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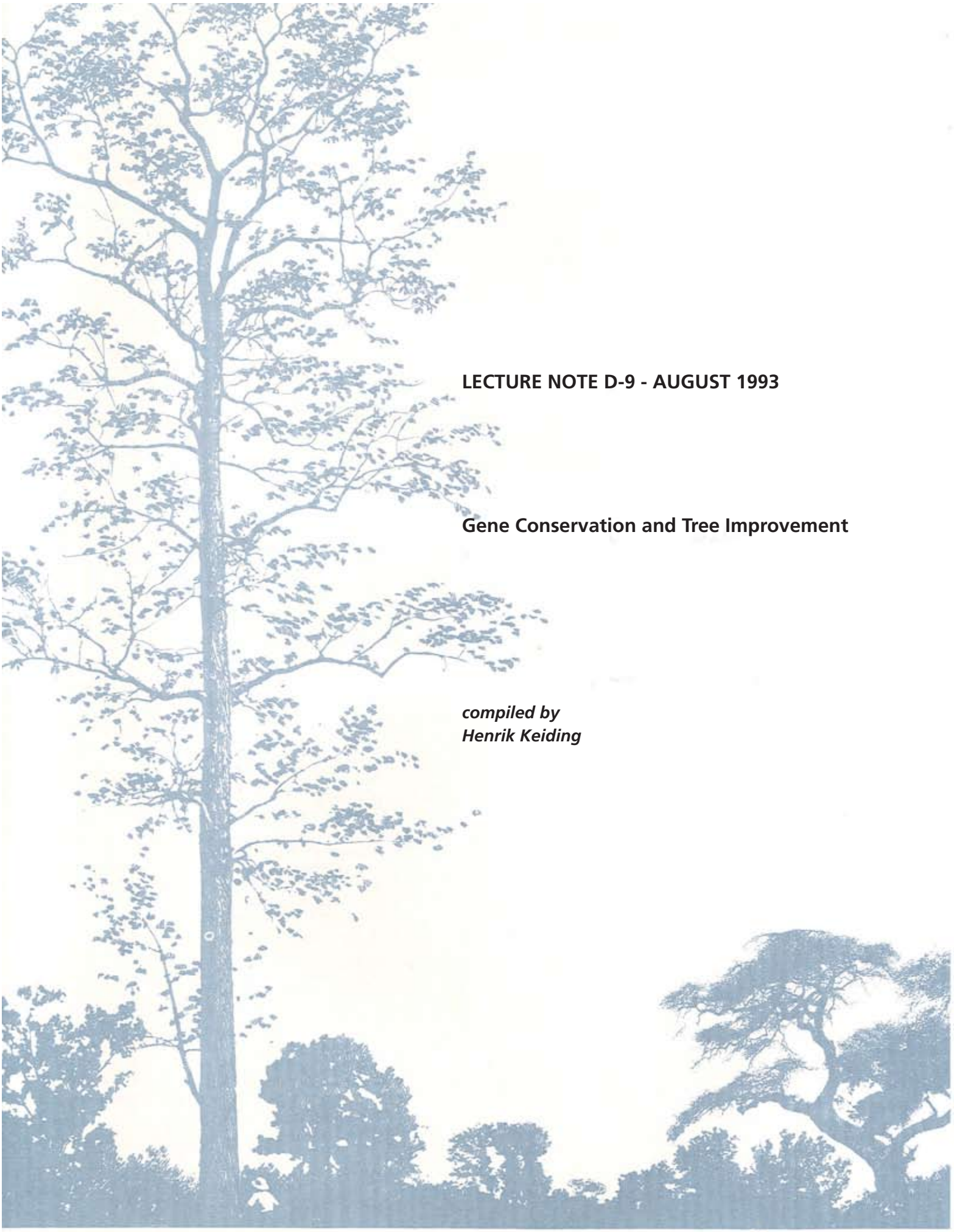

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Gene Conservation and Tree Improvement

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1. Introduction

The **aim** of tree improvement is to increase production and quality of trees in connection with planting. The concept "Improvement" implies that a growing proportion of individual trees in successive generations possess the characteristics that suit the users. The **rate** of improvement is measured, initially, against the performance of base populations or the natural occurrence of the species. It may also be considered a measure of the effectiveness of selection or the ability to remove undesirable genes from the original populations.

The **potential** for improvement or scope for selection depends fundamentally on the genetic variability of a species as it has evolved in nature.

The genetic variability is an expression of genotypic differences between individuals in a population i.e. that individuals have different gene compositions. The more variable the genotypic constitution between individuals (the broader the genetic variability), the better the chance, generally speaking, for a species or population to reproduce and survive or adapt itself to changes in environmental conditions. This circumstance may also provide tree improvement with a greater potential for selecting the genetic compositions aimed at.

However, in tree improvement programmes, only part of the genetic variability is used. The tree breeder will try to select and thereby favour only those gene combinations that serve his particular purpose(s). This process will mean a narrowing of the genetic variability or loss of certain genes, which may have serious consequences in an evolutionary context or with altered goals for the improvement. At the extreme, very high yielding but genetically uniform and vulnerable material may replace more robust and variable plantings with the added risk of large scale disasters due to pests and diseases.

As with other natural and reproducible resources it is therefore necessary to consider the sustainability of the genetic potential or the conservation aspect of tree improvement.

