

Genetic Variation and Conservation of British Native Trees and Shrubs

Current Knowledge and Policy Implications

Richard Ennos, Rick Worrell, Paul Arkle
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Richard Ennos, Rick Worrell, Paul Arkle and Douglas Malcolm

School of Forestry, Institute of Ecology and Resource Management,
University of Edinburgh, Edinburgh EH9 3JU

FORESTRY COMMISSION, EDINBURGH

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Arkle, P.	Malcolm, D. C.
Ernos, R. A.	Worrell, R.

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Enquiries relating to this publication should be addressed to:

The Research Communications Officer
Forest Research
Alice Holt Lodge
Wrecclesham, Farnham
Surrey GU10 4LH

Front cover: Upland birch and oak woodland at Newtyle Hill, Perthshire. The birch is naturally regenerated from a local population; the oak was planted in the past from seed of unknown origin. (RICK WORRELL)

Back cover: *left* Bog woodland of Scots pine in the foreground and a native Scots pine stand in the background at Abernethy Forest, Inverness-shire. (RICK WORRELL)
right A remnant of upland birch woodland with hazel, rowan and willow in a gully at Glen Roy, Inverness-shire. (RICK WORRELL)

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Foreword

This Technical Paper, which results from a review commissioned by the Forestry Commission in 1998, is the first attempt at setting a comprehensive framework for the development of knowledge and policies for the genetic conservation of our native trees and shrubs.

For obvious practical reasons, foresters have always tried to select trees for planting which are well adapted to site conditions, and a lot of effort over many decades has gone into identifying and testing suitable seed sources for the more commercial species.

Since the Earth Summit in 1992, there has been growing international recognition of the importance of genetic resources as the basis for biological diversity of all kinds. In forestry we have seen a growth of interest in the genetic conservation of our native trees and shrubs over the past few years, as the amount of planting of native species has increased. In response to this interest our forestry practice guidelines (summarised in *The UK forestry standard* published by the Forestry Commission in 1998) encourage the use of local planting stock in planting in native woodlands. A prime example of this is the case of the native pinewoods of northern Scotland, where patterns of genetic variation are relatively well understood thanks to research by the Forestry Commission in the early 1980s. A very successful scheme has been running for some years now to promote the use of local origins of Scots pine within the historic range of the native pinewoods.

Even so, there remains a lack of widely available knowledge of the pattern and significance of genetic variation for most of our native trees and shrubs. Terms such as 'genetic purity', 'genetic integrity', and 'local origin' are used frequently but, without clear and consistent definitions, they may serve only to confuse. At the same time, the use of tree breeding techniques for improving desirable characteristics such as vigour and timber quality has increased in importance for some commercial species, and this raises questions about the desirable balance between the use of unselected and selectively bred genetic material.

This Technical Paper seeks to tackle these issues. It reviews our understanding of the genetic variation of the native trees and shrubs of Britain, identifies important issues relating to the conservation of genetic diversity, and proposes a research and policy development agenda for the management of the genetic resources of our native species.

While the report is entirely the work of the authors and does not therefore necessarily reflect the views of the Forestry Commission, we very much welcome the main message of the report, that we need better understanding and development of more comprehensive guidance on genetic conservation. We have decided to publish the report in full as a Technical Paper in order to help stimulate wider discussion of this important topic.



Tim Rollinson
Head of Policy & Practice Division
Forestry Commission, Edinburgh

Summary

Genetic variation within forest tree species is a fundamental component of forest biodiversity and is the basis of variability at both the species and tree stand levels. Despite its importance, the management and conservation of this aspect of our forest resource has only recently come under close scrutiny.

The objectives of this Technical Paper are:

- **To provide an accessible account of genetic variation and its behaviour in forest tree species.**
- **To review knowledge of the genetic resources of native tree and shrub species.**
- **To highlight the issues which need to be addressed when developing a genetic conservation policy for British forestry.**

These objectives are set out in Chapters 1, 2 and 3.

Genetic variation falls into two distinct classes (Chapter 1). Selectively neutral variation detected by molecular marker techniques is of no adaptive significance. However its analysis can be used to make inferences about population history, gene flow and mating systems, all of which may be of relevance in conservation. Adaptive variation, measured in provenance and progeny trials, underpins local adaptation in present day populations and allows populations to respond genetically both to environmental change and to artificial selection imposed in tree improvement programmes. **Genetic conservation should chiefly be concerned with:**

- maintaining and enhancing adaptation of native populations and
- safeguarding the ability of populations to respond to future natural or artificial selection.

Work on genetic variation in British native trees and shrubs (Chapter 2) has concentrated on studies of selectively neutral variation, and is restricted to a small number of chiefly northern and upland species. The few reports available from provenance trials indicate significant differences in adaptive characters between British and continental European populations. In some species, notably Scots pine and birch, planting stock from much of continental Europe performs poorly in Britain. There is some evidence of adaptive differences between populations within Britain but this topic has received little research attention. It is clear that human activity has altered and continues to alter the genetic resources of native species through processes such as fragmentation, dysgenic selection, and gene flow from exotic and commercially selected genetic material.

A genetic conservation strategy for British forestry (Chapter 3) must address and provide guidance on a number of issues including:

- choice of seed sources and regeneration methods
- influence of exotic provenances
- conservation of small and isolated populations
- establishment of forest reserves and gene banks
- forest design
- use of genetically improved material
- adaptation of trees to future climate and other environmental change
- provisions for different species and different woodland types
- influences of tree genotypes on woodland fungi and fauna.

To address these issues the following main elements of policy are available:

- Development of a policy statement in national forestry policy
- Development of guidance on a range of policy and technical issues
- Development of a small number of key regulations
- A major and sustained research input
- A programme of promotional events, training and awareness raising
- Publications describing genetic conservation policy and providing technical guidance for practitioners.

Genetic guidance should be integrated with all relevant areas of forest management. Genetic issues are often poorly understood by practitioners and education for a wider appreciation of their importance is required. Development of a genetic policy is constrained by lack of research information. The principal research priority is to establish comprehensive provenance and progeny trials with our native species to gain an understanding of adaptive genetic variation within Britain.

Genetic diversity and conservation

Introduction

The conservation of biological diversity is now widely acknowledged as a priority in forest management and forms the substance of major new policy initiatives in national and international forestry programmes. Biological diversity can be recognised at a number of different levels, from ecosystem diversity through species diversity to 'within species' or genetic diversity. Much of the emphasis in this area has been on species or ecosystem conservation. However attention is now being turned towards genetic conservation, and the importance of this subject has been made explicit in recent international policy statements (see Appendix 1).

