

## ARTICLES

# Gene Conservation of Broadleaved Tree Species – a Scandinavian – Baltic Perspective

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This paper gives an overview of gene conservation of broadleaved tree species with an emphasis on northern European species. Objectives in gene conservation are discussed and it is concluded that *safeguarding the potential for adaptation* is the most prominent objective. A grouping of species with common features are discussed. Population size is one important criterion for grouping. Whether a species is involved in intensive breeding, stage in ecosystem, pollination vectors, and threats are other criteria for classification. The knowledge about genetic variation in adaptive traits is limited for most broadleaved tree species. Methods for gene conservation of one species representative of each group are suggested. The multiple population breeding system plays a central role in the methods suggested. Establishment of clonal archives or seed orchards of rarely occurring species to increase the effective population size is suggested.

**Key words:** Gene conservation, objectives, methods, northern broadleaved tree species

## Introduction

The term gene conservation intuitively suggests to most geneticists and non-geneticists that gene conservation should encompass as much genetic variability as possible. The existing variability is a result of the past history of the species. During history the evolutionary factors have influenced today's structure. Therefore, it is essential for gene conservation to know about these factors and the dynamics of the species to enable development of solid gene conservation methods.

This presentation will mainly be limited to the tree species in the Scandinavian and Baltic region. Within the frame of EUFORGEN much work has been carried out as regards gene conservation of broadleaf tree species. Thus four out of five networks treat broadleaf trees. One common feature of these tree species is the limited knowledge of quantitative genetic variation. In many other respects the species vary considerably. This in turn means that no uniform gene conservation can be developed for all species but possibly for groups of species. Therefore, a discussion of possible groupings of the species is sensible. Before this classification is carried out it is useful to discuss the objectives of gene conservation

## Objectives

Soulé and Mills (1992) stated that *Conservation genetics exists for one reason only - to promote the fitness of targeted populations*. Within the network for noble hardwoods we have phrased the objective in an analogous way: *To safeguard the potential for adaptation of a species*. As a corollary of this, gene resource populations shall have large additive variance. Additive variance is best safeguarded if there is random mating in populations since deviations from random mating may lead to fixation of alleles.

Many tree species are distributed over large areas and for that reason occupy different selective environmental neighbourhoods (SEN) in the sense of Brandon (1990). In a SEN there are no ranking changes among the trees with respect to fitness. This means that natural selection has caused an adaptive differentiation within most tree species if there is restricted gene flow among different SENs and limited genetic drift (cf. Eriksson, 1998). Such an adaptation does not lead to any perfection even if the adaptedness is improved (Eriksson et al., 1993, Garcia-Ramos and Kirkpatrick 1997). Therefore, the existing adaptedness should be included in gene conservation not as a target but as a starting material (Eriksson et al., 1993). To include existing

adaptedness, knowledge about genetic structure, *ie* the genetic variation within and among populations, is a key issue in gene conservation.

A preservation of the existing genetic structure of wild apples and wild pears is another objective. The rationale behind this objective is that introgression from cultivars should further reduce the adaptedness of these wild species.

## Grouping of species

### *Life history traits*

Population size, mating system, and stage in ecosystem might be the basis for a grouping. Population size covers everything from the extreme situation of large random mating populations to widely scattered single trees. The two extreme situations are easy to distinguish but there are transitions with small and scattered populations without any gene flow among the populations. This will give rise to large but non-adaptive genetic variation among populations in contrast to the adaptive variation that may exist in random mating populations. Therefore, a grouping of species whether they are commonly or rarely occurring is justified.

