

WHAT DO FIELD TRIALS TELL ABOUT THE FUTURE USE OF FOREST REPRODUCTIVE MATERIAL?

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Introduction: the forestry perspective of climate and vegetation shift

In view of the current concern over climate change, the fundamental question is how forest cover and tree populations will react, and what the chances are to maintain and enhance their adaptability. Modelling of vegetation shifts according to various climate change scenarios has been widely applied in the temperate zone. For Europe, it has been forecast that the Mediterranean scrub will invade the British Isles, broadleaved forests might grow in the High Alps instead of conifers, and that treeless grasslands could conquer not only the Carpathian Basin, but also the central part of eastern Germany and Poland.

Apart from the great uncertainty in forecast scenarios (especially regarding the amount of rainfall), the preparation for expected changes of this magnitude presents tasks not encountered before in forestry. The large-scale preparation and conversion of forests to future climatic conditions will present grave

economic and technological challenges. However, it would be a very biased approach to treat this problem solely as an economic and ecological question, since forests bear also important cultural, aesthetic and emotional values. The existence of forests is an important element of life quality in the European tradition.

Predicted climate change demands that a high priority be assigned to the study of the climatic requirements of forest tree species and zonal forest types (i.e. vegetation types determined primarily by macroclimate), especially of their xeric or lower limits, which are determined by tolerance to water stress and high temperatures. The climatic (zonal) limit of greatest concern is the lower limit of closed temperate forests and its dominant species towards continental grasslands or Mediterranean scrub, because the shift of this limit has dramatic consequences for forestry and ecology, as well as for life quality in general.

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The neglected synthesis of ecology and genetics in climate change studies

Any prediction about the effects of future climate change scenarios on stability and yield of forests requires information on the tolerance and adaptability of tree species. The maintenance of adaptive and evolutionary capacity has to be considered as a precondition for stability of forest ecosystems (Ledig and Kitzmiller 1992; Eriksson et al. 1993; Mátyás 1997). It is strange to observe that, although the mentioned requirement is hard to interpret without genetic background, there are practically no ecological or conservation biology studies dealing with climate change effects that incorporate the aspect of genetic regulation of the response. Applied ecology papers dealing with the responses of species to climate change (reviewed by Hulme 2005) cover limited geographical areas and short periods, and usually concentrate on responses in abundance with time or spatial distribution. Practically none of the papers reviewed by Hulme (2005) deals with the genetics of adaptation.

Nor have quantitative response to change and limits of tolerance—seemingly trivial questions—been among the priority themes of current genetic research. One of the reasons for this neglect lies in the limited scientific reputation of research in quantitative trait variation. In addition, such studies are time-consuming and expensive. It also has to be conceded that until recent decades, behaviour of populations under

changed or extreme conditions had little practical relevance.

Current forest genetics research concentrates on molecular genetic analysis because this approach promises a faster elucidation of genetic regulation of stability and tolerance, although ecological interpretation of molecular markers with adaptive value has remained dubious in most cases. Out of genetic forces shaping variability, the random effects of migration, mutation and drift have been studied most, while adaptive response to selection has received significantly less attention.

Options of genetic adaptation on population and individual level

The genetic system and adaptability of trees have been shaped by eons of evolution. On an evolutionary scale, most species are ephemeral creatures on Earth. Forest trees, especially the evolutionarily more ancient conifers, certainly belong to the more persisting class of species. Tree species have not only successfully survived changing geological periods, but also endure during an individual's lifetime considerable fluctuations of environment without the chance of escaping to more favourable habitats. Environmental instability, evolutionary history and genetic forces have shaped the natural adaptive strategy of trees; a life form with extremely long generation times, incomparably high within-population genetic diversity and heterozy-

gosity, and immense population sizes, both areally and numerically.

There are various genetic and non-genetic mechanisms operating on the individual, population, species and ecosystem levels, balancing changes in environmental conditions. On species and ecosystem or landscape levels, a possibility of responding to large-scale changes in the environment is migration through seed (and pollen) dispersal. Palaeoecological evidence of migration during the epochs of glacials and interglacials is abundant—and this is the response mechanism expected and described by most ecologically-oriented future scenarios as well. 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 genetic diversity. Long-term genetic adaptability is therefore directly depending on the conservation or even reconstruction of adaptive genetic variance.

On the individual genotype level, environmentally influenced phenotypic plasticity provides the ability to survive in a wide range of environments, without genetic change in the classic sense. Plasticity means that the phenotypic expression of genes is influenced by the

environment, thus the organism may modify its responses within genetically set limits. Phenotypic plasticity will set the limits of environmental heterogeneity in which a genotype or population can endure within its lifetime.