In the following some of the principal effects of operating with small populations (small compared with the total genetic variability) will be discussed.

2. Genetic Resources of an Improvement Programme

A »genetic resource« is defined as »a unit« of heritable variability of actual or potential value.

A »resource« is a stock or reserve upon which one may draw when necessary.

In other words, units of genetic variability in one form or another must be accessible if they shall fulfil their function.

Genetic resources occur at different levels of selection or intensity of breeding and therefore also with different degrees of genetic variability. Examples of genetic resources arranged, principally, in decreasing order of genetic variability are natural forests, ex situ conservation stands, selected seed stands, seed orchards, and clonal planting. See Fig. 1.

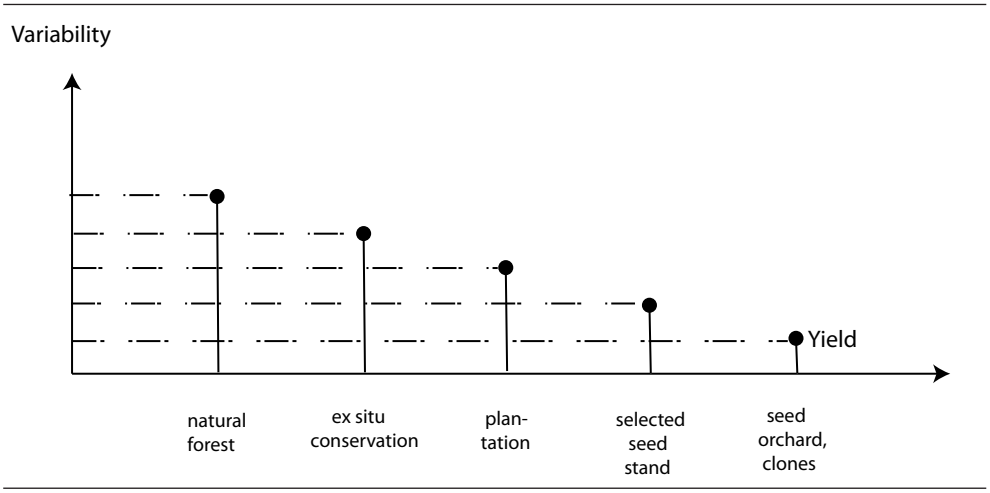

Fig. 1. A schematic outline of the connection between "yield" or progress in improvement and the levels of variability of the different genetic resources. [see also Lecture Note A-4.]

The crucial question then is how much of the original genetic variability we need to retain or conserve in a long term improvement programme in order to secure sufficient flexibility in utilization of the improved material.

There is no clear-cut answer to that because tree species exposed to selection and breeding have different genetic constitutions and react differently to breeding. Furthermore the knowledge of the genetic structure, breeding systems and reproductive biology is rather limited for most tropical species.

However, some of the observations and results from population genetics may inform us of the consequences of narrowing genetic diversity in the efforts to obtain improvement for specific purposes.

3. Sampling And Selection

A tree improvement programme operates implicitly only with part of the total genetic variability i.e. the part that exhibits a better average performance of the desirable traits than the base population.

When samples are taken from the base population, the genetic composition of the selected material will be less variable than that of the total base population evolved by nature because certain gene combinations may be lost or deliberately excluded in the pursuit of favourable characteristics chosen by man. This procedure will continue in subsequent generations of selection and will cause further reduction of genetic variability.

3.1 Effects of sampling on genetic variability

The subject of sampling is of fundamental importance for the founding and planning of a tree improvement programme. How do we combine conservation of genetic diversity with progress in quantitative and qualitative characters of the trees? How should we sample and arrange breeding populations for improvement programmes of different time perspectives?

The simple answer to that is that we have to know the genetic structure of the individual species, their breeding systems, reproductive biology, and mode of occurrence i.e. optimal and marginal areas to mention some of the more important characteristics. The equally simple statement regarding most tropical tree species is that this knowledge is usually limited.

We therefore have to use experiences from other crops in which studies of population or quantitative genetics are more advanced.

When taking out samples from the base populations, we reduce the frequencies of genes and their alleles. The rare ones of the latter are the ones that will be lost first. The significance of the loss will depend on the size of the sample, i.e. number of individuals per sample, and how representative the samples are of a species' distribution to different environmental conditions. There are other factors that influence the lowering of genetic variability in the smaller populations such as relationship of trees from which seed has been collected. This will be discussed later. See 3.3.

The most significant reduction of genetic variability in small populations takes place in subsequent generations, for populations of the same size, as demonstrated for the *Drosophila* fly. See table 1.

Table 1: The retention of genetic variance in small populations of constant size for a number of generations of *Drosophila* fly (Frankel & Soulé, 1981).

Population size *(N)*	Percentage genetic variance remaining after 1, 5, 10 and 100 generations			
	1	5	10	100
2	75	24	6	<< 1
6	91.7	65	42	<< 1
10	95	77	60	< 1
20	97.5	88	78	8
50	99	95	90	36
100	99.5	97.5	95	60

The table shows that the smaller the population, the more the genetic variance is reduced in subsequent generations.

It should be noted that these results for the *Drosophila* fly are indicative only. Other figures apply to other animal and plant species but the principle is the same. If population size in second and following generations is en-larged, the reduction in variance will be slower. Further, as to forest tree species the change in generations takes a much longer time so the effect on genetic variance will be correspondingly slower in showing up.

