

# Migratory, Genetic and Phenetic Response Potential of Forest Tree Populations Facing Climate Change

Csaba MÁTYÁS<sup>1</sup>

Institute of Environmental Sciences, University of West Hungary, Sopron, Hungary

**Abstract** – Forest trees are especially vulnerable to climatic oscillations due to their long lifespan. Out of the possible mechanisms of acclimation and adaptation, natural selection and migration will play a subordinate role because of the relatively high speed of expected changes. Phenotypic plasticity retains on the other hand primary importance. Analysis of common garden experiments and of health monitoring data indicate that response across the distribution area will be differentiated. The low-latitude, low elevation periphery is especially threatened, while growth in the northern part of ranges will accelerate (in case moisture conditions will remain favourable). Comparing the velocity of predicted changes and the constraints of the buffering mechanisms of species for adaptation, it is obvious that *human interference will be essential for the maintenance of ecosystem stability*. Forest genetic and ecology research results have to be synthesised to better elucidate the requirements of stability and response of forest ecosystems under predicted climatic conditions.

**Adaptation / ecological genetics / phenotypic plasticity / migration / natural selection / tolerance**

**Kivonat** – Klímaváltozás és az erdei fás populációk migrációs, genetikai és fenetikai alkalmazkodási potenciálja. A hosszú életű fás növények különösen kiszolgáltatottak a környezeti változásoknak. Ennek megfelelően széleskörű az az eszköztár, amely lehetővé teszi a gyors alkalmazkodást. A természetes szelekció és a migráció – habár az előrejelzésekben szinte kizárólagos jelleggel szerepelnek – a klímaváltozáshoz alkalmazkodásban alárendelt szerepet kapnak a változás gyorsasága miatt. A fenetikai (fenotípusos) alkalmazkodásnak ezzel szemben nagy a jelentősége. Az elemzések szerint a fenetikai reakció az elterjedési területen belül eltérő: a melegedés az északi árearészben növedékgyorsulást, míg az área déli szegélyén vitalitás-gyengülést és mortalitást vált ki. A peremhelyzetű populációk veszélyeztetettségét alátámasztják az országos EVH háló adataiból készített elemzések is. Az eredmények megerősítik, hogy a klimatikus változást a peremhelyzetű populációk természetes szabályozási mechanizmusai nem lesznek képesek kompenzálni, hanem ehhez *emberi segítségre, gondosan tervezett beavatkozásra van szükség*.

**Adaptáció / ökológiai genetika / fenotípusos plaszticitás / migráció / természetes szelekció / tolerancia**

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<sup>1</sup> cm@emk.nyme.hu; H-9401 SOPRON, Pf. 132

## 1 INTRODUCTION: THE NEED FOR SYNTHESIS

Climate change mitigation, the maintenance of stability of forest ecosystems are serious challenges for both research, forest management and forest policy in the 21<sup>st</sup> century. In this respect, adaptability and adaptedness appears to become a crucial problem. The longevity of trees makes a fast adjustment to changing conditions more difficult than in agriculture. Long-term adaptedness and stability should therefore be of higher concern in forestry than possible gains in timber or fibre yield. The fundamental question is how tree populations and species will react and what the means are to maintain and enhance their adaptability.

Studies analysing the expected response of forest ecosystems to changing environmental conditions are either predicting spontaneous migration of forest tree populations (ecologically oriented studies) or investigating the prospects of adaptation through natural selection or random processes, such as gene flow (genetic studies). A proper synthesis of ecological and genetic information is seldom done, genetic and functional ecological aspects are investigated independently from each other.

Efforts to clarify the genetic background of adaptive traits and adaptation have progressed considerably and have yielded meaningful results. It is no surprise however that the molecular revolution of the recent decades has contributed relatively little yet to the synthesis with ecology. This is partially due to the fact that molecular genetic investigations in biology are concentrated on model organisms (often genetically screened) in artificial environments. Also, majority of species selected for such studies are either micro organisms, annual plants or animals (e.g. *Drosophila*, *Arabidopsis* sp., snails etc.).

There is a widely accepted opinion to exclusively judge adaptability based on genetic diversity on the biochemical-molecular level, often at loci of no or questionable adaptive importance. Quantitative response (growth, phenology) to ecological cues are insufficiently investigated, although their practical value for climate change effect mitigation and for selecting of suitable reproductive material is high. Out of the main genetic forces shaping the genetic structure of species, the random effects get too much attention as compared to ecologically interpretable, directed processes. To study adaptively important, quantitative traits in field tests is however indispensable not only for validation of genetic markers, but also to assess “nongenetic” regulatory effects such as phenotypic plasticity and ecological interactions – in order to put genetic results into a meaningful ecological context.

On the other hand little of the genetic results have penetrated ecology. Most ecological studies treat species as monolithic units, not counting with the intraspecific genetic variation pattern. Also, many functional ecological studies are confined to investigate traits in a single environment. Testing across multiple environments is however important, as reaction to ecological factors, relevance for competition and selection may drastically change. Finally, strong practical constraints on both migration and natural selection are seldom considered.

