental conditions declines gradually — depending on available genetic variability — to mass mortality when the genetic and ecological possibilities of adaptation are exhausted (Figure 1);
- quantitative, adaptive responses (growth, phenology, health) measured in comparative tests may be utilized to forecast the effects of climatic change, as the response of populatons at the test site can be interpreted as a simulation of environmental changes.

The problem of the xeric forest and tree distribution limits

Out of the complexity of biotic-ecological factors determining distribution lmits, in this paper the climatic and genetic ones are dealt with in detail, for the conditions of xeric (rear) limits on continental plains. The "front" and "rear" or upper and lower limits of distribution of widely distributed, zonal species differ by the limiting climate factors temperature and aridity, respectively. Thermic limits are determined by relatively accurately measurable temperature conditions which makes modelling relatively reliable. Xeric (aridity) limits of distribution are determined by climatic aridity, modified by local soil water regime conditions. These limits are more difficult to trace than thermal limits. Beyond methodical difficulties, xeric forest tree limits have received much less attention in the past because of their peripheral situation, away from regions of mainstream European interest.

Xeric forest and tree limits at the planar border zone between closed forest and woodlands (forest steppe) are especially vulnerable and ecologically very important. Their importance is increasing with predicted climatic changes. Beside certain Mediterranean and Submediterranean regions (such as the Spanish Meseta or Aquitany in Southern France), this belt reaches from East-Central Europe (Moravian, Carpathian Basin) across the plains of Southeast Europe (Romania, the Ukraine, South Russia) far into Southern Siberia.

Xeric limits are fuzzy on flat terrain, where species and vegetation types occur mosaic-like and follow the pattern of small-scale topographic, water regime and soil variation. These distribution limits are strongly affected by biotic interacions, competition, diseases and pests, and various obstacles to regeneration.

It has to be emphasised that low elevation distribution limits of tree species and forest types have been under continuous and strong human impact due to high population density and easier accessibility as compared to upper limits. Therefore, present-day distribution patterns reflect long lasting anthropogenic effects. Still, on a larger scale, present xeric limits at least indicate genetic-physiological limitations of climatic tolerance.

Ecological and genetic options to adapt to changes at the xeric limits

Early symptoms of climate change effects at the xeric limits, such as loss of vitality, sporadic mortality, forest health problems indicate the constraints of adaptability. There are both genetic and non-genetic mechanisms operating on the individual, population, species, ecosystem levels, balancing changes in environmental conditions. On species and ecosystem or landscape level, a non-genetic possibility of responding to large-scale changes in the environment is *migration through seed dispersal*, including species substitution (succession, immigration) provided there are suitable species available. Paleoecological evidence is abundant on migration during the epochs of glacials and interglacials (Davis and Shaw 2001), and this is the underlying response mechanism modelled and described by practically all ecologically-oriented future vegetation shift scenarios as well.

Extensive studies on *long-distance gene flow through pollen* have shed light also on this very effective mechanism of constant replenishment of genetic resources, which most probably contributes to the unexpectedly high diversity and adaptability of tree populations (Hamrick *et al.* 1992). It is self-evident that migration and gene flow are functional across the whole range of distribution. Both mechanisms have however limited importance at the xeric limits, because they *rather support the escape of species and genes instead of the persistence* in marginal situations.

Genetically set adjustment mechanisms sustain persistence both on population and individual level. On the level of populations, *natural selection* adjusts the average fitness of a population to changing conditions. The directed genetic change of the population's gene pool towards an optimum state is genetic adaptation in the strict sense. It is a well accepted concept that the basic precondition for fast and effective genetic adaptation lies in sufficiently large variation, i.e. in sufficient genetic diversity. Long-term genetic adaptability is therefore directly depending on the conservation or even reconstruction of broad adaptive genetic variance. The progress of selection will also depend on the intensity of selection pressure, as described by Fisher's theorem (Mátyás 2004). This progress may be counterbalanced by gene flow and migration.

Selection by climatic effects is certainly a key element among ecological factors. Although seemingly obvious, the role of selection in tracking changes is not uniformly seen. Some authors presume that climate selection is ineffective, plays a subordinate role or is at least very slow (Bradshaw 1991, Huntley 1991, Savolainen *et al.* 2004). The classic works of Turesson (1925) and Clausen *et al.* (1940) on annuals, and Langlet (1971) for trees support however the strong selective power of climate effects, backed by more recent papers such as Linhart and Grant (1996), Davis and Shaw (2001), Etterson and Shaw (2001), Jump and Penuelas (2005).

On the individual (genotype) level, *phenotypic plasticity* provides the ability to survive in a wide range of environments, without genetic change in the classic sense. Plasticity is the *environmentally sensitive production of alternative phenotypes by given genotypes* (DeWitt and Scheiner 2004). The term has been coined in zoology, where it has been applied in a relatively restricted manner for certain environmentally induced developmental or morphological phenomena. For plants, plasticity has to be interpreted relatively broadly (Bradshaw 1965). In our interpretation, derived from the practice of forest tree breeding, the ability of the genotype (clone), or of the population to maintain relative (usually superior) fitness across a wide range of environments is regarded as phenotypic plasticity or stability (Mátyás 2006a).

Plasticity implies that the phenotypic expression of genes is influenced by the environment, thus the organism may modify its responses within genetically set limits. It is especially effective in modular organisms such as trees, where the growth and development cycle may be strongly influenced by the environment. Phenotypic plasticity will set the limits of environmental heterogeneity within which a genotype or population can persist in its lifetime. In ecological literature, plasticity is often regarded as a non-genetic adaptation mechanism. It has to be emphasised that this trait is definitely heritable and underlying also climatic selection (Mátyás 2006a).

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[1] Phenotypic plasticity is a trait which may be interpreted and measured also on population level as the average effect of individuals. Common garden experiments prove that significant differences exist between populations: see in following chapters

When analysing the chances to adapt to the rapidly changing climate, it is important to comprehend which of the described mechanisms will gain importance in the timeframe of expected scenarios, and which mechanisms might be even negligible, and to discern between adaptation options in the current and future generations.

Processes of adjustment in the extant (currently growing) generation

Phenotypic plasticity provides the ability of individual, instant acclimation without any change in the inherited genetic resources of the population. Mainly for reasons of difficulty of experimental analysis, reaction norms and limits of adaptability set by phenotypic plasticity are rarely considered in connection with adaptation. It is an often underestimated issue both in forest genetics and ecology, in spite of the fact that *considering the speed and magnitude of predicted changes, phenotypic plasticity is the most important and practically only natural buffering mechanism* (Mátyás and Nagy 2005).

Natural selection is eliminating the genotypes of low fitness in the lifetime of a population. Although some studies on adaptation deal with selection processes and with changes in the genetic composition, few studies have been implemented in practice under conditions of severe change where populations are reaching their tolerance limits. In such extreme situations, the effectiveness of adjustment through selection ceases and mass mortality and even local extinction may follow (Lynch, Lande 1993, Mátyás and Yeatman 1992). Compared to plasticity, spontaneous natural selection plays therefore a smaller role in supporting persistence than generally assumed.

Processes of adjustment in the following generations

The progeny generation of parents selected by ecological factors will be altered on ecosystem level by migration (including gene flow) and succession. Preconditions for effective adjustment in both cases are landscape connectivity, availability of propagules and suitable speed, tracking the pace of change.