However, in spite of the difference between *Drosophila* and forest trees the fundamental effect on variability when operating with small populations should be kept in mind, as this is an essential part of any improvement programme.

3.2 Heterozygosity and homozygosity

In order to understand the consequences of sampling and selection in relation to conservation of genetic variability, it is necessary to look at the basic elements which decide the expression of the various characteristics i.e. the *genes* and their *alleles*.

For this purpose the following extract of "The packaging of genetic information" is cited from "Managing Global Genetic Resources. Forest Trees".

> "A gene ... is the basic unit of heredity and has one or more specific effects on an organism. ... the term "locus" refers to the position of a gene on the chromosome, and it is sometimes used interchangeably with the term "gene" when referring to regions ... that are influencing a trait.
>
> Alternate forms of a gene found at the same locus are called alleles. Some genes have many alleles, which allow for multiple gene products and therefore multiple phenotypes. For example, multiple alleles have been identified for many of the genes that code for human blood proteins. The

allelic frequency refers to the proportion of loci in the population occupied by each allele ...

Most organisms are diploid, meaning they carry two copies of each gene. If both copies are the same allele, the individual is said to be homozygous; if the two copies are different alleles of the gene, the individual is heterozygous for that locus ...

Variation can readily be observed at several levels: between species, between major types within a species, between populations within a major type, and between individuals. An individual's genetic composition, or genotype, in conjunction with the environment in which that individual is found naturally, determines the phenotype or observable characteristics.

Certain traits are controlled by a single gene and are referred to as qualitative ... Many characteristics, however, are influenced by a larger number of genes; these are called quantitative or polygenic traits. The cumulative action of these genes influences the expression of the trait, but the effect of any single gene is small and cannot generally be isolated in the phenotype. Important production traits, such as yield, growth rate, and straightness, are examples of polygenic traits. Occasionally, a »major« gene (one that has a stronger influence on the trait) can be detected, but there is nevertheless modification of the trait by other genes with smaller effects.

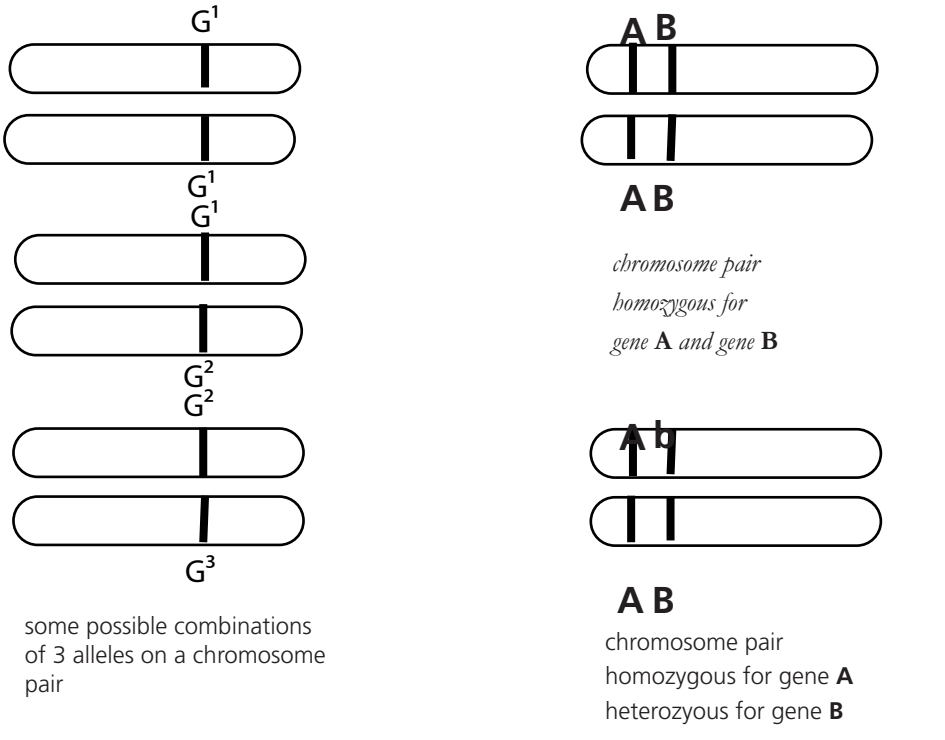

Fig 2. Some possible combinations of 3 alleles, G_1, G_2, and G_3 (left) and the meaning of homozygosity and heterozygosity (right). From Longman's Illustrated Dictionary of Botany.

3.3 Importance of heterozygosity

Genetic variability is expressed by the average heterozygosity per locus. Heterozygosity indicates the presence of a recessive and dominant gene at the same locus, as illustrated in figure 2. The alternative forms with two, both either dominant or recessive, genes at the same locus are termed homozygous. Heterozygosity is generally linked to viability or ability to reproduce and is therefore an important feature of the sampled populations to retain, or to consider in a conservation context.

"Among geneticists and breeders there is a heterozygosity consensus; this is the belief based on extensive laboratory and farm experience that fitness (viability, vigour, fecundity, fertility, etc.) is enhanced by heterozygosity, and that any decrease in genetic variation will be paralleled by a diminution of fitness. Enhancement of fitness due to increased heterozygosity is called heterosis, and it is virtually universal in outbreeding domesticated plants and animals." (Frankel & Soulé, 1981).