To achieve a more balanced approach, comprehensive studies are necessary for a deeper understanding of the functioning of ecosystems, of evolutionary diversification on genetic and species level and of the real value of biodiversity in stability and resilience of living systems.

### 1.1 Interpretation of ecology, genetics and evolution of observed wealth of variation in fitness

Contemplating the wealth of hereditary and phenetic variation in fitness on all scales and levels (qualitative and quantitative, geographic or within population), the famous question of Hutchinson (1959) about the reasons for existence of so many species, could be raised on within-species level as well; why is genetic variation so excessive not only in obviously neutral but also in strongly adaptive traits, such as length of growing cycle, phenotypic behaviour etc.

There are three possible approaches to answer this question: a historic-evolutionary, a genetic and an ecological one; all three are needed to correctly understand processes in natural populations and ecosystems.

According to the *ecological interpretation*, variation between individuals of a species is maintained by the temporal and spatial heterogeneity of environmental conditions, differences in age, in habitat conditions, in density etc. It seems that both on within-species and on between-species level, i.e. in genetic and also in species diversity, correlations with environmental (ecological) heterogeneity exist.

The *genetic* explanation of existing variation is based on the simultaneous dynamics of different directed and random genetic processes (natural selection, mutation, gene flow, drift, introgression, inbreeding etc.) and on existing constraints in the genetic system of the species (e.g. trade-off effects, genetic correlations).

*Historic processes of evolution* are random: speciation and extinction events, withdrawals to refugia and migrations in connection with glaciations and smaller-scale climatic oscillations. All these events leave marked genetic footprints.

Depending on historic, ecological and genetic circumstances, the generated diversity (both on species and genetic level) can be manifold. Members of the population will consequently utilize the given environment in multiple, alternative ways. Therefore it is important to realize that variation within a population (and in the ecosystem) in itself represents an adaptive value. The question however remains, *how and to which extent this diversity plays a role to counterbalance climatic oscillations*.

## 1.2 Options for balancing environmental changes

There are various genetic and non-genetic mechanisms on both individual, population, species and ecosystem level, balancing changes in environmental conditions. On *species and ecosystem/landscape level*, a possibility of responding to large-scale changes in the environment is migration through seed (and pollen) dispersal. Paleoecological evidence on migration during the epochs of glacial periods and interglacials is abundant – and this is the option generally described by most ecologically-oriented future scenarios as well.

On the *level of populations*, natural selection adjusts the average fitness of the population to changing conditions through genetic adaptation. Fisher's well known fundamental theorem on fitness change illustrates that the precondition for fast and effective genetic adaptation is provided by sufficiently large genetic diversity. *The maintenance of long-term genetic adaptability is therefore directly depending on the conservation or even reconstruction of adaptive genetic variance*. This is not to say that natural selection is able to follow and buffer environmental oscillations (Savolainen et al. 2004).

On *individual genotype level*, environmentally induced phenotypic plasticity and genetic carryover effects (Jablonka et al. 1995, for review see Martienssen - Colot 2001) provide the ability to survive in a wider range of environments without genetic change in the classic sense. Phenotypic plasticity will set the limits of environmental heterogeneity in time and space, a genotype or population can endure within its lifetime (*Figure 1*). Limits of distribution and cultivation are set by the decline of fitness across the environmental cline (in the figure: from left to right). If ecological interactions (i.e. competition) or certain biological constraints (e.g. failing natural regeneration) are counterbalanced by cultivation, limits can be extended beyond natural distribution limits. The genetically set tolerance limit varies on individual level, provoking selection. Weather extremes and disease outbreaks push the population toward mass mortality on off-limit sites.

