The role of biodiversity in forest ecosystems and for sustainability

# Genetic diversity in forest trees – its importance and potential human impact

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# Introduction

At present, humanity faces significant environmental changes. Worldwide, forests are declining at unprecedented rates. This loss is primarily due to human population growth, which, in the last 50 years, has doubled and is predicted to reach its peak – approximately 9 billion – in 2050 (UN/ESA 2001). The population growth exerts pressure on forests for agricultural purposes and/or fuel-wood consumption. According to the FAO (1999) the global net annual loss was 112,600 square kilometers for 1990–95. While population growth is of great concern in the less developed countries, developed countries are largely to blame for drastic changes in global climate as a corollary of steady growth of industrialization. Recent evidence shows that the 20<sup>th</sup> century was the warmest in the last 1000 years, especially due to emission of CO<sub>2</sub> and other greenhouse gases (IPCC 2000). Without doubts biotic impoverishment is an inevitable consequence when humanity continues to misuse natural resources (SISK *et al.* 1994).

This contribution will firstly and briefly describe why genetics is important for the stability of forest ecosystems [for a more detailed view see GREGORIUS (1996)]. Secondly, information will be compiled how humanity has affected genetics in forest trees during ancient and recent times. Among others, LEDIG (1992), MÁTYÁS (1999, *loc. cit.* Chapter 5) and JENNINGS *et al.* (2001) have reviewed this issue in depth. Often, direct cause-effect relationships are difficult to discern, as there may be complicated or a cascade of effects. Also, various influences – both anthropogenic and natural – may interact, enhancing the impact and complicating the interpretation. Polygenic inheritance and the fact that certain traits are only expressed after several years of growth under field conditions complicate genetic comparisons. On the other hand, genetic markers provide some insights into the evolution of forest tree species by studying natural populations. Increasingly, the field of forest genetics is benefiting from genomics and the ability to analyse more accurately the genome via fine linkage mapping, genome sequencing and patterns of differential multiple gene expression (see p. 369 ff., this volume). But this area is still in its infancy and data are not yet available for

European forest tree species and both quantitative and population genetics come up against limiting factors. Therefore, the reader should have low expectations awaiting unequivocal evidence rather educated guesses can only be provided in most cases.

#### Forest ecosystem stability and its genetic component

The stability of an ecosystem depends (1) on the ability to avoid displacement from its present state by a disturbance (resistance) and (2) on the speed with which the ecosystem returns to its former state after it has been disturbed (resilience). Since the fifties of the late century, ecologists have debated whether diversity breeds stability. The theory, simplified, is that communities with few species are less stable than complex or more diverse ones (see p. 477 ff., this volume). Furthermore, temporal and spatial variation or species interactions are discussed in this context. However, variation within species is scarcely considered although genetic diversity is accepted as prerequisite for adaptational processes in general (for review see PIMM 1984)

The integrity of open dynamical ecosystems by keeping the material, energy and information well balanced while constantly influenced by external forces of the abioceon are achieved by adaptation. Hence, the forest ecosystem's state depends both on internal and external forces. Certain external inputs into the biocoen or internal forces evoke adaptational demands to which the biocoen – or to be more precise – the population constantly reacts through state alterations which in turn are outputs to the adaptational demands (Fig. 1). Since the population cannot instantly react due to genetic stolicity or the adaptational reaction may be further slowed down by environmental dichotomy (LEVINS 1968, *loc. cit.* p. 12, GREGORIUS & KLEINSCHMIT 1999), the output seldom if ever matches the adaptational demands.

While material and energy balances are frequently defined as important components for the integrity of ecosystems, the information balance has only a vaguely defined meaning. However, the information balance must be recognised as a prerequisite for the integrity of ecosystems because they control material and energy flows. As GREGORIUS (1996) has put it: 'Adaptation of these flows to variable external conditions is among the most fundamental tasks of such control. On the one hand, variability of the information controlling the adaptational processes is thus indispensable. On the other hand, a certain degree of constancy of this information is required in order to guarantee consistency of adaptational processes. Apparently, this information must be of a biological nature, and has its material basis in the hereditary substance DNA (or RNA in some cases), as is well known. The implied temporal continuity of this information is realizable only within populations, the genetic systems of which organize the information balance.'

Therefore, the ability of tree populations to adapt to environmental changes is the basis for the stability of forest ecosystems. Forest tree species can adjust to environmental signals through only three mechanisms:

(1) *Physiological adaptation*. The organisms adjust to a new environment through internal self-regulating mechanisms. If the individual tree carries many different alleles (*i.e.*, has a high degree of heterozygosity) it can better buffer against fluctuating environmental conditions.



**Figure 1.** Adaptational processes in an open dynamic system: Inputs required by environmental conditions determine adaptational demands and trigger systems reactions via mediation of the system's state. Different degrees of adaptedness of the output (open arch) and the systems reactions (ellipse) are indicated by different fits of the symbols [from GREGORIUS (1996), redrawn].

(2) *Epigenetic adaptation*. This heritable adaptation that is not based on classical (Mendelian) rules. Epigenetic adaptation may be triggered by environmental signals, may regulate gene expression over generations and may have long-lasting effects. Mechanisms similar to genomic imprinting are presumed to exist in forest trees.

(3) *Collective (= evolutionary) adaptation*. The population adjusts its genetic composition by eliminating those individuals (*i.e.*, through natural selection) that have exceeded their physiological adaptive range. The range of collective adaptation is determined by the extent to which the gene pool can respond to environmental factors (see p. 199 ff., this volume).

In all three mechanisms, genetic diversity plays a key role: without genetic diversity, all adaptational processes are inconceivable. However, it is still debated among geneticists how much genetic diversity is needed for the long term existence of populations (for review see BOOY *et al.* 2000).

Compared to other plants, forest tree species are genetically highly variable and exhibit comparably less genetic diversity among different populations, although only generalisations are possible until genome-specific data are available (HAMRICK *et al.* 1992). Clearly this pattern is strongly influenced by the breeding system. The genetic diversity of predominantly selfed, monocotyledonous species is generally much lower, but the among-population component is much higher than in European forest tree species that are mainly outcrossing and wind-pollinated.

# Potential threats to genetic diversity

# Deforestation and fragmentation

In reviewing European history, a close connection is apparent between cultural development and deforestation; the contemporaneous fall of ancient society and environmental ruin have been inescapable. Consciously or unconsciously, directly or indirectly, humans have changed forests in size, composition and in dependence on climatic conditions. This has led to so-called secondary forests or, in worse cases, to total deforestation. Utilizing forest genetic resources for fuel and timber, and clearing forests for agricultural crops, domestic animals and human dwellings have altered the gene pool of many forest tree species (for review see CHEW 2001). Certainly a major threat has been deforestation. Classical writers have reported that in Ancient Times deforestation was widespread and severe. It has been recorded that it was difficult to find suitable timber for construction, shipbuilding or war material and that timber sources were generally bound to inaccessible locations in mountainous regions. In the Mediterranean region, names such as Elatea (= Firtown), Pityossa (= Pineville) and Xylopolis (= Timber City) still remind us of locations where formerly forests were found, while today barren land or only traces of forests remain. Generally, destruction began close to villages, urban areas, or mining sites, and forests were pushed back to hilly or secluded regions. This process has not been limited to Ancient Rome or Greece but is also found more recently in other parts of Europe. For example, whereas Scots pine (Pinus sylvestris L.) forests in Scotland are mentioned in historical documents, these forests have disappeared since the 17<sup>th</sup> century due to grazing and burning culminating in the huge demand for timber imposed by the Napoleonic wars (STEPHEN & CARLISLE 1959); it is speculated that the difficult timber extraction in more inaccessible glens has saved remnant, scattered populations that cover less than 11,000 hectares (GOODIER & BUNCE 1977). Although baseline data are missing for the undisturbed Caledonian Scots pine, allozyme and monoterpene studies showed that the genetic diversity is still high compared with continental populations and also an assessment of morphological data supports the hypothesis that the extinction of Scots pine in large parts of its former range in the British Isles has not caused a serious impact on the genetic diversity (KINLOCH et al. 1986). However, in many cases local populations are eliminated and certain species are even driven to extinction such as Sicilian fir (Abies nebrodensis [Lojac.] Mattei), which is listed as critically endangered on the IUCN red list (http://www.redlist.org) and is today only found on Monte Cervo, Monti Nebrodi, Monte Scalane and Polizzi Generosa in Sicily (Italy). Unexpectedly, high estimates of genetic diversity in the relic Sicilian fir were found compared to Abies alba Mill. based on allozymes, terpenes, and different types of DNA markers (VICARIO et al. 1995).

Today, it is very difficult to assess the extent of deforestation and it is even more complicated or even impossible to estimate the extent to which genetic diversity of forest tree species has been affected. Moreover, deforestation is accompanied by fragmentation, habitat alteration and very often transfer of forest reproductive material and it is practically impossible to differentiate among these factors. Of course, it is selfevident that, in cases where a species has become extinct, its complete gene pool is lost, while its gene pool is 'only' altered when local populations were destroyed. LEDIG (1992) tried to estimate the effects of deforestation in ponderosa pine (*Pinus ponderosa* Dougl.). This widely occurring North American pine varies significantly along altitudinal gradients in California as evidenced by field studies. If the genetic variance for the trait height growth is divided by the length of the gradient, then roughly 2 % of the total genetic variation is associated with every 100 m change in elevation. Comparing actual elevation distribution with historical records shows that in many areas ponderosa pine has been moved upslope. Extrapolation suggests that locally 6 % of the original genetic diversity has been lost where chaparral has replaced the pine forest in the lowland. In Europe, the natural alpine timber line is supposed to be approximately 250 m lower than under non-anthropogenic influences (KRAL 1971. *loc. cit.* p. 130). Estimates of how genetic variation is distributed along the elevation gradient are not available, but it is very plausible that also forest tree species in this region have lost some of their genetic variation.

The genetic impact of deforestation depends strongly on the natural population structure. In the simplest structure, all trees form a single, large, randomly mating population. While certainly forest tree populations do not mate randomly in a strict sense, there are genetic patterns that come close to this simple type. Other natural structures include the main-satellite type where some peripheral populations exist which benefit from gene flow from the main population. Genetic diversity may differ among satellite populations as well as between a satellite and the main population. A more complex pattern is that of a group of isolated populations that do not significantly exchange genetic information. Island populations may be of varied size. Swiss stone pine (Pinus cembra L.) (with the exception of Pinus cembra var. sibirica [Du Tour] Loudon) – a species that exists in several disjunctive small populations in the Alps, northern-eastern, eastern and southern Carpathians - exhibits this island structure. Also many pioneer species have a scattered distribution and often must create new founder populations from few individuals which leads to a more ecotypic variation pattern (REHFELDT & LESTER 1969). Deforestation has probably a higher genetic impact on these species than on species with a more clinal genetic pattern such as *Pinus sylves*tris or Picea abies (L.) Karst.

If the natural genetic pattern is unknown and losses through deforestation cover a range of different climatic conditions, genetic impact is certainly severe. Usually the climate is a much more important selective factor than edaphic or biotic conditions. This must be also taken into account when deforestation is assessed in mountainous regions because of the strong environmental (climatic) gradients.

Deforestation has often also led to fragmented forests, leading to reproductively isolated populations (YOUNG & BOYLE 2000). When those populations are small, inbreeding and (perhaps even more important) stochastic effects may finally extirpate local populations. The same fragmentation process has different effects depending on the natural population structure as described above.

In their simplest form, fragmentation effects resemble genetic sampling effects. The change in gene frequency is random in the sense that its direction is unpredictable, but its magnitude is predictable in terms of the variance of the change. Thus, the variance

of the change of the gene frequency  $(\sigma_{\Delta p}^2)$  depends on the gene frequency (p) and on the local population size (N), as follows:

$$\sigma_{\Delta p}^2 = [p(1-p)](2N)^{-1}$$

Hence, the smaller the population size and the more extreme the gene frequency, the higher the probability of a genetic change simply resulting from the dispersive process. An approximation of the amount of genetic variation (heterozygosity *H*) that remains following a reduction of a large population containing *N* individuals after *t* generations is  $H_{t} = \begin{pmatrix} 1 \\ 1 \end{pmatrix} t$ 

$$\frac{H_t}{H_o} = \left(1 - \frac{1}{2N}\right)^2$$

While heterozygosity is less affected by a reduction, rare alleles fare worse. The expected allelic richness (number of alleles) a remaining in the population of the effective size N is

$$E(a) = \sum_{i} (1 - (1 - p_i)^{2N})$$

where  $p_i$  equals the frequency of allele *i*. Allelic structure can suffer seriously from bottlenecks. Experimental studies examining the change of genetic variation due to bottlenecking cannot be performed in long-lived forest trees. But in organisms with shorter regeneration cycles field experiments can be carried out supporting the abovementioned expectations (*e.g.*, LEBERG 1992). In forest trees species fragmentation effects can be concluded from genetic differences among different sized populations. Such experiments were conducted, for instance, in bog pine (*Halocarpus bidwillii* [Hook. f. ex T. Kirk] Quinn) (BILLINGTON 1991) and white box (*Eucalyptus albens* Benth.) (PROBER & BROWN 1994) (Fig. 2). Very severe bottlenecks as typical for many wild populations can be even inferred from allele frequency data in remnant populations (LUIKART & CORNUET 1998, LEDIG *et al.* 1999).

