DYNAMIC *IN SITU* CONSERVATION OF GENETIC RESOURCES IN FAGACEAE: CONCEPTS, GOALS AND SILVICULTURAL CONSEQUENCES

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Abstract:--Conservation of forest genetic resources may be realised in different ways. Thus, *in situ* as well as *ex situ* conservation or static as well as dynamic gene conservation are basic concepts differing on principle. In Europe, forest genetic resources are often to be maintained *in situ* in certain gene reserves but genetic conservation may also be performed within stands being managed by routine forestry and especially silvicultural practices. Clear conservation concepts as well as a unambiguous definition of the goals are often lacking. Conservation of genetic resources within certain gene reserves means that genetic conservation is an objective with relatively high priority. As a consequence, in respectively designated conservation stands other objectives can in contrast only be of subordinate importance and forestry practice, especially silviculture, will have to serve primarily the achievement of the management objective "conservation of genetic resources". Using three widely distributed Central European genera of *Fagaceae,* i.e. *Quercus, Fagus* and *Castanea* as an example, some concepts of the conservation of genetic resources in definite gene reserves as well as silvicultural consequences are outlined and critically discussed. In this context we could show that quite different approaches of gene conservation are needed for the three closely related genera.

INTRODUCTION

Generally, the conservation of genetic resources serves various motives and objectives. Depending upon the selected goal and the available external conditions there is a huge number of methodical options. These have been explained and discussed in detail by various authors such as Ziehe et al. (1989). At present it is largely acknowledged that dynamic methods of conservation of genetic resources are to be given preference over static methods with the latter being reasonably applicable in special situations only. Additionally, it is also widely accepted in literature that *in situ* conservation is to be given preference over *ex situ* methods as long as possible (e.g. Ziehe et al., 1989; Hattemer, 1995, 1996). However, feasible concepts for the conservation of forest genetic resources are still missing. Although our knowledge of evolution and population ecology of the forest tree species is still poor, it seems to be appropriate and important to make concrete proposals, based upon the state-of-the-art, as to which procedures should be pursued in gene conservation efforts. Some concepts of conservation of genetic resources are to be introduced and discussed using Central European *Fagaceae* species as an example. Moreover, criteria for the selection of genetic resources as well as preliminary proposals for silvicultural practice concerning gene conservation stands in consideration of the genetic peculiarities within the genera *Fagus, Quercus* and *Castanea* are derived.

Concepts for the selection of gene conservation stands

Considering the entirety of all presently discussed gene conservation efforts, they can be reduced to few basic objectives (Ledig, 1986, 1988; Ziehe et al., 1989). At first there is the traditional goal of the conservation of the genetic basis for certain phenotypes of economic interest, not at least as a base for a further advancement of forest tree breeding. This traditional goal is increasingly replaced or broadened

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by other, evolutionarily relevant goals like the conservation of genetic adaptability or the continuation of a preferably large degree of genetic variation as such (Ledig, 1986, 1988; Ziehe et al., 1989). The last named goals are, however, fairly identical, so that it appears appropriate to summarize them under the collective term "conservation of genetic adaptability". Beyond this, the continuation of adaptedness to the real and likely very specific environmental situation should be named as another fundamental aim, which in particular within the framework of preventive nature conservation still plays a comparatively large part.

If several of these goals are to be achieved, an order of ranking will have to be defined. This essentially depends on the extent of predictability of future environmental conditions (Gregorius, 1991, Hattemer, 1995).

Analogous to the definition of the target system of gene conservation, the priority compared to other goals like *e.g.* timber production, recreational function or hunting has to be determined. "Gene conservation stands" in the narrower sense should only be designated, if this target system assumed the highest or at least a very high priority over the other management goals. Otherwise, conservation of genetic resources can and should be taken likewise into account, however, in the case of a conflict of different goals they will have to recede in favour of other objectives. However, expensive activities for genetic conservation will only be reasonable, if their long-term effectiveness is ensured. If „conservation of genetic resources" is the highest ranking goal, all instruments of forestry practice, in particular silviculture, will have to primarily serve this management objective. Consequently, other forest objectives can thus only be pursued, if conflicts with the goals of gene conservation are excluded.