Isozyme studies have revealed that mating system influences the genetic structure of a species. Wind-pollinated species have generally a higher within-population/ among-population variation ratio than insect-pollinated species (*e.g.* Govindaraju, 1988). This is attributed to gene flow over larger distances of wind-pollinated species than in insect-pollinated species. This does not mean that every wind-pollinated species has wider pollen dispersal than every insect-pollinated species. Many population geneticists have pointed out that markers such as isozymes do not reflect the variation in adaptive traits (*e.g.* Karhu *et al.*, 1996, Lynch, 1997). Since among-population variation in quantitative traits is easier to distinguish than differences in marker traits (Lewontin, 1984), it is highly likely that differences in quantitative traits are larger among populations than for markers. Empirical data support this hypothesis (*cf.* Eriksson, 1995). An insect-pollinated species will in most cases need a larger number of gene resource populations than a wind-pollinated species. However, this difference is probably of another magnitude than differences between rarely and commonly occurring species.

Pioneer species are in the extreme case characterised by very low within-population variation. Typically, pioneers invade open areas with fairly homogeneous growth conditions that thus not call for a large genetic variation. Rather, once a genotype with good

adaptedness to the prevailing conditions at the open area arises, it would, teleologically speaking, be an advantage in the short-term perspective to rely on that genotype. Therefore, asexual propagation like in *Taraxacum vulgare* would be advantageous. Contrary to this, climax species experience during their lifetime heterogeneity both in space and time. Therefore, genetic variation in populations will be advantageous. The climax – pioneer difference is analogous to the contrast wind-pollination – insect-pollination and is probably of a lower magnitude than the classification: rarely occurring – commonly occurring.

### *Breeding*

Long-term breeding efforts require breeding populations with satisfactory additive variance. If this requirement is fulfilled, gene conservation is well taken care of in breeding. Therefore, species included in long-term breeding programmes do not need separate gene conservation programmes and whether a species is included in long-term breeding might be used in classification of species.

The improvement objectives might include one or several traits. When breeding objectives comprise such disparate traits as high-quality timber and nuts it is not self-evident that improvement can be achieved in one common breeding population. This is still more accentuated in the case of chestnut and walnut, in which selection for nut quality and yield has gone on for millennia while timber improvement has not taken place to any large extent. Therefore, a special treatment of gene conservation of multipurpose species is justified.

### *Threats*

Entire species or populations of species might be endangered for several reasons. One reason is serious pests and diseases. Especially wych elm (*Ulmus glabra*) populations from the larger part of the distribution area of this species are severely affected by the Dutch elm disease. Only in the northernmost area of the distribution there is no disease problem thanks to the absence of insect vectors. European white elm (*Ulmus laevis*) is affected to a lesser degree by this disease. Silvicultural regimes and forestland conversion to other land uses is a threat executed by man. Transformation of riverbanks to man-made environments has caused considerable disturbances and fragmentation in riparian forests. Thinnings may intentionally or unintentionally be a threat to species. Economically less valuable species are cut during thinnings or rare spe-

cies are cut owing to ignorance of staff. Especially the serious threat from the Dutch elm disease deserves a special treatment.

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Gene conservation of one tree species from each group will be used as an example of how gene conservation might be carried out.

### Commonly occurring species

#### *Intensive breeding*

The only species from our region included in anything approaching intensive breeding programme is silver birch (*Betula pendula*). It is well known that clinal variation for growth traits and growth rhythm traits exists (cf. The review by and Jonsson and Eriksson, 1986).

In Finland the silver birch breeding is separated in four breeding zones, each with 300 trees. The breeding is designated as open nucleus breeding; *i.e.* each main population will have 300 trees and among those trees 50-70 (nucleus) are selected for establishment of seed orchards/clone trials. It is foreseen that transfers between the main population and the nucleus may take place in future. Thus the nucleus is open. If the Finnish breeding programme is carried out according to the presentation above, the breeding population is satisfactory for gene conservation as well.

At an effective population size of 50 the loss of additive variance is 1 % and the coefficient of inbreeding increases also with 1 % per generation. Such a loss of variance and increase of inbreeding is not regarded as a threat to future breeding (*e.g.* Danell, 1993). A prerequisite is that each tree contributes equally to the progeny, which can be achieved by artificial crosses.

