

Utilization of genetic and ecological adaptation research results for planning conservation of forest genetic resources in view of environmental changes¹

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Introduction

Climate change mitigation, maintenance of stability of forest ecosystems and proper use of forest propagation material are serious challenges for research in the 21st century. All are linked by ecology-related aspects of forest genetics, first of all by the question of adaptation.

The issue of adaptedness appears to become a crucial problem for forestry in view of expected climate instability. 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 are the means to maintain and enhance their adaptability.

Studies analyzing 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 (genetic studies). Two basic shortcomings of are frequently encountered in the research work:

- a proper synthesis of ecological and genetic information is seldom done;
- strong practical constraints on both migration and natural selection are in the majority of cases not considered.

In the paper the research challenges are reviewed with regard to the above problems.

Answers of ecology, genetics and evolution to genetic variation of fitness

Contemplating the wealth of hereditary 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 (and, as an analogy, diversity of species) is maintained by the heterogeneity of environmental conditions both in time and space differences in age, in habitat conditions, in density differences etc. It seems that both on within-species and on between-species level, i.e. in genetic and species diversity, correlations with environmental (ecological) heterogeneity exist.

¹ The paper is based on a keynote speech held at the Institute of Forest Genetics in Hamburg, on the occasion of the retirement of Prof. H. Muhs in 2004

The *genetic* explanation of existing variation is based on the simultaneous dynamics of different genetic processes (natural selection, mutation, migration, drift, introgression, inbreeding etc.).

Genetic effects are partly related to the mostly random, *historic processes of evolution*: to speciation and extinction events, to withdrawals to refugia and migrations in connection with glaciations and warmings.

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 and should be maintained and protected. To understand the evolution of variation in a trait, all the mentioned factors have to be considered. With changing conditions, the fitness value of a trait will change as well.

For instance, wide crown shape in conifers to utilize available resources and to keep away competitors, and narrow crown shape to avoid snow brake are both adaptively important values. While the former is especially vital in richer ecosystems with high species diversity, narrow crown shape is selectively preferred in rather monospecific, higher altitude surroundings. 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 proper distribution of phenotypes (see Fig.1).

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 glacials and interglacials is abundant – and this is the option generally described by most ecologically-oriented future scenarios as well (its relevance will be discussed later).

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*.

On *individual genotype level*, environmentally induced phenotypic plasticity and 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.

Studies on adaptation prevalently deal with selection processes and with changes in the genetic composition, respectively allelic diversity of the populations. Mainly for reasons of difficulty of experimental analysis, *limits of individual and population tolerance set by phenotypic plasticity* are less frequently among either ecological or genetic considerations regarding adaptation. However, spontaneous natural selection in connection with forecast climate change will play a relatively minor role compared to plasticity due to the speed of expected changes, as explained later on. Plasticity will gain therefore an increasing role as a preferred trait for forest reproduction material in artificial regenerations, in nature

conservation and restoration ecology. For this reason phenotypic plasticity is investigated more in detail in the followings.

Missing synthesis

Analysis of phenotypic plasticity involves not only genetics and ecology but also physiology and contributes to a more complex view of plant response in the environment. In many studies however, genetic and functional ecological aspects are investigated independently from each other. “Environmental tolerance” seldom appears in genetics, while “reaction norm along an