Effective conservation of genetic diversity or genetic resources requires a thorough understanding of the nature of genetic diversity, its biological importance, its behaviour, and the effects that various forms of management may have on the quality and quantity of genetic diversity. Debate and discussion of genetic conservation issues has frequently been hampered by a general lack of understanding of these basic concepts, and further confusion has been generated by problems related specifically to terminology.

An increasing number of terms and concepts are being deployed in forest genetics, principally:

- scientific terms relating to genetic variation and genetic processes;
- taxonomic terms;
- terms related to genetic management.

Many of the scientific and taxonomic terms are only partially understood by policy-makers and forest managers. In addition a small number of terms deployed in genetic management have been coined by foresters and woodland ecologists and it is useful to define these scientifically. Different terms for very similar concepts are sometimes used in different contexts, for example, provenance, ecotype, race, strain. Inconsistent use of such synonyms can lead to confusion. There is considerable benefit in adopting an agreed suite of important terms, promoting their use and discouraging the use of less useful ones or of

synonyms. The aim of this introduction is therefore to give a concise summary of the basic concepts that must be understood before an informed debate on genetic conservation can begin. To help in this task a definition of technical terms (printed bold in the text) with comments and recommendations on their use is provided in Boxes 1.1, 1.2 and 1.3.

Having dealt with these background issues, we discuss the importance of genetic variation and outline an agenda for genetic conservation. This sets the scene in Chapter 2 for a detailed review of our knowledge of genetic diversity and genetic resources in British forest tree species. Building on this information, Chapter 3 gives an outline of those forestry issues for which we consider genetic conservation to be relevant. We argue that a formal genetic conservation policy is required to ensure that genetic considerations are taken into account in decision-making. The final part of Chapter 3 considers how we might progress towards a comprehensive genetic conservation policy for British forestry and set research priorities.

The nature and behaviour of genetic diversity

The **genetic variation** found within species represents a natural, renewable, biological resource. The sum total of genetic variation within a species can be thought of as its **genetic resources**. Like all other types of biological resources, genetic resources are amenable to management, sustainable or otherwise. The outcome of this management is predictable so long as the factors controlling the level and behaviour of genetic resources are fully understood.

Genetic variation is continually created within a species at each generation by mutation. This takes place at a very low, but detectable, rate (the probability of mutation per average gene per generation is approximately 10^{-5}). The variation generated falls into two contrasting categories. On the one hand, it may have no effect on the performance of the individual possessing it and is then known as **selectively neutral variation**. The vast majority of variation detected by molecular methods (DNA markers, isozyme markers) is of this nature.

Box 1.1 Basic genetic concepts

GENOTYPE The genetic information possessed by an individual. It interacts with the environment to produce the phenotype.

PHENOTYPE The observed characteristics of an individual, morphological, anatomical and physiological. This is determined by an interaction between the genotype of that individual and the environment in which it is grown. Changes in either genotype or environment can cause changes in the phenotype.

ENVIRONMENT The conditions under which a tree (i.e. the genotype) is grown. This includes all the abiotic (climate, geology, topography, etc.) and biotic (pests, pathogens, competition, etc.) elements.

POPULATION A collection of interbreeding individuals of the same species that occupy a particular geographic area. Usually conceived of as a single forest stand or collections of stands within a catchment. Sometimes population is used in the context of much larger units of forest, e.g. the population of juniper in south Scotland. In this case it is scientifically more correct to use the term **metapopulation**.

EVOLUTIONARY UNIT Group of populations with a common evolutionary history.

METAPOPOPULATION A collection of populations which are linked by gene flow.

GENEPOOL The sum of all the genotypes within a species in a particular population or region.

GENETIC VARIATION Any variation among trees and shrubs in the genetic information they possess. This information is coded in the DNA, and expressed in all aspects of the tree's growth, structure, etc. Some of this variation has effects on the phenotype of a tree (called adaptive variation) while some has little or no discernible effect (called selectively neutral variation; see below).

GENETIC STRUCTURE The spatial arrangement of genetic variation within and among populations.

GENETIC DIVERSITY The range and sum of genetic variation within a population or populations. The term diversity, which simply means the state of displaying differences, dissimilarities or variety, has acquired an extended meaning which signifies the sum of the variation (as in biodiversity). Where genetic differences can be scored, it is possible to measure genetic diversity quantitatively.

GENE FLOW The transfer of genes between populations. This may occur by both pollen and seed.

BREEDING SYSTEM The way in which adult trees produce the next generation (sexual, asexual reproduction).

MATING SYSTEM The way in which sexual reproduction takes place in a population. This may be through crossing with other members of the population (outcrossing), by self-fertilisation (selfing) or by a mixture of the two.

GENETIC DRIFT The process whereby the frequency of alleles in a population changes from one generation to the next as a consequence of chance sampling events. Genetic drift leads to the loss of all types of genetic variation from populations and this is most pronounced in small populations.

ADAPTIVE VARIATION Genetically determined variation in phenotype (i.e. morphology and performance) upon which natural (and artificial) selection operates. The distribution of this type of variation is determined by natural selection, and reflects the environment in which the trees/shrubs are growing.

SELECTIVELY NEUTRAL VARIATION Genetically determined variation which has little or no effect on the phenotype or performance of a tree/shrub. The distribution of this type of variation depends solely on mutation, genetic drift, population size and migration and can therefore be used to infer historical events in the evolution and migration of species.

PATTERNS OF VARIATION Patterns in the distribution of genetic variation within populations. Patterns may be geographic (spatial) or describe the proportion of variation found within or between populations.

ADAPTATION The process of becoming physiologically suited to an environment.

ADAPTED Suited to the environment.

ADAPTABILITY/ADAPTEDNESS The degree of adaptation.

There are several indicators of adaptation which are deployed in different circumstances:

- ability to reproduce and leave descendants in the next generation (=fitness) is the key criterion in natural populations;
- survival and growth rates are often used for crop species. For crop species the best adapted genotypes are those which produce the highest economic return in the crop environment when harvested.

These indices of adaptedness do not measure the same thing.

STAND A delineated population of trees possessing sufficient uniformity in composition.

SEED SOURCE Trees within an area from which seed is collected.

PROVENANCE

– **Usage 1.** The location from which a seed lot (or cuttings) used to produce planting material was collected.

Note that *provenance* in USA is equivalent to *origin* in Britain.

– **Usage 2.** A sub-division of a species consisting of genetically similar individuals related by common descent and occupying a particular territory to which it has usually become adapted.