In the breeding programme outlined for Sweden by Danell and Werner (1990), a selection of 1,100 plus trees, of which 900 should originate from a representative selection within Sweden was suggested. Additionally 200 trees should be selected in progeny trials with material of Finnish, Baltic, German, or Polish origin. Four zones of cultivation according to latitude with an elevation border at 300 m ASL was suggested. This programme would be satisfactory for gene conservation of silver birch in Sweden. However, the funding for silver birch breeding did not allow the executing organisation, SkogForsk, Sweden, to implement this programme. For southern Sweden a breeding programme is carried out with clone trials (Lars-Göran Stener pers. comm.). Based on the results from this testing, southern Sweden will have one or two breeding populations each with at least 50 trees. In Sweden approximately north of latitude 60

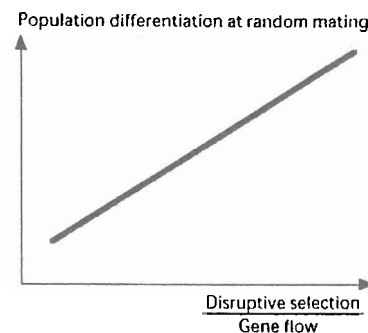
there will be no breeding with domestic material. In this part of the country breeding does not take care of gene conservation. The number of trees in the southern part of the country is at the lower limit of trees required for long-term gene conservation.

#### *No breeding or low-intensity breeding*

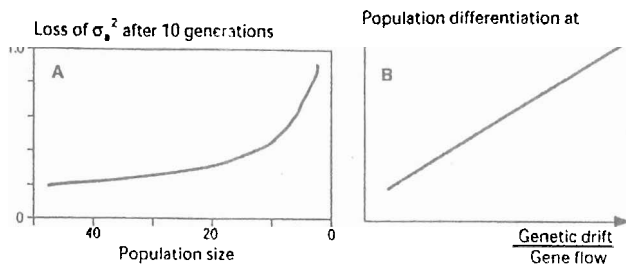
I will select *Tilia cordata* as an example of a species belonging to this group. Most of the information emanates from the excellent review on gene conservation of limes by Svejgaard Jensen and Kanger (1999). They reported that *Tilia cordata* mostly grows in mixtures with hardwoods and especially in oak hornbeam forests but it might be a component of the dominating forest in east Europe. In Scandinavia there are problems with seed maturation that might be the reason for its northern range of distribution (Pigott and Huntley 1981). *Tilia cordata* hybridises with *Tilia platyphylla* but the differences in time for flowering is a constraint to spontaneous hybridisation.

According to Svejgaard Jensen and Kanger (1999) there are no breeding activities and almost no genetic information available. This means that educated guesses about the population differentiation have to be relied upon.

I have treated the sampling of gene resource populations in absence of genetic knowledge earlier (Eriksson, 1998). The focus of that paper was on the evolutionary factors that promote and prevent among-population differentiation. In random mating populations the strength of the two counteracting forces, disruptive natural selection and gene flow, determines the degree of among-population differentiation that will take place in a species (Fig. 1). In species with small population sizes



**Figure 1.** Schematic illustration of the influence of the counteracting forces, disruptive natural selection and gene flow, on the expected among-population differentiation. The stronger the disruptive selection in relation to gene flow, the larger the differentiation.