Environmental signals might also trigger genetic carryover effects. Genetic carryover effects (imprinting, 'after-effects') are lasting changes in genetic regulation, which can be inherited (Jablonka et al. 1995; for a review, see Martienssen and Colot 2001). First proofs of existence of such effects in certain forest trees were detected in boreal populations of Norway spruce (*Picea abies*) (Skrøppa and Johnsen 2000) and some other conifers. The significance of genetic carryover in adaptation is so far unclear and should be treated with caution.

When preparing to meet the challenges of changing climate, it is important to realize which of the described mechanisms will gain importance in adaptation, what their action time frame is, and which mechanisms might be even negligible.

Processes of adjustment in the extant (currently growing) generation

Natural selection is eliminating the genotypes of low fitness and tolerance in the lifetime of a population, and this leads to better adaptation. Although some studies on adaptation deal with selection processes and with changes

in the genetic composition, few studies have in practice been implemented under conditions of severe change where populations are reaching their tolerance limits. In such margin situations, the effectiveness of adjustment through selection ceases and mass mortality may follow.

A much less observed mechanism, phenotypic plasticity, provides the ability of individual adjustment 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. Compared with plasticity, spontaneous natural selection will play a smaller role than presumed, due to the speed of expected changes, as explained below. Plasticity should gain therefore an increasing role as a preferred trait for forest reproductive material in artificial regeneration, nature conservation and restoration ecology.

Processes of adjustment in the following generations

Studies on long-distance gene flow through pollen have shed light on this very effective mechanism of constant replenishment of genetic resources, which probably contributes to the unexpectedly high diversity of boreal tree populations. A possibility for responding to large-scale changes in the environment

is also migration through seed dispersal. Preconditions for effective adjustment in both cases are landscape connectivity (availability of pollen or seed) and suitable speed, matching the pace of change. The constraints for both are discussed below.

Constraints to spontaneous adaptation and why human interference is needed

A basic question of mitigation strategy is how much natural genetic processes, such as migration, gene flow and natural selection, will spontaneously compensate for the effects of climate change. Migration and genetic adaptation are investigated here as they are usually taken for granted in climate change modelling.

Is forest community change by spontaneous migration automatic?

It could be argued that, as in the past, species and communities will keep pace with changes and counterbalance these changing scenarios by colonizing new habitats. Authoritative studies on the effects of climate change on vegetation cover take the automatic adjustment of distribution areas of species (i.e. adaptation through migration) for granted, irrespective of the migration possibilities and potentials. Analogies could be taken from observation of spontaneous changes in the insect fauna. However, there are fundamental differences between the migration potential of insects and

of forest trees. It should be emphasized that changes in distribution areas and vegetation cover are predicted to be of such a magnitude that they could never happen through natural succession and migration of forest trees. There are two obvious reasons for this.

Firstly, the natural migration ability of forest trees is slower than the forecast scenario change. Effective species migration has to match, *inter alia*, the pace of expected change. For Central European conditions it can be shown that, based on a scenario of an average temperature increase of 2°C in 35 years, isotherms would move north at an average speed of 3 km per year, and vertically 12 m per year in altitude (see Box 1). This has to be compared with the natural migration speed of tree species. It is known from palaeobotanical studies that tree populations migrate—depending on migration abilities—at rates of 0.1 to 0.4 km per year (Davis and Shaw 2001). The difference between the expected and the potential value is roughly one magnitude for horizontal migration (vertical

migration seems to be possible if geomorphologic and distribution patterns are favourable).

Secondly, insurmountable obstacles to migration are the intensely managed and fragmented landscapes of temperate Europe. Even if tree migration could catch up with the speed of climate shift, and if migration routes were available, spontaneous changes would be impeded due to the nearly total human domination of forest ecosystems through forest management, which has regulated regeneration and species composition for centuries. As much as it is an obstacle, this situation also offers a serious opportunity for human support to natural processes.

Another constraint to migration into new habitats is the limited availability of such new habitats, due to unfavourable geomorphological and distributional conditions. Typical examples are populations restricted to mountain tops, such as Spanish fir (*Abies pinsapo*) in northern Africa (Eriksson and Ekberg 2001)

Box 1. Comparison of migration and isotherm shift velocities

Natural migration velocities through seed dispersal (from palaeobotanical data):

- *Quercus*, *Fagus*: 100 to 250 m/year
- *Betula*, *Pinus*: 200 to 400 m/year

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

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

or Scots pine (*Pinus sylvestris*) in Spain, which simply have nowhere to migrate. In general, any tree species settled in a habitat that does not provide a spatially contiguous escape route will be affected. In addition to high-altitude tree species, coastal Mediterranean species may also be exposed to this threat.