Provenance is used at a range of scales from national (e.g. Scottish provenance of Scots pine; continental provenance beech) to local (e.g. Dunkeld provenance of birch). Synonyms for provenance include:

- **geographic race** and **geographic strain**. This is used in the USA and relates to large scale sub-divisions of species.
- **ecotype**. This is used by ecologists and usually relates to scales smaller than race. See **ecotype** below.

Provenance is a term used in forest genetics and only rarely in the context of other plants and crops.

REGION OF PROVENANCE For a species or sub-species this is the area or group of areas subject to sufficiently uniform ecological conditions in which stands or seed sources showing similar phenotypic or genetic characters are found.

ORIGIN For an autochthonous stand or seed source, the origin is the place in which the trees are growing.

For a non-autochthonous stand or seed source, the origin is the place from which the seed or plants were originally introduced.

The origin of a stand or seed source may be unknown.

NATIVE AND INDIGENOUS Naturally occurring within a country or region^a.

These terms are used particularly in relation to *species*. They are also sometimes used in respect of *populations*, *provenances* and *origins*. The term:

- **native (indigenous) population** usually means an autochthonous population, but can also be a planted population derived from an origin within the same country or region of provenance;
- **native (indigenous) origin** means an origin located in the same country or region;
- **native (indigenous) provenance** usually means material derived from an origin within the same country or region (the seed source itself may be autochthonous or planted).

(^aNote that at a locality scale nativeness graduates into site specificity. For example, *Alnus glutinosa* never grows on gravelly morainic knolls in Deeside, but it is native to the region.)

AUTOCHTHONOUS STAND OR SEED SOURCE One that has been continuously regenerated by natural regeneration in this generation and (as far as can be determined) in all previous ones.

The stand or seed source may be regenerated artificially from reproductive material collected in the same stand or seed source or autochthonous stands or seed sources within close proximity; equates with the following terms used to describe woodlands: *genuinely native* and *natural origin*. Use of the term could be promoted.

INTRODUCED, EXOTIC, NON-NATIVE, FOREIGN Transferred by people from another country or region.

These terms are used particularly in relation to *species*, in which case the transfer is beyond the natural range of the species concerned. They are also sometimes used in respect of *populations*, *provenances* and *origin*, in which case the transfer is within the natural range of the species concerned. The term:

- **introduced (exotic, non-native) population** usually means a population of a native species derived from material from another country or region;
- **introduced (exotic, non-native, foreign) provenance or origin** means material derived from an origin located in another country or region.

Strictly there is no such thing as a non-native origin (origins are by definition autochthonous), but *planting material* can be described as being of non-native origin. The juxtaposition in an expression such as 'the wood was of native species of non-native origin' can lead to an element of confusion. *Foreign* is usually used in relation to seed/cuttings imported from a foreign country; therefore the boundary is administrative rather than ecological.

NATURALISED A naturalised species is an introduced species which is to able function ecologically in its new environment.

Indicators of naturalisation include ability to:

- regenerate and colonise,
- occupy successfully an ecological niche,
- acquire associated flora and fauna.

ECOTYPE A population of trees/shrubs, smaller than a race, of similar genotype which occupy and are adapted to a specific set of ecological conditions.

ISOLATED, ISOLATION Populations which are too far apart for significant gene flow to take place.

LAND RACE An introduced population which has become adapted to its new environment through natural selection.

Land races of forest trees are typically faster growing than the population from which they were originally derived.

Alternatively the variation generated by mutation may affect the **fitness** of individuals, defined formally as their relative genetic contribution to the next generation. This form of variation is termed **adaptive genetic variation**. Adaptive variation is best detected by measuring differences in **phenotype** and performance between populations, families or clones *when these are growing under common environmental conditions* in properly designed field trials. Examples of adaptive genetic variation are genetically determined differences in date of bud burst, in growth rate, or in disease resistance expressed in such trials. All of these traits are expected to influence the reproductive fitness of individuals. Genetic variation detected by comparing samples from different populations in such trials is known as **among population genetic variation**. Comparison of samples from different families (groups of individuals with at least one parent in common) or clones within a single population can be used to give estimates of **within population genetic variation**.

The distinction between selectively neutral and adaptive variation is a very important one because the behaviours of these two types of variation in a population are quite different. However it must be acknowledged that the distinction between the two is not absolute. Genetic variants may arise in a population which initially have no effect on individual fitness and would be classified as selectively neutral. However at a later date, perhaps due to changes in environmental conditions, the individuals possessing this variant may be at a reproductive advantage or disadvantage. The same genetic variation is now adaptive. An example might be variability in a disease resistance gene which is selectively neutral in the absence of the pathogen, but is selectively important in environments where the pathogen is present. Despite this complication it is still appropriate to regard the vast majority of variants detected by molecular methods as selectively neutral.

When genetic variation is generated within a population of trees, it is transmitted to the next generation during reproduction. The **breeding system** of the species controls this transmission process. Breeding systems may be asexual

(involving no rearrangement of the genetic material) or sexual. Sexual reproductive systems or **mating systems** are typically classified firstly along a continuum ranging from completely self-fertilising, in which all offspring are produced as a result of self-pollination, to complete outcrossing, in which all offspring are the result of pollination by another member of the population. Most forest trees show very high levels of outcrossing, close to 100% (Muona, 1990).

Different mechanisms may be responsible for ensuring outcrossing. These range from self-incompatibility systems such as those found in rowan and cherry, to separation of the sexes as present in willows and aspen. Breeding systems may also be characterised by the pollen vector involved. This may vary from wind in pine, oak and aspen to insects in rowan, cherry and lime. Pollen vectors affect the distance travelled by pollen, with, on average, greater pollen dispersal by wind than by animal vectors.

The fate of genetic variants in a population after their creation by mutation is governed by a number of further processes. Genetic variation is lost from populations by chance every sexual generation, by a process known as **genetic drift**, at a rate that is inversely related to population size. The frequency of adaptive genetic variants (but not selectively neutral variants) in the population is also directly altered by natural selection. Genetic variants that raise fitness will increase in frequency over time, enhancing **adaptation** to the environmental conditions and creating a locally **adapted population**.

Species of trees are made up of a number of populations. These are, to a greater or lesser extent, able to exchange genetic variants by seed and/or pollen migration between populations. Such exchange of genetic material between populations by seed and pollen migration constitutes **gene flow**. Gene flow will alter the distribution of genetic variation among populations which was established by genetic drift and selection. Gene flow has a large influence on the distribution of selectively neutral genetic variation. Thus in many forest trees where pollen dispersal between populations is very effective, there is very little variation for genetic

Box 1.2 Taxonomic concepts

SPECIES Trees/shrubs which have a high degree of similarity can generally interbreed only amongst themselves and show persistent differences from members of allied species.