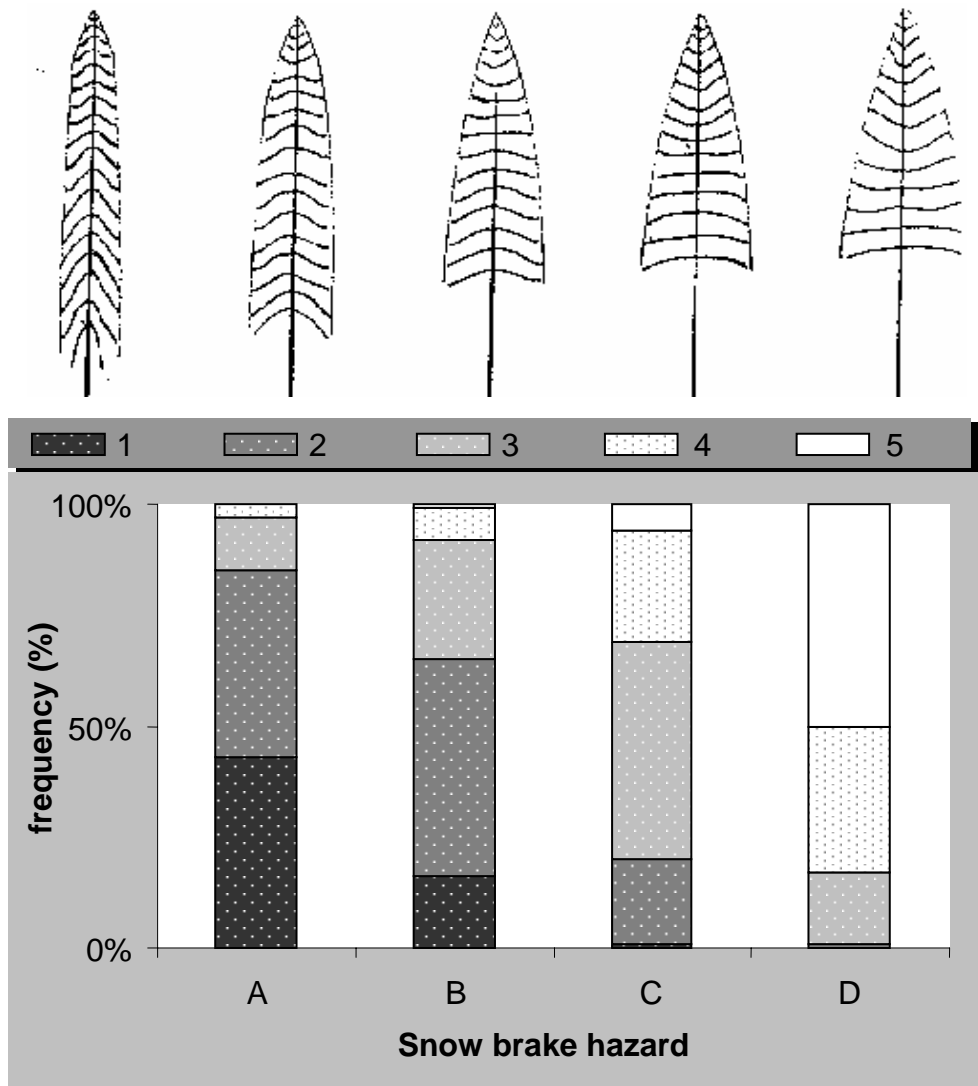


Figure 1. Frequency of spruce crown types in the Slovenian Alps: an example of genetic adaptation, phenotypic plasticity or carryover effects?

The diagrams 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)

environmental gradient” is not a frequent theme of ecological studies. Very often 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. A complementary approach of quantitative genetics and ecology may shed light on the evolutionary and adaptive background of the trait. Comprehensive studies are necessary to achieve a deeper understanding of the functioning of ecosystems, of the evolutionary diversification on genetic and species level and of the real value of biodiversity in stability and resilience of living systems.

It is no surprise that the molecular revolution of the recent decades has contributed little yet to the synthesis of genetics, evolution and 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 microorganisms or animals (e.g. *Drosophila* sp., other insects, snails etc.).

Phenotypic plasticity in broader evolutionary context

Phenotypic plasticity as phenomenon also connects ecology, genetics and evolution. A common definition for 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 (as all biological processes are influenced by the environment) 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.

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. Although seen by many as “nongenetic”, plasticity is 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.

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.

Case study of trees: ecological and genetic response to fast changes

In case of long-living sessile organisms, such as trees, relatively fast changes in heterogenous environments require special strategies and may pose also specific constraints. Long-living forest trees and heterogeneous climatic conditions across a topographically variable landscape or latitudinal cline represent obviously ideal conditions for the evolution of such 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.