It must be noted that only effects at single loci are considered so far and losses of quantitative genetic variation, which are particularly important for adaptive traits, are difficult to estimate. To the best of the author's knowledge, fragmentation effects have not been investigated on quantitative traits in forest trees.

Fragmentation also increases demographic stochasticity. Genetic diversity at the among-population level may be increased, particularly when the number of migrants per generation is very small ( $N_em << 1$ ) (WRIGHT 1931). But normally, gene flow (via pollen and seed) among populations of forest tree species is high and as a result genetic neighbourhoods tend to be large. The result is that, following severe fragmentation, remnant populations may be smaller than pre-fragmented genetic neighbourhoods. Thus, the potential to maintain the original genetic structure depends on the ability of pollen and seeds to cross deforested zones. This potential is probably high because most European forest tree species are wind-pollinated and

anemochoric and long transfer of pollen and seeds are typical (see p. 171 ff., this volume).

#### Exploitation

Humans have selectively used forest resources by skimming (or 'high-grading') populations when the tallest, biggest or highest-graded trees have been removed. Changes of the genetic composition are inevitable but are subtle. In principal, the genetic loss produced by dysgenic selection depends in a qualified manner on:

(1) the selection differential which is the selection truncation; and

(2) the (narrow-sense) heritability of the traits [*i.e.* 



**Figure 2.** Relationship between genetic diversity measured as allelic richness (mean number of alleles per isoenzyme locus) and remnant population size in the bog pine (*Halocarpus bidwillii* - open symbols) and in white box (*Eucalyptus albens* - full symbols). [Data for bog pine are from BILLINGTON (1991) and for white box from PROBER and BROWN (1994)].

the contribution of the (additive) genetic effect to the phenotypic variation].

The expected (mean) change in trait value of progeny in the next generation (R, selection response) equals the selection differential (S) times the heritability ( $h^2$ ) of the trait:

 $R = Sh^2$ 

From this relationship, it can be easily deduced that genetic effects (R) from one generation to the other will be small if only the very best trees will be removed from the forests and/or the trait is less genetically controlled, *i.e.*,  $h^2$  is small. Otherwise, if only culls are left following a harvest and if heritability is high, genetic effects can be very high. In fact, the more trees harvested (and thus, the less demanding the loggers with respect to what they cut), the more rigid are the effects per generation, *i.e.* dysgenic selection is high (Fig. 3).

Although estimates of heritabilities vary with species, populations within species, families within populations, and age following compilation of different traits in *Picea abies* may be used for some guidance (Table 1). Rather than providing exact values the order of magnitude is important. It is obvious that the data of different experiments which in a strict sense cannot be compared often resulted in high estimates especially based on phenology or related traits.



**Figure 3.** Expected genetic loss when populations are selectively used. When only the very best trees are utilized, genetic losses are supposed to be small. Conversely, when the majority of trees are harvested, leaving only a small number of culls, genetic effects are much more pronounced in the next generation [from LEDIG (1992), redrawn].

Table 1. Heritabilities (broad-sense) in Norway spruce compiled according to different studies cited in SCHMIDT-VOGT (1986, *loc. cit.* p. 232) and after SCHOLZ *et al.* (1979).

Trait	Heritability
Tree height	0.30-0.95
Stem diameter	0.60-0.71
Wood density	0.56-0.84
Flushing	0.56-1.00
Resistance (late frost)	0.98
Resistance (fluorides)	0.60

However, even when estimates of heritabilities are intrinsically problematic and selection intensities over generations remain vague or are not available, some lessons can be learned from history. For more than 5,000 years, people of the Middle East used only the tallest and straightest trees of the Lebanon cedar (Cedrus libani A. Richard) for shipbuilding and construction. If moderate heritabilities are assumed for these traits, only minor effects per generation are estimated. However, small effects have

accumulated over many generations since timber of Lebanon cedar was highly demanded. Already Alexander the Great (333 A.D.) was forced to transport the wood for his fleet from the Anti-Lebanon, a mountain range located in southwestern Syria and eastern Lebanon. Today, this species is limited to a total of approximately 2,000 hectares, a far cry from its previous extent of 500,000 hectares in Lebanon (AYASLIGIL 1997). As a result of this overexploitation, only small patches of cedar forests with mostly crooked stems and long branches were left behind (MAKKONEN 1967). Over the long term, genetic impacts on Lebanon cedar have been significant. Similar effects are expected also in more recently affected European forests, for example with *Pinus sylvestris* in Scandinavia. For several centuries, harvesters have cut the tallest trees close to waterways. Today, negative effects of this harvesting practice are still seen along the most heavily used streams used for wood rafting in Sweden (LINDQUIST 1946). Damaged trees, trees with poorly shaped stem forms or spiral growth or very big (at that time usually difficult to cut) trees were not used. This has probably affected the genetic composition within a species.

#### Habitat alteration

Due to anthropogenic influence, the natural habitat for certain forest tree species has been significantly modified. For example, alteration of the riparian ecosystem across the natural range of black poplar (*Populus nigra* L.) took place in the past. With hydraulic engineering, native poplar stands were displaced by agriculture and other human activities. Black poplar was deliberately removed from flood plains forest near 1900 because of its poor wood quality, and hybrid poplar replaced indigenous poplar populations. Moreover, in the still untouched regions, the regulation of the water level avoided flooding which favoured the succession of poplar stands by hardwood forests.

In contrast, some forest tree species have been favoured by human activity. In the European Alps, for instance, the distribution of European larch (*Larix decidua* Mill.) has been significantly increased within its natural range. For dairy farming, original native forests have been selectively cut with the exception of larch trees, resulting in low-densely stocked pure larch stands, called larch meadows (*i.e.*, 'Lärchenwiesen') (Fig. 4). Larch trees were used for timber production and also for seed production (because of the ease of seed collection) during the 'larch fashion' in the 18<sup>th</sup> and 19<sup>th</sup> centuries (MÜNCH 1936a).

On a global scale, the transfer of different organisms is presumably the most significant anthropogenic influence on the habitat. Insects, fungi and plants have been moved around the globe for centuries, and have affected selection, genetic drift and the reproductive pattern of numerous organisms. In natural forest ecosystems host and pathogen populations have often co-evolved resulting in dynamic host-parasite interactions. Examples in North America include *Rhabdocline pseudotsugae* H. Sydow needle cast in Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) (STEPHAN 1973), *Cronartium ribicola* J. C. Fischer blister rust in five-needle pines (MILLAR & KINLOCH 1991) or Chestnut blight by *Cryphonectria parasitica* (Murrill) Barr (BRASIER 1990). In Europe, introductions of new pathogens have also changed the gene pools of indigenous tree species. For example, elm (*Ulmus glabra* Huds. emend. Moss) cannot be used for timber production in many regions due to the Dutch elm disease (DED). Although this disease has not resulted in extinction yet, DED has eliminated elms



**Figure 4.** Larch meadows ('Lärchenwiesen') have been the result of dairy farming in the European Alps. With the exception of larch trees, all other woody species were harvested. Larch trees were used for timber and seed production and provided shade for livestock. In certain areas of Alps, distribution of *Larix decidua* was significantly increased [photo taken from MÜNCH (1936a)].

from forests and it is very difficult to forecast how the artificial host-pathogen relation ship will develop. Before 1900, DED was unknown in Europe. It first appeared in the north-western region around 1910 and forestry has faced two pandemics during the last 100 years (BRASIER 1996). For more details on host-pathogen interactions see STEPHAN and GEBUREK (p. 477 ff., this volume).

Certainly, island flora have been imperilled from introduced invasive plants and animals as the modified flora of Galapagos Island (MAUCHAMP 1997) or Hawaii (MOULTON & PIMM 1986) clearly demonstrate. Feral goats and pigs - often liberated already in the 18<sup>th</sup> century on islands as a naval tradition to provide food for sealers, whalers or shipwrecked mariners - are now regarded as pests and threaten endemic populations. While in grassland/shrub habitats a dynamic equilibrium may be reached between released-animal populations and native vegetation, effects in forest ecosystems may be long-term and potentially catastrophic. Forests may be completely destroyed and replaced by grassland or barren ground if ungulates prevent natural regeneration. In Europe, translocation of wild ungulates was less severe but has been locally of significance. Probably most detrimental was the introduction of mouflon (Ovis musimon Pallas) - indigenous in Sardinia and Corsica into central Europe since baroque periods (ULOTH & PRIEN 1985). Due to its feeding and gregarious behaviour, this species has partly extirpated highly adapted plant populations, for instance in precipices in Austria (W. RUHM, pers. comm.). While uncontrolled browsing of ungulates have not threatened forest tree species in Europe, the ill-advised release of ungulates has driven species or subspecies close to extinction elsewhere. For instance, Pinus radiata var. binata (Engelm.) Lemmon which occurs naturally on the Isle of Guadalupe is uniquely resistant to Dothiostroma septospora (Dorog.) Morelet (COBB &

LIBBY 1968) and *Endocronartium harknessii* J. P. Moore (OLD *et al.* 1986). As mentioned by LEDIG (1992) this variety was reduced from 383 (census 1968) to only 45 individuals (census in 1988) due to ungulate browsing.

Nowadays human activities strongly alter the habitat through environmental pollution. Pollution is a multi-faceted issue which additionally stresses forest tree populations and which has contributed to forest decline in Europe and other regions for many years (BUSSOTI & FERRETTI 1998, see also p. 111 ff., this volume). Genetically, environmental deterioration has three important implications:

(1) Evolutionary rates under environmental stress may differ from a pollution-free environment. Experimental evidence suggests that a combination of high genetic variability of ecological, physiological and morphological phenotypes, high rates of mutation and recombination, and some protection from stress through shock proteins could collectively trigger an accelerated evolutionary change. Ultraviolet-B (UV-B) radiation may serve here as an example. The release of chlorofluorocarbons has decreased the Earth's protective shield against UV-B and genomic alterations must be assumed (KARNOSKY *et al.* 1999 and references cited therein).

(2) Genetic differentiation is a significant determinant of adaptive potential and thus has implications for ecosystem resilience. Evolutionary rates may not be fast enough to counteract severe genetic erosion.

(3) Diversity in managing forests, for example, a shift towards more tolerant species, causes additional habitat alterations.



**Figure 5.** Environmental pollution affects the gene pool of forest trees in a manifold manner [from GEBUREK (2000), modified].

Genetic variation is the pivotal point which may be affected during different developmental stages (Fig. 5).

In most forest tree populations, differences in resistance to gaseous and non-gaseous pollutants exist. Generally, slow-growing and genetically highly variable populations seem to be less affected than fast-growing and genetically less variable populations. Expectedly, intraspecific variation in resistance to pollutants increases from the population to the family level and is highest among single individuals. Generally, heritabilities are high and, in combination with severe selection pressure, result in comparably fast changes in genetic composition. Under field conditions, pollutioninduced genetic alteration has been detected both by marker studies as well as in



**Figure 6.** Pollution-induced injuries in two seed collections (1955 and 1964/66) of *Pinus strobus* exposed to high pollution in the field trials. For more details see text [based on data from KRIEBEL & LEBEN (1981)].

common-garden experiments (for review see GEBUREK 2000).

That evolution through pollution has taken place is nicely demonstrated by an eastern white pine field study. Seeds of Pinus strobus L. were harvested in 1955 from high-pollution localities in the U.S. States of West Virginia, Georgia, and Ohio. All seedlings were planted in a heavy-polluted region in northern Ohio. A second seed collection was done in 1964/66 after seed stands have been approximately exposed for 10 years. Pines of the second seed collection showed significantly less pollution symptoms (Fig. 6, KRIEBEL & LEBEN 1981).

# Today's forestry

In today's forestry, tree populations are mainly genetically altered through regeneration and stand treatment. The question how forests are to be regenerated and which reproductive material is to be used is of prime importance. Genetic effects are manifold both when forests are regenerated naturally or artificially and many authors have discussed this issue (*e.g.*, SAVOLAINEN & KÄRKKÄINEN 1992, GEBUREK & THURNER 1993, MÜLLER-STARCK *et al.* 2000).

# Natural regeneration

When forests are regenerated naturally, the number, spatial distribution of mating trees and their selection mode, flow of pollen and seeds including wanted and un-

wanted flux from outside sources, and finally time and duration of regeneration are important. Hence, different forms of natural regeneration such as strip cutting, shelterwood cutting, group selection felling, selective silvicultural system, selective logging (target cutting), and close-to-nature silviculture will have different genetic effects.