Environmental signals might trigger also *genetic carryover* (imprinting, 'after-effects') effects. These are lasting changes of genetic regulation, which can be inherited (for a review, see Martienssen and Colot 2001). Theoretically, spontaneous mutations might contribute to the replenishment of adaptive potential as well. These mechanisms are however too slow to become effective in a rapidly changing environment. There are also further genetic, migratory and evolutionary constraints to effective tracking (Loeschke 1987, Kremer *et al*. 1999, Mátyás 2006a).

Selection at the xeric limit

Selective pressure is connected with the ecological-climatic position

The selective pressure increase when approaching the xeric limits have been seldom studied (see review of Kingsolver *et al*. 2001). Observations on tolerance are scarce even in forestry practice, as forest management strives to operate well above the tolerance limits to secure economic returns.

Having investigated the health condition of sampled trees in the permanent heath monitoring network in Hungary, it turned out that the effect of selection pressure growing towards the xeric limits can be traced for climate indicator species such as beech or sessile oak. The climatic position in relation to the distribution limit significantly determines vitality: the larger the distance from the limit, the better the health status.

For example, when expressing average climatic moisture stress by the ratio of July mean and average summer precipitation, a very close correlation with leaf damage classes were found for both species. Figure 2 shows the average damage classes for beech represented in permanent monitoring plots in Hungary. It is visible that approaching the genetically set limits of tolerance, health status declines and reaches even mortality at marginal locations.

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[2] Such effects were detected also in certain forest trees, e.g. in boreal populations of Norway spruce (Picea abies) (Skrøppa and Johnsen 2000). Similar effects are suspected in a progeny trial of the same species (Ujvari-Jármay and Ujvari 2006). The general significance of genetic carryover in adaptation of trees is so far unclear and should be treated with caution.
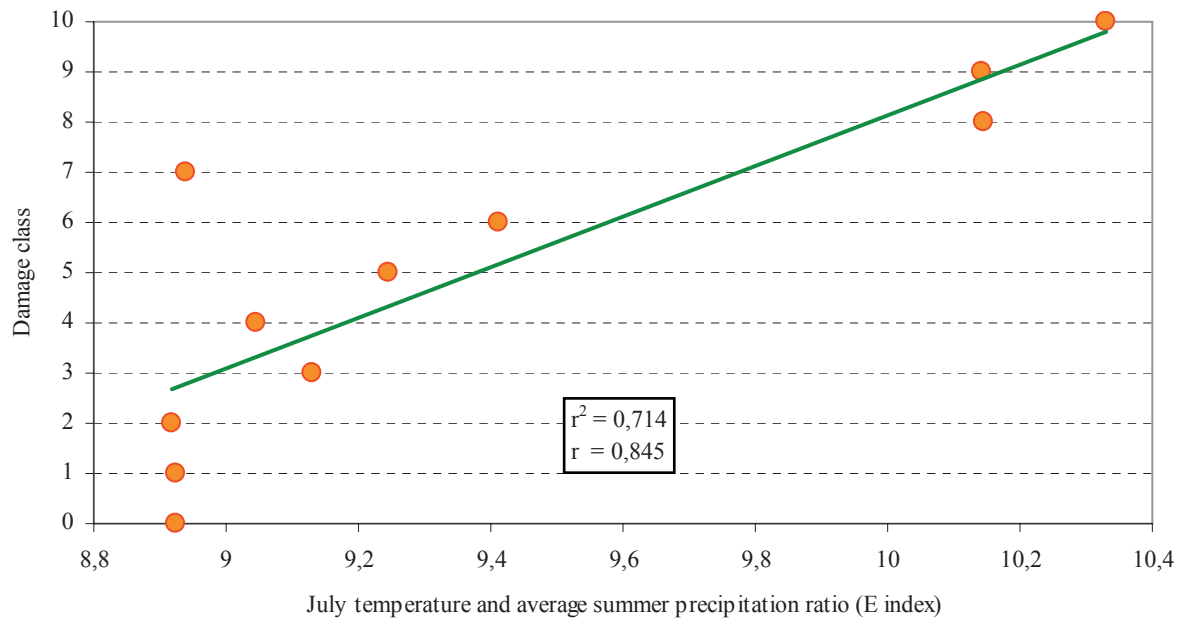

Figure 2. Approaching the genetically set limits of tolerance: average moisture stress versus leaf damage classes of beech in permanent monitoring plots in Hungary. The graph shows the change in health status from healthy (class 0) to dead (class 10) along a climate gradient of increasing summer moisture stress (screened data averaged for 1991 to 2001; analysis by G. Veperdi)

Genetic effects of past climatic selection

The selective effect of local environment on the genetic pool of plant populations has been demonstrated for adaptive traits in a large number of studies (for review, see Linhart and Grant 1996), however few studies provide information on the concrete action of climate selection on plants. Similarly, out of the very rich literature on intraspecific genetic variation of forest trees, papers dealing with adaptive response to climate/weather events are rather the exceptions.

To prove the hypothesis of increasing selection towards the tolerance limit (see Figure 1), gene loci of adaptive/physiological relevance have to be studied. In Hungary, a systematic genetic inventory was carried out in sessile oak and beech stands along climate severity gradients (Borovics 2007). Results show a strikingly distinctive selective effect at allozyme gene loci. The effect depends on the adaptive role of the investigated gene or of the allele. In the majority of cases a frequency increase of certain, adaptively favourable alleles (gene variations) has been observed, which leads to decrease of diversity and higher level of fixation towards the xeric limits. In a few cases, where heterozygotes seem to support tolerance, increasing heterozygosity was also observed. These results are all the more surprising as the sampled stands have been under prolonged human (silvicultural) influence.
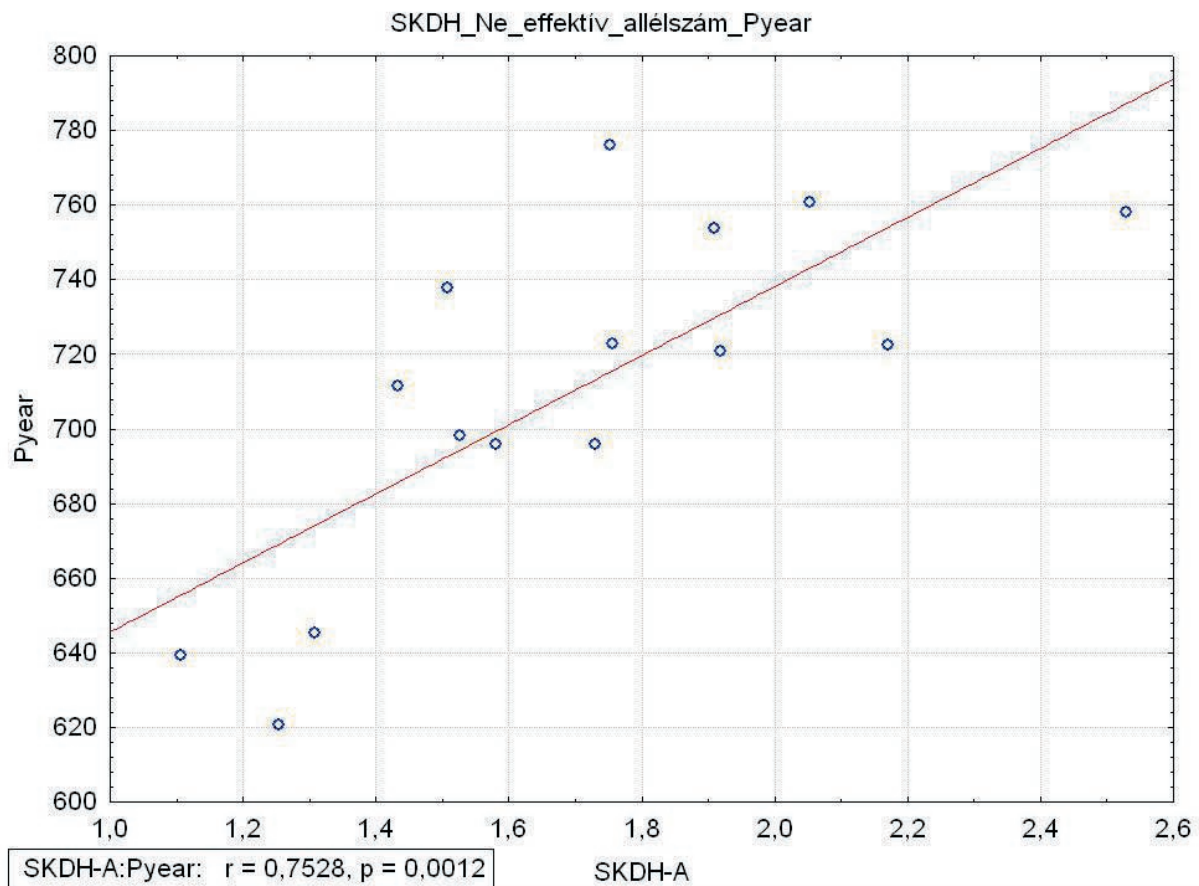
Figure 3. Frequency increase of the genotype "33" at the SKDH-A gene locus in sessile oak towards the xeric limit. The average annual rainfall (Pyear) serves as surrogate for the ecological distance from the xeric limit (Borovics 2007)