SUB-SPECIES A major subdivision of a species based on distinctive, persistent, naturally occurring morphological characteristics.

VARIETY A particular distinctive genotype which either occurs naturally or is produced by artificial selection/breeding.

markers over large geographic regions. However gene flow has a much lower impact on the distribution of adaptive genetic variation. Substantial differences in adaptive genetic variation can occur between populations even in the presence of considerable gene flow when there are large differences in the selective environments that they occupy. It should be noted however that the maintenance of these genetic differences in the face of gene flow requires the continuous selective removal of maladapted **genotypes** resulting from gene flow and imposes a 'migrational genetic load' on the population concerned.

Following the interaction of all these processes, a particular level and patterning of genetic variation is established within a species. This spatial pattern of genetic variation is often referred to as the **genetic structure** of the species. It is important to realise that the genetic structure of a species is different for different types of genetic variation. Moreover genetic structure is a property which is not fixed but will change through time as a consequence of different patterns of gene flow, genetic drift and selection. For genetic variants that have no effect on fitness, genetic structure will be influenced by population history, mutation, genetic drift and migration.

The effect of population history on genetic structure is especially apparent when the species has undergone periods of contraction and expansion in the past caused by climatic fluctuations. Thus a species may have been confined in the past to a limited number of isolated refugia. These isolated populations may diverge for selectively neutral genes by chance through the process of genetic drift, since there is no gene flow between them. On subsequent range expansion, all populations derived from a particular refugium will possess the selectively neutral genetic variants characteristic of their refugial population, and will differ from populations derived from the other refugia. Thus large scale patterns of selectively neutral genetic variation may be largely shaped by population history. Groups of populations derived from the same refugium with a common evolutionary history are often referred to as **evolutionary units** (Moritz, 1994). A good example of evolutionary units within species is seen in oaks. Three evolutionary units of oak derived from refugia in Spain, Italy and the Balkans can be recognised in western Europe using genetic markers (Ferris *et al.*, 1998).

Evolutionary units within a species are detected using selectively neutral genetic markers which themselves may have no ecological relevance. However there are a number of arguments that

suggest that there may be biologically important genetic differences between different evolutionary units that need to be taken account of in genetic conservation. The first is that genes within an evolutionary unit have been selected together to interact well (they are coevolved). Interbreeding of differently coadapted genotypes could result in the break up of these desirable genetic combinations and the production of offspring with reduced fitness. This phenomenon of 'hybrid breakdown' is well documented when interbreeding occurs between different species, but is not well documented for interbreeding between different evolutionary units within species.

The second reason for supposing that ecologically significant genetic differences occur between different evolutionary units within a species is that the populations making up an evolutionary unit are derived from a refugial population evolved under a selective regime that is likely to have been different from that in other refugia. Though adaptive variation moulded by selection in the refugium will be highly modified by selection subsequent to range expansion, some elements of adaptive genetic differences between the evolutionary units evolved in the refugia may remain, as the ghosts of past natural selection. These arguments suggest that although selectively neutral genes provide no direct information on patterns of adaptive variation, they can have a role in defining evolutionary units within a species, and these evolutionary units may differ genetically in ecologically important ways.

The population structure of selectively neutral markers contrasts with that of selectively important genetic variants that influence adaptation. For selectively important genetic variation, genetic structure within an evolutionary unit is not homogeneous but reflects the pattern of environmental variation to which the populations have adapted. Thus in the same populations of oak in Europe that show east-west differences in genetic markers representing different evolutionary units, genetically determined differences in adaptively important flushing date change along a north-south axis, with earlier flushing in more southerly populations. This occurs in all three evolutionary units, and is clearly an adaptation to the different lengths of growing season encountered. Thus genetic structure is completely different for the two types of genetic variation in oak. Selectively neutral variation reflects past history and changes on an east-west axis, and adaptive variation reflects patterns of environmental variation across the range of the species and changes on a north-south axis.

The final point to consider is temporal variation in

genetic structure. Alterations in both levels of genetic variation and genetic structure will naturally arise as changes occur in factors such as population size, migration and environment. Populations kept at low population size for many generations maintain lower levels of genetic variation than populations maintained at high population size. When populations are transferred by man into new environments, and left to reproduce, genetic changes occur which increase adaptation to the exotic environment as a consequence of selection, and **land races** are produced. Thus levels of both genetic variation and genetic structure within species (the **genetic resources** of that species) are not fixed but are dynamic and will change continually over time as a consequence of many natural processes.

The importance of genetic variation

As outlined above, genetic diversity within species takes a variety of forms, while its abundance and distribution are altered by a large number of different processes. The resulting genetic resources are also subject to change in response to a wide range of factors. Having indicated the complexity of the subject, it is now essential to provide an analysis of the importance of each of the forms of genetic variation described above, so that the justification for genetic conservation is clear. This then allows priorities to be set and an agenda for genetic conservation policy to be drawn up.

By its very definition, selectively neutral genetic variation has no effect on the performance or fitness of individuals, it can be regarded as evolutionary noise, and there would appear to be no justification for the conservation of such variation *per se*. The only exception to this statement is where selectively neutral variation becomes selectively important as a consequence of changes in the environment. Nevertheless analysis of selectively neutral variation with molecular techniques does enable us to recognise evolutionary units within species. As we have argued, such evolutionary units may possess different adaptive traits as a consequence of their past history, and deleterious consequences may arise if interbreeding between different evolutionary units occurs. Thus although the effects may not be large, on the precautionary principle, it would be unwise to encourage the mixing of genetic material from very different evolutionary units within a species. Indirect information from selectively neutral markers therefore has a role to play in genetic conservation to ensure that this precaution is taken.

Adaptive genetic variation is of direct importance to the species which possesses it for three reasons.

- The present patterns of adaptive variation that exist between populations ensure high fitness across the range of current environmental conditions. These patterns of adaptive variation have evolved over a number of generations in response to natural selection by both abiotic and biotic components of the environment.
- The future ability of tree populations to respond genetically to environmental change is dependent on the adaptive genetic variation which they either contain within them or have access to via gene flow from other populations. The level of actual, or potential, adaptive variation within populations determines directly the rate of response to natural selection.
- From the point of view of commercial forestry, the future **genetic improvement** of a species is absolutely dependent on a supply of appropriate genetic variants. It is from this resource that **improved genotypes**, defined as those best adapted to managed environments and commercial needs, are selected. The greater the genetic resources available, the swifter will be the response to selection, and the more successful will be the tree improvement programme.