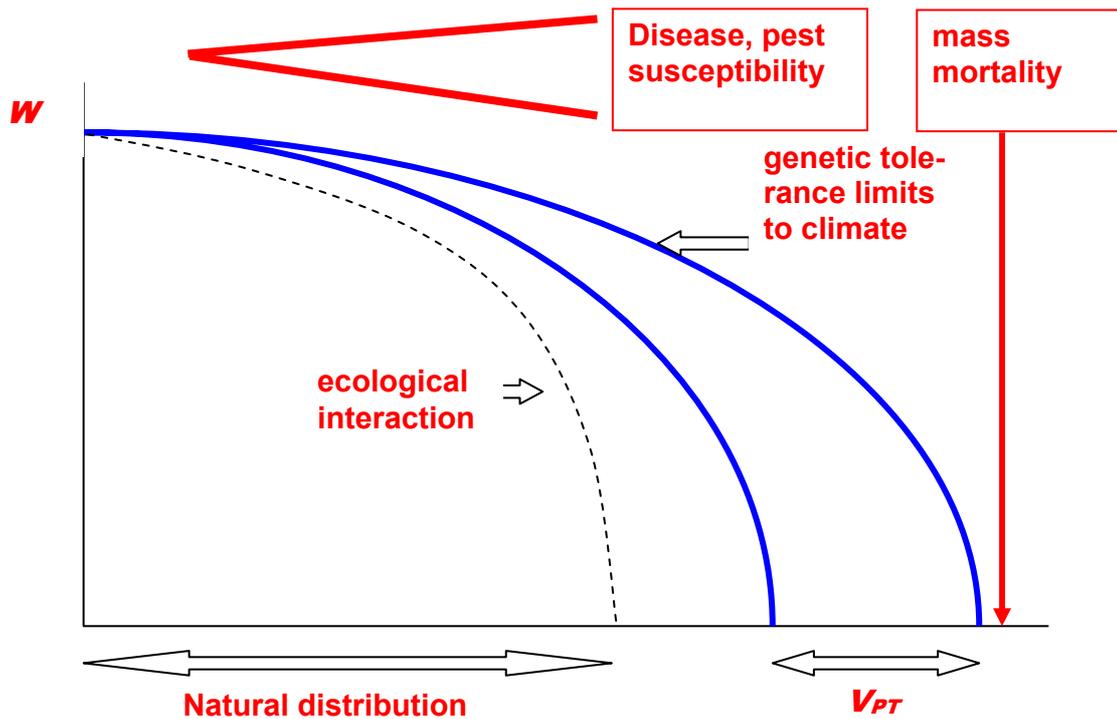


Figure 1. Ecological-genetic model of fitness decline and mortality triggered by worsening of climatic (site) conditions. The phenotypic variance of limits of tolerance ( $V_{PT}$ ) represents the basis of natural selection. Due to interactions in the ecosystem, the natural distribution is usually stronger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

With changing conditions, the fitness value of a trait will change as well. For instance, wide crown shape in conifers facilitates to utilize available resources and to keep away competitors; narrow crown shape helps to avoid snow brake; both are adaptively important values. While the former is especially vital in strongly competitive ecosystems with high species diversity, narrow crown shape is selectively preferred in rather monospecific, higher altitude environments. The fitness of the two types are inversely related to each other, representing a *functional trade-off*. It can be expected that divergent adaptive forces will determine the distribution of phenotypes. The observed distribution of crown types shown in Figure 2 may have been generated – apart from random effects - either by gradient-dependent distribution of different alleles responding natural selection, by carryover effects (female parental effects) or by a perfectly functioning plasticity with no genetic change in the populations, but with highest probability by the simultaneous effect of all mentioned mechanisms.

## 2 RESPONSE POTENTIAL AND CONSTRAINTS

From the viewpoint of long-living sessile organisms, such as trees, environments are temporarily and spatially extremely heterogeneous, as compared to the lifecycle and dimension of occupied space. This fact requires special strategies and may pose also specific constraints. Long-living forest trees are therefore especially threatened by fast changing climatic conditions and are ideal organisms to study the parallel evolution of phenetic and genetic adaptation mechanisms. The necessity of efficient adjustment arises not only if progenies of trees migrate into new environments, but also if populations stay in their habitat but climate conditions change. In the followings some genetic and ecological considerations are briefly discussed.