One of the most comprehensive studies comparing naturally regenerated and planted forests was conducted by MACDONALD *et al.* (2001) in North America. She and her co-workers compared 57 populations of *Pinus contorta* Dougl. ex Loud. differing in history. Stands both regenerated naturally after fire or commercial harvest exhibited significantly higher heterozygosities and allelic richness than stands that were planted after harvest. This finding is in line with observation in Europe where the genetic diversity in *Picea abies* stands from artificial regeneration was slightly smaller than in naturally regenerated ones (GÖMÖRY 1992).

Silvicultural systems that enhance natural regeneration often encompass a reduction of mature trees. In severely fragmented forest stands, inbreeding may be due to either increased self-pollination or mating among consanguineous trees through more recent common ancestry in fragmented populations. But empirical data showing increased inbreeding following forest management are very limited. Knowledge is restricted as to how population density affects outcrossing rates (Table 2).

Forest tree species	Outcrossing in low stand density	Outcrossing in high stand density	Reference
Abies amabilis	.637	.737	El-Kassaby (1999)
Larix laricina	.537768	.908	KNOWLES <i>et al.</i> (1987)
Larix occidentalis	.876	.903	El-Kassaby & Jaquish (1996)
	.912	.793	
Picea abies	.956	.955	Morgante <i>et al.</i> (1991)
Pinus attenuata	.860	.914	BURCZYK <i>et al.</i> (1997)
Pinus caribea	.894	.984	Zheng & Ennos (1997)
Pinus ponderosa	.850	.960	Farris & Mitton (1984)
Pinus jeffreyi	.949	.971	Furnier & Adams (1986)
Pseudotsuga menziesii	.950	.880	Neale & Adams (1985)
	.930	.920	· · ·

Table 2. Influence of forest stand densities on outcrossing rates in some selected conifers.

Simplifying, the more individuals that are effectively involved over time and in space (belonging to different demographic cohorts) and the lesser gene flow from outside sources, the smaller the genetic distance between the stand to be regenerated and the next generation will be.

If the mating system is only little affected, then genetic differences between adults and natural regeneration should be also negligible or small for the same type of (neutral or semi-neutral) marker. Several comparative allozyme studies between adult trees and young seedlings indicate that genetic differences are non-existent or not palpably (Table 3).

Expectedly no differences in heterozygosity between adults and understorey were found. Since most natural regenerations result from a limited number of mates, effects – if any which are detectable by this type of marker – should be rather detected by allelic richness since this parameter is much more sensitive when the effective population is reduced. But even when this more sensitive measure is used, differences were very small at isoenzyme loci. More recently highly informative DNA markers were used in a comparative genetic study in *Eucalyptus sieberi* L. Johnson. While in the managed population the expected heterozygosity based on 10 restriction length polymorphisms and 2 microsatellites was only slightly smaller than in the unharvested control (.476 vs. .486), 9 % of allelic richness of the parental generation was lost in the regeneration (GLAUBITZ *et al.* 1999).

#### Artificial regeneration

Since the invention of artificial seeding in the 14<sup>th</sup> century and its dissemination through NOE MEURER's (1582) book on hunting and forest rights, forests have been widely regenerated by human activities. Artificial regeneration can very effectively affect forest genetic resources during sampling of seed trees, harvest techniques, and the processing of forest reproductive material. Special attention must be paid for the origin of the seed source, since reproductive material has been very often translocated across wide distances. Furthermore the mode by which artificial stands are established either by seeding or planting are important. Last but not least, human impact on the gene pool of forest trees also depends on whether clonal material is used and in extreme cases if genetically modified planting stock would be commercially used.

# Artificial regeneration: origin of forest reproductive material

To serve early industrial activities in Europe, especially salt production and ore mining, extensive forest areas were harvested and later artificially regenerated by planting or sowing. Since the early 19<sup>th</sup> century, artificial seeding and planting became common in whole Europe and soon required reproductive material in great quantities irrespective of its origin. First introductions of European larch (*Larix decidua*), for example, date back to the 15<sup>th</sup> century, but probably were not significant before the transition from the 16<sup>th</sup> to 17<sup>th</sup> century. From 1680 to 1750, larch seeds were imported to Bavaria from sub-montane locations in southeast Carinthia (southern periphery of the Central Alps). Especially in eastern and north-eastern Germany, larch seeds were nearly exclusively used from nearby sources in the Sudeten and Upper Silesia (today a southernwestern region of Poland) until the first half of the 19<sup>th</sup> century. Many of the early

Forest tree species	Heterozygosity in adult trees <i>vs.</i> offspring	Allelic richness in adult trees <i>vs.</i> offspring	Reference
Abies alba <sup>1</sup>	.229 / .234 .230 / .237 .214 / .214	1.87/1.87 ª 1.94/2.00 ª 2.28/2.21 ª	Müller-Starck et al. (2000)
Abies amabilis <sup>2</sup>	.085 / .071	2.1 / 2.2 ª	El-Kassaby (1999)
Fagus sylvatica <sup>1</sup>	.290 / .273 .267 / .253 .281 / .287	31 / 30 <sup>b</sup> 26 / 25 <sup>b</sup> 23 / 25 <sup>b</sup>	Starke (1996)
Larix decidua <sup>1</sup>	.155 / .156 .172 / .167	2.33 / 2.60 ª 2.33 / 2.27 ª	Müller-Starck <i>et al.</i> (2000)
Picea abies <sup>1</sup>	.197 / .185 .189 / .167 .199 / .194 .192 / .193 .202 / .190	2.35 / 2.22 <sup>a</sup> 2.35 / 2.47 <sup>a</sup> 2.30 / 2.39 <sup>a</sup> 2.26 / 2.39 <sup>a</sup> 2.22 / 2.13 <sup>a</sup>	Müller-Starck <i>et al.</i> (2000)
Pinus sylvestris <sup>1</sup>	.469/ .441	27 / 23 °	YAZDANI et al. (1985)
Pinus mugo <sup>1</sup>	.236 / .246	3.33 / 3.11 ª	MÜLLER-STARCK et al. (2000)
Pseudotsuga menziesii <sup>1</sup>	.211 / .180 .200 / .210 .197 / .190	24 / 22 ° 25 / 24 ° 2.86 / 2.76 ª	Neale (1985) Adams <i>et al.</i> (1998)
Tsuga heterophylla²	.093 / .109	2.0 / 2.4 ª	EL-KASSABY (1999)

Table 3. Heterozygosity and allelic richness in adults *vs.* their naturally regenerated offspring in some selected tree species based on allozyme studies.

<sup>1</sup> observed heterozygosity, <sup>2</sup> expected heterozygosity

<sup>a</sup> average number of alleles, <sup>b</sup> total number of alleles at marker loci, <sup>c</sup> number of alleles in adults / number of alleles found in offspring that were also detected in adults

introductions were initially very successful and triggered further reforestations with larch. Mainly starting from the end of the 18<sup>th</sup> century, Tyrolean seed sources were predominantly used, for example, in the Harz Mts. (Germany) where larch cultivation very early gained momentum. The use of Tyrolean seed sources, which became fash-ionable after 1775 in Europe, finally reached its peak of artificial distribution around 1820 to 1840. In the Saxonian state forest (Germany) alone, 10 tonnes of larch seeds were used from 1836 to 1843. Beginning in 1850, a disastrous decline of introduced larch plantations finally ended the so-called 'larch fashion'. Alpine larch populations turned out to be extremely susceptible to early and late frost, this stress allowing entrance for fungus infections such as larch canker (*Lachnellula willkommi* [Hartig] Den-

nis.). Historical records showed that the Tyrolean seed sources that originated mainly from higher altitudes (montane to subalpine zone) caused many failures. For example, extensive larch plantations in Brandenburg and other Prussian provinces of that time which were established at the instigation of von Burgsdorf (1770–1790) totally failed. From a genetical point of view, intensive transfer of larch seeds has had severe effects. While failures in areas where larch is not indigenous may 'only' have caused severe economic losses, transfer of non-indigenous sources into areas of high genetic value (such as into the Sudeten Mountains) may have caused both ecological and economic effects (LANGNER 1935, MÜNCH 1936a, ŠINDELÁŘ 1999).

The history of the Reichenhaller and Salzburger Alps may serve as an other example. By the 16<sup>th</sup> century, the Royal Alpine Ordinance issued by Ferdinand I had caused extensive clear-cutting of forests. Deforestation was closely linked to the high demand of salineries, ore mines and opportunities of easy extraction and transportation of logs. Generally, *Picea abies* and *Larix decidua* were favoured and finally led to elimination of hardwoods over extensive areas. Over an area of more than 100,000 hectares, artificial planting and sowing reached a peak between approximately 1840 and 1875. By 1784, more than 11,000 kg of seeds from Norway spruce and silver fir were sent from Munich to the Reichenhall forests (VON BÜLOW 1964). At least during longer periods, inappropriate Norway spruce seed sources, predominantly originating from low elevations, were used.

Other well known historic examples of inappropriate use of forest reproductive include the transfer of *Pinus sylvestris* from German sources to Sweden (WIBECK 1912) and to the Baltic region (VON SIVERS 1895) as well as planting of inappropriate *Alnus glutinosa* L. Gaertn. populations from a Belgian source that was widely used in several European countries (MÜNCH 1936b).

However, translocation of forest reproductive material is not confined to historical occurrences. In Australia alone, some 25-30 tonnes of forest tree seeds are annually exported. Approximately 4 million hectares eucalypts and 1.3 million hectares acacias have been planted exclusively with Australian sources in Asia (MIDGLEY & BOLAND 1999). Movement of forest reproductive material continues also today across Europe. However, it is very difficult to keep track of origin of seeds and plants, because, at least for Member States of the European Union (EU), several Directives were issued in the past by the European Commission to overcome trade barriers (see p. 75 ff., this volume). For the EU Member States, it became complicated to keep track of forest reproductive material moving into the national territory and not in all countries are such data recorded. For Germany, the proportion of foreign versus domestic seed sources is illustrated for the time period 1983 to 2000 (Fig. 7). It is obvious that, for Acer platanoides L., Quercus robur L. and Tilia cordata Mill., the proportion of foreign sources are meaningful. For these species nearly every third plant, which is planted by end-users, is of non-German origin. Moreover, there are no public data available on how many plants are transferred from one seed zone to another.

The impact on autochthonous populations by plant transfer in regions where inappropriate seed sources were used is unknown since in most cases the extent of translocated material remains vague unless ill-adapted stands completely collapse before reaching maturity. To track down translocations of forest reproductive material



**Figure 7.** Transfer of forest reproductive material in Germany. Relative proportion of foreign *versus* domestic seed quantity (bright grey bars) and plants (dark grey bars), respectively, in Germany averaged from 1983 to 2000. Data were made available by courtesy of the Bundesanstalt für Landwirtschaft und Ernährung, Frankfurt a. M., Germany.

within countries, Resolution S2 (Conservation of Forest Genetic Resources) agreed upon during the first Ministerial Conference on the Protection of Forests in Europe held in Strasbourg 1990 recommended – at least for public forests – to keep records covering the exact identity of the reproduction materials used for planting and regeneration (MCPFE 1990). Unfortunately, the use of reproductive material is not documented or data are not made publicly available in most European countries.

Evolutionary factors shape the introduced population. In some cases, if there is sufficient genetic diversity in the translocated population, there can be sufficient adaptation to the new environment. For example, evidence for microevolution in an escaped common pear (*Pyrus communis* L.) population in Canada was based on an altered growth pattern. Younger trees phenotypically like and unlike the founders were analysed. Trees similar to the oldest trees were significantly slower in growth rate than trees that were phenotypically dissimilar suggesting adaptation to climate and other environmental site conditions (WALDRON *et al.* 1976). In Europe, so-called 'landraces' of European and North American forest tree species are well recognised. In

tionally well (personal observation) and landraces perform exceptionally well in common-garden experiments (KLEINSCHMIT *et al.* 1974). Another example is Norway spruce, translocated within its native range. Experiments in Scandinavia show that the growth cessation, and consequently the sensitivity against frost, has significantly changed in the course of translocation. Certainly the adaptation to the new environment can be primarily explained by classical selection but is also driven by early epigenetic effects (JOHNSEN 1988).

Artificial regeneration: reduction of genetic diversity in commercial seed lots

The mode by which seeds are harvested in seeds stands strongly affects genetic diversity in the seed lots. Both the number of seed trees, their spatial arrangement, mixing of crops of different ripening years or provenance regions are important issues (HUSSENDÖRFER 1996, GEBUREK & MENGL 1998).