Apart from the importance of adaptive genetic variation to the tree or shrub species itself, it is also relevant to the success of other members of the forest community with which the trees interact (herbivores, pathogens, pollinators, mutualists, etc.). Though rather little work has been done on the subject, it is clear that the adaptive genetic differences between tree populations are large enough to have an impact on the success of co-occurring species. Thus the successful growth of insect larvae may be dependent on the coincidence of leaf flush and egg hatching dates. The use of tree populations with an altered genetically determined flushing date in woodland regeneration programmes could have an adverse effect on the population dynamics of associated leaf consuming insects. More work is required on the degree of local adaptation of herbivores, pathogens, pollinators, mutualists, etc. to determine the seriousness of this type of effect.

Summarising these arguments about the importance of genetic variation, it is clear that adaptive variation should form the chief focus for attention in genetic conservation programmes. This form of variation is directly relevant to present day levels of adaptation of populations; it determines the future evolutionary flexibility of populations in response to environmental change, and is the raw material necessary for commercial exploitation

Box 1.3 Management related concepts

GENETIC MANAGEMENT Intentional manipulation of genetic diversity to achieve desired aims.

It encompasses all forms of management from conservation and restoration of natural patterns of genetic variation, to selection and breeding. It has a similar scope to *genetics*; but genetics describes a *discipline*, whereas genetic management refers to an *activity*.

GENETIC RESOURCE Sum of the genetic variation within a species, usually at regional or national scale, which is presently or in the future of use to people.

It is used mainly in the context of plans to exploit, conserve or manage genetic diversity.

GENETIC CONSERVATION Conservation and restoration of the different elements of genetic diversity (genotypes, populations, patterns of genetic variation, species).

SEED SOURCE Trees within an area from which seed is collected.

REGION OF PROVENANCE, PROVENANCE REGION, SEED ZONE, SEED COLLECTION AREA Division of territory into units for the purpose of identifying seed sources and/or establishing provenance recommendations and/or transfer rules.

The use of the term *region of provenance* is specified under EC reproductive material directives. Seed collection areas are smaller than regions of provenance or seed zones.

ORIGIN REGION Used in Britain to describe divisions into units of the natural distribution of Scots pine for the purpose of identifying seed sources and establishing provenance recommendations / transfer rules.

They are based on information from studies of selectively neutral variation.

SELECTED STAND A stand located within a single region of provenance which has been phenotypically selected at the population level and meets certain requirements.

(ARTIFICIAL) SELECTION, SELECTED Identification and use of specific superior genotypes.

This relates to use of species as crops. Such material is only superior when used in a particular environment. The most common indicators of superiority are high productivity, good form and disease resistance.

IMPROVED, IMPROVEMENT Selected material which has been demonstrated by progeny testing to be superior to the average of the population(s) from which it was derived.

Genotypic superiority is not absolute, but is dependent on the environment in which the genotype is grown.

GENETIC INTEGRITY Shorthand used by ecologists and foresters meaning **existing patterns of genetic variation within semi-natural woodland**. It is applied at local, regional or national scale. The term is now well established, but understanding would be increased if use of the expression 'existing patterns of genetic variation' was encouraged instead.

GENETIC PURITY Similar to genetic integrity but usually used solely in relation to proposed introduction of non-local material into semi-natural woodlands. By inferring that any introduction of material constitutes 'pollution' the term is misleading and should not be promoted.

GENETIC POLLUTION, CONTAMINATION The introduction of undesirable genes or genotypes.

This is a result of transfer of specific genotypes into the proximity of populations composed of different genotypes, leading to cross pollination and colonisation. This may be non-local or improved genotypes contributing genes to semi-natural woodland, or unimproved genotypes contributing genes to seed orchards or improved populations.

LOCAL PROVENANCE, LOCAL ORIGIN Planting material of native species from origins within a relatively short distance of the planting site.

A single definition of 'local' cannot be established. It is within the range of proximity of seed source locations as follows: same wood < local < regional < national < foreign. Local will generally imply that material is from a similar site within the same or neighbouring watershed(s).

TRANSFER Movement of planting material from one location to another by people. 'Long distance transfer' refers to movement across entire regions or countries.

GENUINELY NATIVE AND NATURAL ORIGIN

These terms are used to describe the origin of native woodland by conservationists and field foresters and mean **having regenerated naturally in both the present and (as far as can be ascertained) all previous generations**. Identical meaning to autochthonous. Semi-natural woodland is assumed to be genuinely native / natural origin, though it is difficult to tell in some cases whether it has been through a planted generation in the past.

through genetic improvement. Selectively neutral genetic variation is not of direct relevance to conservation, but may be used as a tool to delineate evolutionary units whose existence must be recognised in conservation, and to study other aspects of the biology and ecology of trees to facilitate the operation of conservation programmes.

Agenda for genetic conservation

Having outlined the importance of genetic variation and pinpointed adaptive genetic variation as the focus for conservation attention, we are now in a position to outline a broad agenda for genetic conservation of forest trees and shrubs which will be elaborated in Chapter 3. The essential aims of genetic conservation should be:

1. To maintain and enhance genetic adaptation, fitness and the long-term potential for evolution in populations of tree and shrub species.
2. To safeguard the continued supply of genetic variation for use in all aspects of forestry, from woodland conservation to tree improvement programmes.
3. To conserve those aspects of the genetic structure of populations which reflect their unique evolutionary history.
4. To maintain and, as far as possible, restore natural genetic processes especially gene flow and natural selection.

The objectives of genetic conservation and genetic management

Genetic conservation is part of the broader concept of genetic management. The other main element of genetic management is the exploitation of genetic variation for the benefit of people, usually through selection and tree improvement (see Figure 1.1).

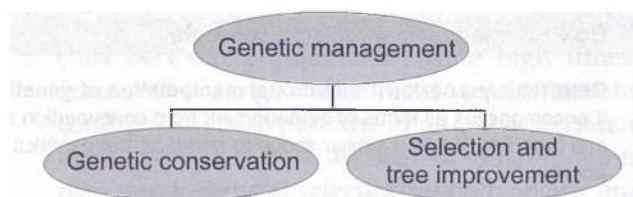


Figure 1.1 The relationship of genetic conservation to genetic management

The objectives of selection and tree improvement may to some extent conflict with those of genetic conservation, so that an appropriate balance between the conservation and exploitation of genetic variation has to be found. This mirrors the balancing of objectives between conservation and exploitation of the resource which takes place in other aspects of forest management.