As an example, the correlation of the frequency of a homozygote genotype with moisture conditions is presented. The frequency increase of the genotype "33" at the SKDH-A gene locus in sessile oak towards the xeric limit is highly significant (r = -0,797, P = 0.0004, see Figure 3). The enzyme produced by this gene takes part in the synthesis of amino acids, of growth hormones and influences lignification. Climatic selection obviously selects for genotypes (individuals) carrying the adaptively most effective allele 3 in homozygote combination (Borovics 2007).

These findings are in contradiction with certain current opinions on the genetic status of populations at the xeric limits. Some authors propose (e.g. Hampe and Petit 2005, Petit *et al.* 2002) that during Quaternary climate oscillations, many populations persisted in habitat islands ("stable edges"). These populations might be very old, and maintain a high level of between-population genetic diversity. Accordingly, marginal populations would harbour most of the species' genetic diversity.

This hypothesis - although permitting genetic drift (= diversity loss) within individual populations - does not seem to hold for lowland xeric limit situations, where stable habitat refugia are seldom found. Persistence of trees in refugia means by definition that other populations not growing in exceptional ecological situations went extinct. Especially under planar conditions, refugia do not provide safe havens of diversity. Also, these isolated populations show the effects of strong selection and diversity loss.

A further questionable opinion is the presumed decline of actual fitness as a result of diversity decline. The loss of adaptive diversity certainly decreases the adaptive potential of the population. Its role in fitness loss is however somewhat overestimated. Narrowing genetic variation under selection pressure has by definition the function of increasing (instead of decreasing) fitness. There is no "optimum" diversity, and the effect of diversity loss on future competitiveness in therefore unpredictable (Whitlock in: Jump and Penuelas 2005).

The observed tolerance loss at the xeric limits to pests and diseases is primarily not the consequence of diversity loss. The attack of insects and pathogens is usually connected either with the changed consumer life cycle (Woods *et al.* 2005) due to changed climate conditions, or the weakened physiological status of the trees (e.g. lower resin or sap pressure permitting the attack), or both.

Cs. Mátyás

Weather extremes: the real drivers of climatic selection

Extremes and mortality

It is self-evident that means of climatic parameters do not characterise correctly the severity of climatic selection at the xeric limits. Even under zonal conditions, the limit cannot be described properly in terms of average climate, as limiting conditions are bound to irregularly appearing extremes, often triggering damage by diseases and pests.

Spontaneous climatic selection is driven at the xeric limits by recurrent droughts. Therefore, if climatic means are used in analyses, they should be regarded rather as surrogates for extreme events. For methodical reasons the analysis of causal relations between drought events and selection has to be confined to selected locations.

In Figure 4 severity and frequency of drought events are shown for a South Hungarian beech forest at the very limits of distribution. The drought index used calculates with the ratio of spring and summer precipitation and average temperature of the 3 summer months. The graph illustrates that single drought events do not threaten the stability of populations. The recurrent drought period lasting five years between 2000 and 2004 however resulted in very serious mortality in the investigated marginal beech stands, in one case the population became extinct. It has been found that for beech, recurrent drought events of 4 to 5 years lead to irreversible mass mortality and local extinction (Berki *et al*. 2007). These cases illustrate in practice the process of retreating margins of distribution as proposed by the tolerance limit hypothesis (Figure 1).
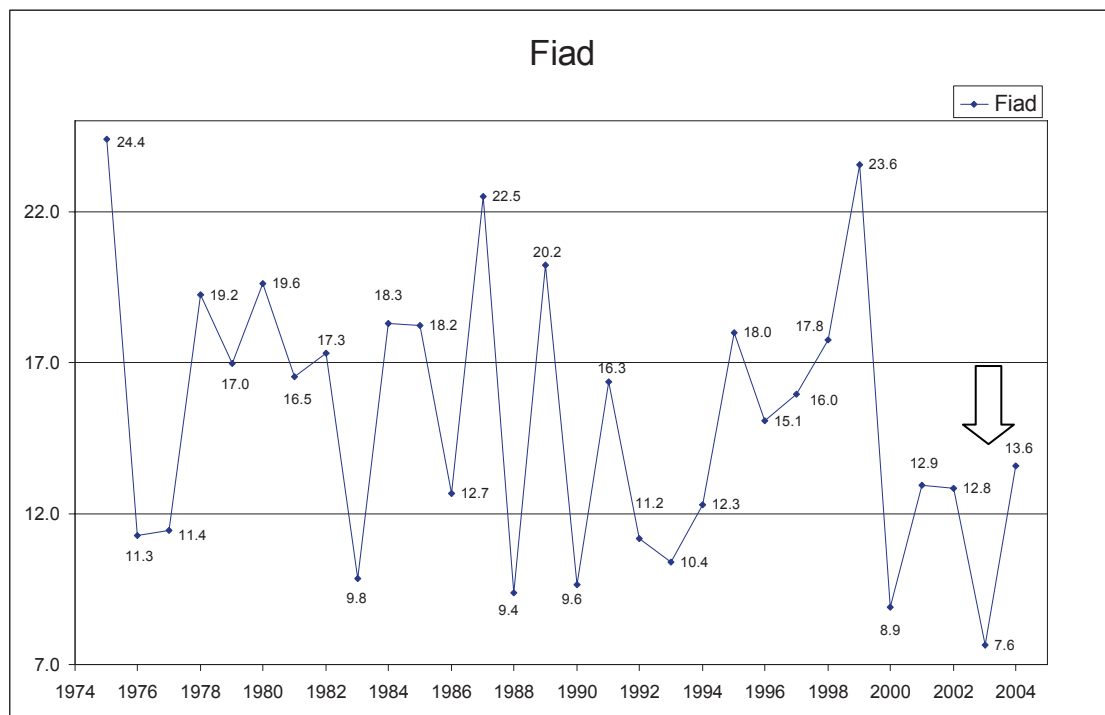