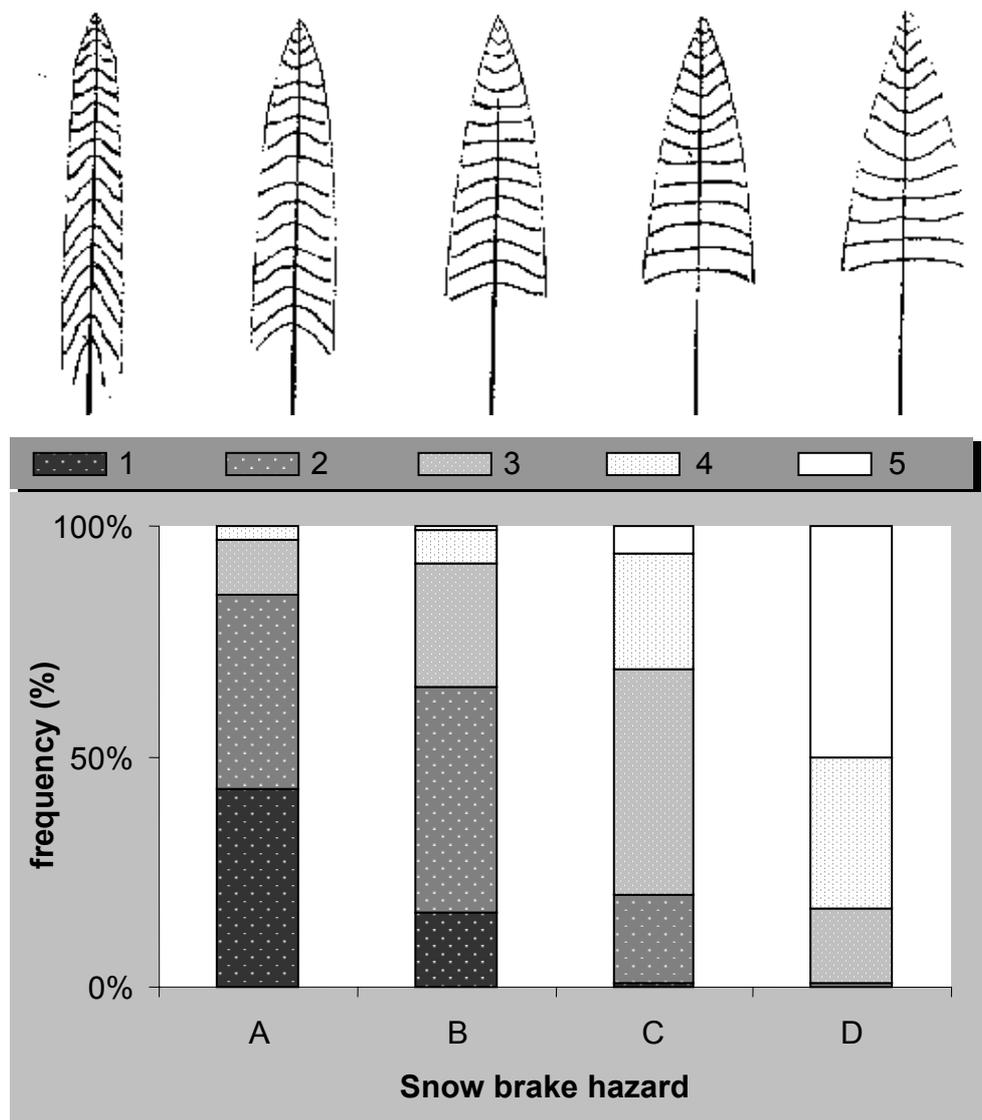


Figure 2. Frequency of spruce crown phenotypes in the Slovenian Alps: an example of interaction of natural selection, phenotypic plasticity, carryover and/or random effects. The columns represent different categories of snow break hazard: A: extreme cold, hazardous sites, B: exposed sites on a plateau, C: transitory sites, and D: low-hazard sites. Percentage of crown types are marked by shading (Mátyás 2004, data from Z. Grec)

## 2.1 Natural selection: constraints in a changing climate

Natural, autochthonous tree populations harbour an unusually high level of genetic variation compared to annual plants, offering ideal preconditions for genetic adaptation, i.e. selection of the fittest phenotypes in changing environments. However, both field observations and theoretical models support the view, that contrary to the general belief, that the population adapts its gene pool to temporal changes by fitness selection, these changes can be expected to be small and the selection process slow and ineffective. Reasons are inherent constraints of the genetic system of species, balancing even extreme selective forces. Some authors suggest that an appropriate genetic adjustment to climatic changes of the predicted magnitude (e.g. in the boreal: 2-4 °C temperature increase) requires numerous, up to 10 or more generations (Tchebakova et al. 2005, Savolainen et al. 2004). Presuming at least 100 years per generation,

this adds up to a millennium – the predicted change however might take place in less than a century. Thus, the *magnitude and speed of expected changes may neutralize* the natural balancing effect of selection.

In the following example basic ecological factors determining zonal forest ecosystems in Hungary are compared to climate scenarios. *Table 1* shows temperature and precipitation data for the main forest zones in Hungary. In spite of relatively large climatic heterogeneity within zones, the average difference between means of zones is very small – especially if the value is compared with the downscaled temperature and rainfall data of climate scenarios for the next quarter of century (*Table 1*). It seems that, theoretically within one tree generation time, the extent of climatic shift may surpass the difference between zonal forest belts. Consequently, present populations of dominant tree species might not be able to keep their present habitat. Due to the persistence of forest ecosystems, the described scenarios do not necessarily lead to a gradual shift of species composition, rather to sudden large-scale mortality events following extreme weather anomalies. Under these conditions the effective functioning of natural selection will be restricted. Such events have been already observed for Norway spruce a decade ago (Mátyás 1997), as well as for oak and more recently also for beech in Hungary,

*Table 1. Average temperature and precipitation data of zonal forest belts in the lowlands of the Carpathian Basin and the magnitude of expected changes (Mátyás - Czimmer 2000)*

	Annual precipitation (mm)	July temperature (C°)
Beech zone	734 ± 65.2	19.1 ± 0.95
Hornbeam-oak zone	702 ± 70.3	20.0 ± 0.79
Turkey- sessile oak zone	616 ± 49.0	20.2 ± 0.70
Forest steppe zone	563 ± 49.0	21.5 ± 0.56
Average difference between zones	57	0.80
Climate change prediction, medium scenario for Central Europe	decrease by 40-60 mm	increase by 1.0-1.5 C°

## 2.2 Species and allelic migration constraints

It could be argued that similar to the past, species and communities will keep pace with changes and counterbalance climatic shifts by colonising new habitats. Migration is frequently modelled by ecologists, by projecting climatic envelopes of present distributional ranges into future scenarios of changed climates.

Effective species migration has to match, however, the pace of expected changes as well. It has been shown that forecast climate changes are simply too fast to be followed by tree populations (Mátyás cited in: Davis - Shaw 2001). In Central Europe, according to a more pessimistic scenario of a temperature increase of 2°C in 35 years, isotherms would wander horizontally in northerly direction with an average speed of 3 km/year and 12 m/year in altitude (*Table 2*). This has to be compared to the natural migration speed of species. It is known from paleobotanical studies (Davis 1981) that tree populations migrate - depending on migratory abilities - at rates of 0.1-0.4 km/year. The difference between the expected climatic shift and the potential migration speed is roughly one magnitude. This means that even in case if migration routes were available and environmental, geographical conditions would not provide obstacles, horizontal migration velocities do not keep up with the expected changes.