Homozygosity generally tends to lower viability because recessive deleterious genes are uncovered i.e. become present at the same loci. Deleterious genes have a negative effect on reproduction and qualities connected with adaptation and vigour. Therefore factors that promote homozygosity, as for instance inbreeding, should be kept at a minimum in the course of sampling and founding of breeding populations.

3.4 Inbreeding

Inbreeding is defined as the mating of related individuals, or fusion of gametes in self-fertilization and takes place when members of the same family (sibs or halfsibs) cross-fertilize or if an individual is fertilized with its own pollen. The rate of inbreeding increases with the degree of relationship and may be expressed as the decrease in heterozygosity per generation of inbreeding. In case of self-fertilization, which is the strongest form of inbreeding, half the loci will become homozygous for each generation and the coefficient of inbreeding, F, is said to be O.5.

The effect of different degrees of inbreeding expressed as increase in homozygosity is shown in fig. 3.

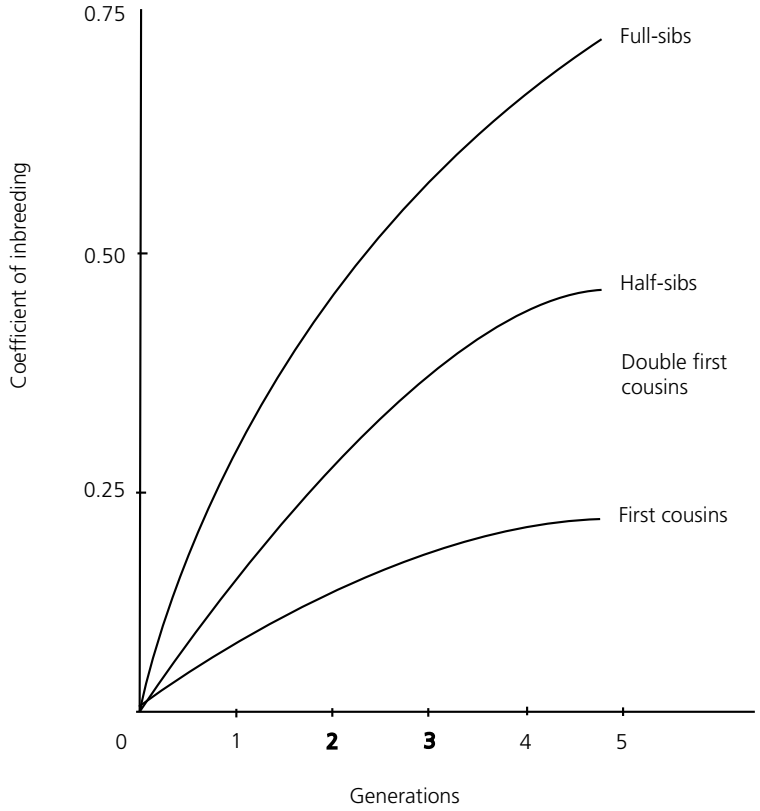

Fig. 3.Increase in homozygosity during inbreeding. After Underwood, 1979, as shown in Frankel and Soulé, 1981.

As indicated above, inbreeding may have a negative effect on characteristics important for breeding and efforts to maintain genetic variability. In order to minimize this effect, the relationship of individuals in base or breeding populations should be kept at a minimum. This should be done by observing certain rules for selection of seed parent trees both in respect of number and of physical distance between trees. The more knowledge we have of the breeding systems, mode of occurrence (scattered or in groups, continuous or discontinuous) and of seed dispersal, the more appropriate the sampling can be. A typical situation in many tropical countries is collection from natural forests for establishment of seed stands and ex situ conservation stands or for provenance testing. A rate of inbreeding of 1-2% (inbreeding coefficient F = 0.01 - 0.02) is generally accepted in samples from larger populations. The justification for this "tolerance" is based on experiences from a broad field of breeding programmes in which the smallest possible size of populations sufficient for continued survival and reproduction have been tested. The size of such a population is termed effective population or Ne. It is stated that a population size of 50 non-related individuals (effective population) would give an inbreeding percentage of 1 based on the formula

F = 2Ne , where F = inbreeding coefficient and Ne = effective population size.

Thus with Ne = 50, F will be 0.01.

In forestry and particularly in connection with provenance research, the minimum number of trees required to represent a population is considered to be 25 which theoretically would amount to an inbreeding rate of 2%. The provision is that seed parent trees are sufficiently far apart so as not to be related, which may differ considerably from one species to another e.g. whether wind or insect pollinated. Mechanisms to prevent self fertilization also play a part.

It should be emphasized that these rules are very general, but often the only ones we have with some background in population genetics. Until more knowledge is obtained about the genetic structure of tree species, they will have to suffice.

However, new techniques for estimating heterozygosity such as electrophoresis coupled with systematic evaluations of provenance trials are beginning to throw more light on the complexity of the genetic constitution of tree species. There are indications of a high degree of heterozygosity in most tree species which may be explained by the comparatively recent introduction of tree breeding.

4. Conservation of Genetic Resources in Relation to Improvement Strategy

Genetic resources have per definition a clear object of being of actual or potential value for provision of improved material.