Are genetic adaptation mechanisms sufficient?

Regarding the genetic component of climatic adaptation, there is no general agreement, even among geneticists, on the urgency and modes of mitigation measures. Some scientists (e.g. Hamrick 2004) argue that in the temperate zone, no silvicultural 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;
- regeneration is secured through the persistence, phenotypic plasticity and long life cycle of forest tree populations;
- palaeoecological data indicate that enough variation accumulates and is saved in refugia, and the selection pressure of recent climatic fluctuations was without effect; and
- genetic adaptation may happen in relatively short periods, within two or three generations.

These arguments may be valid, but primarily in boreal regions with predominantly nature-close conditions, where human land use has yet had no seri-

ous impact. In certain nature conservation areas or national parks, cyclical changes of vegetation do not pose serious problems as long as the dynamism of vegetation and fauna is accepted (Westphal and Millar 2004). However, in landscapes and regions transformed by humans, there is no room left for such fluctuations, especially when approaching the lower distribution limits of a vegetation type or a species. This approach does not consider genetically set tolerance limits, and assumes practically limitless adaptation. And last but not least, ecological and economic consequences for forestry and human life quality are omitted completely from these arguments.

A support for accelerated adaptation of populations is the flux of pollen from distant sources. Depending on random wind trajectories, this long-distance migration probably plays a certain role in adaptation (Lindgren et al. 1995). The speed of adaptation of a gene pool through pollen flow can be assumed to be higher than that deriving from migration by dispersed seed. It is the central and northern part of distribution ranges in the northern hemisphere where influx of pollen might contribute to adjustment to change. Relatively continuous distribution of a species, populations close to the natural state and general application of natural regeneration techniques are, however, general preconditions for effective gene flow. Neither of these can be taken for granted. In addition, the

adaptability-improving role of gene flow comes into effect only in subsequent generations.

Common gardens: sources of valuable information on limits of tolerance and plasticity

From the point of view of selection effects of climatic extremes, studies on tolerance and plasticity traits are essential. Tolerance can be defined as the ability of a genotype to maintain its fitness despite damage. Tolerance is 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 genetically set and will determine the presence or absence of species (Figure 1). Even under zonal conditions, the limit cannot be described properly in terms of average climate, as limiting conditions are bound to irregularly appearing extremes, usually triggering damage by diseases and pests. The effects of climate parameter shifts are frequently modelled but seldom studied; observations on tolerance limits are scarce, as forest management strives to operate well above the tolerance limits to secure economic returns.

The study of the effect of natural selection and the phenotypic response of forest trees presents serious methodical challenges in the field (Berki and Rasztovcics 2004). Such effects are much easier to follow in common-garden tests, i.e.

in provenance trials. Provenance tests established since the second half of the 19th century are probably among the most important contributions of foresters to the science of biology. 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. Nonetheless, these tests have remained unnoticed by evolutionary ecologists.

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 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. Most of these models rely 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. The ecological relevance of these variables is ambiguous.

The idea of transfer analysis, i.e. modelling of responses and forecasting responses to scenarios based on provenance data, was proposed originally by Mátyás and