Table 2. Comparison of migration speed and predicted isotherm shift (Mátyás 2005)

Natural migration velocities through seed dispersal (from paleobotanical data, from Davis 1981):

*Quercus, Fagus*: 100-250 m/yr

*Betula, Pinus*: 200-400 m/yr

Velocity of isotherm shift (scenario: 2.0 °C in 35 years )

Direction	Gradient	Velocity
S ⇒ N horizontal	50 km/°C	3000 m/yr
Vertical (altitudinal)	200 m/°C	11.5 m alt./yr

There are other, more direct reasons which will prohibit the spontaneous mass migration of trees, such as the fragmentedness of man-dominated landscapes, and the comparably very slow development of soil conditions – a constraint in subpolar and alpine environments. In the north boreal and alpine tundra zone the theoretical possibility of a colonisation advance of forest trees exists according to climatic forecasts. It has to be considered, however, that apart from the fact that natural migration speed of forest trees is relatively low, even on the long run the utilisation of climatically improved zones off the present distribution range will be limited by soil conditions. The development of soil profiles takes millennia and the usually shallow, less developed soils of high altitudes and high latitudes will not change fast enough.

Another constraint for colonisation of new habitats is the limited availability due to geomorphological-distributional preconditions. Typical examples are populations restricted to mountain tops such as *Abies pinsapo* in Northern Africa or *A. fraseri* in the Appalachians which have simply nowhere to migrate (Eriksson - Ekberg 2001). In general, any species settled in a habitat which does not provide a geographically contiguous escape route will be affected. In addition to high-altitude species, coastal Mediterranean species may be exposed to this threat as well.

There is, on the other hand, not enough information on the effectivity of *migration through gene flow* within a contiguous distribution area. For many widely distributed species long distance gene flow might influence the gene pool of filial generations. There are indications that distant pollen sources, usually of southern origin, may significantly contribute to pollination in the north (Lindgren et al. 1995). The effect of adaptation of gene pool through gene immigration might be assumed as higher than the migration by dispersed seed. Preconditions are: a relatively unfragmented distribution of the species, the close to undisturbed state of populations (i.e. low frequency of stands planted with uncontrolled, less adapted plants) and the general application of natural regeneration techniques. Neither of these can be taken for granted, except possibly in certain regions of the boreal zone.

## 2.3 Phenotypic plasticity

### 2.3.1 Evolution of phenotypic plasticity

A common definition for phenotypic plasticity\* is the *environmentally sensitive production of alternative phenotypes by given genotypes* (DeWitt - 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. 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 series of environments is regarded as phenotypic plasticity or stability.

\* Phenotypic stability is a synonymous term

According to this approach, stable genotypes or populations are better fit to utilise diverse environments than others. Similar to fitness, plasticity can be measured and analysed on vegetative growth and organic matter production. Phenotypically plastic genotypes should exhibit less morphological, vitality and growth variation across environments than others. Naturally, this relatively constant performance is expected to be in the upper or above-mean range; a genotype with generally bad performance could not be regarded as “plastic” or “stable”.

Although seen by many as “nongenetic”, plasticity is doubtless a genetic trait and certainly influences evolution: individuals carrying more plasticity will show fitness in more environments – on the other hand plasticity will also put a constraint on genetic adaptation of the population by concealing the “true” genotypes.

Statistical evidence for plasticity in plants is supplied by multiple-test comparative trials, where the variance component for genotype  $\times$  environment interaction ( $V_{G \times E}$ ) indicates that the response of test entries (clones or populations) to changing test conditions is different.

According to field tests of numerous species, exclusivity of phenotypic plasticity is certainly not the evolutionary strategy of forest trees as proposed by certain studies (e.g. Maherali et al. 2002). There are obviously trade-off limitations to develop a high level a plasticity and the availability of high genetic variation in itself may put limitations to the further development of plasticity. Although plasticity appears to be highly adaptive, it has to be cautioned, however, against supposing that plasticity as a trait is always a product of natural selection. As shown in the review of van Kleunen and Fisher (2005), there are certain constraints on the development of phenotypic plasticity, which *per se* needs not even be adaptive.