Often the question is addressed whether seeds derived from seed orchards are genetically less variable than from natural stands. Studies comparing genetic diversity of these sources indicated no significant differences (MUONA & HARJU 1989, STOEHR & EL-KASSABY 1997). However, most studies were based on a comparison of expected heterozygosity at allozymes, a genetic measure that is fairly insensitive when drift effects are concerned (see above). One is tempting to speculate that between seed lots from seed orchards and seed stands, difference in allelic richness exist and especially rare alleles are even rarer in seeds harvested in orchards. Moreover, seeds for high elevation afforestation produced in seeds orchards located in low elevation – as it is often done in central Europe – in order to enhance seed production are probably genetically modified by epigenetic effects.

Artificial regeneration: reduction of genetic diversity in clonal forestry

The promise of uniformity in size and shape of trees, with a consequent cost saving in forest management and processing and the promise of continuing significant gains in growth rates made clonal forestry regionally attractive.

However, while selected genotypes increase economic expectation, a major concern stems from the potential reduction of adaptability needed in plantations to protect against catastrophic events. An important question that has been long debated is how many clones (BISHIR & ROBERDS 1999, and references cited therein) in which mixtures (VON WUEHLISCH *et al.* 1990) should be used. Generally it is assumed that using more clones will decrease the potential risk of stand failure, but mathematical models have shown that the situation is more intricate and even under very simplifying conditions the necessary number of clones varies erratically. As a rule of thumb environmentally safe numbers in clonal varieties should not be less than 40 (BISHIR & ROBERDS 1999) but other authors recommend higher number (AHUJA & LIBBY 1993, and references therein). Clonal forestry already started in Japan with sugi (*Cryptomeria japonica* D. Don) in the 15<sup>th</sup> century. Today probably *Eucalyptus* species are most often used in clonal forestry on a global scale. In the tropical and subtropical region approximately 15 million hectares of cloned material is planted. Rubber tree (*Hevea brasiliensis* Müll. Arg.) and radiata pine (*Pinus radiata* D. Don.) are other prime species used in clonal forestry and worldwide several million hectares are managed (SONESSON *et al.* 2001).

In Europe, clonal plantation started in the beginning of the 20<sup>th</sup> century mainly with exotic *Populus* clones. Besides ecological reservations there is a genetic risk due to introgression from exotics (mainly *Populus deltoides* Bartr. ex Marsh., *Populus × euramericana* Guinier, *Populus trichocarpa* Torr. et Gray), but first experimental studies indicated a rather limited gene flow (HEINZE 1997, BENETKA *et al.* 1999). Later in the 1960s, clonal forestry with *Picea abies* begun in Germany (KLEINSCHMIT *et al.* 1973) and was then introduced to other countries. In Sweden, within the framework of different clonal forestry programmes in total more than 15 million rooted cuttings were planted, mainly in southern Sweden (SONESSON *et al.* 2001).

A major concern of clonal forestry is the use of GM trees (STRAUSS et al. 2001). Genetic risks mainly stem from the unstable expression of the transgene(s), physiological processes which may or may not be affected as intended by gene transfer, from the temporal unpredictability of both processes and from an uncontrolled dissemination of transgenes via pollen or seed of GM trees. Plants have surveillance mechanisms to search for and attempt to silence introduced DNA (FIRE 1999) causing genetic instability of GM trees. Furthermore, transgenes cannot be introduced into the genome at a specific location. Hence, populations of GM trees may exhibit variable transgene expression. While genetic instability of traits such as improved biocide or insect resistance, growth or wood properties may be acceptable, instability of sterility genes may cause a serious problem. Since GM trees should not spread their transgenes via pollen or seed, their own flowering genes are generally silenced, which – if unstable – may cause a spread of transgenes. Unfortunately, expression over time can only be studied in field trials. Although an 'escape' of transgenes cannot be totally excluded, many transgenes do not enhance the fitness of its carrier and an unwanted spread is not very likely. However, this may not be the case for adaptive transgenes such as pest resistance genes.

Artificial regeneration: mode of establishment (planting vs. seeding)

During a bumper crop in *Larix, Picea, Pinus, Quercus,* or *Fagus* stands several million and in *Betula* and *Populus* even close to a billion of seeds are shed per hectare, which result under natural condition in less than 1,000 trees/hectare. Albeit great quantities of seeds simply die by chance, an immense reduction of the population is due to viability selection. Hence, artificial seeding with – let's say 50,000 seeds per hectare – mimic natural conditions while planting 1,000 or 2,000 seedlings per hectare reduces strongly the pool on which natural selection can operate. From a genetic perspective forest stands regenerated by means of seeding – appropriate seed sources granted – are the favourable form by which forests stands should be artificially regenerated.

Artificial regeneration: plant processing in nursery

Generally also in nurseries natural selection may act against inbred seedlings (MUONA *et al.* 1987) although selection pressure is likely to be smaller than in stands due to more favourable growing conditions (controlled water and nutrient supply).

Genetic alteration may be due to mass selection in nurseries when certain seedlings are culled. Generally smaller plants or plants injured during mechanized processing are eliminated. It was presumed by HOLZER and MÜLLER (1985) that this selection may affect the genetic composition of the seedling pool, especially the slow growing individuals that are highly adapted to high elevation may be eliminated. As shown by MITTON and JEFFERS (1989) mass selection in *Picea engelmannii* Parry ex Englm. may have favoured highly heterozygous genotypes, but effects were slight. In *Picea abies* and *Abies alba* allozymes were compared between selected and unselected plants (KONNERT & SCHMIDT 1996). Between the different cohorts significant genetic differences were detected. Unfortunately, seedlings were not grouped in open-pollinated progenies in order to quantify maternal effects on the genetic structure of selected and unselected seedlings.

#### Selective thinning in traditional forestry

Genetic alteration of managed stands by a selective thinning are very plausible and depend on selection differential and proportion of additive genetic variance of the respective trait. So far marker studies have failed to detect unequivocal effects. No effects due to selective cutting was found for instance in Picea glauca (CHELIAK et al. 1988) or Pseudotsuga menziesii (EL-KASSABY 1982) and differing allelic richness of preharvested and postharvested virgin forest of Pinus strobus are likely due to sampling effects rather than to management effects as claimed by the authors (BUCHERT et al. 1997). However, in Fagus sylvatica L. significant differences in allele frequencies at a certain locus coding 6-phosphogluconate dehydrogenase were reported. In two stands which both were compared before and after cutting allele frequencies shifted towards the same direction (HUSSENDÖRFER & KONNERT 2000). Interestingly at the same locus, significant differences were also detected in cohorts differing in social classes (dominating trees, mediocre trees, supressed trees) in Picea abies (HOSIUS 1993) and Abies alba (HUSSENDÖRFER & KONNERT 2000). Although allozymes do not reflect the whole genomic variation reasonably (REED & FRANKHAM 2001, but see also AMOS & HAR-WOOD 1998), certain loci may be linked to quantitative traits loci or even may have functions in metabolism that directly or indirectly affect growth.

Effects of the traditional selective thinning in *Pinus sylvestris* stands could be also evaluated in a Polish field experiment. Progenies from different stands presumably originating from the identical source population but differing in thinning intensities and natural selection were field tested. Expectedly, progenies from more intensively thinned stands outperformed less selective ones in growth (WILUSZ & GIERTYCH 1974). LEDIG and SMITH (1981) tested progenies from different *Pinus strobus* stands, in which

badly weeviled trees were either removed by selective thinning or no thinning was applied. Progenies from thinned stands had much lower weevil attacks than from untreated stands.

# Conclusions

There is no debate that it is in humanity's interest to maintain high levels of genetic diversity in forest tree species, thus conferring resilience on forest ecosystems. History has shown that in Ancient Times deforestation and exploitation have had significant effects on the genetic composition of forest trees although evidence is anecdotal. To-day's forestry and habitat alterations, especially through pollution, surely modify the genetic structure of tree populations. So far, the vast majority of studies is grounded on genetic markers, mainly allozymes, that are presumed to be neutral or semi-neutral. All human impacts supposed to act via selection must remain vague when these markers are employed. It is not disputed that in single cases certain allozymes are suitable indicators for adaptation (ZIEHE *et al.* 1999), but reservation is highly recommended when selective effects of silvicultural treatment by means of non-adaptive markers are investigated or when results are generalised. Unfortunately forest geneticits have omitted to perform quantitative genetic studies that tackle human impact on the forest trees in sufficient numbers. Quantitative genetic data are very scarce.

Besides the obstacle that adaptive markers are not available in appropriate numbers, genetic baseline data rarely (if ever) exist, making a comparison of past and current gene pools of forest trees difficult. Possibly new molecular tools will furnish new possibilities. DNA can be extracted from old trees, wood samples or even fossils, allowing, to some extent, a 'reconstruction' the gene pool of extinct populations (SUYA-MA et al. 1996, DUMOLIN-LAPÈGUE et al. 1999). But up to now, general conclusions on selective action can hardly be drawn. So far, molecular tools assessing adaptive variation effectively are simply not at hand and it is obvious that – as in many cases – the lack of detectable selective effects based on markers does not necessarily mean that anthropogenic impacts are negligible. However, when human impact on the gene pool of forest tress is referred to that act through genetic drift or through modifying the mating system, then available marker data are of higher value simply because these processes act on all parts of the genome. Therefore, general conclusions can be more easily drawn, for instance, from studies of how different stand densities or fragmented forests influence the gene pool. But even in such cases an ecological evaluation is very intricate, because it is still unknown how much genetic diversity is needed for a longterm existence of forest trees. Further this paucity is not restricted to forest genetics. The same dilemma is faced by ecologists questioning how much diversity is needed on the species' level in sustained forestry and, moreover, it is not known how species diversity and the diversity within these species interfere. Therefore future forest management should embrace the 'precautionary principle', which means that action must be taken to stave off significant threats to biodiversity (including genetic diversity) without waiting for the last scientific proof about their cause or extent. Forest management practices should consider both the current status of the forest and the desired genetic condition and attempt to bridge any gap within a specified time frame. This requires that forest genetic resources must be assessed, including a better evaluation of anthropogenic effects on the natural conditions. One important task is to identify genetic objectives to be included in the national forest programmes or national biodiversity monitoring programmes. Components to be considered included the natural genetic differentiation pattern significantly influenced through post-glacial re-immigration, possibly mingling of different refuge source populations, and more recently, through various human actions including current forestry practices. Keeping records of the source of forest reproductive material is another desirable principle.

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# Expected climate instability and its consequences for conservation of forest genetic resources

Cs. Mátyás

# Longevity of trees and adaptation to environmental changes

The issue of adaptedness appears as a crucial problem for forestry in view of the 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. Conservation strategies should take into consideration the issue of climate (and other environmental) changes in an evolutionary perspective. Due to the long lifespan of trees, climate fluctuations, other secular changes and rare events must have shaped the natural adaptive strategy of trees both on individual and population level.

On an evolutionary scale, most species are ephemeral creatures of the Earth system – an average species exists for about 10 million years. Forest trees, especially the ancient conifers certainly belong to the more persisting class of species. Trees have not only successfully survived changing geological periods as species, but also endure considerable fluctuations of environment without the chance of migrating to more favourable habitats or of short-term genetic adaptation on the population level during an individual's lifetime, as in case of many animals or annual plants.

The present interglacial period, the Holocene, has lasted for approximately 15,000 years; radiocarbon dating confirmed a relatively recent migrational past of forest trees of a couple of thousand years only in the temperate-boreal forest zone. This timespan is very short with regard to possibilities of close adaptation when compared to the lifespan of trees. In extreme, for the oldest bristlecone pines (*Pinus aristata* Engelm.) of the Californian White Mountains, reaching ages over four thousand years, the whole Holocene might appear as a period of mere three to four generations.

Th. Geburek & J. Turok (eds.) Conservation and Management of Forest Genetic Resources in Europe Arbora Publishers, Zvolen, 2005, 465–476, ISBN 80-967088-1-3

# Life strategy options to mitigate effects of long-term environmental changes

In view of the current concern about global climate change, the fundamental question is how tree populations and species will react and what are the means to maintain and enhance their adaptability. There are various genetic and non-genetic options on both individual and population levels to respond to changes in environmental conditions.

On the level of populations, natural selection adjusts the average fitness of the population to changing conditions. The directed genetic change of the population gene pool towards an optimum state is termed *genetic adaptation*.

R. A. Fisher's fundamental theorem on fitness change illustrates that the basic precondition for fast and effective genetic adaptation lies in the sufficiently large variation, *i.e.* in genetic diversity (Fig. 1). This underlines the fact that *the maintenance of long-term genetic adaptability is directly depending on the conservation of adaptive genetic* 



**Figure 1.** Graphic illustration of R.A. Fisher's fundamental theorem on fitness selection. The improvement of fitness ( $\Delta W$ ) of a population depends on the distance from the 'optimum' fitness ( $W_{max}$ ) and on the within-population genetic diversity – the larger, the faster the adaptation.