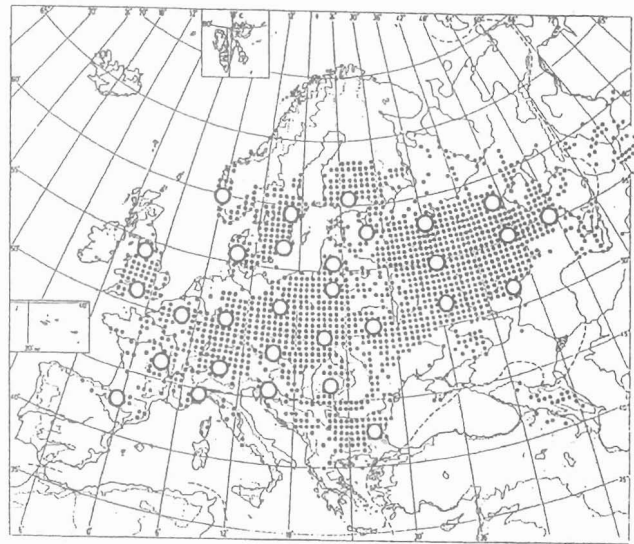


**Figure 2.** *A* – the relationship between loss of additive variance after 10 generations and decreasing effective population size. *B* – schematic illustration of the influence of the counteracting forces, genetic drift and gene flow, on the expected among-population differentiation. The stronger the genetic drift in relation to gene flow, the larger the differentiation.

this differentiation depends on the strength of genetic drift and gene flow (Fig. 2). *Tilia cordata* is generally characterized by small populations and it is expected that genetic drift will be of significance. Since bees mainly pollinate *Tilia cordata* it must be assumed that pollen transport (gene flow) does not take place over long distances. Therefore, genetic drift is probably the strongest evolutionary factor, which should lead to random allele fixation to a large extent. As a corollary of this, the population structure is expected to be rather patchy.

We have earlier argued for the use of the so-called Multiple Population Breeding System (MPBS) for gene conservation (Eriksson et al., 1993). Svejgaard Jensen and Kanger (1999) supported this suggestion. It would certainly be useful to establish seed orchards for different ecogeographic areas that should serve as producers of seed for reforestation of gene resource populations. However, this option is probably unrealistic since there is no funding support for this option. Instead *in situ* gene conservation has to be carried out. By the aid of distribution maps for the species and climatic maps of that area some 30 subpopulations might be pointed out as *in situ* gene resources. One example of how subpopulations may be selected based on ecogeographic information is given in Fig. 3. Whenever possible the gene conservation of lime should be carried out jointly with other broad-leaf tree species in mixed stands.

The *in situ* MPBS method suggested for lime is recommended for many other broad leaf tree species such as alder, ash, beech, birch, maple, oaks, and elms under certain conditions (cf. below). The difference is that there is more genetic knowledge about beech and oaks than for lime. Therefore, the selection of subpopulations of beech and oaks is facilitated. In some countries there is an extensive gene conservation of some species. Thus, there are 255 gene conservation stands



**Figure 3.** One suggestion for sampling of gene resource subpopulations of *Tilia cordata* in absence of genetic knowledge. The map of distribution according to Pigott (1991).

of beech with a total area of 2201 hectares in Germany (Stephan 1998). This is far beyond what is needed from a genetic point of view. Although this might be regarded as a strong guarantee that the gene resources of beech are saved, it might be detrimental politically if gene conservationists in other countries are claiming such a large area for gene conservation of species much less abundant than beech in Germany.

Close to the margin of the distribution the species will be rare and for these regions the gene conservation of rarely occurring species should be followed (see below).

#### *Multipurpose tree species*

Both chestnut and walnut are probably introduced species and have served man for millennia as food resources (Fernandez-Lopez and Alia 2000). Chestnut was a useful crop for poor people as a substitute for cereals since the nuts are rich in carbohydrates. Therefore, selection of material with desired nut quality has gone on for millennia. Nowadays the nuts have become a part of fancy food and many of the cultivars used by poor people in remote areas are threatened owing to the substitute of chestnuts with other carbohydrate products and by human movement from such areas. For the time being there is an interest in improvement of the timber quality of these two tree species which have highly priced wood for furniture. Chestnut occurs both as a domesticated species in fruit orchards and also as a high forest species, mainly in mixed forests in the Mediterranean countries.