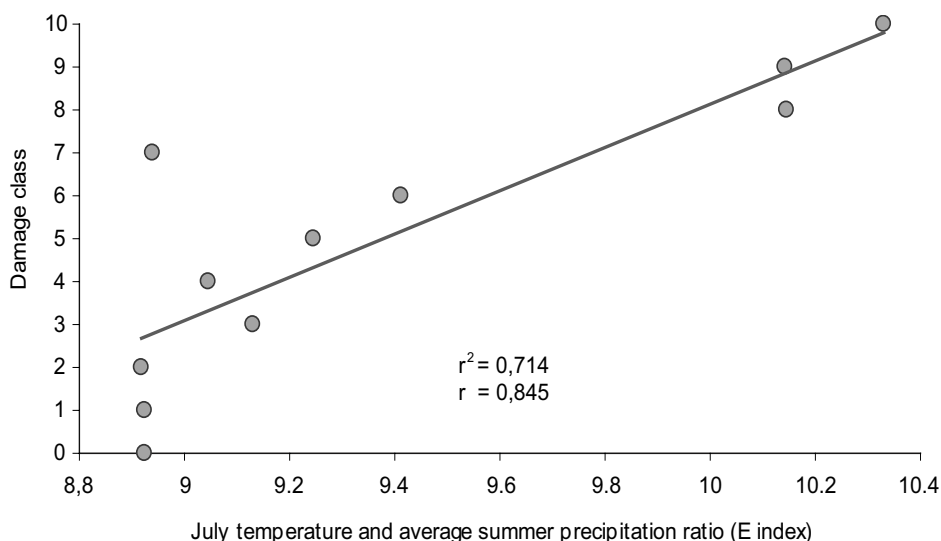


Figure 1. Approaching the genetically set limits of tolerance: average moisture stress climate (E index) of leaf damage classes of beech in permanent monitoring plots in Hungary. The graph shows the change in health status from healthy (class 0) to dead (class 10) along a climate gradient of sites with increasing summer moisture stress (screened data averaged for 1991 to 2001; analysis by G. Veperdi).

Yeatman (1987) and 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 change 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 in-

vestigated (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).

Quantitative response to change

The quantitative assessments of common-garden tests have yielded some generally valid results, which are summarized below.

Width of adaptability: phenotypic plasticity

Analysis of field tests shows remarkable width of adaptability and persistence (and, in consequence, the extended width of 'local' adaptation) in the face of even dramatic changes in thermal conditions and, to a lesser 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).

Value of autochthonous, local source

The superiority of locally adapted, autochthonous populations is an unchallenged axiom in silviculture. The evaluation of provenance tests shows a more differentiated picture. It seems that the fitness of local sources expressed in (height) growth is clearest at locations with extreme conditions. Under more favourable conditions, locally adapted provenances show less superiority (Mátyás 2002).

Asymmetry of response

An important outcome of analysis results 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. It should be noted that a species is not responding as a monolithic unit, due to within-species genetic structure. The boreal limit of tree distribution is temperature dependent. In

provenance tests, populations originating from the upper limit of a species distribution show their maximum performance in much milder conditions. The effect diminishes with increasing temperature sum of the location of origin.

At the southern limit of distribution, drought stress is the main controlling factor. Transfer of populations towards a cooler climate (and better moisture supply) results in accelerated growth. Transfer distance to optimum diminishes with decreasing temperature sum of the location of origin. Accordingly, the reaction of indigenous tree populations to changing conditions will differ according to climatic zones (Figure 2). In the thermally-limited northern-boreal zone, the expected rise in temperature will lead to strong growth acceleration with no significant genetic change. At lower altitudes, in the temperate-maritime zone, growth will accelerate too, along with higher temperatures and increasing or at least unchanged rainfall. In the semi-arid temperate-continental and semi-arid 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. As a result, temperature increase leads to relatively fast growth and productivity loss, and selective mortality (Berki and Rasztovcics 2004; Mátyás 2005). It should be noted that the described phenomena are generalizations. Substantial deviations may be caused by the genetic