#### variance.

On individual level, *phenotypic plasticity* provides the ability to survive in a wider range of environments. Although plasticity does not directly lead to genetic changes, it is also determined by the genetic makeup of the individual (Fig. 2). It is generally believed that heterozygosity may play an important, nevertheless not exclusive role in maintaining plasticity. Plasticity differences could be proven not only on individual (clonal) level, but also between populations. Provenances and regions with known high phenotypic plasticity are of special value for maintaining adaptability of the species.



**Figure 2.** Relation between genotype, phenotypic plasticity and tolerance limits. The genotype 'translates' the environmental conditions into the phenotypic reaction, which could be mortality as well, if values are outside the tolerance limits.

*Genetic imprinting* and after-effects is another element of non-genetic adaptation, which seems to play a role in certain forest trees. A not yet fully understood mechanism, imprinting was detected in boreal populations of Norway spruce and some other conifers. It may change the adaptive behaviour of the individual if the effect is lasting (SKRØPPA & JOHNSEN 1994).

A possibility of limited relevance for responding to large-scale changes in the environment is *migration through seed dispersal*. This was the way to follow climatic changes in the European glacials and interglacials – and impeded migration was the reason for the extinction of many temperate tree species in central Europe. Current possibilities for migration are very limited for two reasons. Firstly, as presented later, for migrationally slow species, expected changes may be too fast to keep pace with. Secondly, and more decisively, human interference (mainly fragmentation and regulated forestry activities) impedes natural, long-distance and long-term dispersal, at least for economically important tree species.

#### Analysis of response to environmental change

From point of view of conservation, the maintenance of the adaptive and evolutionary capacity linked with genetic diversity has to be considered as the precondition for stability of forest ecosystems (LEDIG & KITZMILLER 1992, ERIKSSON *et al.* 1993). To develop proper strategies, adequate knowledge of the adaptational process should be indispensable. Due to its long-term character, direct study is extremely difficult and time consuming. The way and extent of genetic transformation following natural selection may be studied however in the common-garden tests of forest trees, *i.e.* in provenance trials. These tests provide also the opportunity to *investigate the effects of change of environment on productivity and survival* (MÁTYÁS 1994).

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 distance of the location of origin.

Equations describing these phenomena have been developed by a large number of authors, and response functions have been broadly used to define seed transfer rules and to delimit seed zones. Most of these models venture 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; while latitude reliably describes photoperiod and includes also a thermal component, longitude is often related to continentality and rainfall. Temperature regime and, to a lesser extent, rainfall is determined by altitude. In fortunate geographical-macroclimatical settings, *e.g.*, in Sweden, geographical parameters are in a straightforward relationship with ecological factors, facilitating the analysis of selective effect of climatic elements, but in most cases the connections are more obscure.

The use of true ecological variables (*e.g.*, various temperature and humidity parameters) instead of geographical ones has many advantages. First of all, it creates a direct link between genetics and ecology through the possible assessment of the importance of various environmental factors shaping and delimiting intraspecific variation (it should be remembered that the elucidation of effects restricting distribution of species is the main goal of ecology).

Secondly, adaptive responses and variation patterns can be interpreted, generalised, and compared more easily if cleared from strict geographic bonds. Also, test conditions and performance can be described and evaluated in an ecologically more meaningful way. The use of ecological variables therefore facilitates the *analysis of*  *adaptation response*. The data may be used to *model environmental change effects* as described later.

In spite of all this, the use of true ecological variables in ecological genetics of forest tees is less common. An eminent reason for not converting geographic parameters into ecological terms is that in most cases such data are very difficult to obtain and utilize (typically, heavily forested, *i.e.* thinly populated and less accessible areas are the least served by weather stations) and, for the very same reason, are difficult to apply in forestry practice.

# Predicting effects of climate change

The assessment of effects of climate change with the help of multiple regression analysis has been proposed by the author (MÁTYÁS 1994). The use of existing provenance tests to predict such effects is based upon the concept that spatial (geographic) variation may be interpreted as a simulation of responses to environmental change over time, *i.e.* geographical-ecological patterns are interpreted as 'false time series'. A further enhancement is the *application of ecological distance*, *i.e.* differences between the test site and the original location (MÁTYÁS & YEATMAN 1992). Accordingly, response regressions of growth of transferred populations on thermal parameters may be interpreted as a model of response to temperature change scenarios.

The investigation of some conifers indicate that a relative growth increase until a certain limit of transfer into cooler environments is a phenomenon regularly encountered in provenance tests; at least into environments not too close to the upper distribution limits (=physiological tolerance limits) of the species. Relative growth means that data are related to the performance of the local populations. In absolute terms, growth decreases if the temperature sum is lower. On the other hand, the transfer to

Test site			Annual mean temperature change (°C)				
		4.5	4	3	2	1	0
high elevation	cm %	406.9 75.6	422.4 78.5	449.1 83.5	474.8 88.3	506.9 94.3	537.8 100
middle elevation	cm %			475.1 87.3	496.7 91.3	520.0 95.6	544.0 100
low elevation	cm %				504.6	524.1 96.3	100

Table 1. Estimated change of height growth of Californian ponderosa pine families at age 12 as a result of different annual average temperature change scenarios. Responses are calculated for three elevational positions (no reliable estimates are available for the empty cells) (MÁTYÁS 1997b).

sites with higher temperature average affects growth negatively. As an example, Fig. 3 and Table 1 show the interpretation of the general response of populations calculated from the dataset of 45 families of ponderosa pine (*Pinus ponderosa* Dougl.) from the Sierra Nevada in California at 5 sites. The data in the Table were obtained from three-dimensional response regression functions, where the transfer effect, *i.e.* the 'ecological distance' was one of the variables, and the ecological conditions at the test site the other (MÁTYÁS 1997b, see also MORGENSTERN 1996).

It is visible that the growth rate deteriorates with increasing pace as average annual temperature climbs higher. An increase of 1 °C means a growth loss of roughly 5 %; and 3 °C a loss of 13 % of the original height at mid-elevation. The sensitivity difference between high-elevation and mid-elevation conditions, exhibiting a stronger response at higher altitudes, has to be treated with caution and needs further confirmation.

The calculated decline in height growth is only an indication for actual productivity loss, as a similar decline in diameter and basal area has a quadratic effect on stem volume. In addition to growth loss, other consequences of maladaptation increase as a function of growing temperature (or ecological) distances, such as susceptibility to snow break; or the loss of resistance to diseases and pests, which are otherwise often harmless or of minor importance; *e.g.*, saprophytic fungi may turn into real parasites. A direct link between ecological distance and mortality could be proven for *Pinus banksiana* Lamb. (MÁTYÁS & YEATMAN 1992).

Growth vigour loss and increased pest and disease susceptibility will result in decline of competitive ability of the species at the locations close to the lower limits of tolerance. Other species may gradually take over the dominant position. At the upper limit of distribution, temperature increase will result in higher competitive ability and the species will colonise new potential habitats. As a consequence, temperature increase will trigger an upward/northward shift of species distribution areas and of elevational vegetation zones.

It has to be pointed out that a species is not moving as a monolithic unit, due to the within-species genetic structure. Gene flow characteristics of the species, the applied procedures in forest regeneration and use of reproductive material will mainly influence, how the genetic structure will be affected by the area change. For instance in mountainous regions, within the elevational band of distribution, species are structured into altitudinal 'races' or clines. Because of the altitudinal genetic differences, 300 m of elevation is generally proposed as the critical limit of safe transfer by ecological genetic studies on some western conifers. In the case of ponderosa pine, the temperature lapse rate for the distribution area in the Sierra Nevada Mts. in California was established as 0.54 °C/100 m (MÁTYÁS 1997b). It follows that 300 m of elevation equals a temperature increase of 1.62 °C of yet relatively 'safe' adaptation, which does not lead to serious loss of competitive ability. The data shown in Table 1 support this. A further increase of temperature, however, inevitably leads to significant losses in productivity. Under other conditions, in the lower part of the area of distribution, even the cited temperature increase might already lead to the surpassing the tolerance limit of the species; this could be shown for the lowlands of the Carpathian basin (MÁTYÁS & CZIMBER 2000).



**Figure 3.** Growth response (height in cm at age 12) of *Pinus ponderosa* populations to changing ecological distances at five test sites (coded location names in the legend) in California. On the horizontal axis the ecological distance between the test site and the provenance location is given (in °C annual average temperature). It is visible that with increasing average temperatures (positive values), response is rapidly deteriorating. Maximum growth was consistently measured at cooler sites than the original location (negative values), except for the site BH (Badger Hill) which was situated at a very cool location (see also Table 1 and MÁTYÁS 1997b).

# **Climate change scenarios**

To forecast climate change is a difficult and uncertain task. To describe various possibilities, so-called scenarios are worked out which may be interpreted as conditional prognoses. The International Panel for Climate Change (HOUGHTON *et al.* 1996) established for the Northern hemisphere four basic scenarios (see Table 2).

It is obvious from Table 2 that temperature changes in central Europe will be higher than the averages of the Northern Hemisphere.

# Table 2. Scenarios for the next quarter of century in the Northern Hemisphere and downscaled data (in °C) for central Europe (Carpathian basin) (HOUGHTON *et al.* 1996).

Past global temperature increase (1850–1995): +0.5 °C				
Scenario number	1	2	3	4
Average temperature increase on the Norther Hemisphere until 2025	+0.5	+1	+2	+3
Summer temperature change in the Carpathian Basin	+1.1	+1.3	+1,5	+3
Summer temperature change in the Carpathian Basin	+0.8	+2.2	+3	+6
Annual precipitation change (mm)	-40	-66	+0	+40-400
Geographically analogous area	Northern Serbia	Central Bulgaria	Southern Bulgaria	Tuscany

Box 1. Comparison of migration and isotherm shift velocities.				
Natural migration velocities through seed dispersal (from paleobotanical data according to DAVIS 1981): <i>Quercus, Fagus</i> : 100–250 m/year <i>Betula, Pinus</i> : 200–400 m/year				
Velocity of isotherm shift (scenario: 2.0 °C in 35 years)				
DirectionGradientVelocity $S \rightarrow N$ horizontal $50 \text{ km/°C}$ $3,000 \text{ m/year}$ Vertical $200 \text{ m/°C}$ $11.5 \text{ alt. m/year}$				

# Species and gene migration constraints and the need of human interference

It could be argued that similar to the past, species and communities will keep pace with changes and evolve to counterbalance these changing scenarios by adjusting gene frequencies within populations and colonising new habitats.

Effective species migration has to match, however, the pace of expected changes. For central European conditions it could be shown that according to the scenario of a temperature increase of 2 °C in 35 years, isotherms would wander in northerly direction with an average speed of 3 km/year and 12 m/year in altitude (see Box 1). This

has to be compared to the natural migration speed of species. It is known from paleobotanical studies that tree populations migrate – depending on migrative abilities – at rates of 0.1–0.4 km/year. The difference between the expected and the potential value is roughly one magnitude. This means that even in case if migrational routes were available and forest conditions would not provide obstacles – which is seldom the case in the intensely managed landscapes of the temperate zone – horizontal migration velocities do not keep up with the expected changes.

There is, on the other hand, no information on the effectiveness of gene flow within a contiguous distribution area. Judging from available indirect information, the speed of adaptation of gene pool through gene immigration might be assumed as considerably 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: an non-fragmented 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 parts of the boreal zone.

Thus, considering the long regeneration cycle of trees, the pace of the forecast climate changes will be too fast to provide enough time for proper genetic adaptation of populations. A temperature shift will in any case negatively affect a large part of the area of distribution. At low elevations and in the southern outliers of the area, close to the lower limit of the species, temperature increase certainly will lead to the thinning out and disappearance of the species, losing its competitive ability against other species.

At the upper/northern limits, temperature increase will bring an improvement of site conditions. This offers the theoretical possibility of a migration advance for the species on the long run, as often modelled in climate scenarios. 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 utilization 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.

Another constraint for migration into new habitats is the limited availability of space due to unfavourable geomorphological-distributional preconditions. Typical examples are populations restricted to mountain tops such as *Abies pinsapo* Boiss. in Northern Africa or *A. fraseri* (Pursh) Poir in the Appalachians which have simply nowhere to migrate (ERIKSSON & EKBERG 2001). In general, any species settled in a habitat that 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.

It may be concluded that the need for active conservation measures is the most pressing in the southern margins of the distribution areas. However, if the mentioned preconditions are not met, they are to be carried out practically over the whole present range. As a consequence, *human interference will be essential for the maintenance of adaptability under changed conditions in the present area of the species, and also to extend the ran-* ges of species at the northern margins of distribution. This will be especially the case in the boreal zone where possible temperature increases might be considerably higher than at medium latitudes.

### Priorities and need for action

When planning mitigation strategies, conditions in naturally regenerated and planted forests have to be considered separately. In artificially planted, respectively managed forests, species migration of trees is basically halted, which is usually overlooked in model scenarios. Gene flow between stands might not be considered as optimally contributing to the large-scale adaptation of populations either, if the origin of the artificially regenerated stands has not been properly controlled in the past.