There are chestnut populations in the wild and there is a fear that gene flow from cultivars highly bred for fruit production will reduce the adaptedness of wild populations. In certain areas there are serious attacks on chestnut by two fungal diseases caused by *Phytophthora* or *Cryphonectria* species. For this reason the Asian chestnut species, *Castanea crenata* and *C. mollissima*, have been used in crossing work to obtain resistance. Owing to this there is a potential for spontaneous interspecific hybridisation. Species hybrids have another growth rhythm, which might lead to increased exposure to damaging frosts. Besides, hybrids are less drought tolerant. For this reason interspecific hybrids are only wanted for areas without summer drought but with disease problems. The use of coppice forests with repeated regrowth from the same stools creates good conditions for building up strong footholds for diseases and pests. Since there is almost no natural regeneration in this kind of silviculture, natural selection for disease tolerance does not occur.

For populations in the wild the MPBS concept is suggested with a selection of at least 20 subpopulations according to ecogeographic principles. Cultivars from different regions will be gathered in clone collections. In clone collections for regions in which there are disease problems, grafts of the two Asian *Castanea* species might be included to facilitate the production of disease tolerant interspecific hybrids.

#### *European white elm*

Collin (2000) gave an excellent treatment on gene conservation of elms and my treatment is largely based on his report. According to this report the major threat to European white elm is not the Dutch elm disease but the destruction of the riparian habitats, which is the habitat for most European white elms. This destruction has led to low census number of trees in most populations and Collin raises the question whether it is realistic with *in situ* conservation under such conditions. Moreover, a low effective population size probably has led to a great impact of genetic drift. Since the species is wind-pollinated and since the distances between adjacent populations are not large there might be a gene flow between adjacent stands. This would lead to a stepping stone structure of the population variation. The most important measure to take is to increase the population size. Planting of seedlings or cuttings from the same river system could do that. A method also suggested for *Populus nigra*, another tree species of the riparian ecosystem (Heinze and Lefèvre, 1999). A

more radical means would be to collect scions for grafting or vegetative propagation to establish clone archives or clone seed orchards for production of material for regeneration. The disadvantage with the latter method is that it takes more time until the reinforcement of the populations in the wild is possible. The advantage of the seed production is that commercial material might be offered to forest owners.

#### *Wych elm*

It should be noted that DED shows cycles in outbreaks of the disease probably caused by a large die off of mature trees leaving no breeding ground for the *Scolytus* insects.

A great emphasis was given to vegetative propagation for establishment of clone hedges, which are kept low by regular pruning (Collin, 2000). This treatment makes the hedges unattractive to the *Scolytus* insects and thus no transfer of the disease takes place. Cryopreservation has also been utilised for conservation (Collin, 2000). Sampling should be based on educated guesses about existing genetic variation. It is of great significance that screening for tolerance against the DED takes place in the conserved material. *In situ* conservation should follow the general recommendations for other noble hardwoods not included in breeding activities (cf. above) but with a higher number of subpopulations to increase the probability that some will survive. Another reason for increasing the number of subpopulations is the large variability in morphological traits. Wych elm is advantageously included in joint gene conservation of other noble hardwoods. Owing to the risks for attacks of the DED, measures should be taken to promote flowering so that seedlings are available when an attack of DED appears. When such an attack appears Collin (2000) recommended that one should *practice sanitation (prophylactic cuttings and pruning, trap and destroy bark beetles,...) in the conservation unit and its vicinity.*

Finally, systematic research activities are urgently needed to find solutions to the susceptibility to DED.

#### **Rarely occurring species**

The main focus will be given to the wild service tree (*Sorbus torminalis*) which recently has been highly appreciated for production of veneer.

To safeguard the future potential for adaptation of this type of species means that the main emphasis must focus on an increase of the effective population size. Hauser et al. (1994) who focused on conservation of

rarely occurring herbaceous plants also advocated for an increase of  $N_e$  in gene resource populations. For wild apples and wild pears, an additional objective is to preserve the wild species and thus to avoid contamination from cultivated varieties (Kleinschmit and Stephan, 1997).