Figure 4. Drought frequency and the initiation of mass mortality of beech at the location Fiad (South Transdanubia). Years with drought indices (vertical axis) below the 30 year average (<14.5) have been considered as drought events. Mass mortality started after the fourth year of consecutive drought (arrow) (after Berki, Rasztovics 2004)

Expected frequency changes of draught events at the xeric limits

Drought events will happen in line with predicted climatic changes but their frequency and severity may change at a rate different from the averages. Frequency change of drought events have been analysed for Hungary using the REMO climate model of the Max Planck Institute, Hamburg. The predicted frequency of drought years (precipitation decline exceeding 5% of the periodic mean) and of drought summers (precipitation decline exceeding 15% of the seasonal mean) are shown in Table 1. The anomalies are averages calculated for the territory of Hungary, related to the 1961-1990 period. The model indicates relatively modest increases of drought events for the scenario A2, at least for the first half of the 21st century. Still, the average precipitation decline will continually progress, and the average precipitation loss of drought summers may reach 30% (related to the predicted averages). It has to be pointed out that the data refer to *average anomalies*, single drought events may be much more severe. It is highly remarkable in Table 1 that from 2050 onward, the REMO model defines every second summer as drought event: 24 summers out of 50 years (Gálos *et al*. 2007)

Cs. Mátyás

Table 1. Frequency of recent and predicted drought events for Hungary, calculated with MPI's REMO climate model (from Gálos *et al.* 2007)

Period	Drought years		
	number of years	mean of precipitation anomalies (%)	mean of temperature anomalies (°C)
1951-2000	17	-12.42	+0.39
2001-2050	9	-16.52	+1.24
2051-2100	21	-19.07	+3.75
	Drought summers		
	number of years	mean of precipitation anomalies (%)	mean of temperature anomalies (°C)
1951-2000	15	-28.02	+0.95
2001-2050	9	-29.21	+2.00
2051-2100	24	-34.98	+2.86

The described shifts in drought frequency may cause cathastrophic changes in lowland regions at the xeric limit. For the mildest climate change scenario, the following area change of non-forest, open woodland climate has been calculated for Hungary:

Table 2. Present and predicted area of forest steppe climate in Hungary

	present situation	predicted for 2080
Area, million ha	4.92	7.53
In percents of total territory	59.9	81.0

Table 2 indicates a predicted area increase for forest steppe climate by more than 50%, which would mean that open woodlands could potentially replace a significant part of present-day closed forests. Part of the predicted change may be buffered by the plasticity and persistence of populations. Mass mortality is most probable at the rear edges and on sites with unfavourable water regime.

Estimation of aridity tolerance from common garden test results

There are two possibilities to elucidate the genetic background of tolerance:

- quantitative analysis of adaptive response in common gardens, or
- molecular genetic tracing of genetic regulation of adaptive traits.

Contemporary molecular genetics is investing great efforts to clarify the genetic mechanism regulating quantitative traits, however the breakthrough has not been reached yet. Compared to quantitative traits, variation at the molecular genetic (nearly exclusively neutral) loci is inconclusive (Savolainen 1994, Savolainen *et al.* 2004). Therefore the shortcut, simple method of direct analysis of quantitative responses in common gardens cannot be missed.

Transfer analysis of common garden data

The idea of transfer analysis, i.e. modelling of responses and forecasting responses to scenarios based on provenance data, has been proposed originally by the author (Mátyás and Yeatman 1987, Mátyás 1994). The principle of this approach is the use of ecological variables to express the change of environment through transfer to the test site. Adaptive responses to changes can be interpreted, generalized and compared more easily if expressed as ecological distances. To observe tolerance and plasticity, populations (provenances) are assessed in different environmental conditions. Regression analysis can be applied to describe the change in fitness. The slope of the function represents the sensitivity to changes and the possible limits of tolerance. Taking growth and health condition as proxy for fitness, the function is interpreted as the species' reaction norm of fitness to the variable investigated (precipitation, drought). Thus, growth and survival of natural populations adapted to a given site, transferred and tested in other environments as part of common-garden tests, can be interpreted as a simulation of ambient changes at the original location. The transfer analysis facilitates the forecasting of adaptive response and of effects of environmental change (Mátyás and Nagy 2005; Rehfeldt *et al.* 2003). This approach has been applied by numerous researchers (e.g. Persson and Beuker 1996, Rehfeldt *et al.* 1999, Andalo *et al.* 2005, Wang *et al.* 2006).

In common garden tests the response of populations is analyzed under conditions often very different from their original climatic environment they are adapted to. The changes caused by the transfer to the test site are in extreme cases exceeding 5ºC annual mean temperature which is well beyond the predicted climate scenarios for medium latitudes (Figure 9). Therefore field observations provide valuable concrete data on population responses which are otherwise not obtainable from theoretical models.

Traces of severe climate selection (mortality) are seldom observed in juvenile age in common gardens. One reason for this is the original concept of selecting sites for provenance tests: in hindsight it is a pity that extreme test locations provoking high mortality rates have been avoided for obvious reasons. The existing tests are therefore first of all informative in providing data on phenotypic plasticity.

Response to changes of climatic environment

When testing a set of populations at a given site, a characteristic response pattern can be observed, where growth and vigour of populations originating from the area of the test site tend to be the best and the performance of less adapted populations decreases with the ecological distance from the location of origin (Mátyás and Yeatman 1987, 1992). Equations describing these phenomena have been developed by a large number of authors, and response functions have been broadly utilized to define seed transfer rules and to delimit seed zones. Earlier models relied on describing genetic variation patterns on a geographical basis using latitude, longitude and elevation as independent variables to describe variation patterns for a given area. (Shutyaev and Giertych 1997). The ecological relevance of these variables is ambiguous. With the growing availability of digital climatic data, multivariate analyses of provenance trials have provided convincing results on patterns of climatic selection and adaptation. Common garden tests of most tree species verify that populations originating from different climates show specific adaptation to local conditions and, accordingly, respond differently if grown under uniform conditions of a common garden. Height growth response shows significant correlations even with very general climatic parameters such as average annual mean temperature at the location of origin (Mátyás and Yeatman 1987, 1992, Rehfeldt, *et al.* 2003). Calculated regression functions show for most investigated species a very characteristic pattern of growth response, indicating an obviously clinal adaptation to the climate across the range.

For example, for both Norway spruce and Scotch pine, the relation height at 15-16 years of age versus annual mean temperature at origin may be described by a typical response regression function, where in both cases a not very well expressed maximum appears around 6-7ºC annual mean (Figures 5 and 6).

At the same time no clear trend is detectable in within-population variation (Figures 5 and 6), i.e. the magnitude of genetic variation in height between individuals remains roughly the same across the range: neither the central ("optimum") nor the marginal ("edge") populations seem to harbour excessive adaptive variation.