Environmental heterogeneity and the evolution of plasticity

The adaptive response of spruces shown in Figure 1 may have been generated *either by gradient-dependent distribution of different alleles determining crown form, by carryover effects (e.g. female parental effects) or by a perfectly functioning plasticity with no genetic change in the populations.*

According to field tests of numerous species, “perfect plasticity” is certainly not the evolutionary strategy of forest trees. There are obviously tradeoff 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.

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 growing in stable, typical climates and in transitory zones toward other climate types. Due to the difficulties of collecting relevant climatic information, very few hints can be traced.

The author has found indications of higher plasticity in Norway spruce and Scots pine for climatically unstable, transitory zones of Eastern Europe and for jack pine (*Pinus banksiana*) in the Ottawa Valley (Mátyás 1996). A similar zone supporting the evolution of plasticity of Douglas fir was presumed in inland British Columbia and Oregon, which seems to be supported by recent research results (S. Aitken, pers. comm.).

Parallel to phenotypic plasticity, environmentally induced carry over (epigenetic) effects are relatively common in plants and seem to represent an adaptive advantage in changing environments (Jablonka et al. 1995). Investigations on 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 series 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 far-northern populations than toward the south, supports this view.

These phenomena underline the importance of spatial and temporal heterogeneity, out of which the temporal fluctuation has received relatively little attention. The development of phenotypic plasticity may be also considered as an alternative strategy of evolution in addition to the “classic” generalist and specialist concept.

Natural selection constraints

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. In addition to the general genetic constraints briefly mentioned in the introduction, 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 2). 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).

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, Czímber 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

Table 2. Scenarios for the next quarter of century in the Northern Hemisphere and downscaled data for Central Europe (Carpathian Basin) (Mátyás 2005)

Past global temperature increase (1850-1995): +0,5 °C				
Scenario number	1	2	3	4
Average temp. increase on the Northern Hemisphere until 2025 (<i>in °C</i>)	+0,5	+1	+2	+4
Summer temp. change in the Carpathian Basin (<i>in °C</i>)	+1,1	+1,3	+1,5	+3
Winter temp. change in the Carpathian Basin (<i>in °C</i>)	+0,8	+2,2	+3	+6
Annual precipitation change (<i>mm</i>)	-40	-66	±0	+40-400
Geographically analogous area	North Serbia	Central Bulgaria	South Bulgaria	Tuscany

Species and allelic migration constraints

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

Effective species migration has to match, however, the pace of expected changes. It has been shown that forecast climate changes are simply too fast to be followed by tree populations (Mátyás 1997a cited in: Davis and Shaw 2001). In Central Europe, according to a 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 (see Table 3). 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 migrative 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 3. Comparison of migration and 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
> 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 – an overlooked constraint in subpolar and alpine environments. In the north boreal/subpolar 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. Thus, contrary to general belief, the site potential will not follow at once the improvement in climate. It is quite surprising, that this typically ecological feature is recurrently overlooked in ecological studies.

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 and 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 be an effective mechanism to alter 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. Within contiguous distribution ranges gene frequency adjustment through migration of pollen could be sufficient to match the pace of changes. Preconditions are: a relatively unfragmented distribution of the species, the close to natural state of populations 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.

Regional differences in adaptive response

Thus, considering the long regeneration cycle of trees, the pace of the forecast climate changes will be too fast to provide enough time for either genetic adaptation or spontaneous migration of populations. Populations will respond with the change of site conditions, in accordance with their genetically set phenotypic plasticity. Plasticity responses may be forecast from reaction norms, if available.

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 2 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 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 2) 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.