In Germany collection of scions for grafting of rarely occurring species was carried out (Kleinschmit, 1994). The grafts are planted in seed orchards or clone archives that are expected to produce propagation material for reforestation of progeny plantations (Fig. 4). Such progeny plantations are not necessarily aimed for progeny testing rather to increase the population size of the species. This is a cost demanding operation that cannot be carried out in most countries owing to funding limitations.

A useful alternative for increasing the population size of rarely occurring species is to produce seedlings and offer them free of charge to forest owners. This is to some extent applied for rare oaks in Apulia, Italy (Schirone pers. comm.). This type of a low-cost increment of the population size could advantageously be done in many other situations as long as exotic material is not included. I anticipate that many forest owners would be most interested in establishing such plantations to participate in the saving of biodiversity.

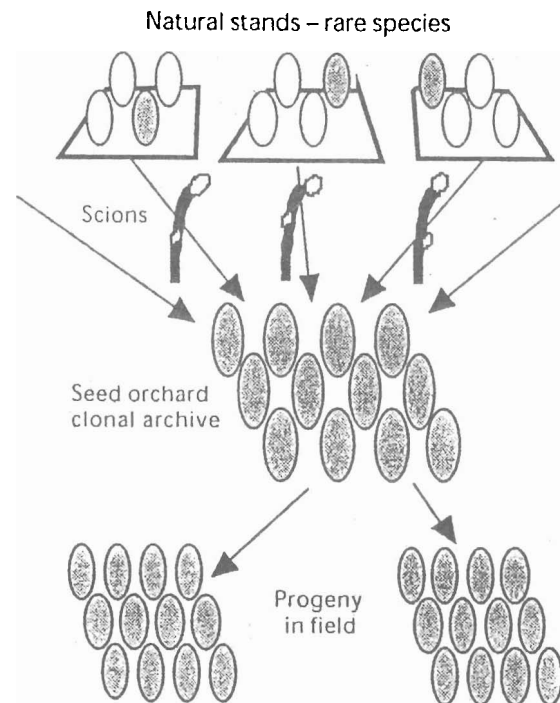
A considerable risk for the rarely occurring tree species is the poor knowledge about tree taxonomy among foresters responsible for silvicultural operations. Therefore, it is highly likely that many of these trees have been cut during thinning operations. This has probably taken place only with respect to economic considerations without intention to risk the existence of a species. Therefore, teaching in taxonomy must be improved in foresters' education.

Rotach (1999) gave useful recommendations on how to promote rarely occurring trees by silvicultural means. In many cases they are not competitive with dominating trees in their ecosystem. Therefore, thinnings must be done such that the rarely occurring species are not out-competed by the climax species. Rotach (1999) pointed out the importance of forest margins, coppice forests, and forest patches in agricultural land for conservation of the light-demanding, slow-growing species of low stature like wild, apples, wild pears, and *Sorbus* species.

As stated previously many species are rare close to the margin of their distribution. Therefore, any gene conservation agency can utilise the methods suggested for rarely occurring species for all species, which are rare under the domains of their responsibility.

### General remarks about methods in gene conservation

Most of the broadleaf tree species are so called ecological keystone species in the sense that many other species are dependent on them for their existence. To match the objective of gene conservation of associated species it might be useful to extend a few of the subpopulations of the MPBS method to cover 200-300 hectares (cf Varela and Eriksson 1995). Within such a large subpopulation a large variation in site indices should be aimed at since many associated species are dependent on different habitats (cf. Berg et al 1994). Since different species are dependent on different stages of development within an ecosystem one way is to keep different age classes as is illustrated in Fig. 4. It is also important that a certain area is set aside as a nature reserve without any human intervention.



**Figure 4.** Schematic illustration of the method applied in Germany to increase the effective population size of some of the rarely occurring species. Separate orchards are established for different ecogeographic zones.