In general, in the main area of distribution of widely dispersed species with effective gene flow, there is still no emergency for active preventing measures if the stands have been properly managed and regenerated. Active preparatory measures should have priority in case of rare, fragmented species with limited or impeded dispersal ability (artificial regeneration, weak flowering/seeding). Species occupying habitats of extreme character should get also special attention (see Box 2).

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

- isolated populations on the southern or continental margins of the distribution area;
- isolated mountains with no 'reserve altitude';
- locations where conditions are unsuitable in the potential migration area (high alpine or boreal conditions);
- areas regenerated with reproductive material characterized by low adaptability;
- populations with high phenotypic plasticity.

*Populations at the southern/continental distribution limits* are specially threatened due to strong productivity loss, *i.e.* weakened competitive ability and hindered sexual reproduction. Investigations have shown that changes in climatic conditions may affect reproduction processes, flowering, pollination and seed production, 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 shrubs and weeds) demand additional efforts to maintain genetic diversity and adaptive potential.

There is a generally accepted opinion to judge adaptability based on genetic diversity on the biochemical-molecular level. It should be pointed out that the approach to interpret genetic diversity only in terms of qualitative parameters is too narrow. Adaptively important, quantitative traits should receive at least the same attention. The maintenance or reconstruction of non-adaptive, random allelic frequency patterns is, at the same time, less pressing. A typical example would be the maintenance of random, non-adaptive geographic variation patterns due to colonisation.

Box 2. Urgency of preventive action: species characteristics to be considered.			
Low urgency	High urgency		
Continuous distribution High density Naturally regenerated Effective gene flow Spontaneously spreading Extensive, zonal habitats Reproduction unaffected	Fragmented, isolated distribution Small populations Artificially regenerated Limited replenishment of gene pool Low dispersal capacity Extreme sites as habitats Disturbances in flowering and seeding		

A programme mitigating expected climate instability effects should concentrate on selecting the proper populations in the problem areas and on establishment of breeding populations in less exposed surroundings. In addition, regeneration practices and rules for reproductive material transfer and trade have to be revised and adjusted to the necessities of changed conditions.

In case of seriously *threatened minor species and populations*, evacuation into archives, conservation orchards and progeny stands might appear necessary. These activities should be integrated into already existing network programmes; a typically international, collaborative task.

# Conclusions

Common garden tests have been established up to now mostly with easy-to-propagate, widely distributed species. The majority of species in large-scale test networks are conifers, which occupy often the initial phases of succession in temperate forest communities. It is, therefore, not certain that the observed phenomena apply to all widely distributed species. The described modelling method has its limitations as well, as the effect of climate variables at a given test location cannot be evaluated in its full complexity. For instance, in the described approach latitudinal transfer (change in photoperiod) has been neglected, although it might have some effect on light-sensitive species.

With the above limitations, the described effects of temperature change on growth and productivity of tree populations seem to have a rather general validity, even though the magnitude and type of response is determined by the actual genetic structure and tolerance of the species. As a result, temperature increase leads to relatively fast growth and productivity loss and selective mortality. Apart from economic consequences, growth decline affects also the functioning of the forest ecosystem as carbon sink in a twofold manner. With increasing temperature, the quantity of sequestered carbon decreases and simultaneously the decomposition rate of dead organic matter accelerates, causing additional carbon release into the atmosphere. 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. Forest trees as longlived, immobile organisms will especially need human interference in order to enhance gene flow and adaptation to altered conditions, in spite of an impressing adaptive capacity. National forest policies have to incorporate this task into the agenda of the next decades. To counteract genetic erosion and extinction, populations and outliers along the southern (or low-elevation) limits of species distribution areas will need special attention.

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# Host-pathogen interaction in forest ecosystems

# B. R. Stephan & Th. Geburek

# Introduction

An 'ecosystem' is defined as a dynamic complex of plant, animal and microorganism communities and their non-living environment interacting as a functional unit. Fungal microorganisms, together with species of phanerogams, mosses and lichens, and numerous animal species, are an essential part of forest ecosystems and are of great significance for biodiversity. Biodiversity is defined in this context as 'variability among living organisms from all sources including, inter alia, terrestrial, marine and other ecosystems and ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems' (UNEP/CBD 1992, Article 2).

In natural ecosystems, self-regulating structures between living organisms and their abiotic environment are typical (ELLENBERG 1996). Most adaptive processes will be characterized by changes in both genetic structures (of all organisms in that particular system) and environmental conditions, where the latter precede the former (adaptation lag). However, in a stable environment, environmental conditions (biotic and abiotic) do not change over time or change only in a cyclically recurrent manner. Host and pathogen populations (co)evolve until a genetic equilibrium is reached. Different environmental conditions (including biotic and abiotic stress) are necessary and are regulating forces for the common adaptation. Such systems are generally well balanced and are characterized by a high buffering capacity against 'natural' disturbances. In contrast, severe disturbances often exceed the ecosystem's stability. In highly disturbed forests, epidemics can develop more easily and faster, and can even drive host plant populations close to extinction. Anthropogenic impacts of various kinds especially have affected natural forest ecosystems during the last century in Europe (see p. 437 ff., this volume) and, in doing so, the interaction between host plants and their pathogens has often been impaired. Natural forest ecosystems have been changed into human-made communities, often homogeneous with relation to tree species and tree age. Accordingly, often ecologically less heterogeneous forest communities are found. Such communities are less homeostatic and are more vulnerable to biotic and/or abiotic agents. In this paper, we would like to describe the interaction of host trees and their pathogens under both stable and disturbed conditions.

### Host-pathogen interaction in stable forest ecosystems

Ecological homeostasis or stability is a characteristic of natural forest ecosystems, which is also controlled genetically in an open dynamic system to its environmental conditions (GREGORIUS 1997, see also p. 438 ff., this volume). Conventionally, ecosystem stability is defined by two factors: resilience and resistance. The greater the resilience of an ecosystem, the shorter its recovery or return time to equilibrium following a perturbation (LEPS *et al.* 1982, PIMM 1991), while resistance is the ability of the system to avoid displacement during periods of disturbance in its environment (LEPS *et al.* 1982). A simple model is described in Fig. 1. The stable ecosystem will be considered here as not affected by direct anthropogenic activities. But such conditions are, of course, very rare in central Europe.

During evolutionary processes, dynamic equilibria have been reached between host plants and their pathogens. Hence, resistance (see also Box 1) of host plant populations against pathogens is typically found. Host plant populations are not totally eradicated by the pathogen population. The coexisting parasite population is not normally so aggressive that it destroys its host. But, even in stable forest ecosystems, local epidemics are important since they trigger natural succession (*e.g.*, COOK *et al.* 1989, SCHARPF 1990).

#### Box 1. Differing degrees of specificity in the host – pathogen relations.

*Immunity*: Not subject to attack by a specified pest or pathogen.

*Resistance*: Ability of a tree to limit the development of a given pest or pathogen throughout the whole or a part of a growing cycle.

*Susceptibility:* Corresponds to a zero resistance level of a tree with respect to a given pest or pathogen.

*Tolerance*: Ability of a tree to tolerate the development of a pest or pathogen whilst displaying disorders that are without serious consequences for its growth, appearance and yield.

The co-existence of host and pathogens is often but not necessarily a result of coevolution (= reciprocal evolutionary change), which is the change in the genetic structure (frequencies of genes or genotypes) of one species (or on a smaller scale of the deme) in response to the genetic change in another. The genus *Nothofagus* (southern beech indigeneous in South America), for instance, co-evolved with *Cyttaria* (*Ascomycetes*), a fungal species causing tree cancer (HUMPHRIES *et al.* 1986). Populations of host plant and pathogens have passed co-evolution under natural conditions over long periods. Fossil rust fungi of trees were already detected since the Miocene period (5–25 million years B.P.) (PIROZYNSKI 1976). In the biotrophic living rust and smut fungi especially, a distinct specialization for well-defined host plant taxa is found. Such interaction can be noticed in so-called gene-for-gene concepts (CRUTE *et al.* 1997). These concepts are based on FLOR's (1956, 1971) observations in races of flax (*Linum usitatissimum* L.) and the flax rust (*Melampsora lini* [Pers.] Lev.). In the case of race-specific or genetically-determined resistance, the host plant is able to thwart an infection

# **Ecological Status**





# Host-Pathogen Interaction

# **Stabilizing factors**

Host and pathogen coevolved, high resistance, high resilience capacity, tree species (deme) well adapted to pathogen.

# Predisposing factors

Host and pathogen are still in equilibrium, low resistance, moderate resilience, tree species (deme) less adapted to pathogen.





# Destabilizing factors

Host and pathogen are not longer in equilibrium, buffering capacity exceeded, tree species (deme) not adapted to pathogen, *e.g.*, introduction of 'new' pathogen into forest ecosystem.

**Figure 1.** Ecosystem status under different scenarios of host–pathogen interactions. In this simple model, the mass of the marble refers to the resistance (big marble = high resistance, small marble = low resistance). The depth of the valley refers to the resilience (no depth = no resilience (not shown), high depth = high resilience) [from LARSEN (1995), modified].

by the rapid deployment of defense functions. This defensive act by the host relies in part on the presence of a so-called host resistance gene (R), which in some way permits the plant to recognize a specific pathogen. However, this recognition can only occur if the pathogen possesses a gene of its own called an avirulence gene (A) that is



Figure 2. The 'gene-by-gene system' [from FLOR (1956), modified].

matched to the host's R-gene. Because correspondence between host and pathogen genes leads to recognition and defense, this form of resistance has been termed 'genefor-gene' or race-specific resistance (Fig. 2). Also, from many other pathogens, special forms (*formae speciales*) are known, for instance, in diseases of cereal crops, where a distinct adaptation between host plant variety and its respective parasitic fungal race exists (CRUTE *et al.* 1997, *loc. cit.* Part 2).

Adaptedness under different environmental conditions can be

tested in common garden experiments (see p. 275 ff., this volume). For instance, progenies from Scots pine individuals (*Pinus sylvestris* L.), selected because of their relative resistance to the needle cast disease (*Lophodermium seditiosum* Minter, Staley & Millar) in the Black Forest (southwest Germany), were heavily infected by this fungus, when planted at low elevations in the Rhine valley while progenies from local demes were not damaged (STEPHAN 1984).

Different microorganisms occur in forest ecosystems: pathogens, parasites, saprophytes, epiphytes, endophytes, as parasites of weakness or of injury, primary or secondary disease agents and, last but not least, as facultative or obligatory ones. But, microorganisms are generally only recognized if they occur as pathogens on host plants and cause conspicuous damage. Among the many organisms within a forest ecosystem, various potential pathogens exist. However, parasitism is relatively rare. Only 2 % of the high number of fungi can be considered as pathogens. Many species have their ecological niche in or on host trees without causing damage. The symbiotic co-existence within the mycorrhiza of trees should be stressed here. Many microscopically small fungi live in green conifer needles, leaves or other plant tissues. External symptoms are mostly not visible. Such organisms obviously live symbiotically as socalled endophytes in the respective plant tissues (PETRINI 1991). In many plant species, a great number of endophytic fungal species could be isolated from externally healthy organs. Some examples are compiled in Table 1. Generally, older needles or leaves were colonized more frequently by endophytes than young ones. Often the numbers of endophytes and the species involved increase during the summer and are positively correlated with stand density. Their role in the host plant is not yet well known in detail.

Pathogens are characterized by manifold traits. They can live as highly specialized biotrophic or as necrotrophic organisms, but transitions also exist. Pathogens can be specifically found on particular host plant species. On the other side many fungi are unspecialized with a very broad host spectrum. They can be pioneers in their ecosys-

Tree species	Plant organ	Number of detected fungal species	Reference(s)
Abies alba	Needle Twig	142 37	Canavesi (1987) Sieber (1989)
Picea abies	Needle Needle Twig Wood	63 4 53 7	Mack (1989) Stephan & Osorio (1993) Sieber (1989) Roll-Hansen & Roll-Hansen (1979)
Pinus nigra	Needle	56	JURC et al. (1995)
Pinus strobus	Needle	73	Bérubé et al. (1998)
Pinus sylvestris	Needle Xylem, stem	7 53	Rack & Scheidemann (1987) Petrini & fischer (1988)
Arctostaphylos uva-ursi	Leaf, twig	197	Widler & Müller (1984)
Fagus sylvatica	Leaf	64	Sieber & Hugentobler (1987)
Prunus spp.	Leaf, twig	175	Magnuson (1987)

Table 1. Number of endophytic fungal species found on some selected hosting tree species.

tem niche or climax species, and they can be associated with many other microorgan isms. Finally, microorganisms, including pathogens and endophytes, are consumers in the natural ecosystem and contribute to the catabolism and mineralization of natural substances (*e.g.*, MULLER *et al.* 2001).