In the case of preventive gene conservation efforts, in which the object has not yet been implicitly defined by the target system, the next issue of interest refers to the selective criteria of the stands and populations to be conserved. This, however, is rather difficult, since until now only few clearly formulated and applicable criteria for the selection of genetic resources are available.

Regarding the possible objectives given above, it is quite apparent that the conservation of genetic resources for the purpose of maintaining such genotypes which correspond to particular traits, will usually fail, because of the fact that the knowledge of what kind of gene loci are involved in the expression of a character is missing. Thus, in this case the selection of stands can only take place based on the existence or frequency of certain phenotypes in the stand itself and – most favourably – additionally in its progeny.

However, much more interesting than this are the two other objectives mentioned – the conservation of adaptedness and/or adaptability. The conservation of adaptedness to a broad spectrum of environmental conditions in the range of a species requires the conservation of such populations which -in view of their genetic structures- preferably represent the sum of all populations of this species. Hence, such kind of populations are to be selected, which are characterised by a preferably low genetic differentiation.

In this context it seems, however, noteworthy, that a differentiation between populations does not necessarily give rise for conclusions regarding the extent of genetic variation (variability and diversity, respectively) manifested in them. Thus a population may possess a high degree of genetic differentiation either because of a fairly high variability or diversity; but also *vice versa, i.e.* that a single or a few populations reveal a particularly low variability in diversity, while the majority of the rest of the populations is very variable. In addition to this, a population may attain a high extent of genetic differentiation if, though being comparable in its degree of genetic variation with the other populations, it differs in its specific endowment with genetic types (genotypes and mainly alleles). So, if intending to incorporate in a gene conservation programme besides preferably representative populations also such ones just containing particularly rare genotypes (perhaps resulting from adaptation processes or genetic drift), the low degree of differentiation is insufficient as a sole criterion. Instead, especially highly differentiated populations have to be involved additionally.

Furthermore, the preservation of a preferably high adaptability can be the objective of gene conservation. Here, populations distinguished by high operating and, above all, latent capacities of adaptation are to be focussed on. In this regard the measures of genetic differentiation are not necessarily helpful. Instead, we will need parameters of genetic variation and diversity as selective criteria.

Finally, a combination of the two last-named selective concepts in terms of a conservation of both less differentiated populations and such ones distinguished by their above-average genetic variability and/or diversity is conceivable.

According to the above deliberations, it may be just the last mentioned conception that seems to be a proper basis, at a reasonable expense, in particular for the preventive designation of genetic resources. In this place yet another requirement within the framework of genetic conservation programmes of forest trees is noteworthy, *i.e.* the application of tools to control the success. Independent of the primarily defined objectives and the selected concept it is important to test also in what regard the objectives could be achieved. This comprises especially a regular genetic investigation of the progeny of the selected stands (see below) in view of those characters and parameters, which were decisive for the original designation.

Additionally, also phenotypic characters are appropriate besides the genetic markers, which are indicative of the vitality of forest tree populations and provide some evidence for a sufficient adaptability.

Without any control as to the achievement of objectives the designation of genetic resources does not make much sense: as will be explained below the presently existing base of data and criteria in connection with gene conservation is still rather poor. Hence, the regular modification of the procedure by involving the latest scientific findings is a must, as was already pointed out in the introduction. In this respect, the long term controls to be regularly conducted are indispensable because in this way the connection is created between the concrete object and the sum of the knowledge to be newly gained in the future.

Selection and management of gene conservation stands by the example of the *Fagaceae*

Selection of gene conservation stands

The peculiarities of the reproduction systems of *Fagaceae* on the one hand as well as the knowledge of the genetic structures gained until now indicate joint characteristics but also point to interesting peculiarities within this family. If the above-named facts are elucidated, the question which parameters should be focussed on regarding the genetic adaptedness and adaptability suggests itself.