In order to secure this potential for continuous use the sources must be either conserved or preserved.

As the terms »conservation« and »preservation« are often used synonymously, it may be appropriate to quote Frankel & Soulé (1981):

»We use the term 'conservation' to denote policies and programmes for the long term retention of natural communities under conditions which provide the potential for continuing evolution, as against 'preservation' which provides for the maintenance of individuals or groups but not for their evolutionary change" and: "The genetic resource of domesticates are, for the most part, in a static state. The exceptions are the wild relatives of crop plants and the wild plants used by man, such as forest and pasture species, which are located in natural communities. Some local breeds of livestock also retain a fairly dynamic state. All other genetic resources are maintained 'frozen' - which in many cases is literally true. Their evolutionary potential is enormous, but it needs to be realized through recombination, mutation and selection which, of course, is in the hands of the plant and animal breeders.«

Thus, conservation of genetic resources in a tree improvement programme applies, according to the quotations above only to seed sources (stands) in natural forests and ex situ conservation stands. It may be a matter of opinion whether selected seed stands in plantations, inclusive landraces, and other types of seed production areas, in which free exchange of gametes takes place, should also be included. When seed, pollen and tissue cultures are stored, the genetic resources they contain are fixed and thus preserved for future application.

The following four sections (4.1-4.4) illustrate the interrelationship between improvement strategy and conservation of genetic variation.

4.1 Seed sources in natural forests

The entire range of distribution of a species constitutes the total genetic variation as it is formed by evolutionary forces. This is the genetic base from which seed procurement and tree improvement may develop. Only a limited part of the whole genetic base may be applied in a tree breeding strategy, either for technical reasons in connection with seed collection or because of restriction in scope and time scale of the improvement programme.

Thus the identification of seed stands in natural forests of indigenous species, which is a common feature of many tropical countries, has to take into account both the technical feasibility (access, age, size etc.) and the genetic representation. The latter may again be determined by the conditions under which the species is intended to be planted.

In relation to an improvement strategy the aspects of "technical feasibility" and "genetic representation" have to be weighted according to time scale perspectives, scope of planting and relative importance of species. In the short term, emphasis may be laid on accessibility and other technical aspects in order to obtain seed. Emphasis may also be laid on protective measures, because many natural stands are vulnerable if not threatened.

The longer perspective should be considered as soon as possible in the planning of tree improvement, and the securement of a broader genetic representation should be attempted. Among other things this may imply an extended search for and identification of seed sources.

Demarcation and management of seed collection units in natural forest types of mixed composition of tree species correspond in terms of methodology to *in situ* conservation. While this is regarded as the most desirable method of conservation, it may not be the most practicable for seed collection, as the protection of a single species or provenance may depend on the interplay with other species i.e. the conservation of the whole ecosystem in which they occur. Therefore the transfer of the genetic resource in the form of planted seed stands may be necessary.

See next section 4.2 and, for a more detailed treatment of the subject, Lecture Note B-2.

4.2 Establishment of seed stands

As indicated above, the protection of seed stands in natural forests is frequently difficult to maintain, which combined with rational seed production necessitates establishment of seed stands. The common procedure will be collection of seed from the natural stand and planting the offspring for later seed production. This process implies a transfer of genetic potential which in terms of conservation is comparable to ex situ conservation, and as such involves both genetic and technical considerations as well as their mutual interdependence.

With regard to genetic consideration and with the presumption that as much as possible of genetic variation should be transferred, the method of sampling plays an important role. This has already been described in general in section 2 and 3, where it was emphasized that number of unrelated individuals, functioning as seed parents, should not be less than 25 or 50 depending on allowance for increase in inbreeding coefficient (2% or 1%).

Besides relationship and number, the forestry value (phenotypic value) of the

seed mother trees is often a criterion for selection, which means that a certain reduction in genetic diversity may take place. It is doubtful, however, that the phenotypic selection at this "wild" stage will influence the quality of the offspring very much, and therefore with greater advantage is postponed to the even-aged seed or conservation stands.

The »technical« considerations concern the effect of the new and changed environments of the seed stands on flowering and seed production, which again may affect the genetic constitution of the offspring (2nd generation and following). It would be a great advantage if favourable conditions for seed production could be secured before establishment take place, but far too often this knowledge is lacking. Other technical aspects which have an effect on the genetics of the offspring are size of seed stand and management. These are treated in details in Lecture Note B-2, but in respect of management special mention of the thinning regime should be made as the conservation and improvement objectives have, apparently, conflicting objectives.

Ex situ conservation aims at maintaining as much of the genetic variation of the original sources as possible. Therefore thinning for improved physical conditions for flowering and seed production i.e. sufficient space between trees, should be strictly objective. This means a systematic removal for instance of every second tree in a row irrespective of the quality (vigour, straightness, seed production) of the individual tree. Some problems may arise when natural selection has caused the death of trees and spacing therefore has become irregular.

For improvement and seed production purposes a "genetic" thinning may be carried out in which a combination of spacing and removal of the poorest phenotypes takes place. The adaptation of an ex situ conservation stand to its present site (1st generation) will be brought about by natural selection. The genetic constitution of the stand at the reproductive (mature) stage will be different from the one at the time of planting. It may have lost some of its diversity, but may have won in respect of adaptability in the following generations.