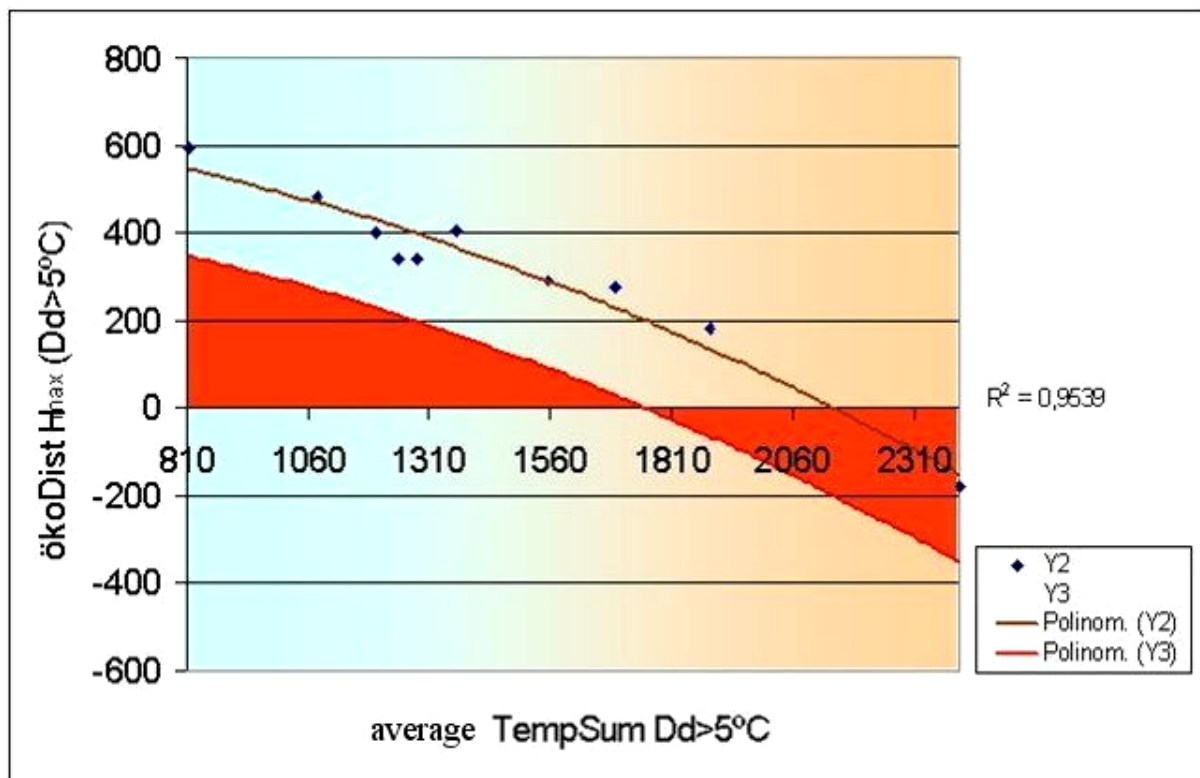


Figure 2. Increment response prediction (vertical axis) of differently adapted Scots pine (*Pinus sylvestris*) populations for an annual temperature rise of +200 degree-days change scenario. The model was constructed for a cross-section of the Scots pine distribution area from North to South, i.e. from low to high temperature sum climates (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.

How are these considerations reflected in present-day research?

Efforts to clarify the genetic background of quantitative traits and adaptation have progressed considerably and has yielded meaningful results. However little of these results have penetrated forest ecological research. Even recently published textbooks on forest ecology and on effects of environmental change contain little or no genetic component of relevance.

Similarly, relatively little ecological input can be discerned in forest genetics research. 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.

There is a generally accepted opinion to judge adaptability based on genetic diversity on the biochemical-molecular level. It should be pointed out that to interpret exclusively only on the basis of qualitative parameters (even if QTL-s are applied) is too narrow. Adaptively important, quantitative traits observed in field tests are 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 observations into an ecological context.

Proposals for the future 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 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. A special drawback of field testing in forestry is the fact, that for obvious reasons (no interest in low-yield, risky sites) there are few trials where quantitative responses can be studied under extreme conditions.