Genetic markers are existing until today mainly on the basis of enzyme polymorphisms. Thus, such biochemical-genetic markers may serve as a pragmatic criterion for the selection of gene conservation stands. It needs to be discussed, if or to what an extent phenotypic characteristics, with the knowledge of the genetic control being absent, can or should likewise be taken into consideration besides genetic criteria. Here in particular such characteristics should be remembered, which can be used as a criterion for the vitality of a stand. However, referring to such phenotypic criteria as the sole or main basis for decision making should be abstained from.

However, also the use of genetic parameters that were determined based upon isoenzymic gene loci needs to be critically reviewed. The advantages and drawbacks of this group of markers have already been thoroughly discussed elsewhere (e.g. Herzog, 1988). Thus, the hint may suffice in this regard that expressed and presumably in most cases also adaptive genetic information is the object of consideration. This seems to be an important argument in favour of the use of isoenzyme systems. The main disadvantage of the latter, namely the restriction of being few in number, not randomly selected gene loci requires also to involve molecular marker systems, *i.e.* those at the level of DNA, if these are available for routine investigations (Krabel et al., 1998).

Concerning the reproduction system of *Fagaceae,* anemophily is a property which just bears great importance for selection of gene conservation stands. It seems to be responsible for the low degree of genetic inter-population differentiation in beech *(Fagus sylvatica,* Comps *et al.,* 1990, Gömery et al., 1992, 1997; Starke et al., 1995; Turok, 1995; Konnert, 1995; Larsen, 1996; Hazier *et al.,* 1997, and *Fagus taurica,* Gömery et al., 1998) as well as in oak (concerning the Southwest European distribution area of *Quercus robur* and *Quercus petraea,* Kremer et al., 1991), with a comparatively high genetic variation occurring simultaneously at the intra-population level.

On the other hand, the ability to vegetative propagation, undoubtedly existing in oak as well as in sweet chestnut *(Castanea sativa),* has obviously various consequences concerning the anthropogenic effects on the genetic structures. In oaks, the coppice system, which used to be practised, had virtually no consequences regarding the parameters of genetic variation in the high timber forests that had emerged from the former coppice stands (Herzog 1998). Compared to this, the data referring to the genetic structures of sweet chestnut *(Castanea sativa,* Fineschi et al., 1994) reflect influences of a regular vegetative propagation.

While beech shows, fairly uniformly, a high genetic variation at the intra-population level as well as small differentiation values at the inter-population level, this holds only partly true for oaks stocking in Central Europe. Here too, we mostly encounter comparatively high variation parameters at the intra-population level, but at the same time a rather high differentiation at the inter-population level. The latter does not follow any unambiguous geographic cline (Müller-Starck et al., 1993; Herzog, 1993, 1994, 1996a,b; Herzog and Müller-Starck, 1993; Herzog and Krabel, 1994, 1996, 1998).

The conclusions for selection of gene conservation stands solely resulting from these observations are thus rather different with respect to the genera of one and the same botanical family. Hence, in beech, relatively few but large populations or even metapopulations are to be introduced in gene conservation programmes, since obviously a broad evolutionary continuity is given here.

Oak does not reveal such a pattern in all regions of its range. Instead, in Central Europe we partly encounter a very high differentiation, sometimes between immediately adjacent stands. From this one may conclude, that there was quite a considerable anthropogenic influence by forestry over the past few decades. This requires a different procedure in gene conservation: because of the supposedly artificial establishment of numerous stands the metapolulation is getting less important here, while the individual (perhaps also small) stand, provided that it comprises genetic characters worth of conservation, shifts to the focus of interest. The still intensively discussed issues of taxonomy of the Central European oaks, based on the differentiability and hybridisation of pedunculate and sessile oak (Kleinschmit et al., 1995a,b; Hertel and Degen, 1998) are not to be further deepened here, but even in this context consequences for the selection of gene conservation stands are becoming apparent. In the case of doubt this question should be answered in terms of a large-scale deregulation, *i. e.* the affiliation of a population in question to a species or the presence of definite or unequivocal hybrids between pedunculate and sessile oak should not be a primary factor in the designation of gene conservation stands.