The effect of temperature conditions on the height growth of populations have been studied in six Scots pine tests situated in the centre of European Russia (Mátyás and Nagy 2005). The climate is there continental, summers may show moisture deficit. In order to exclude the effect of site quality, data were standardized by expressing height in percents of locally adapted populations. Tested populations were grouped according to their adaptedness into northern, central and southern groups. Regressions relative height versus temperature sum difference of the vegetation period at the test and original location (Delta STVEG) were calculated. The comparison of the regressions show that the three groups behave very similarly and display a marked depression in growth with increasing aridity of test site (in figure 7: to the left), i.e. introduced to more arid conditions than they were adapted to, populations react with growth decline expressed in relative height. On the other hand, the transfer into cooler (= more humid) environments (in figure 7: to the right) resulted in growth acceleration compared to the local, autochthonous populations (Mátyás and Nagy 2005).

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[3] Multivariate analyses using numerous climate parameters supply even better results. For the sake of simplicity, annual means are used in the following examples
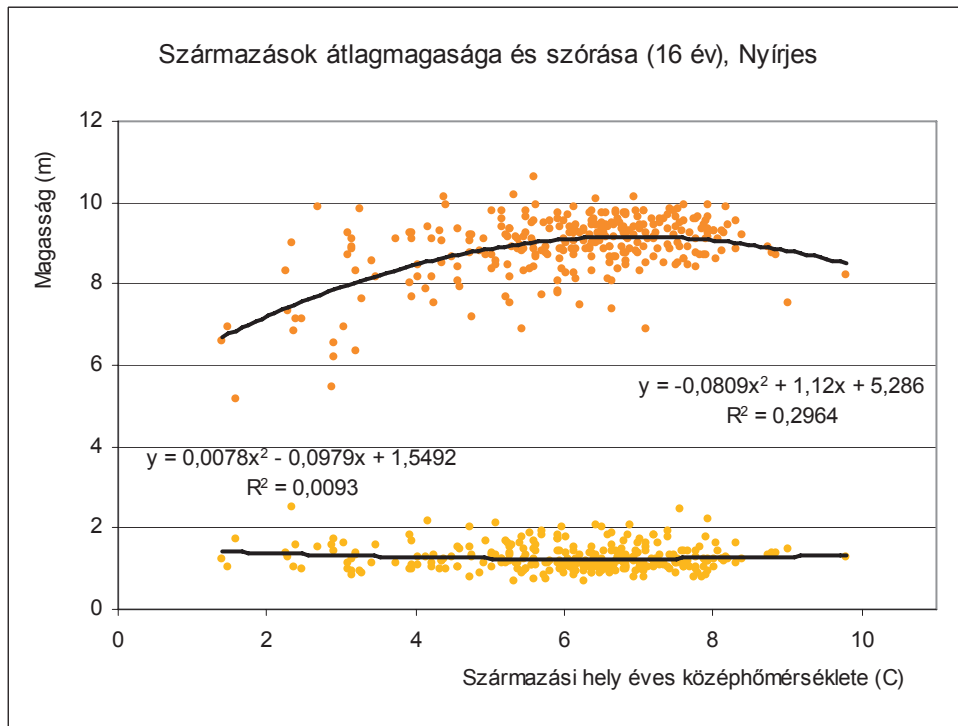
Figure 5. Average height (vertical axis) and within-population standard deviation of height at age 16 of Norway spruce in the Nyírjes (IUFRO) provenance test, versus annual mean temperature of the location of origin (horizontal axis) (data: É. Ujváriné-Jármai, unpubl.)
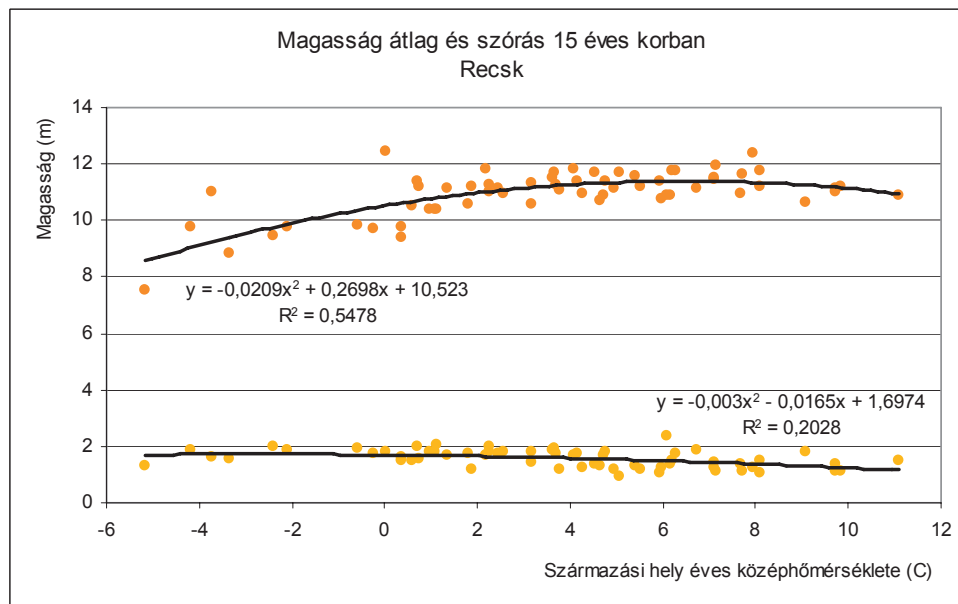

Figure 6. Average height (vertical axis) and within-population standard deviation of height at age 15 of Scotch pine in the Recsk provenance test, versus annual mean temperature of the location of origin (horizontal axis) (data: L. Nagy 2007 unpubl.)
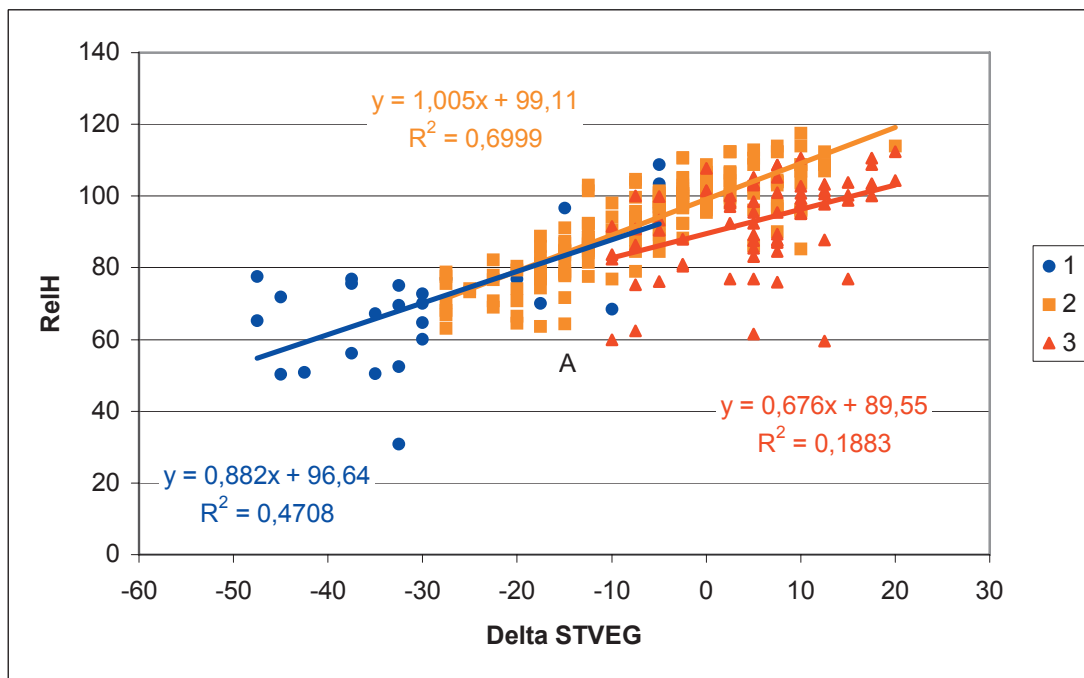
Figure 7. Linear regressions relative height (RelH) versus change of temperature sum due to transfer (delta STVEG) by groups of provenances of Scotch pine in 6 Russian tests (1: northern, 2: central, 3: southern group) (Mátyás and Nagy 2005)