Genetic thinning may further enhance the quality of the offspring. In this process a weighting of conservation for their highest possible variability against adaptation and quality has to be considered.

For further discussion of the subject reference is made to Technical Note No. 14.

4.3 Introduced species and provenances

Introduced species or exotics have been, and still are, widely used in planting programmes. Formerly, the main interest was attached to species for plantation forestry and industrial wood production, and relatively few genera (eucalyptus, pines, cupressus and teak) have dominated the scene. More recently, many more genera and species have been introduced for testing and utilization in circumstances other than plantation forestry e.g. agroforestry, shelterbelts, erosion control etc.

The application of introduced species on a larger scale should and often does follow a stepwise approach via species trials, species/provenance trials combined, and proper provenance trials of promising species. Sometimes a growth trial on a medium scale is carried out after the species trial and before actual plantings.

Often, however, the classic pattern of early introduction and subsequent extension to large scale plantings rests on a small population whose origin is unknown or very vague. The introductions of teak (Tectona grandis) to East and West Africa or to Trinidad are examples of that. Apparent success in growth and yield may not call for any particular conservation measures and improvement by individual tree selection and isolation in clonal seed orchards to further improve qualitative characters may be undertaken.

In this connection and with the possible formulation of an improvement strategy it may be asked whether new sources (provenances) from a wider range of the species' distribution would increase the possibilities for further progress. There provenance trials are established for many of the most widely used exotics as a means to supplement the breeding base. The international provenance trials of Central American pines, eucalyptus species, teak, Gmelina and South East Asian pine species are examples of this sequence of events.

Frequently the early introductions have been included in later provenance trial as "local provenances" or landraces, both inside and outside their country of domestication. In many if not most of the trials the local provenance ranges among the best in their countries of domestication in respect of growth and adaptation but often display qualitative characteristics which may be less advantageous. Without going into details about this phenomenon, landraces should not be ignored in connection with conservation of genetic resources. Two outstanding examples of important domesticated strains are teak in Tanzania and Gmelina arborea in Brazil.

4.4 Provenance trials as sources for genetic conservation

When some provenances after assessment and evaluation of trials are found to be promising or superior, the extended use of such sources will naturally arise.

Firstly an attempt may be made to obtain larger quantities of seed from the original sources for establishment of seed or conservation stands locally. It will rarely be safe to rely on continuous supply of seed from the sources of origin. If a bulk sample is available or obtainable, the same procedure as outlined for seed stand establishment from natural, indigenous species may be applied. The ex situ conservation project for provenances of Pinus caribaea, P. oocarpa, Eucalyptus camaldulensis and E. terecticornis from 1975, coordinated by UNEP and FAO (FAO/UNEP Project on Conservation of Forest Genetic Resources 1108-75-05) may illustrate the integrated efforts to combine conservation and improvement. The background for promoting a world wide ex situ conservation programme was the desire to conserve the genes of the most valuable, and to some extent threatened, sources of these species. Their performance

was evaluated in a number of provenance trials distributed throughout the tropics. In order to make the programme manageable, only a few provenances (2-4) of each species were included. Bulk samples were collected from the original sources and distributed to countries interested in the establishment of conservation stands in accordance with certain technical requirements on establishment, management and seed distribution.

The programme resulted in the establishment of a number of ex situ conservation stands throughout Africa and in South East Asia, the details of which appear in appendix 1. From a seed-procurement and tree-improvement point of view the respective host countries of the conservation stands have obtained their own seed source and breeding base, from which extended planting programme may be made, and an enlarged breeding population of a valuable provenance.

It is expected that a conservation stand of 10 ha and an initial number of 1100-2500 (3 x 3 and 2 x 2 m planting distance) trees, will transfer the majority of the genetic variation. In the course of time and development of the trees, natural selection at the particular site will probably change the genetic composition of the offspring which will gradually become more "specialized" or "domesticated". While this may be satisfactory in a narrow sense i.e. for the local conditions, it may cause a loss of genetic variation compared with the original source, which it was the broader objective of the programme to conserve.

However, by having the same provenance established at a number of places under different environmental conditions, the genetic pool will approach the genetic variation of the original source when all ex situ conservation stands are considered collectively. On the condition that seed from different ex situ conservation stands can be exchanged freely, the international community may still have most of the original genetic variation at its disposal.

Unfortunately, after the original sources have been tested in provenance trials, seed from these are often difficult if not impossible to obtain. The reasons may be either the disappearance or depletion of the source area or that restrictions on export of seed have been imposed by the host country. Because of these experiences, collections and storage of bulk samples for conservation purposes of individual provenances concurrently with the actual provenance collections are strongly recommended. They have in fact been practised for some of the internationally coordinated provenance trials e.g. Pinus kesiya 1988-1989. Where seed from the original sources cannot be obtained for one reason or another, the founder population is limited to the stand or plot in its new surroundings and measures to conserve it have to be taken.

In provenance trials the individual plots of the experiment constitute the sole genetic resource, and have to be separated from the other provenances in the trial in order to avoid contamination from inferior provenance or unintentional hybridization. A mass vegetative propagation with subsequent isolation of ramets - an unselected clonal seed orchard - has to be established. This has recently been practised in connection with the international series of teak and Gmelina provenance trials.

5. Conclusion

Conservation in relation to tree improvement is a matter of provision and protection of a base of genetic variation or a number of genetic resources to which selection may be applied and improved material obtained.