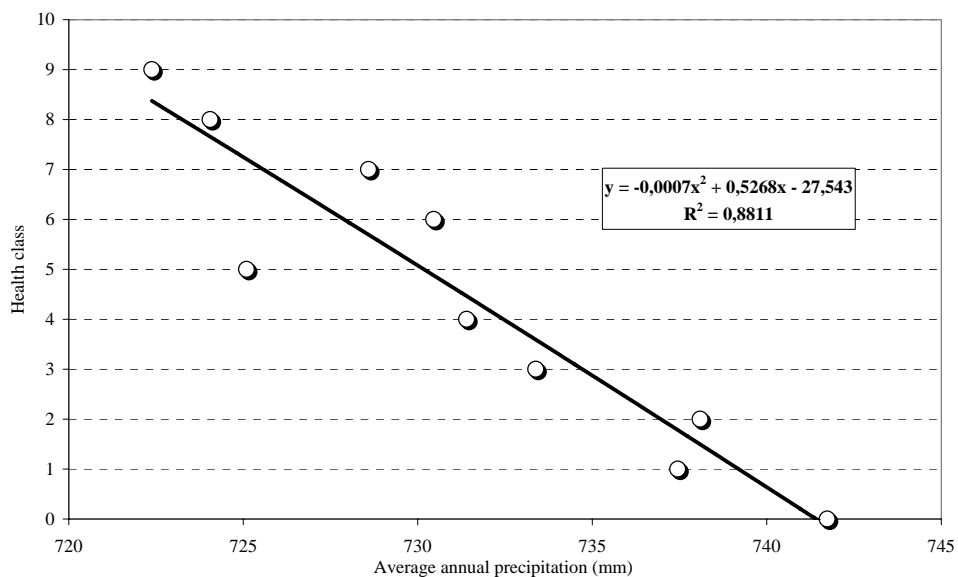
The importance of plasticity for “standard” forest management, for use of forest reproductive material and for mitigation strategies of expected environmental changes is self-evident. The understanding of the balance between natural selection, genetic constraints and other strategies as plasticity and 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.

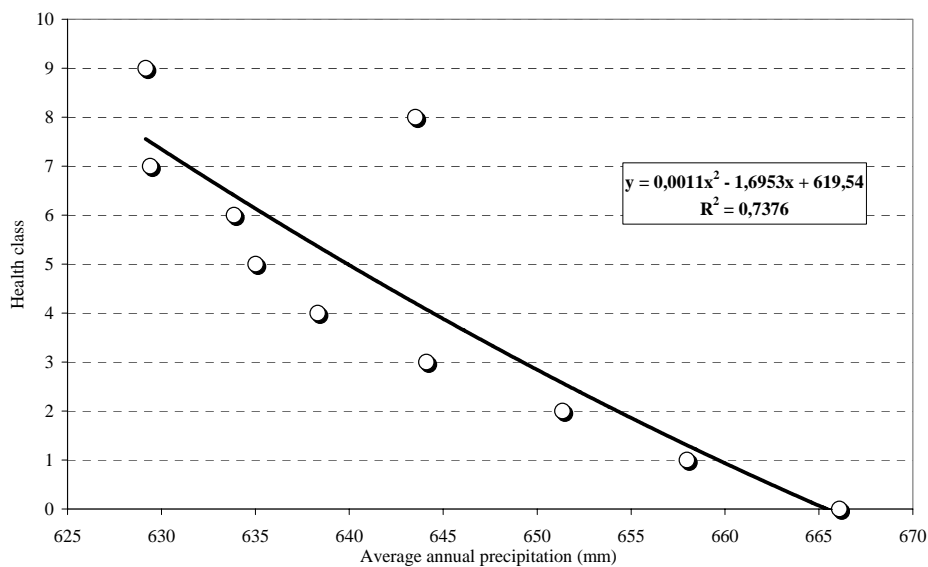
Preparing for mitigation - need for human interference

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.



BEECH (*Fagus silvatica*)



SESSILE OAK (*Quercus petraea*)

Figure 3. 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 concrete network points, for the years 1960-1990, indicating their position in the zone of distribution. Health classes have been assessed in 10 percentiles of leaf loss; 0 = healthy, 9 = 90 % leaf loss, calculated from Hungarian data of the European Forest Health Monitoring Network by G. Veperdi, 2005 (data source: State Forest Service, assessments between 1989 and 2002)

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 native tree species have few possible 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 (Figure 3).

As a consequence, *human interference will be essential for the maintenance of adaptability under changed conditions in the present areas of distribution, and also to adjust (extend) the ranges of species at the northern peripheries.* 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 shed more light in the discussed issues of predicted stability and response of forest ecosystems.

Acknowledgement

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