Generally, utilisation of a species is positive for its conservation since this means that there is an economic value of the species that mostly promotes understanding for the necessity of gene conservation. Supply of local seedlings or seeds to forest owners free of charge is a low-cost alternative for conservation of the species.

**Concluding remarks**

Before any methods are suggested it is important to clearly identify the objectives of gene conservation. The EUFORGEN network for noble hardwoods has identified the following objective as the prime objective:

*To safeguard the potential for adaptation of the species*

This objective is the most important objective according to my understanding. Methods to meet the objective of safeguarding the potential for adaptation are summarised in Table 1. To preserve the wild status

**Table 1.** A summary of suggested gene conservation activities for different groups of species to meet the objective: *to safeguard the evolutionary potential of a tree species*. From the textbook "Forest genetics – an introduction" by G. Eriksson and I. Ekberg

Commonly occurring	Species included in intensive breeding	<i>Ex situ</i> MPBS + complementation with populations in the wild when needed
	No breeding or low-intensity breeding with genetic knowledge	<i>In situ</i> MPBS selected according to genetic knowledge
	No breeding or low-intensity breeding without any genetic knowledge	<i>In situ</i> MPBS selected on ecogeographic principles
	Multipurpose breeding: wood and nuts	MPBS for wood in naturalised forests + clonal archives for nuts
	Endangered by Dutch elm disease	Low clonal hedges + <i>in situ</i> MPBS whenever possible
	Rarely occurring With possibilities for investments	Clonal archives + progeny plantation for each ecogeographic zone
	Rarely occurring low-cost alternative	Promotion of the growth conditions + delivery of seedlings free of charge to forest land owners

of species such as wild apples and wild pears is another objective.

Most broadleaf tree species from Scandinavia and the Baltic countries are not included in any breeding programme. Therefore, the genetic knowledge is limited for most species. Educated guesses about genetic variation among populations have to be relied upon to

identify gene resource populations. Life history trait characteristics of the various species give some assistance for the guesses. Thus, species with a considerable gene flow among populations is expected to have less population differentiation than a species with restricted gene flow if the two species share the same distribution area. Variation in climatic and edaphic conditions in the distribution area will also give hints about potentials for population differentiation.

Generally the *Multiple Population Breeding System* concept is suggested for all commonly occurring species. It is taken for granted that each subpopulation in this case has an effective population size of at least 50. For species in intensive breeding the breeding population is generally satisfactory for gene conservation. For regions, in which there is no breeding, *in situ* gene resource populations have to be identified. For lack of funding the *in situ* method must be applied for species not included in breeding. Preferably joint gene conservation for several species could be applied. For multipurpose species such as chestnut and walnut separate gene conservation for populations in the wild and cultivars is suggested. It is assumed that these two types of population have deviated so much that joint gene conservation will not be sensible. The main threat to tree species in riparian ecosystems is the conversion of such ecosystems to other land uses. The MPBS method might be used in this case too, but in many instances there might be a need to increase the  $N_e$ . In such cases the increase has to be done with trees from the same ecogeographic region. The great threat to wych elm by the Dutch elm disease requires that clone archives are established and kept as low hedges to avoid attacks by the disease vector. Whenever possible the *in situ* MPBS system might be used for populations in the wild.

The approach used in Germany for some of the rarely occurring species is recommended whenever financial support is available. For this type of species seed orchards or clone archives are established with material from different ecogeographic zones. This is done to increase the  $N_e$ . The progeny will be planted in forests and natural selection will have an influence on the next generation. When funding for such intensive gene conservation is not available it is useful to promote the growth conditions in the stands where rarely occurring species grow. Since these species are rarely occurring it means that foresters not always are aware of their existence and many trees might be thinned unintentionally owing to lack of knowledge. An im-

provement of the taxonomic knowledge among foresters at various levels is highly desired. Offering plants of the rarely occurring species free of charge to owners of forestland is another useful means to increase their number.

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