Figure 7 illustrates that the simulation of climatic warming, i.e. the transfer into warmer environments, results in significant decline of productivity in the warmer part of the range, where moisture is in deficit in certain periods of the year.

Width of adaptability: phenotypic plasticity

Analyses of field tests show remarkable width of adaptability and persistence (and, in consequence, the extended width of 'local' adaptation) in the face of even drastic changes in thermal environment and, to a less extent, in moisture supply. This phenomenon indicates the substantial conservatism in the climatic adaptation of numerous tested tree species, which has an inherent genetic basis and may have been enhanced by evolution (Mátyás and Nagy 2005).

For illustration, data from three test sites of the international Norway spruce provenance experiment (Krutzsch 1974, Ujvari-Jármay and Ujvari 2006) are shown. Height at age 16 was measured for 300 identical populations of various origin at climatically widely differing test sites in Hungary (Nyírjes), south Sweden (Abild) and north Sweden (Lappkojberget). Response regressions were calculated with the mean annual temperature of the locations of origin of the populations for the three sites (Figure 8). Comparing the three response functions, the first conclusion is that in spite of large environmental differences represented by the tested populations, the response does not indicate narrow (strictly local) adaptedness. It seems also that fitness differentiation increases towards more favourable environments, i.e. southward. This phenomenon is attributable to the fact that manifestation of genetic differences is favoured by improving site conditions.

Table 3. Temperature and height data of Norway spruce experiments to figure 8.

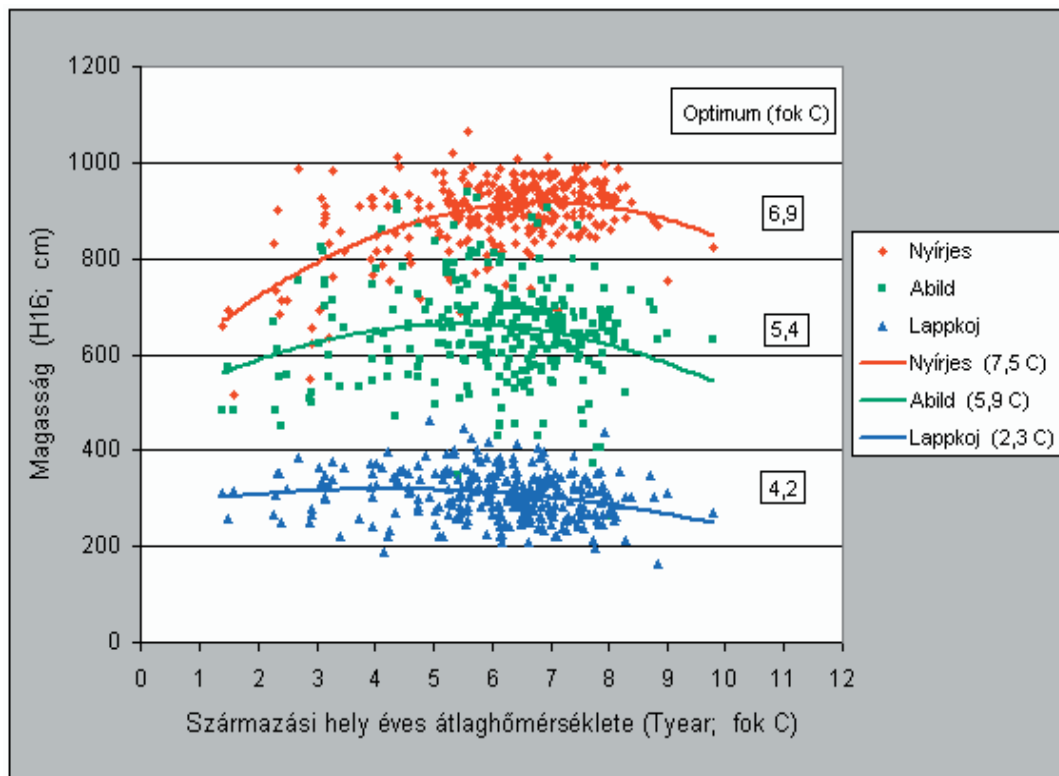|	Experimental site data		Response function	
test name	mean annual temp. (T_{exp} °C)	mean height of test (cm)	temp. at maximum (T_{max} °C)	mean height at T_{max} (cm)
Nyírjes (H)	7,5	890,3	6,9	915,4
Abild (S)	5,9	643,1	5,5	659,7
Lappkojberget (S)	2,3	305,4	4,5	317,1

Figure 8. Regression of 16-year average height (vertical axis) of identic Norway spruce provenances versus mean annual temperature at origin (horizontal axis) in three IUFRO provenance tests Nyirjes, Abild, Lappkojberget. Mean temperatures of the test sites are shown in the legend, maximum values of the curves in the graph (Ujváriné-Jármai, unpubl.)

When comparing the calculated response regression maxima for annual means with the test site data, it turns out that the "fittest" populations at two milder locations originate from somewhat cooler environments, while at the harsh northern location, populations from milder environments perform somewhat better (Figure 8, table 3). According to table 3, the difference between the annual mean temperature corresponding to the response regression maximum and the test site mean is negative at milder sites, indicating that populations from cooler climates perform better ($\Delta T = T_{max} - T_{exp}$). The opposite result appears at the harsh northern site, where populations from milder environments outperform local ones. This surprising phenomenon was reported from some other boreal tests as well (e.g. Andalo *et al.* 2005).