Using the general guidelines set out above, management proposals can be assessed for their potential effects on genetic resources. In this way the conservation of genetic resources can be brought under the same umbrella as other forms of conservation and resource management, and be included jointly in decision-making processes.

Much of our forest resource is of exotic species one or more generations after introduction, or of long naturalised species such as sycamore. The genetic management of these exotic or naturalised species should have broadly the same aims as those outlined above. Thus where exotic populations have evolved land races these should be accepted as valuable sources of locally adapted genetic material. Sufficient genetic variability should be introduced within exotic species to ensure adaptation in response to climatic change and for tree improvement programmes.

Genetic resources of forest tree species: review of the literature

Introduction

As indicated in Chapter 1, two contrasting types of genetic variation can be studied in tree populations, selectively neutral and adaptive genetic variation. As we explained, these two types of variation behave in different ways. The pattern and abundance of adaptive genetic variation is affected by natural selection, whereas this is not true for selectively neutral variation. This means that studies of the two types of genetic variation yield different types of information which must be interpreted in different ways.

Analysis of selectively neutral genetic variation is ideally suited to the investigation of mating systems, gene flow, loss of genetic variation through genetic drift, and population history. However studies of selectively neutral markers do not provide insights into patterns of genetic adaptation among populations and cannot reliably be used to infer levels of adaptive genetic variation within populations. To investigate these topics data from provenance and progeny trials are needed.

Given these differences in the information that can be derived from study of selectively neutral and adaptive genetic variation, these topics will be dealt with separately to avoid confusion. The first section of this literature review is therefore a compilation of studies on selectively neutral genetic marker variation, arranged by species. In many cases the studies include data from populations in continental Europe, since these shed light on the colonisation history of Britain after glaciation.

The remaining sections deal with information that is available on adaptive genetic variation. This concentrates first on the natural patterns of adaptive genetic differences that occur between populations of our native tree species. Factors affecting these patterns are analysed and the differences between individual species are highlighted. Anthropogenic influences on present day patterns of variation are then reviewed, and the manifold effects of changes in genetic structure brought about by movement of seed source are investigated. Finally, some general conclusions are drawn from the existing research base and comment

made on the strengths and weaknesses of our knowledge of forest genetic resources in Britain. Native species included in this literature review are from Soutar and Peterken (1989).

Studies of selectively neutral variation

Oak (Quercus robur and Q. petraea)

Molecular marker studies of oak have concentrated chiefly on large scale geographic patterns of variation across Europe, including Britain. The data have been used in conjunction with fossil pollen evidence to make inferences about the sites of glacial refugia (Bennet *et al.*, 1991), and the recolonisation routes used by oak from 10 000 BP onwards after glaciation.

Quercus spp. are inferred, from chloroplast DNA markers, to have had three distinct refugia during the last ice-age glaciation, namely southern Iberia, southern Italy and the Balkans (Bennet *et al.*, 1991; Ferris *et al.*, 1993, 1998; Johnk and Siegmund, 1997). Separation of these refugia was sufficiently long, over many glaciations, to allow differentiation for cpDNA to occur between refugial populations. Oaks migrated north from these refugia colonising a large area in western Europe and Britain from the Iberian refugium. A relatively narrow strip within Europe northwards from Italy to Sweden and western Finland was colonised from the Italian refugium. To the east of this area, colonisation was from a refugium in the Balkans.

Differentiation for a variety of nuclear markers also indicates an east-west cline in gene frequencies across Europe, providing further support for the hypothesised routes of recolonisation (Kremer and Zanetto, 1997). However the amount of differentiation is much lower for nuclear markers due to lower initial differentiation in refugia, and extensive gene flow via pollen after recolonisation.

Local patterns of genetic markers have also provided clues about the mode of colonisation after glaciation. Rather than a compact wave of advance, this spread appears to have occurred at low densities by sporadic events of long-distance dispersal. Long-distance dispersants are likely to have established colonies in advance of the main

distribution (Hewitt, 1996). Colonisers would reproduce at a high rate at the expense of later migrants (Hewitt, 1996). As a result, a patchy genetic structure from a series of subpopulations will have been created (Nicholls and Hewitt, 1994; Hartl and Clark, 1997).

Petit *et al.* (1997) discerned patches of several hundred square kilometres in oak in western France by examining chloroplast DNA (cpDNA). These patches were virtually fixed for single haplotypes in both *Quercus robur* and *Q. petraea*. They suggest that long-distance seed dispersal events followed by interspecific exchanges were involved during post-glacial colonisation (Petit *et al.*, 1997).

Ferris *et al.* (1995) identified an East Anglian population clearly distinct from others in Britain. They suggest that this differentiation most likely arose due to expansion locally of a cpDNA type carrying a new mutation at the time of colonisation of East Anglia, creating a large patch of the novel haplotype (Figure 2.1).

Pine (*Pinus sylvestris*)

Considerable evidence is available on the origins of genetic variation of Scots pine (*Pinus sylvestris* L.), which in Britain is native only to the Scottish

Highlands. Studies of selectively neutral monoterpene and isozyme variation revealed substantial levels of variability despite the remnant nature of the populations. The north-western group of populations was found to be distinct from the remainder (Forrest, 1980; Kinloch *et al.*, 1986; Figure 2.2). Later studies of mitochondrial DNA (mtDNA) have upheld the genetic distinctiveness of western populations (Sinclair *et al.*, 1995; Figure 2.3). The suggestion is that Scots pine invaded from two sources. The distinct north-west populations were derived from south-west Ireland with the remainder arriving from continental Europe via England (Bennet, 1995; Sinclair *et al.*, 1995).