Concerning *Castanea sativa* the number of available investigations dealing with this question is still rather small; but according to the results of previous authors, it seems appropriate to look primarily for such stands, which are capable of generative reproduction over longer time periods. Beyond this, the facts pertaining to oaks hold likewise true here.

Management of gene conservation stands

Silvicultural management of the forest stands can take place in different ways. At present, depending on the region and land owner, we encounter the whole spectrum, starting from a type of management being not influenced by the goal of gene conservation and oriented by the previously agreed aims up to a management according to the principles of natural forests or more fittingly expressed "absence of management". These extreme points should be avoided in stands which primarily serve the purposes of conservation of genetic resources. In the former case the question arises as to which end a special designation is performed, unless there is the preparedness to change the order of ranking of hitherto valid goals in regard to the newly introduced objective. Thus, an unaltered acceptance of the hitherto valid forms of management in connection with newly designated gene conservation stands is supposed to be appropriate in exceptional cases only. If, however, the conservation of genetic resources is not of prime ranking, the special designation of the stands concerned does not make much sense either, especially because the commitments accruing from international conventions anyway require, at least for the forests under public law, to preserve biodiversity including the genetic resources.

Conversely, a renunciation of forest management in connection with the designation as a gene conservation stand seems to be rather improper, because the condition regarded for various reasons as valuable and therefore worthy of conservation (in terms of a snapshot during the stand lifetime over decades or centuries) is, in most cases, virtually the result of a more or less intensive forest utilisation over decades. To designate such stands as a wilderness area (Totalreservat) implies the risk that quite different genetic structures may emerge under the new selection conditions. Moreover, succession processes may cause that single tree species will become rather rare or even disappear, among them possibly also the target tree species.

Consequently, for the future management of gene conservation stands a careful approach is desirable and drastic changes should be avoided. Nevertheless, silvicultural methods should be taken into account in view of their effects on the genetic structures, and be modified, if appropriate.

Concerning the regeneration of gene conservation stands, the natural regeneration or at least the regeneration from the local seed material is favoured on a regular base. This requirement, seeming to suggest itself intuitively, has, however, to be questioned: gene conservation stands are, as outlined above, stands having a certain, often-unknown genetic structure which has predestined them for selection. Hence, the long-term objective is to conserve this structure. Moreover, the aspect of dynamics is complied insofar as, with respect to changing environmental conditions, also an alteration of the genetic structures by way of an adaptation to the latter is permissible and even desirable. Against this background the natural regeneration indeed seems to be an appropriate method to ensure the preferably large-scale identity of mature stand and progeny with respect to their genetic structures. In this connection, also the refusal of reproductive material (seeds, plants) which has not been derived from the stand concerned appears to be appropriate for gene conservation stands. Nevertheless, the following factors should be involved in the considerations about regeneration of gene conservation stands: just in the case of anemophilic species like the *Fagaceae* it is surely advisable to include in the conservation concept not solely the population to be conserved, but likewise the surrounding stands as pollen donators in terms of a metapopulation (e.g. Hattemer, 1996). Dynamic gene conservation as such does in the first place not interfere with the introduction of reproductive material from outside. However, assuming that the specific conservation objective just strives for a high identity between parent stand and progeny stand (see above), the usage of local reproductive material from the stand concerned appears to be most appropriate when natural regeneration is insufficient in the designated gene conservation stand. If the stands to be preserved are already characterised by very small population volumes, which do neither allow a natural regeneration nor a collection of sufficient reproductive material, so, based on the objectives of gene conservation, it is to be weighed up, whether perhaps an *ex situ* conservation is indicated (above all, under lasting detrimental environmental impacts) or whether planting or, yet better, seed material from other regions is to be introduced for complementation of those stands. At a first sight, only small differences in genetic structures of the seeds in various years of partial or scattered mast. However, these differences are of the same magnitude than the differences between various beech stands (Krauhausen, 1985, Gregorius *et al.,* 1986). These authors found comparative results for the genetic differentiation between various parts of the stand (upper, mid- and lower slope), which, in part, is higher than that between different seed years.