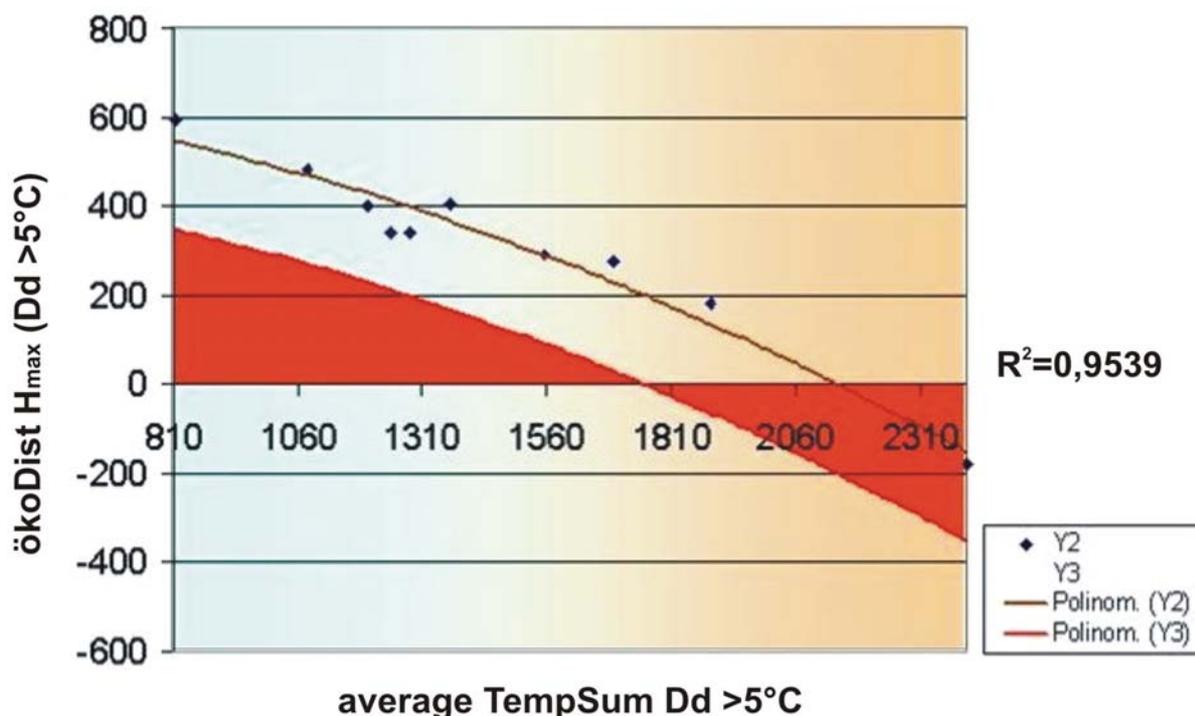
### **2.3.2 Plasticity and climatic oscillations**

A major factor in supporting the evolution of plasticity is the unpredictable nature of main ecological factors. The first factor which offers itself for examination is weather and climate. *Could it be that different levels of climatic stability might be linked to differences in plasticity?* Such connections may be found for example when comparing reaction norms of populations adapted either to stable, typical climates or to transitory zones toward other climate types. Due to the difficulties of collecting relevant climatic information, very few hints can be traced.

Riley and Spolton (1974) analysed the conformity of annual weather types with the actual climate zone and delineated zones of lower stability for Europe (out of 30 years at least 5 years of untypical weather). They found that a zone of relatively high instability divides in East-Central Europe the maritime and continental climate. If the hypothesis of links between plasticity and environmental (climatic) fluctuation holds, phenotypically plastic populations should have evolved in more than one species in this region. As a matter of fact, comparing this zone with East European provenance regions of higher plasticity both in Norway spruce and Scots pine, the author has found surprising similarities (Mátyás 1986). For jack pine (*Pinus banksiana*) a zone of elevated plasticity could be identified in the Ottawa Valley, being climatically a transitory zone as well (Mátyás 1986). A similar zone presumably supporting the evolution of plasticity of Douglas fir is suspected in inland British Columbia, Washington and Oregon, which seems to be substantiated by recent research results (S. Aitken, pers. comm.).

### 2.3.3 Assessment of phenotypic response

Phenotypic response of populations in changed environments may be predicted from data of provenance (common garden) tests, as has been proposed by the author (Mátyás 1996). As an example, in *Figure 3* we show the prediction for height growth response across the distributional range for Scots pine (details may be found in Mátyás - Nagy 2005). Using transfer analysis techniques, a response curve for maximum height performance (Y2) was calculated from data of provenances representing a transect of the European distribution area, from north to south, i.e. with temperature sums from 810 to 2310 average degree-days above 5°C. Through the lowering of the regression line by 200 degree-days, that is by approx. 1°C temperature rise in the vegetation period (Y3 in *Figure 3*) we have simulated a virtual climate change scenario. The shaded areas below the curve stand for increment responses of populations in different parts of the range. These indicate that in the northern half of distribution (left side of the graph) an increment acceleration can be expected, while on the southern limits (right side) Scots pine populations will perform much below their original potential, which may mean also mortality.