The analysis has also shown that phenotypic plasticity of populations from certain geographic regions display characteristic differences which may be determined by local microevolution. As an example, the height growth response of Norway spruce is shown for three selected regions of provenance: Eastern Carpathians, the Beskids, and Harz Mts. Figure 9 shows that an increase of average annual mean temperature of up to 4°C has no significant effect on the 16-year height of East Carpathian provenances in the test. At the same time the populations from the Harz have reacted with a decline of roughly 15%. In cases, where the mean temperature of the test site Nyirjes was similar to the one at origin of the population ($\Delta T = 0$), the average height of provenances from all the three regions was similar ($H_{16} = 9.5$ m). The results support the higher plasticity of the Eastern Carpathian populations. Similar results have been gained by Norway spruce breeders as well.
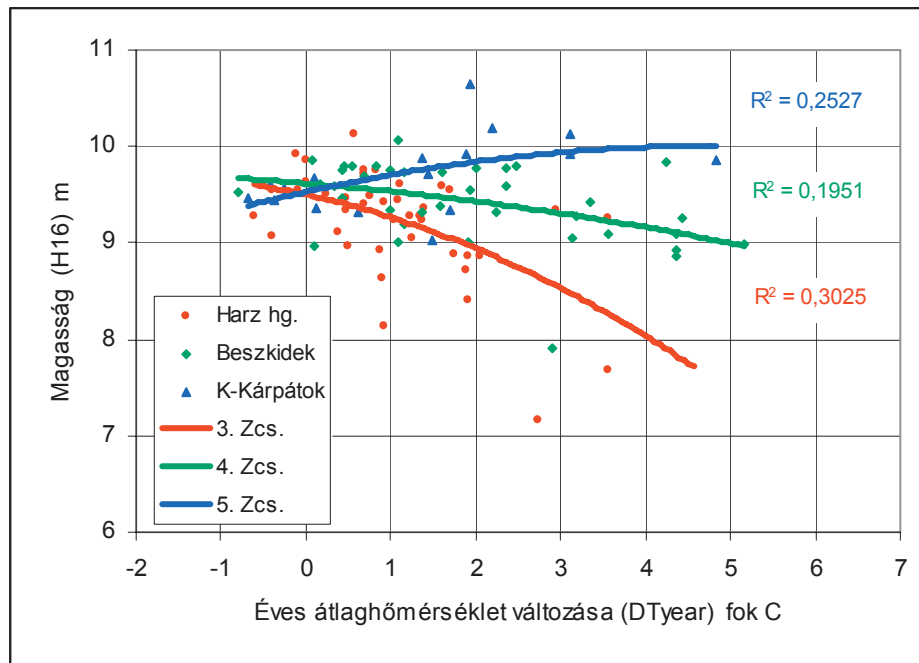
Figure 9. Effect of mean annual temperature change (horizontal axis, positive values stand for warming) on 16-year height of Norway spruce provenances. The three provenance groups Harz, Beskids, E. Carpathians show different levels of plasticity (best: E. Carpathians) (Ujváriné-Jármai, unpubl.)

Discussion

Adaptation maintains non-equilibrium state

Common sense would suggest that in any environment, the growth of the locally adapted population should represent the maximum, compared to populations adapted to other environments. This principle has been adopted instinctively by foresters already for centuries and it appears among the basic rules of reproductive material commerce and utilization to the present day.
As described before, the maximum of the response functions does not coincide with the climatic conditions of the test site, with other words: locally adapted populations do not perform best. This *adaptation lag* (Mátyás 1990) runs against accepted principles of evolutionary optimization and needs further examination.

The explanation, that the lag may originate from the difference between the environments of natural regeneration under forest cover (the populations are assumed to be adapted to) and the grossly artificial conditions provided in a common garden test (nursery-grown plants, site preparation, weed competition excluded etc.) seems to be evident. Eriksson (Eriksson and Ekberg 2001) coined the term "domestication fitness" to explain the difference to locally adapted fitness. Apart from the fact, that this effect arises rather from cultivation (cultivation fitness: Mátyás 2004) than from domestication, it does not explain fully the peculiarities of response maxima measured in various environments.

When looking for a parsimonious explanation, one should keep in mind that there is no reason to suppose the two adaptive mechanisms, (genetic) selection and phenotypic plasticity as acting alternatively or independently. On the contrary, they should be considered as jointly functioning forces, determining a certain position in the "adaptive landscape". Although lacking experimental proof, this concept surfaced already in literature (cited in Fournier *et al.* 2006): a question to be answered by common garden data. A logical explanation could be that *plasticity buffers the effect of natural selection*. It seems that genotypes "camouflaged" by plasticity are genetically adapted to more favourable site conditions. Consequently, reaction norms of such populations display shifts of the maximum performance towards better climates. One has to remember, however, that "better" has a different meaning at opposite limits of distribution. Close to the xeric (aridity, lower) limits humidity is restraining, so lower temperatures (even at equal precipitation) mean more favourable conditions. At the thermic (northern, upper) limits, temperature sum is at minimum, and more southern sites appear as more favourable.

Therefore, reaction norm of populations adapted to climates close to the xeric limit, must show an increased growth performance northward of the original location. This effect is shown in figure 7. It indicates that *populations under climatic selection pressure adapt to local conditions simultaneously by genetic (natural) selection and by utilizing phenotypic plasticity. Apart from climatic conditions normatively optimal for a given species, populations toward the climatic limits of distribution display an increasing genetic adaptation lag, which is compensated by phenotypic plasticity.* Accordingly, autochthonous, local

populations, considered as "perfectly" adapted, are in reality under constant stress, and perform better in more favourable environments, presenting the *effect of adaptive non-equilibrium.*

The proposed term of adaptive non-equibrium means that within the distribution area of a (zonal) species, climatic adaptedness can be considered to be in an equilibrium state only in a narrow optimum zone. Approaching the thermic and xeric limits, the local populations get under increasing climatic stress due to the suboptimal functioning of genetic selection, which is buffered by phenotypic plasticity.

In contemporary ecology, the paradigm of non-equilibrium state of forest ecosystems is generally accepted. This refers to the regulation conditions at the level of species. It seems that **the paradigm of non-equilibrium state of natural systems may be valid also at the genetic level of adaptation to the (climatic) environment**. Non-equilibrium state in genetic respect implies that in most cases, locally adapted populations cannot maintain an optimum fitness. condition as shown earlier.

"Decoupling": local adaptive optimum disturbed by changes?

The "decoupling" of local populations from the climate they are adapted to is a popular hypothesis applied for trees as well. The assumption is based on the equilibrium concept, i.e. that local populations are genetically well adapted to the local climate and any change will have detrimental effects. As a result, fitness loss will appear and extinction risk may increase across the whole range (see review of Jump, Penuelas 2005). A corollary of the hypothesis is the immigration of preadapted individuals (Davis, Shaw 2001) or even of preadapted populations (Rehfeldt *et al.* 2003). Besides the fact, that long-distance immigration of individuals or populations into existing ecosystems has a low probability, reference is made to the dominance of plasticity in adaptation as described before: tree populations experiencing climate warming will first utilise the available potential of phenotypic plasticity, which may lead even to growth acceleration, depending on the position within the range.

Consequences for bioclimatic modelling

The non-equilibrium concept, if valid, has important implications with regard to construction of climate envelopes and vegetation shift models. Classic climate envelope models are developed on the basis of the equilibrium hypothesis, assuming that local, autochthonous populations are optimally adapted to their environment. As a consequence, any change of the climatic conditions to the worse should trigger decline or even local extinction. The non-equilibrium concept proposes that these models predict local disappearance too pessimistic: the genetic/physiological possibilities for persistence are not instantly exhausted under changing conditions, with the exception of populations at extreme, marginal sites.

Conclusions for prediction and climatic modelling of adaptive response

Asymmetry of response

An important outcome of transfer analyses is the asymmetry of response. The effect of environmental change on populations in different parts of the distribution range is divergent as different climatic factors exert their selection pressure.