"Provision" implies the search for and identification of genetic resources through exploration and studies of breeding systems and genetic structure of the individual species. The latter usually involves investigations of variation between and within populations in provenance trials. The more recently developed techniques for allozyme studies such as electrophoresis may be more widely used for estimates of heterogeneity.

"Protection" or conservation measures are essential for the securement of a sustained supply of genetic variation. This is even more important in an improvement context as advancement in breeding will lead to a narrowing of the genetic variation, as illustrated in fig. 1. If the broader genetic base is still accessible, mishaps to the genetically uniform but high yielding crops, may be remedied by incorporating genes which are resistant to pests or diseases. In other circumstances where the objectives of the improvement programme have changed and new gene combinations are required, the maintenance of a broad genetic base may also prove necessary.

Conservation of genetic resources in connection with tree improvement is directed towards individual species or populations within species. In their natural occurrence they are found in association with other species or constitute a part of an ecosystem in which all living organisms interact with each other and the environment. Thus the specific conservation object of a tree improvement programme often has to be considered in a broader perspective i.e. in corporation with nature conservation where sustainability of diversity in tree species, flora, and fauna is the main criterion. This situation is likely to occur more frequently in the coming years following the increasing need to identify and secure seed sources of local indigenous species (Lecture Note B-2).

It is therefore important that different objectives for conservation are clearly stated and a management plan worked out which will consider the different interests as far as possible.

Finally, it may be understood from discussions in the preceding sections that effective conservation of genetic variability is dependent on thorough knowledge of the species in respect of occurrence, mode of reproduction, breeding system, genetic structure and a number of other features related to them. Information from different sectors such as ecology, botany and genetics are required to get a full picture of the factors that influence the genetic set-up of the individual species and their reaction to selection and improvement.

Some of this knowledge may be available for the more widely used species, but generally much more exact knowledge is still required for the planning of and

argumentation for conservation, improvement and consequently for seed procurement programmes.

In the absence of sufficient knowledge of the individual species, which is prevalent for most tree improvement programmes and tree seed projects at this time, there seem to be at least three important fields of action to observe:

1. Apply basic and generally accepted rules (of thumb) for sampling from base populations to establish trials, seed production areas and breeding populations. See chapter 3.

2. Describe and register the simple facts about the actions concerned with identification and establishment of conservation areas. See for instance Lecture Note B-2, seed source registration.

3. Implement, improve and support studies and testing of factors connected with and influencing the maintenance of genetic variability, e.g. reproduction biology and breeding system.

6. References

FAO 1974
Proposal for a Global Programme for Improved Use of Forest Genetic Resources. FO: MISC/ 74/15. Rome.

FAO 1985
FAO/UNEP Project on the Conser-vation of Forest Genetic Resources. Final report (6106-75-05/1108-7505).

FAO 1989
Plant Genetic Resources, Their Conservation in situ for Human Use. Issued jointly with IUCN, UNESCO, UNEP. Rome.

Forest Genetic Resources Work Group 1991
Managing Global Genetic Resources: Forest Trees. National Academy Press, Washington, D.C.

Frankel, O.H. and Soulé, M.E. 1981
Conservation and Evolution. Cambridge University Press

Keiding, H. 1991
Genebanking at Danida Forest Seed Centre. Opera Botanica. 113: 29-33 Copenhagen

Keiding, H., Wellendorf. H. and Lauridsen, E.B. 1986
Evaluation of an International Series of Teak Provenance Trials. DFSC publ.

Keiding H. and Barner, H. 1990
Identification, Establishment and Management of Seed Sources. Lecture Note B-2, DFSC.

Keiding H. and Graudal, L. 1989
Introduction to Conservation of Forest Genetic Resources. Lecture Note A-4, DFSC.

Lauridsen, E.B., Wellendorf H. and Keiding, H. Evaluation of an International 1987
Series of Gmelina Provenance Trials, DFSC publ.

Schonewald-Cox, Christine M., Chambers, Steven M., MacBryde, Bruce and Thomas, W. Lawrence, (editors) 1983
Genetics and Conservation. A reference for managing wild animal and plant populations. The Benjamin/Cummings Publishing Company, N.Y.

Sugden, A. 1984
Longman Illustrated Dictionary of Botany. Longman, York Press.

Underwood, J.H. 1979
Human Variation and Human Evolution. Prentice-Hall, Eaglewood Cliffs, New Jersey.

Willan, R.L. 1984
Provenance Seed Stands and Provenance Conservation Stands. Technical Note no.14, DFSC.

7. Glossary - Definitions

ALLELES - alternate forms of a gene found on the same locus. See fig. 2.

ALLOZYME - any of the multiple forms of a multimeric enzyme the subunitsof which are coded by alleles of the same gene.

BREEDING SYSTEM - a term used to cover all those variables apart from mutation which affect the genetic relations of the gametes that fuse in sexual reproduction. The variable components of the b.s. are numerous and often not easy to estimate. Two main groups may be distinguished (1) Those which affect the ability of particular gametes to fuse or parents to mate, and (2) those which affect their probability within the limits set by the first. The variables under (1) comprise an aspect of the b.s. known as the mating system.

The b.s may be an essential factor controlling population structure and evolutionary divergence (evolutionary rate).