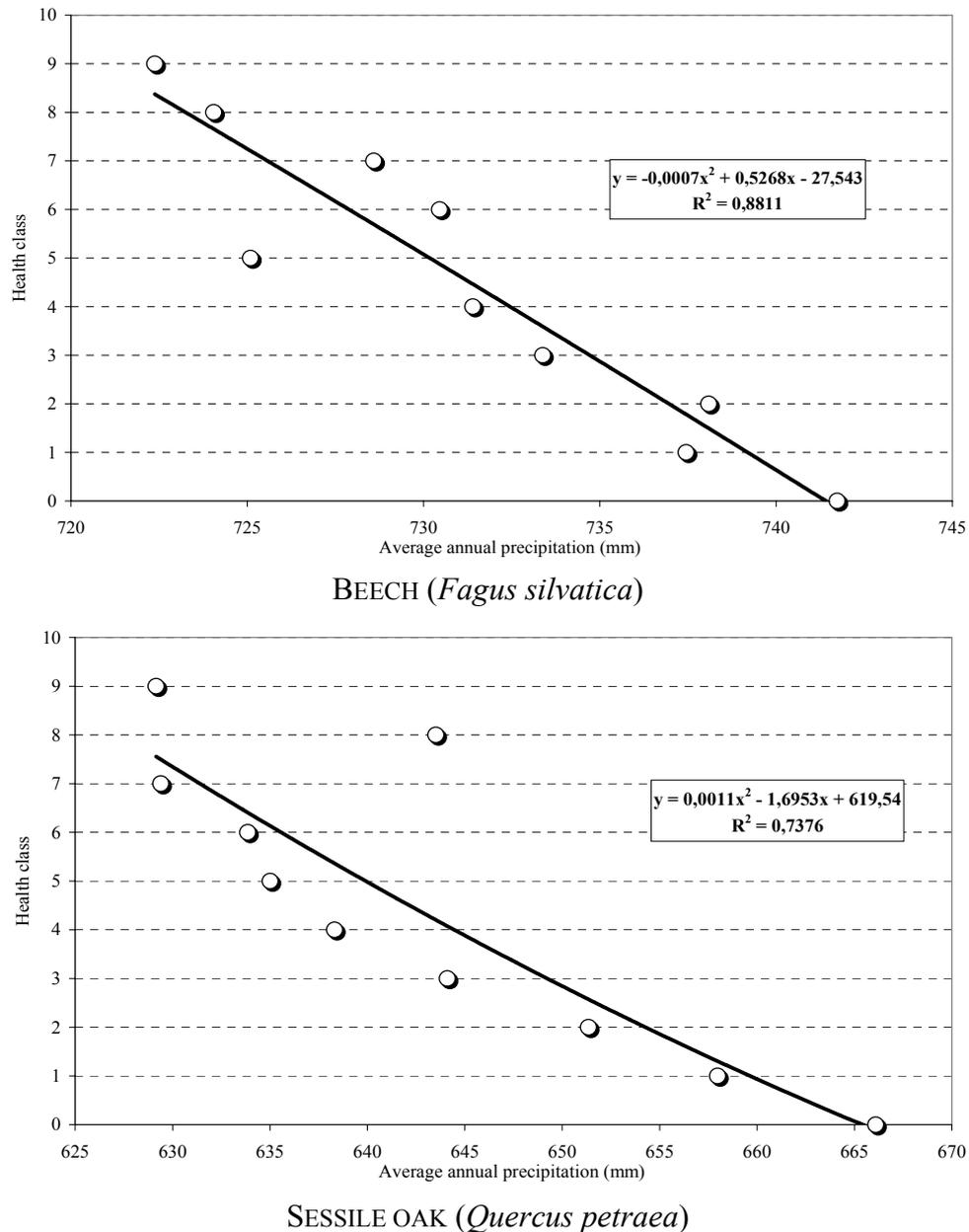


*Figure 3. Increment response prediction (vertical axis) of differently adapted Scots pine (*Pinus sylvestris*) populations for an annual temperature rise of +200 degree-days change scenario. The model was constructed for a cross-section of the Eurasian distribution area of Scots pine from North to South, i.e. from low to high temperature sum climates, utilising calculations of Rehfeldt et al. (2003) (from Mátyás - Nagy 2005, see explanation in text)*

The model illustrates that phenotypic response to changes will be differentiated. While species-specific reactions, and other ecological effects (synchrony changes with competitors or consumers etc.) may diversify the overall picture; it may be assumed, that in general at the upper/northern limits, temperature increase will bring an improvement of site conditions, resulting in increment acceleration in forest tree populations. At low elevations and in the southern outliers of the distribution, close to the present lower limit of the area, temperature increase and lower humidity certainly will lead to the thinning out and disappearance of the species, losing its competitive ability against other species.

### 2.3.4 Limits of tolerance

Although ecologically set limits of tolerance are integral parts of modelling considerations, it is rather difficult to concretely define such limits as shown in *Figure 1*. One reason is the lack of relevant experiments. For obvious reasons (little interest in low-yield, risky sites) there are few trials where quantitative responses can be studied under extreme conditions in forestry. In addition, correlation between climatic parameters and vitality are usually sought on basis of weather conditions for an antecedent period triggering disease symptoms or pest outbreaks.



*Figure 4. Climatic limits of tolerance and plasticity on species level, set by recent deterioration of health condition of forest trees: correlation of leaf loss of beech and of sessile oak vs. average annual precipitation. Rainfall data refer to the past climate of analysed network points, for the years 1960-1990. Health classes have been assessed in 10 percentiles of leaf loss; 0 = healthy, 9 = 90% leaf loss. Evaluated from Hungarian data of the European Forest Health Monitoring Network by G. Veperdi (2005). Data source: State Forest Service, average of assessments between 1989 and 2002*

To test the hypothesis that worsening of climatic conditions lead to health decline and finally to death, data of the Forest Health Monitoring Network have been analysed. In this study climate data were set against health condition of sample trees at observation network points over a prolonged period. Climate parameters were determined from digital surfaces.