The reaction of indigenous tree populations to warming will differ according to climatic zones. In the thermal-limited northern-boreal zone, the expected rise of temperature will lead to marked growth acceleration. At lower altitudes, in the temperate-maritime zone, growth will accelerate too, along with increasing or at least unchanged rainfall. In the subhumid temperate-continental and subhumid Mediterranean zones, however, even relatively minor temperature increases, coupled with growing drought stress, will trigger loss of compatibility, higher susceptibility to diseases, and increased mortality. At the xeric limits warming leads to relatively fast growth and productivity loss, and selective mortality (Berki and Rasztovics 2004; Mátyás 2005). It should be noted that the described phenomena are generalisations. Substantial deviations may be caused by the genetic system of the species, the evolutionary-migratory past and regional or local climate effects. For example, there are indications that in certain regions of the boreal zone, where moisture stress is already present due to low precipitation, higher temperatures and increased drought stress may also lead to incremental decline (Lapenis *et al.* 2005).

Changes in genetic diversity following climatic stress

Expectable genetic changes will be minor in the northern part of the distribution range despite the speed of predicted changes. Improved growing conditions can be utilized through the plasticity potential of tree populations, without much selection. As inherited plasticity will determine the response to changes, there is little room left for genetic adaptation. In temperate-Atlantic Europe, where moisture stress is predicted to stay low, populations will also be well buffered by their adaptability.

The situation is completely different along the xeric limit of main tree species, and at the limit of closed temperate forests. Here, natural selection becomes effective in the form of irregularly appearing health decline and mortality waves following weather extremes. The symptoms of pests (gradations) and diseases might be mistaken for primary causes (this was the case in many countries in recent decades). High selection rates will certainly exert a strong effect on the genetic resources of exposed populations, and if stress situations aggravate, it may lead to local population extinction, even for once well distributed,

dominant species. This underlines the importance of management and conservation of forest genetic resources (Ledig and Kitzmiller 1992, Mátyás 2000).

Caveats for the climatic interpretation of xeric limits

To forecast climatic limits of genetically set tolerance has its constraints. The followings have to be pointed out:

- It is a well known ecological rule that actual distributions of species are regulated by complex, often hidden interactions which may modify tolerance limits. Genetically set (potential) limits may be *per definitionem* wider than realized actual ones.

- Due to the longevity and persistence of forest trees, the determination of fitness limits may be misleading. Short-term 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.

- The sequence of consecutive extreme weather events and linked biotic damages will concretely decide over survival or mortality at the fitness limits. Therefore *the use of climate (mean) data should be regarded as surrogates only for weather extremes.*

- The change of climatic environment affects also consuming and pathogenic organisms, the selection pressure by consumers may be rearranged. Forecasts in this respect are unreliable, especially because up to date unknown or unimportant pests and diseases may appear. Environmental shifts may also lead to changing interactions between host and consumer.

- The limited precision of predicted precipitation changes in scenarios is of special significance in particular at the xeric limits which are extremely sensitive to relatively minor humidity variations.

- Significance of correlations is in itself no proof for a causal relationship, this has to be investigated and verified.

Conclusions for mitigation and management

No mitigation measures needed?

Although genetic, migratory and evolutionary constraints are generally acknowledged (Namkoong 2001, Loeschke 1987, Davis, Shaw 2001, Mátyás 1990, 2006a), some scientists (e.g. Kelly *et al.* and others cit. in Jump, Penuelas 2005, also Hamrick 2004) claim that no measures will be needed to mitigate the effects of changing conditions because

- there is enough genetic variability in the populations, which might be further replenished by migration and gene flow;

- interannual fluctuation has the same magnitude as predicted changes of milder scenarios, so populations are prepared to adjust by preadapted individuals;

- regeneration is secured through the persistence, phenotypic plasticity and long life cycle of forest tree populations;

- paleoecologic data indicate that enough variation accumulates and is saved in refugia, and the selection pressure of recent climatic fluctuations was without effect;

- genetic adaptation may happen in relatively short periods, 2-3 generations.

Some of the opinions have been already answered in preceding chapters. The argument of limited consequences of vegetation and area shifts may be valid first of all in boreal regions with predominantly nature-close conditions, where human land use had no serious impact yet. In natural landscapes or national parks cyclical changes of vegetation do not pose serious threats as long as ecological space for retreat is available. In landscapes and regions transformed by humans there is however no room left for such fluctuations, especially not close to the lower distribution limits of a vegetation type or a species. At the xeric limits of distribution, migration or gene flow from better adapted populations is not happening.

Regarding interannual fluctuations, tables 2 and 3 indicate that with increasing mean temperatures, severity of extremes will increase too: aridity stress will therefore increase, which will cause additional stress at the xeric limits.

Fast genetic adaptation is in contradiction with the accepted assumption of strong biological and ecological constraints. At the (zonal) xeric limits, an unlimited adaptation to declining environment is unthinkable, due to the evolutionary tradeoffs and constraints. This is proven by remarkable area changes in the geological past.

Therefore the need of human intervention in mitigation has to be underlined (Hulme 2005, Mátyás 2006a). Due to ecological constraints to spontaneous adaptation, the policy of artificial translocation should be preferred instead of extensive enhancement of connectivity, at least with regard to tree species.

Consequences for forest management

The urgent necessity to put into practice the findings of quantitative genetics cannot be questioned. In addition some aspects of forest management should not be overlooked when predicting responses and formulating mitigation strategies. Most of Europe's forests have been and still are under strong human influence, and are managed according to periodic management plans. Especially close to the xeric limit the proportion of nature-close forests is low, regeneration is mostly artificial. E.g. in Hungary, the rate of artificial regeneration is over 70 % on the Great Plain (forest inventory, 2001). The possibilities left for spontaneous processes, such as migration, succession are limited, forest stand composition is determined by forest policy and economic considerations. This means also that adjustments in species composition and in adaptive genetic potential will be achieved faster and more effectively compared to natural, spontaneous processes.

In drought stress climates, incremental loss and higher incidence of diseases and pests will challenge the economics of forest operations, and will move emphasis more to maintenance of ecological functions and conservation of stability and of genetic resources (Geburek and Turok 2005).

Summary

The analysis of quantitative data of common garden tests supports the concept that these tests offer unique possibilities for the realistic simulation of effects of climate scenarios. Within a species, the response of a population depends on its adaptedness to its original environment.

Response at the xeric limits is insufficiently studied in spite of its ecological importance. At the lower (or rear) limit of distribution, selection pressure narrows genetic variation and the increase in frequency of extreme events may result in growth decline and mortality. In the humid part of range, climate selection is less effective.

The asymmetry of response in different environments support the hypothesis that the simultaneous action of plasticity and selection *maintains an adaptive nonequilibrium also at genetic level, similar to the one at ecosystem level.* This brings consequences for response and climate envelope modelling. Adaptedness to local environment cannot be considered as basis for response prediction. In the distributional range of low moisture stress, warming will release plasticity pressure which leads to growth acceleration instead of "decoupling" from adapted climate. The opposite growth trends in Western and boreal Europe, versus Southeastern-continental and Mediterranean Europe can be explained by the described phenomenon.

As expected rapid changes in the next decades will affect first of all the extant (already existing) forest stands, adaptation potential will mainly depend on the level of phenotypic plasticity. The importance of this trait should be recognized not only in breeding and improvement, but also in selection and use of forest reproductive material. The retrospective analysis and international comparison of provenance test data is considered as important and necessary, justified by the uniqueness and non-repeatability of these tests.

Bioclimatic modelling of forests and trees based on actual distributions has many limitations. The aspects of genetic regulation should be considered among them.

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