ECOTYPE - a group of plants within a species adapted genetically to a particular habitat, but able to cross freely with other ecotypes of the same species.

ECOSYSTEM - an ecological system in which organisms interact with each other and with their non-living environment and in which there is a more or less closed cycle of nutrients.

EFFECTIVE POPULATION SIZE (NE) - the size of an ideal population that would have the same rate of increase in inbreeding or decrease in genetic diversity by genetic drift as the population being studied. The effective population size of a true population is usually much less than its real size.

ELECTROPHORESIS - a technique for separating molecules based on their differential mobility in an electric field. Each type of molecule has a specific electrical charge, shape, a specific attraction to the solution in which it is kept, and a specific molecular weight. All these charac-teristics "fingerprint" the compounds in a solution so that they can be separated (here, largely on the basis of electrical charge) from other molecules.

EVOLUTION - the transformation of the form and mode of existence of an organism in such a way that the descendants differ from their predecessors. Evolutionary changes are brought about by the primary evolutionary forces which produce and sort out genetic variations and operate in a field of space and time.

The principal causes of biological e. are: (1) **Mutations** supplying the raw materials, (2) **selection** shaping these raw materials into the biologically fit genotypes of races and species, (3) random **genetic drift** which can produce rapid changes in gene frequency in small populations, (4) differential **migration** and **gene flow** which can shift gene frequencies via exchange of individuals and genetic information between populations, (5) **isolation** and **annidation**

which may act in a way similar to selection as a directive force in evolution and prevent the mixing of differentiations arisen in the population.
FITNESS - in population genetics, a quantitative measure of reproductive success of a given genotype, i.e. the average number of progeny left by this genotype as compared to the average number of progeny of other, competing genotypes (= adaptive value, selective value).

GAMETE - a haploid sex cell, whose function is to join with a gamete of the opposite sex, to form a diploid zygote.

GENETIC VARIABILITY - the formation of individuals differing in genotype, or the presence of genotypically different individuals, in contrast to environmentally induced differences which, as a rule, cause only temporary, non-heritable changes of the phenotype. Genetic variance is the term used to denote that portion of the phenotypic variance which is caused by variation in the genetic constitution of the individuals in a population. G.v. is a universal feature of breeding populations and a necessary preliminary condition for evolutionary change. The g.v. of a population is usually measured by the average heterozygosity per locus.

GENETIC DRIFT - (1) any change, either directed ("steady drift") or undirected ("random drift") in gene frequency in a population (2) Irregular (random) fluctuations in gene frequency in a population from generation to genera-tion due to finite population size (in "effectively" small populations whose effective breeding size either remains small or periodically be-comes small) or randomly fluctuating selection intensities (g.d. in the sense of random drift only). These fluctuations in gene frequency may lead to the fixation (random fixation) of one allele and the extinction of another without regard to their adaptive value. Random drift is a po-tential evolutionary factor is referred to as the "Sewall Wright effect".

GENOTYPE - the allelic composition of a single locus, several loci, or the entire chromosome set of an individual.

INBREEDING COEFFICIENT - the probability that two alleles of a particular locus in an individual are identical by descent.

PHENOTYPE - the observable characteristics of an organism regarded as the result of the interaction between the genotype and the environment.

For further definitions and explanation of genetic and biological terms the following two publications may be consulted:

1. Rieger, R., A. Michaelis, M.M. Green: 1991
Glossary of Genetics, Classical and Molecular. 5th edition, Springer-Verlag, 1991.

2. Sugden, Andrew:
Longman Illustrated Dictionary of Botany. See REFERENCES.

Appendix

FAO/UNEP Project on the conservation of forest genetic resources (1108-75-05)

Summary of *Ex-situ* conservation stands (1985). Area in ha.

Host countries / Species Provenances	Congo	Ivory Coast	Kenya	Nigeria	Zambia	Tanzania	India	Thailand	Philippines	Ex situ total	No. of localities
Euc. Camaldulensis											
Petford				2.6				22.0		24.6	2
Katherine				1.5		8.0				9.4	2
Gibb River								19.9		19.9	1
Euc. Terecticornis						8.0				8.0	1
Cooktown	9.1			1.6	19.0					29.7	3
Mt. Garner	9.8			3.0	11.0	8.0				31.8	4
Total Eucalyptus	**18.9**			**8.6**	**30.0**	**24.0**		**41.9**		**123.4**	
Pinus caribaea						7.0				7.0	1
Alamicamba (Nicaragua)	16.4	7.0		1.4		19.8	5.0	10.2	10.0	69.8	7
Los Limones (Honduras)	20.0		7.5	8.0		20.0	8.2	12.6	10.0	86.3	7
Poptun (Guatemala)	8.2	8.1					7.2	13.1		36.6	4
Pinus oocarpa											
Bonete (Nicaragua)	20.0			18.4	20.0		9.2			67.6	3
Mountain Pine Ridge (Belize)	10.1	9.4		14.7	20.0		10.9	14.9		80.0	6
Yucul (Nicaragua)	20.1	9.0		30.5	10.0		4.0	18.7		102.3	7
Total pines	94.8	33.5	7.5	73.0	50.0	56.8	44.5	69.5	20.0	449.6	
Grand total	113.7	33.5	7.5	81.6	80.8	80.8	44.5	111.4	20+.0	573.0	