Beech (*Fagus sylvatica*)

Studies of selectively neutral traits in beech (*Fagus sylvatica* L.) in Europe have also identified separate refugia and indicated their importance in determining existing patterns of genetic variation (e.g. Leonardi, 1995). Patterns of genetic variation for cpDNA have been used to infer the origin of beech in Europe. Genetic variability in beech is greatest in the south of its range and northern populations appear to have only received a proportion of the cpDNA diversity present in southern populations. On the basis of their analysis of chloroplast DNA, Demesure *et al.* (1996) suggest

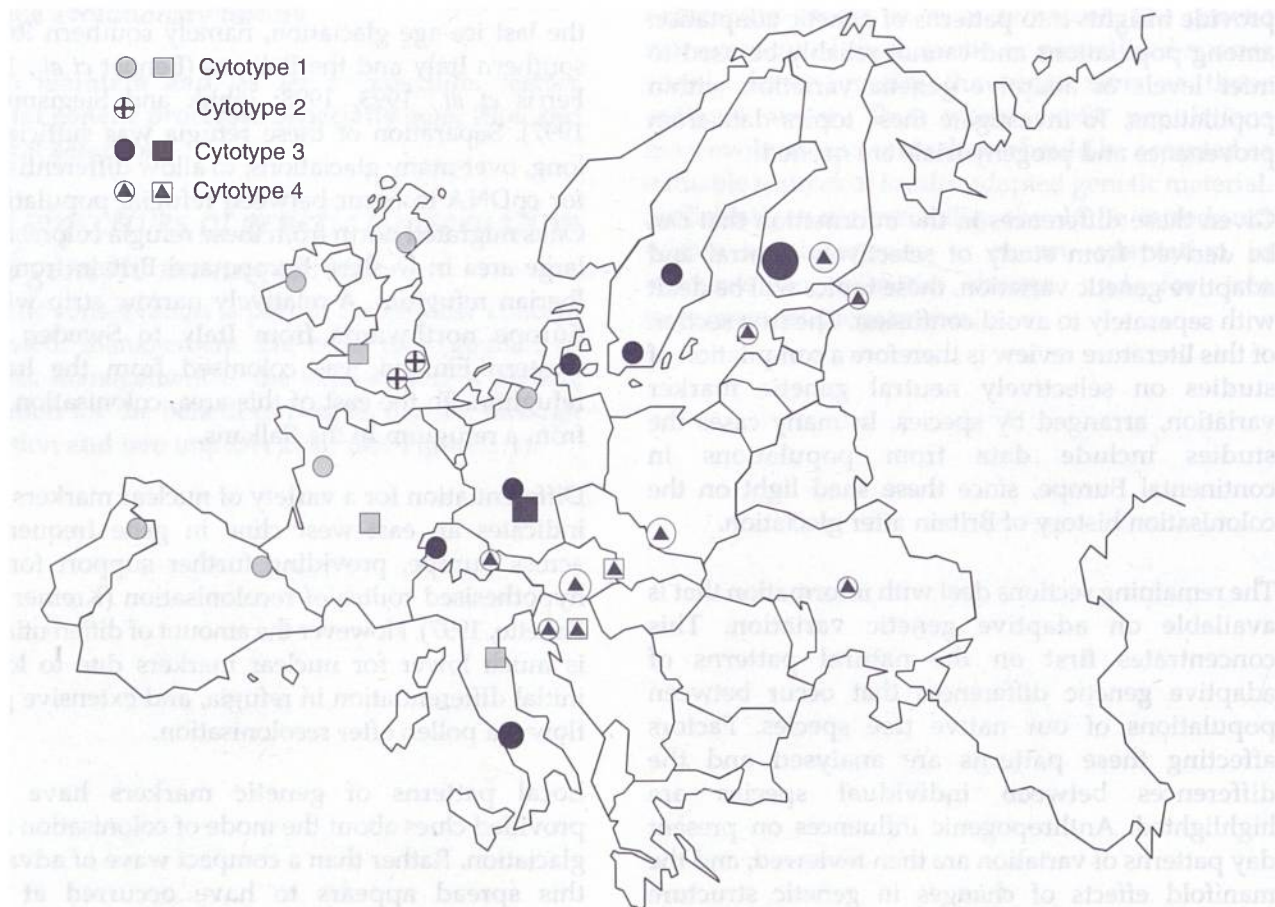


Figure 2.1 Distributions of the four cytotypes determined by cpDNA sequencing in European samples of *Quercus robur* (circles) and *Q. petraea* (squares). Symbol size is proportional to the number of individuals studied. After Ferris *et al.* (1998) by permission of Blackwell Science Ltd

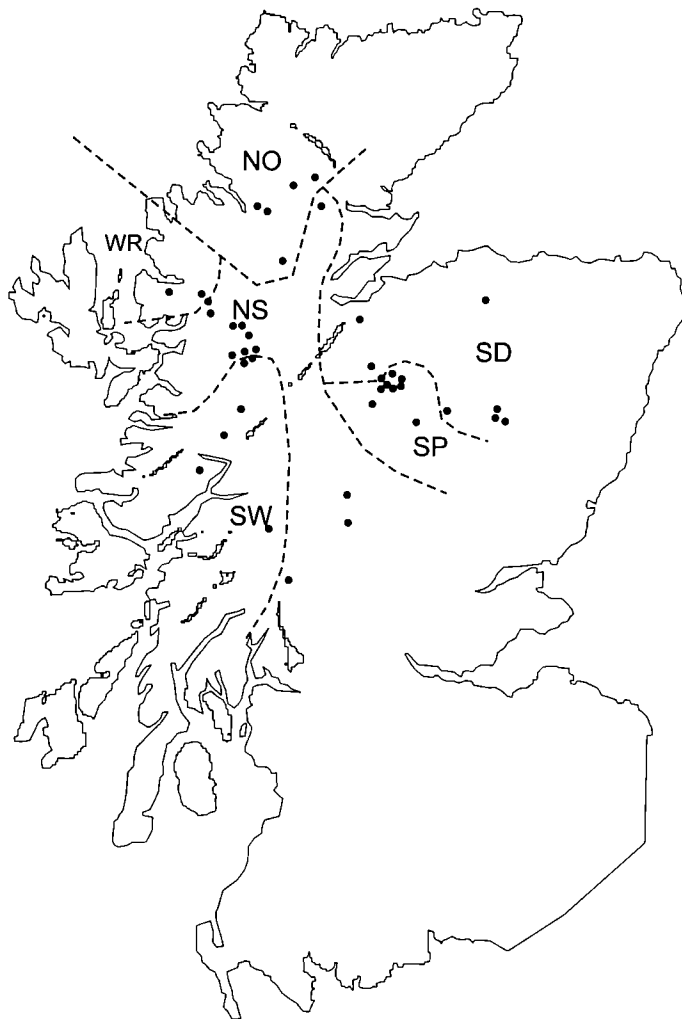


Figure 2.2 Map of Scotland showing sites sampled and division of natural range of Scots pine into regions of biochemical similarity. NO: north, NS: central north-south, SD: outer Speyside-eastern Deeside, SP: central Speyside, SW: south-west, WR: Wester Ross