The parameters of trees with similar health score were averaged. In *Figure 4*, precipitation averages calculated according to this method are shown for leaf loss classes 1 to 9 (10, mortality could not be included because of low number of data and random effects). As the lower limit of distribution is defined by moisture supply as minimum factor, precipitation means may be interpreted as the ecological position of the sample point in the zone of distribution, i.e. as the distance from the xeric tolerance limit (Veperdi 2005).

The graphs indicate very close relationship between health and precipitation at the xeric (lower) limit of the distribution range of both sessile oak and beech (it has to be stressed that the precipitation data refer to climate, i.e. 30-year averages!). The nearly linear, highly significant correlation depicts the loss of vitality towards the xeric end of the distributional niche of the species without regard of actual extreme weather conditions. Comparing the two species, a difference of 80 to 90 mm annual rainfall<sup>†</sup> can be observed between the response of beech and the more drought-tolerant sessile oak. The result shows that the assessment of species-specific tolerance limits on climatic basis is possible. Its usefulness for strategy planning is self-evident. However, *climatically defined critical limits* are not necessarily the exclusive constraints for the species. Pests and diseases may strike much earlier, depending on weather extremes (droughts) and their frequency.

## 2.4 Carryover effects

Parallel to phenotypic plasticity, environmentally induced carryover (epigenetic) effects are relatively common in plants and seem to represent an adaptive advantage in changing environments (Jablonka et al. 1995). Investigations on some forest trees (e.g. Skroppa and Johnsen 2000) have proven that, for instance, parental effects may also contribute to the effective adjustment to spatially or temporally changing conditions. It need not be a chance that – although observed on a number of species – most striking effects have been observed on conifers in boreal environment. Especially in both topographically and climatically variable conditions (Norway!) the maintenance of proper adaptedness needs small-scale adjustment which is obviously more “costly” by genetic adaptation through selection alone. The observation that parental effects in Norway spruce were more explicit in northern populations than toward the south, supports this hypothesis. Due to the unknown importance and extent of carryover effects in forest trees in general, it is however advisable not to count too heavily with carryover effects in buffering climatic oscillations.

## 3 PREPARING FOR THE FUTURE

### 3.1 Importance of plasticity studies

More synthesis between genetics, evolution and ecology, as well as between qualitative (molecular) and quantitative aspects of genetics is needed. To avoid isolation, geneticists should endeavour to improve communication towards related fields where their results may find practical application.

Phenotypic plasticity and tolerance will play in the adaptation of forest stands to changing environmental conditions an increasing role (*Figure 3*). Genetic background of respective QTL-s should be investigated as priorities. New field tests are indispensable to collect more

<sup>†</sup> note that closely matching average rainfall difference between beech and sessile oak is presented in *Table 1!*

evidence. Existing field trials should be evaluated for these purposes even if considered statistically less valuable, and new comparative tests be established. Locations at lower limits of distribution are of special interest. In addition to ecological and genetic modelling, data from comparative test series are essential to bring assessments and forecasts closer to reality.

The importance of phenotypic plasticity for “standard” forest management, for use of forest reproductive material and for mitigation strategies of expected environmental changes is self-evident. The understanding of the balance between natural selection, genetic constraints and other strategies as plasticity and carryover effects is essential for predicting responses and tolerance limits for dominant species in forest ecosystems.

The fact that mitigation of climate change effects has a very strong genetic component, has not yet penetrated forest and nature conservation strategies. It has to be made clear that implications to yield and profitability and ecological processes (succession, degradation and structural changes) are serious and significant.

### 3.2 Preparing for mitigation - need for human interference

Climate change research results indicate that because of the conservative nature of the genetic adaptation process, and of the relative speed of expected changes, even agricultural crops will demand a strategy to facilitate adaptation. Long-lived, immobile organisms, such as trees will especially need human interference in order to enhance adaptation to altered conditions, in spite of an impressive adaptive capacity. National forest policies have to incorporate this task into the agenda of the next decades.

More attention should be paid to alternatives of genetic adaptation, which seem to act faster and without the diversion of sexual reproduction. *Phenotypic plasticity is the adaptive answer to fast changes of the environment*, within the generation time of present-day forest genetic resources. This trait has been undervalued as priority in selecting forest reproductive material sources and also in gene conservation.

The need for active measures is the most pressing in the southern peripheries of the distribution areas. Because of grave environmental changes, human interference and mitigation is especially urgent in regions lying in the transitory zone of closed forests toward open woodlands and steppe, such as in continental Southeast Europe and low elevation areas of the Mediterranean. In these regions water supply is already now a minimum factor and presently native tree species have few sensible alternatives. Deteriorating climate parameters trigger pandemics and uncontrollable mortality already now, leading to loss of crown closure, spontaneous change in species composition rates and yield decline, which will affect profitability of forest operations.

As a consequence, *human interference will be essential for the maintenance of adaptability of forest trees under changed conditions in the present areas of distribution*. Due to the long-term impact and high risk of necessary measures and the low reliability of forecasts, it is imperative that forest genetic and ecology research join forces to better elucidate the discussed issues of predicted stability and response of forest ecosystems.

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