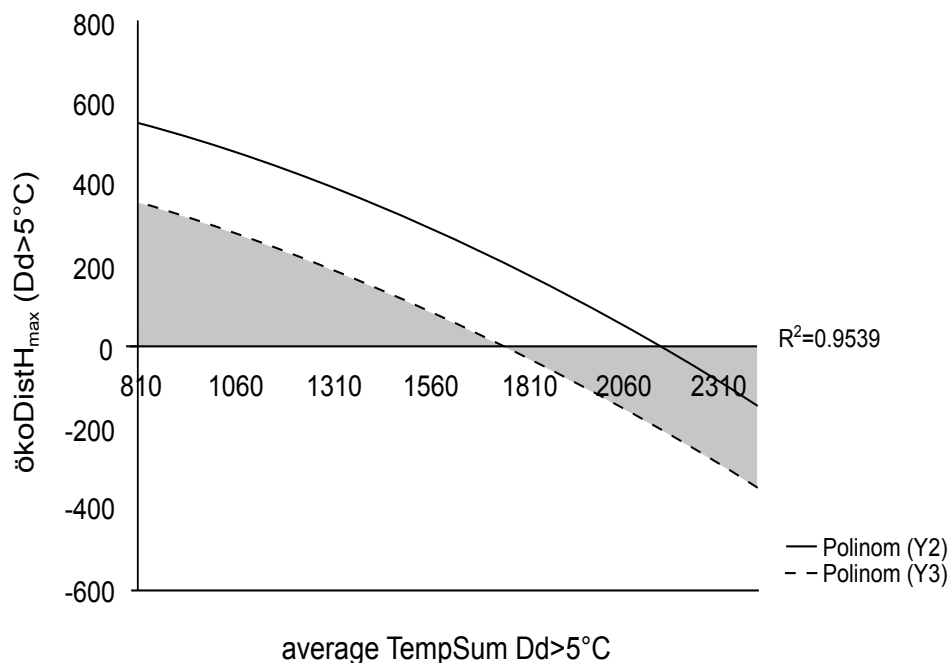


Figure 2. Schematic characterization of response to an ‘annual temperature rise of +200 degree-days’ climate scenario along a N–S transect of differently adapted populations of Scots pine (*Pinus sylvestris*) in eastern Europe. The horizontal axis is the local sum of degree-days. The shaded area indicates direction of growth response: positive in the North and negative in the South (source: Mátyás and Nagy 2005).

system of the species, the evolutionary-migratory past, and regional or local site 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 distribu-

tion range despite the speed of predicted change. Improved growing conditions can be utilized through the plasticity potential of tree populations, without much selection. As inherited plasticity will determine the response to change, there is little room left for genetic adaptation. In the temperate-Atlantic Europe zone, 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 for-

ests. 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 mortality 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.

Response of communities

Studies on quantitative genetic variation patterns and adaptive response indicate significant differences between species' reactions—a result of differences in their genetic systems and evolutionary history. Therefore, potential distribution areas of different species will not shift uniformly. A corollary is that changing climatic conditions will generate communities not identical with the present ones. The coupled grave effect of changes in fauna and flora of forest ecosystems are not discussed here as this question is well covered by literature on species biodiversity change and conservation.

Effect on ecosystem carbon balance

Expected warming also affects the functioning of the forest ecosystem as

a carbon sink. Increased drought frequency leads to growth decline and the quantity of sequestered carbon decreases. Simultaneously, the decomposition rate of dead organic matter accelerates, causing additional carbon release into the atmosphere. In areas favourably affected by temperature increase, growth acceleration leads to higher yields, as observed already across Western Europe (Kramer and Mohren 2001). Closer to the boreal limit, however, the carbon balance might turn strongly negative because of accelerated decomposition rates.

Consequences for forest management

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 towards maintenance of ecological functions and conservation of stability and of genetic resources.

Thus, considering the long regeneration cycle of trees, the pace of the predicted climate change will be too swift to permit sufficient time for proper genetic adaptation of tree populations. A temperature shift will in any case negatively affect a large part of the area of a species' distribution. At low elevations and in the southern outliers of distribution areas, close to the lower (xeric) limit of the species, temperature increase will certainly lead to the thinning out and local extinction of the species.

At the northern limits, temperature increase will bring an improvement in site conditions. This offers the theoretical possibility of a migration advance for the species, as often modelled in climate scenarios. However, even in the long term, the utilization of climatically improved zones outside the present forest limits will be constrained 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. Consequently, contrary to general belief, high altitude and high latitude site potential will not immediately follow the improvement in climate.

It can be concluded that mitigation policy cannot rely on natural self-regulation and acclimation of ecosystems. Tasks are imminent both in forest management and in conservation of genetic resources. The two areas are closely linked by our knowledge of the genetics of forest trees, which provides the

basis for action. As a consequence, human interference will be essential for the maintenance of adaptability under changing conditions, not only in the present distribution range of the species, but also to extend the ranges of species at the northern peripheries of their distribution. This will be especially the case in the boreal zone, where possible temperature increases might be considerably higher than at medium latitudes (See Box 2).

Conclusions: tasks for mitigation

In general, in the core distribution area of widely dispersed tree species with effective gene flow, there is still no emergency for preparatory measures if the stands have been properly managed and regenerated. Active preparatory measures should have priority in the case of rare, fragmented tree species with limited or impeded dispersal ability. Species occupying extreme habitats should also receive special attention (see Box 2.).

Box 2. Urgency of preventive action: species characteristics to be considered

Low urgency	High urgency
Continuous distribution	Fragmented, isolated distribution
High density	Small populations
Naturally regenerated	Artificially regenerated
Effective gene flow	Limited replenishment of gene pool
Spontaneously spreading	Low dispersal capacity
Extensive, zonal habitats	Extreme sites as habitats
Reproduction unaffected	Disturbances in flowering and seeding

However, even major, widely distributed tree species need special consideration in the following situations:

- where there are isolated populations on the southern or continental fringes of the distribution area;
- where there are isolated mountain populations with no 'reserve altitude';
- in locations where conditions in the potential colonization area are unsuitable (high alpine or boreal conditions);
- where the areas were regenerated with reproductive material of obviously low adaptability; and
- where there are populations with high phenotypic plasticity.