In contrast to higher plants, microorganisms are haploid over long parts of their life cycle. Therefore, mutations, recombination, or selection processes have immediate effects. Generally, microorganisms with short generation cycles adapt fast to changing environmental conditions. The genetic variability of fungi is very pronounced, being caused by sexual recombination, mutation, heterokaryosis, subsequent somatic recombination and parasexuality (TINLINE & MACNEILL 1969).

The above-mentioned examples are mainly referring to situations of host-pathogen interactions of limited local scale. But all these evolutionary factors may also be seen at a regional or even greater scale. In general, trees as well as their pathogens are widely distributed. Environmental conditions of the various locations differ and individual populations have adapted to their habitat. Therefore, the interaction between a certain host and pathogen species can differ significantly among locations. Ecological and genetic processes should be investigated also in a spatial context (BURDON & THRALL 1999, 2001). Spatially structured groups of populations, so-called metapopulations, were affected by different conditions, causing different (co)evolutionary processes in local populations. Various demographic and genetic effects of hosts on their pathogens and *vice versa* must be assumed. But studies on those relations in forest ecosystems are scarce. In this context, the interaction between *Populus* spp. and the leaf rust

*Melampsora* across North America can be considered. In the dry interior part of western Canada the natural *Populus* species contain major resistance genes, whereas on the more humid Pacific west coast, resistance to that leaf fungus seems to be controlled by many minor genes (BURDON *et al.* 1996). These differences cause different dynamics. Disease epidemic cycles are very pronounced in the dry interior part, while the disease is more stable on the Pacific coast. Also, fungal pathogens occur in mosaic-like populations, well known from the very variable root and butt rot causing fungal species *Heterobasidion annosum* (Fr.) Bref. and *Armillaria mellea* (Vahl) Kummer. These important pathogens can be found worldwide, often acting as pathogens of various host plants. Genetically different intersterility groups exist, even in the same forest ecosystem (*e.g.*, COETZEE *et al.* 2000, GONTHIER *et al.* 2001, WERNER & LAKOMY 2002).

# Host-pathogen interactions in disturbed forest ecosystems

The ecological stability of natural forest ecosystems is mainly disturbed by human activities, often indirectly favouring certain pathogens. In particular, species composition, demographic and structural diversity as well as genetic diversity are impaired in disturbed forest ecosystems. Plantations consisting of monocultures, the use of genetically homogeneous material (clones), or the use of forest reproductive material lacking sufficient adaptability are predisposing factors. However, these factors within hostpathogen interactions have not been studied in detail. As a warning sign it may be recollected that severe epidemics were documented on large monoclonal plantations of Populus × euramericana Guinier susceptible to the Marssonina brunnea leaf spot disease. In the North Italian riparian region of the river Po, this disease killed thousands of trees in the sixties (CASTELLANI & CELLERINO 1969). The fungal parasite Marssonina brunnea (Ell. & Ev.) P. Magn. (syn. Drepanopeziza punctiformis Gremmen) also caused similar losses of the black poplar clones 'Regenerata' and 'Marilandica' used for afforestation of the Dutch polders (GREMMEN 1984). Such risks can be reduced if a sufficient number of clones with genetically different disease resistance are used (LIBBY 1982). Also, in agricultural ecosystems it has been proven that epidemics are frequently more severe in genetically uniform plantings than in more diverse plantings (e.g., WOLFE 1985, see also Box 2). The mixtures of varieties or clones may have some effects also on the genetic composition of the associated pathogen population.

The interactions between host and pathogens can be inferred especially if plant species are introduced into a new environment or if non-indigenous microorganisms are imported into an ecosystem. Effects are often negative, as numerous examples have shown.

As examples, four host-pathogen interactions will be used, which have caused severe economic damage in the past in forests. Two of them are concerned with conifers, whilst the other two refer to broadleaved species.

#### Box 2. Diversity and stability - theoretical models.

Four hypotheses about the role of diversity in contributing to ecosystem stability have been proposed (cf. JOHNSON et al. 1996). Diversity originally referred to species but may be also broadened to the genetic level. The diversity-stability hypothesis predicts that as species (genetic) diversity increases so too does ecosystem productivity and resilience (MACARTHUR 1955). The rivet hypothesis likens the species (genes) in an ecosystem to rivets in an aeroplane (EHRLICH & EHRLICH 1981); the removal of rivets (species, alleles or genotypes) beyond a critical number will cause the aeroplane (ecosystem) to crash catastrophically. This suggests that the ecosystem will continue to function normally if there are only a few extinctions. However, the loss of a single critical species or a single critical gene (e.g., a major resistance gene) also may cause instability within the ecosystem. The redundancy hypothesis proposes that certain species are able to expand their role in the ecosystem to compensate when neighbouring species are lost (WALKER 1992). This implies that species are segregated into functional groups and species in a given group can expand to fulfil the role of other species in the same functional group should some become extinct. The redundancy hypothesis may be also related to the genetic level assuming that certain gene products may substitute others. The idiosyncratic hypothesis proposes that although ecosystem function changes when diversity changes, the magnitude and direction of the change is unpredictable because of the complexity of the ecosystem and the varied responses of the species (LAWTON 1994).

# Example 1: needle cast disease of Douglas fir (Pseudotsuga menziesii [Mirb.] Franco)

The ascomycete, Rhabdocline pseudotsugae H. Sydow, is native in western North America, where it has been known as needle blight of Douglas fir since 1917 (WEIR 1917). SYDOW & PETRAK (1922) described the fungal species scientifically as R. pseudotsugae. The fungus lives biotrophically in one-year-old needles of Douglas fir within the total distribution area of the tree species (PARKER & REID 1969). The conditions for infection are optimal, particularly in the natural distribution area of the green variety (var. menziesii) of Douglas fir along the western coastal range with long rainy periods and lower temperatures in springtime, when needles are flushing. Between host and pathogen, high genetic resistance has been co-evolved in populations of the green Douglas fir race. In the coastal range the fungus belongs to the indigenous host-pathogen community causing no severe impact. High humidity and relatively low temperatures, necessary for the infection of the flushing needles during spring time, are rare events in the mountains at higher elevations, where the blue (var. *glauca*) and gray (var. caesia) varieties of Douglas fir occur naturally. These environmental conditions are not favourable for *R. pseudotsugae*. Therefore, the fungus is of minor importance in these areas causing no genetic resistance to this needle fungus in gray and blue varieties of Douglas fir. Consequently, 'green' Douglas fir populations are more resistant than 'gray' and 'blue' ones from higher elevations, as shown in common garden experiments (STEPHAN 1973a, 1980, HOFF 1987).

Douglas fir was introduced into Europe (Scotland) by David Douglas in 1827 (BOOTH 1877). In the following hundred years, seed from many populations of differ-

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ent varieties has been introduced and used for afforestations in several European countries without any severe health problems. The plantations remained healthy until the year 1922, when the first severe Rhabdocline needle cast attack occurred in Scotland and southern England (DAY 1927). It is questionable whether the disease had been already introduced accidentally from North America to Europe by 1914 (WILSON & WILSON 1926). The spreading of the disease in central Europe between 1925 and 1934 was later described by RHODE (1932, 1934). In the old world, the needle disease was first observed in northern Germany, spread epidemically in a very short time period and endangered drastically the cultivation of all Douglas fir varieties, but especially the blue and gray ones. These were often grown together with the green variety in the same areas, where the environmental conditions for infections were optimal. In the thirties, it had been already observed that the green Douglas fir variety remained healthier than the blue and gray ones, when attacked by the fungal pathogen (e.g., VAN VLOTEN 1932, LIESE 1935). As the green Douglas fir variety is fortunately not only more resistant to needle cast, but at the same time also superior in economic traits such as height and diameter growth, the highly susceptible blue and gray varieties are generally not recommended for use in Europe (e.g., KLEINSCHMIT & BASTIEN 1992). By this action the spreading of the *Rhabdocline* needle cast disease can be limited. Symptoms of this disease are shown in Fig. 3.

Interestingly, PARKER & REID (1969) could show that two species with five subspe-



**Figure 3.** Needle cast disease on Douglas fir caused by *Rhabdocline pseudotsugae*. Photograph by N. von Wallwitz.

cies exist within the taxon *Rhabdocline*, each with subtle different morphology, life cycle or symptomatology. Probably the subspecies *Rh. pseudotsugae* ssp. *pseudotsugae* Parker & Reid was introduced to Europe (MORIONDO 1972, STEPHAN 1973b).

#### Example 2: blister rust of five-needle pines

A very serious problem for growing five-needle white pines (subgenus *Haploxylon*) is the so-called blister rust disease (*Cronartium ribicola* J. C. Fischer). This disease attacks trees of all ages worldwide where these pines are growing naturally or where they have been artificially introduced. In Europe, the eastern white pine (*Pinus strobus* L.) especially is affected (Fig. 4), where the disease causes significant economic losses.

The blister rust fungus C. ribicola (Basidiomycetes, order Uredinales) is a biotrophic microorganism. During its life-cycle, it requires an alternation of different systematic positions between host plant species (typical three-species-pathosystem). Therefore, the life-cycle of the fungus can only be completed if two host plant species are present within a close neighbourhood. The blister rust fungus occurred originally only in north central Asia on Pinus cembra var. sibirica (Du Tour) Loudon, and some other fiveneedle pines, and on various indigenous species of the genera Ribes (Grossulariaceae) and Pedicularis (Scrophulariaceae). In Tertiary times, the nordic five-needle pine migrated into the Alps during the course of the glacial periods and formed a relic area with the species Pinus cembra L. The rust fungus immigrated simultaneously with these pines and the alternate host species also and survived here. These Eurasian areas can be considered as the main genetic center, where host and pathogen coexisted over long periods, and where host tolerance as well as virulence of the parasite are in a dynamic equilibrium (LEPPIK 1970). Thus, the Eurasian five-needle pines possess a high resistance to Cronartium ribicola, as documented in tests (e.g., DELATOUR & BIROT 1982, STEPHAN 1985, 1986).

In the nineteenth century, plantations were established in Europe with the fast growing five-needle eastern white pine (*Pinus strobus*) from eastern North America. These plantations came in close contact with the endemic Alpine and Siberian *Pinus–Ribes* system. At that time it was not yet known that *P. strobus* was highly susceptible to the white pine blister rust fungus. A first severe fungal attack of eastern white pine was observed in the Baltic Provinces in 1865. Over the following years, the disease appeared epidemically through the whole of central Europe and reached Switzerland in 1895. The further use of *P. strobus* for afforestation was jeopardized and in some areas prohibited. Main hosts of the fungus in Europe are *P. strobus* and the shrub black-currant (*Ribes nigrum* L.).

Blister-rust-infected seedling plants of eastern white pine caused the accidental import of *Cronartium ribicola* from Europe to eastern North America in 1909 and the fungus was later (1921) found on *Ribes nigrum* in the surrounding areas of Vancouver (B.C.). As *Cronartium ribicola* did not occur naturally on the North American continent, the fungus came into a blister-rust-free area. Therefore, the indigenous five-needle white pines had no genetic resistance or tolerance to the fungus. The introduced pathogen spread very quickly (about 30 km per year) within the natural distribution



**Figure 4.** Blister rust (*Cronartium ribicola*) on Eastern white pine (*Pinus strobus*). Photograph by B. R. Stephan.

area of the numerous five-needle white pine species in North America. The spreading was facilitated by numerous Ribes species occurring in the North American forests. Most of these Ribes species were also susceptible to the rust fungus and thus, they acted as alternate hosts. Trees of all ages were attacked. The fungal pathogen has caused heavy mortality of fiveneedle pines in North America. Populations have been dramatically reduced in natural ecosystems. In several pine species, distinct and significant losses caused genetic impoverishment of populations, e.g., in western white pine (Pinus monticola Douglas ex D. Don) 90-95 % of the original population was lost. Therefore, their genetic diversity was, and still is, endangered (BINGHAM & GREM-MEN 1971). It can be assumed also that the genetic diversity of the various alternate host species of the genus *Ribes* is impaired, but this has not been investigated yet.

Extensive and expensive resistance breeding programmes have been established in North America

in the past. However, such activities did not provide a solution. Nevertheless, in some five-needle pine species, *e.g.*, in western white pine (*P. monticola*) or in sugar pine (*P. lambertiana* Dougl.), the breeding led to more resistant progenies (DAOUST & BEAULIEU 2004, KRIEBEL 2004, MCDONALD *et al.* 2004). In both pine species major genes for resistance to blister rust were found (KINLOCH & DAVIS 1996, HUNT *et al.* 2004). Differences concerning infections of 69 *P. strobus* provenances by *Cronartium ribicola* have been observed also under North German conditions (STEPHAN 1974). Simultaneously with breeding programmes, control activities with chemicals were started also, making considerable attempts to eradicate the alternate hosts (species of *Ribes*) in the forests. However, these activities were unsuccessful.