Apart from exceptions, regarding pedunculate and sessile oak in mast years there is a comparatively great similiarity between the initial stand and the progeny grown from the seed material (Herzog, 1998). Moreover, also the procedure applied in seed collection, expectedly, affects the genetic structures in the seed material. So Ziehe *et al.* (1998) were in a position to show that a harvest taking place primarily punctually, i.e. using nets underneath heavily fructifying stands appears to represent the mature stand less properly than the picking-up of beech-nuts from the soil according to a grid.

Concerning the seed harvest, in gene conservation stands the following can be concluded: If possible, a large number of parent trees should be involved in the seed harvest. Not least, this would also have favourable effects on the representation of plastidial and thus maternally inherited genetic information. On the other hand, an immediate seed collection from the parent trees is not obligatory, provided that the nuts can be systematically picked up from the ground. At the same time, the harvest of few, heavily fructifying individual trees of a stand should be regarded as obsolete.

As outlined above, the orientation by the provenance can merely be a clue for stand establishment in gene conservation stands. Likewise, mention was made of the fact that a natural regeneration creates, in most cases, the best preconditions to implement objectives of the conservation of genetic resources. Therefore, natural regeneration should be more often discussed also in regard to oaks, although, presumably, the problems linked with it are more complex than in beech. Especially the fact that oaks are light-demanding and thus the necessity to open up the stands so as to encourage regeneration at a very early point of time, or the comparatively rare occurrence of mast years - at least in the past- may prohibit natural regeneration on a larger **scale.**

If, as already discussed, natural regeneration is impossible for certain reasons, so from the genetic point of view seeding is preferable over planting. However, if planting is unavoidable, it should, if possible, be carried out using reproductive material from the same stand. High numbers of plants and avoiding intensive seed sorting, so as to possibly allow for long phases of adaptation processes under the site-relevant environmental conditions also should help to maintain genetic adaptability (see also Ziehe et al., 1995).

Concerning the tending of young stands it may be assumed that goals of gene conservation and high-grade timber production during this phase of stand life are well compatible, and thus via young stands with great stem numbers a relatively high genetic adaptability may be obtainable even beyond the first decade of tree life.

Regarding the next phase of stand development the question is raised for the effects of tending interventions (thinning) on genetic structures and, in particular, on allele frequencies. As for beech an investigation conducted by Lauber *et al.* (1997) exists, in which merely slight impacts on the genetic structures have been ascertained.

Finally, Konnert and Spiecker (1996) dealt with the consequences of utilisation by exploitable size and selection thinning in beech. It could be shown by the authors that in view of a utilisation by exploitable size distinct allelic distances occurred between the remaining and the removed group of trees. Within the framework of selection thinning the elite trees that ought to be encouraged because of their value, were greatly coincided with the largest-diameter trees of the stand. Since besides the elite trees also other stand members are to be incorporated in the reproduction, this procedure, as a whole, tends to slightly better approach the state of natural stand development. Thus, a first conclusion is the demand that in gene conservation stands the methods of utilisation by exploitable size should be withheld so that the first interventions are only conducted when the stand has entered the stage of regeneration. In principle, the following has to be adhered to for gene conservation stands: Stand members to be removed and those which will remain should not be too highly differentiated, and stand members to be harvested including their progeny should be sufficiently represented in the succeeding generation. This presupposes a preferably lengthy reproductive phase. The latter, in turn, requires long rotational periods. According to our present knowledge and against the background that the ability to fructification hardly declines with increasing age, and in view of the general tendency towards prolonged rotational periods (von Lüpke, 1993) this is supposed to be unproblematic as to its implementation.

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