Populations at the southern or continental distribution limits are threatened in particular due to strong productivity loss, i.e. weakened competitive ability and hindered sexual reproduction (Mátyás 2000). Investigations have shown that changes in climatic conditions may affect reproduction processes, which may influence regeneration and dispersal ability of the species. In addition to decline in fructification and higher mortality of mature trees, low regeneration success and high interspecific competition (especially with shrubs and weeds) demand additional efforts to maintain genetic diversity and adaptive potential. In the case of seriously threatened minor tree species and valuable populations, active gene conservation measures will be necessary through evacuation or transfer to gene banks. At the same time, the maintenance or reconstruction of

non-adaptive, random allelic frequency patterns is less pressing. A typical example of this would be the maintenance of random, non-adaptive geographic variation patterns due to colonization, such as detected for European white oaks (Petit et al. 2002).

Mitigation priorities

When deciding on priorities in conserving and utilizing climatically threatened genetic resources of tree populations, genetic information on adaptability should be used, if available. There is a generally accepted approach to judging adaptability, based on genetic diversity at biochemical or molecular level. Much of recent evidence indicates, however, that inference based on quantitative genetic characteristics, such as phenotypic plasticity and adaptedness on the basis of molecular genetic parameters, is at present unreliable. Therefore, adaptively important, quantitative traits should receive at least as much attention as molecular genetic diversity. For the quantitative assessment of these traits, field experiments are indispensable and will remain so for the coming decades.

Forest management

Climate change mitigation is a newly emerging aspect of regulating the use of forest reproductive material. The present guidelines usually leave this aspect unconsidered in most countries. Rules and guidelines should be reconsidered in the

light of recent research findings. The general need to reconsider regulations should be utilized as an opportunity to reach flexible, effective, genetically sound, continent-wide guidelines that derive from generally accepted principles. To reach consensus on these questions should be an eminent task for the coming years.

Artificial support for migration, i.e. guided transfer of identified provenances and preferring populations exhibiting plasticity, offer probably the most efficient possibilities for mitigation through proper use of forest reproductive material. Among the possible silvicultural management options, the most efficient interference is the proper selection of tending measures in threatened regions by regulating species mixture, canopy closure and stem density in order to improve stability. Genetically, supporting effective gene flow by selecting proper natural regeneration techniques might be sufficient in the mildest cases of climatic threat. When planning silvicultural mitigating strategies, tasks in natural and anthropogenic forests have to be considered separately.

Conservation of forest genetic resources

There is a strong need to put into practice the principles and guidelines of gene conservation that have been formulated as a Europe-wide common effort under the auspices of EUFORGEN. This calls for cooperative action irrespective of national boundaries.

Research

The challenge of environmental instability introduces new dimensions for forest genetic research and demands a review of current research priorities. It points towards more efforts to elucidate natural selection processes and regulation of phenotypic responses. Both continent-wide international collaboration and trade opportunities for forest reproductive material have developed enormously following the political and economic changes in Europe in recent years. For the use of forest reproductive material, this means new challenges, both positive and negative. Scientific collaboration through international research networks must deal with these changing challenges and find proper answers. In parallel, there is a need to review results of common-garden tests established during the last century and to identify gaps in our knowledge, with the aim of agreeing on new, complementary test networks to provide a solid foundation for future use of reproductive material.

Need for a common plan of action

The fundamental basis of adaptability is the genetic variability inherent in natural tree populations. Climate change research results indicate that, because of the conservative nature of the genetic adaptation process, and the relative speed of expected change, even agricultural crops will demand a strategy to facilitate adaptation. Long-lived, immobile organisms, such as trees, will

especially need human interference, in spite of an impressive adaptation capacity. To counteract genetic erosion and extinction, populations and outliers along the southern (or low-elevation) limits of species' distribution areas will need special attention.

Through international cooperation, guidelines for adaptive silviculture and for the use and transfer of forest reproductive material have to be adjusted in the face of climate change. The tasks and principles described have to be incorporated into the agenda of national forest programmes. To elaborate genetically sound guidelines, strengthening of field experimentation should be promoted. In a period of scarce financial support for this, efforts should be joint and based on international cooperation and sharing of responsibilities.

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