White pine progenies with relatively high blister rust resistance under North American conditions became infected when brought into other environments, for instance, to France (DELATOUR & BIROT 1982) or Germany (STEPHAN 1986). This pattern could be explained by the existence of different races of *C. ribicola* in North America,

Europe and East Asia. At least four different races of C. ribicola with a different host spectrum may exist (STEPHAN & HYUN 1983). Many races exist in the eastern Asian center of origin. It can be assumed that only one race of C. ribicola with restricted genetic variation has been introduced into eastern North America. Isoenzyme studies in eastern Canada showed that in 155 samples of the pathogen from 21 P. strobus populations, all 21 of the studied gene loci were monomorphic (BERUBÉ & PLOURDE 1995) while small but significant genetic differences between C. ribicola populations were found (HAMELIN et al. 1995, HAMELIN 1998). The genetic differentiation was more pronounced between populations from western British Columbia and eastern Canada. It may be speculated that different C. ribicola types were introduced into eastern and western North America at the beginning of the last century. However, these populations harboured lower levels of genetic diversity than the original fungal populations in Europe and Asia. Also, further molecular genetic studies, restricted to C. ribicola sources in western North America, revealed much intra-site variation, but no geographic pattern (WHITE et al. 1996, KINLOCH et al. 1998). Inoculation studies with various blister rust inocula showed a different virulence between inland and coastal sources of the fungus (MEAGHER & HUNT 1999).

#### Example 3: chestnut blight

The chestnut blight is another pathogen introduced into an area where the parasite was previously absent. The disease is caused by the ascomycetous fungus *Cryphonectria parasitica* (Murrill) Barr (syn. *Endothia parasitica* [Murrill] And. & And.). It is a necrotrophic pathogen found on species of the genus *Castanea*, but rarely on *Quercus*. The fungus infests bark and cambium of stems and branches causing an interruption of the uptake and transport of water and nutrients. The upper parts of an infected tree fade.

The pathogen is native in Asia, where it can be found in stands of local chestnut species (e.g., Castanea mollissima Blume, C. crenata Sieb. & Zucc.) without causing severe damage. A co-evolution similar to the pine-blister-rust system can be assumed also for chestnut blight. Severe infections caused by this pathogen were found for the first time near New York in 1904 (BRASIER 1990). The disease was probably introduced with plants of the resistant Japanese C. crenata and later spread to the highly susceptible North American chestnut (C. dentata [Marshall] Borkh.), which had not developed any protection against the newly introduced pathogen. The disease spread with a speed of approximately 37 km per year through the entire natural range of the American chestnut. Nearly all of the C. dentata stands were destroyed until 1950. BINGHAM et al. (1971, loc. cit. p. 438) wrote: 'the disease swept through the equivalent of a 9 million acre forest composed of pure Castanea dentata in less than 50 years, and reduced the species from a highly valuable forest and horticultural tree to an infrequent and insignificant shrub'. That was not yet the end of the catastrophe, however. Around 1930, the disease appeared accidentally also in Europe, introduced presumably with Japanese chestnut plants, and spread quickly through plantations of Castanea sativa Miller in Italy, South

France and Switzerland. Unfortunately, the pathogen is still expanding and, since 1992, has occurred also in southwestern Germany (SEEMANN *et al.* 2001).

In the 1950s, a sudden, very peculiar decrease of dying chestnut trees was observed in North America. Although the tree bark was infected, the pathogen did not invade the cambium. From those infected trees, fungal strains could be isolated that had less virulence, the so-called hypovirulent strains. Cryphonectria-hypovirus 1 (CHV1) was found to be the main cause responsible for the fungus disease. The virus caused changes of the fungus so that it was no longer dangerous for the tree. The hypovirulent feature was transmissible in experiments through hyphal bridges (anastomoses) into virulent fungal strains. The hypovirulence could also be transferred by asexual spores, but not by the fungal ascospores. Double-stranded ribonucleicacid (dsRNA) could be identified as the cause of the hypovirulence in avirulent Cryphonectria strains (VAN ALFEN et al. 1975). The dsRNA caused this mycovirus disease of the fungus. A gradual spreading of this fungal disease has been observed within attacked European chestnut populations during the last decades, and simultaneously a decrease of severe damages has been noted. It is of great interest that the speed of spreading of hypovirulence is much slower in and among North American chestnut populations than in the European ones. Vegetative incompatibility between C. parasitica strains is an important factor influencing the natural spread of the hypovirus. The number of types within the pathogen populations with different vegetative compatibility (vc types) is larger in North America than in Europe. Therefore, hypovirulent fungal strains more rarely come across compatible virulent strains. This results in a slower distribution of hypovirulence. The vegetative compatibility is obviously controlled by distinct alleles, eventually even by genes. In the meantime a high genetically controlled diversity was found also in the mycovirus. The use of hypovirulent fungal strains as biological control measure is discussed and already used in southern Switzerland. This method is probably more advantageous than resistance breeding (BRASIER 1990, HEINIGER & RIGLING 1994, ROBIN et al. 2000).

#### Example 4: Dutch elm disease and plane tree cancer

Dutch elm disease (DED) is one of the most destructive tree diseases of the last century. Millions of elm trees (*Ulmus*) have been killed in Europe, North America and some parts of Asia during the past 100 years. Wilting elm trees were observed for the first time in the Netherlands around 1920. The necrotrophic ascomycete *Ophiostoma ulmi* (Buism.) Nannf. was identified as the pathogen, and the disease got its misleading name Dutch Elm Disease (DED). Also for this host-pathogen interaction, the gene center can be assumed to be in eastern Asia, from where the fungus has probably spread to Europe. East Asian species of *Ulmus* (*e.g.*, *U. pumila* L.) show a much higher resistance to the pathogen and were used for crossing experiments in later years. A low xylem vessel diameter prevents the spreading of the fungal spores within resistant trees (*e.g.*, SOLLA & GIL 2002).

A first epidemic of the disease spread very rapidly from the Netherlands throughout the European elm populations by 1929 and reached Middle East Asia by 1939. Particularly in the Netherlands, where 95 % of the elms were of one clone ( $U. \times hollandica$  Mill. 'Belgica') at that time, some areas lost more than 70 % of their elms (HEYBROEK 1966). This fact emphasizes again (see poplar – *Marssonina* – leaf disease) the great danger of using genetically uniform and confined plant material. Also, in southern Britain the disease has caused the death of so many elm trees that it has changed large parts of the landscape, where elms were the characteristic tree species.

The pathogen was introduced into North America around 1930 and became widely established in the *U. americana* L. populations. This pathogen form was much more aggressive in North America than in Europe, where damages decreased gradually.

A second epidemic began around 1940, when a very highly aggressive fungal form was suddenly observed in Illinois (U.S.A.). The North American race NAN developed and was introduced presumably from an area of Toronto to Great Britain around 1960, where it developed the European race EAN. This aggressive race spread over other parts of Europe and reached Tashkent in the 1970s. The two aggressive races NAN and EAN were described by BRASIER (1991) in the meantime as the new species *Ophiostoma novo-ulmi* Brasier. The current pandemic of DED is caused by these two highly pathogenic races.

As with the chestnut blight disease, DED also is a highly complicated host–pathogen system, to which different fungal species and/or races, elm populations, hybrids or clones, bark beetle species (*Scolytidae*) as necessary animal vectors, and a cytoplasmatically transmittable disease (mycovirus) of the fungus *Ophiostoma* contribute (see also GIBBS 1978, BRASIER 1990). In addition, human activity has played an important role in the distribution of this disease. The mycovirus of *Ophiostoma*, the socalled d-factor, also has a double-stranded RNA structure (BRASIER 1983). It can be assumed that the virus disease has already contributed to the decrease of the first epidemic. The vegetative compatibility between mycelia of the non-aggressive fungal race (*O. ulmi*) is interestingly greater in Europe than in North America. This has had an obvious positive effect on the speed of distribution of the mycovirus in Europe and could explain the slower decrease in the disease found in North America.

The main points of the current epidemic will be summarized here (BRASIER 1990, 1996). The two fungal species, *O. ulmi* and *O. novo-ulmi*, are involved with the three races: 'non-aggressive', EAN and NAN. These races have their own specific physiological characters and genetically determined variations. Genetic interactions and gene flow are controlled by three recognition mechanisms between the mycelia: vegetative incompatibility, sexual mating, and fertility barriers between the species or races. Sexual and asexual, as well as pathogenic and saprotrophic populations can be distinguished. The fitness of races is influenced by different aggressiveness, growth rates and kinds of reproduction, asexual conidia or synnemata, and/or sexual formed perithecia with ascospores. Finally, in this very complicated host–pathogen system, selection pressures may play an important role caused by the host populations (various species of *Ulmus*, different rate of resistance against the fungi and the animal vectors), by the vector populations (involved are at least four species of bark beetles with great differences in the efficiency as vectors of the disease), by other microorganisms during the saprophase, and by climatic differences in the respective areas.

Dutch elm disease is not only highly interesting because of the worldwide destructive distribution, but also because of the assumption that it presents a host–pathogen interaction at a very early moment of co-evolution and could, therefore, be an example for older systems that are nowadays rather stable.

It can be assumed that DED has caused great losses in the genetic complement of elm in the past. Resistance breeding programmes have been around for a long time, but successes have been minimal. Clone collections and clonal archives have been established by several European countries during recent years. More than 700 clones of various elm species are now registered in data banks for genetic conservation measures (COLLIN *et al.* 2000, FRANKE 2001). Tissue cultures are kept by cryopreservation at -196 °C, so new elm plants can be regenerated at a later date, if *Ophiostoma* has lost its aggressiveness by mutation, mycovirus disease or through other means.

Closely related to *Ophiostoma*, is the ascomycetous fungus *Ceratocystis fimbriata* (Ell. & Halsted) Davidson f. sp. *platani* Walter (BUTIN 1996). This very aggressive pathogen causes severe cancers and wilt diseases of plane trees (*Platanus* spp.) and was observed for the first time in Italy around 1972 (PANCONESI 1981), and later also in France, Spain, Switzerland and Turkey. The fungal pathogen was obviously introduced from North America into the Mediterranean area, which was previously free of that pathogen. *Ceratocystis fimbriata* has not yet invaded into the more northern countries, and this should be avoided if possible, using, for instance, phytosanitary measures.

# Effects of host-pathogen relationships on ecosystems

The extent of the positive or negative effects from the relationships between host and pathogen on the development of an ecosystem is only partially known and not very well investigated to date. Microclimatic changes or other stress factors are able to stimulate the development of an epidemic by an endemic fungus in a relatively short period. It is, for instance, known from Californian pine forests that every 10 years, natural epidemics occur caused by the needle disease pathogen *Elytroderma deformans* (Weir) Darker (SCHARPF 1990). In particular, natural forests of *Pinus ponderosa* Dougl. and *P. jeffreyi* Grev. & Balf. show high mortality rates. Thus, the succession and species composition of the developing forest are strongly influenced by the epidemic. Rainy periods, the flushing of young pine needles and the presence of mature fungal fruitbodies must coincide and are necessary for the development of an epidemic.

In natural conifer forests of Oregon and British Columbia, the root rotting fungus *Phellinus weirii* (Murr.) Gilbertson attacks the susceptible *Tsuga mertensiana* (Bong.) Carr. preferentially to the two other conifers *Abies amabilis* (Dougl.) Forbes and *Pinus contorta* Dougl. ex Loud. (COOK *et al.* 1989). Under specific environmental conditions, changes of the phytocoenosis are caused by *Phellinus*.

# Conclusions

The adaptation to changes in biotic and abiotic pressures is the principal objective of the conservation of forest genetic resources. While future changes in climate are predicted to affect also the gene pool of forest trees (see p. 465, this volume), prompt changes in pest pressure are even more probable. In agricultural crops, several approaches such as gene rotation, gene combinations, cultivar mixtures, and gene deployment were proposed to manage co-evolution of pathogens with host plants to prolong resistance (*e.g.*, MUNDT 1994). In forest trees, however, it is unlikely that these approaches will or can be used. Nevertheless, some lessons from host-pathogen interactions can be learnt:

- In stable ecosystems most hosts and pathogens are in a dynamic balance that is often, but not necessarily, a result of co-evolution. This balance is maintained by a high genetic variability both in hosts and pathogens;
- Plantations consisting of genetically uniform forest reproductive material favour epidemics and should, therefore, be avoided;
- Host-pathogen interactions regarding symbiosis, mutualism and/or co-evolution should be also assessed in a spatial context;
- Unintentional transfer of pathogens across regions or the import into a new environment, thus changing the biotic environment, drastically promotes epidemics or pandemics;
- Consequently, a transfer of host plants and/or pathogens should be avoided. Reaction norms of host plant populations should be tested in advance;
- A total elimination of pathogens, for instance, by control measures or resistance breeding, is impossible.

Summarizing, the conservation of sound natural ecosystems should be generally the most important target of all activities.

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