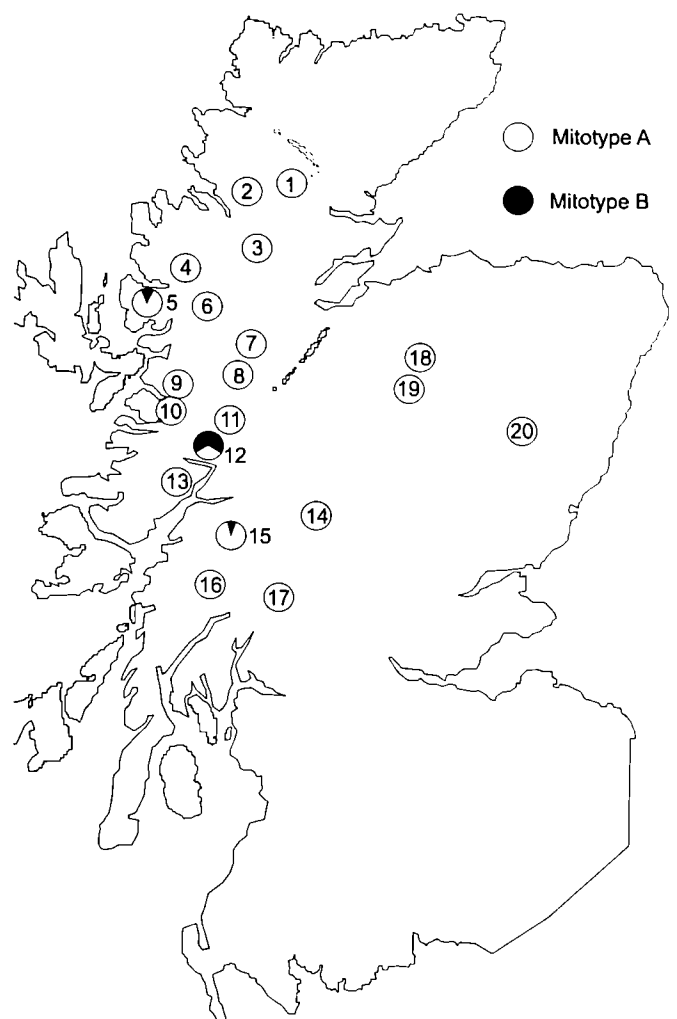


Figure 2.3 Distribution of mitotypes within 20 natural populations of *Pinus sylvestris* in Scotland. Populations are: 1 Glen Einig, 2 Rhidorroch, 3 Strath Vaich, 4 Loch Maree, 5 Shieldaig, 6 Achnashellach, 7 Glen Strathfarrar, 8 Glen Affric, 9 Loch Hour, 10 Glen Barisdale, 11 Glen Garry, 12 Glen Loy, 13 Conaglen, 14 Rannoch, 15 Doire Darach, 16 Glen Orchy, 17 Glen Falloch, 18 Abernethy, 19 Ryvoan, 20 Glentarn

that the Carpathian refuge was the most important in determining the genetic structure of beech in Europe. Recolonisation was rapid from the Carpathians and blocked out migration from southern Italy (Demesure *et al.*, 1996).

This predominance of a single refugial source has led to a degree of uniformity in the selectively neutral variation in European beech populations based on studies of cpDNA. From this it can be inferred that genetic diversity in southern English populations, where beech is considered to be native in Britain and represents the north-western extreme of its distribution in Europe, may be lower than in southern European populations. However small, isolated populations of beech at its northern limits in Denmark have been found to retain substantial isozyme variability with allele frequencies comparable to those found in larger beech forests (Larsen, 1996).

Aspen (Populus tremula)

Easton (1997) found substantial isozyme variation within populations of *P. tremula* in Scotland. Analysis of genotype frequencies suggested a little inbreeding in the populations, possibly caused by sexual reproduction between a limited sample of the total clones in these populations which have a very low frequency of flowering individuals. Despite the lack of sexual reproduction, clonal diversity has remained high. Within a single wood over 20 clones of aspen could be distinguished. However selectively neutral variation showed little differentiation between regions (2–3%), and this was attributed to substantial gene flow by pollen and seed at the time of establishment of the populations. The clones from the southern region of Scotland were the only group to be in any way different from the rest. This was attributed to the geographic isolation of populations in this area.

Black poplar (*Populus nigra*)

Recent upsurge in interest in black poplar (*Populus nigra* subsp. *betulifolia*) has led to a number of studies of its genetic variability. Isozyme diversity in continental Europe is high (Legionnet and Lefevre, 1996; Arens *et al.*, 1998), close to the mean value for wide ranging species. Most of this variation is within populations with little differentiation between individual stands due to substantial interpopulation gene flow. High levels of differentiation have only been found in relation to major physical obstacles. Thus a high degree of differentiation was seen among *P. nigra* populations within the French Alps region, where the mountains constitute an obstacle limiting gene flow (Legionnet and Lefevre, 1996). Isolation of Britain from mainland Europe may also have led to differentiation for selectively neutral markers.

The subspecies *betulifolia* of *Populus nigra* is only considered to be native to northern France, western Germany, southern Britain and parts of Ireland (Rogers, 1995). It is now considered to be severely threatened (White, 1993; Tabbush, 1996a; Turok, 1996), with only 2000 individual trees remaining in Britain (Rogers, 1995). This has prompted research to determine its current genetic status (Forrest and Cottrell, 1996; Winfield *et al.*, 1998). Results have detected moderate to low levels of genetic diversity within regions. Furthermore, geographic distinctions have been identified, with origins in East Anglia being clearly different from those in the Welsh and Severn areas (Forrest and Cottrell, 1996). However, recent examination of the latter area has shown that levels of genetic diversity throughout the Upper Severn region are relatively low (Winfield *et al.*, 1998).

Elm (*Ulmus glabra*)

In contrast to *P. nigra*, examination of *Ulmus glabra* (wych elm) in north-east France has revealed high levels of genetic diversity. Further examination of *U. glabra* has also shown levels of genetic diversity in planted trees to be comparable to those from natural forests (Machon *et al.*, 1997). The regenerated and cultivated trees are probably genetically similar because the latter are likely to have been propagated from natural populations. The lack of genetic differentiation may therefore be due to the absence of artificial breeding programmes, and long natural regeneration period (Machon *et al.*, 1997). Extrapolation of results from French studies of *U. glabra* to the British context is difficult because elm is believed to have entered this country by a westward route across the dry bed of the North Sea to England (Birks, 1989). Therefore, British populations may differ considerably from those in France.

Birch (*Betula* spp.)

Howland *et al.* (1995) examined natural populations of birch (*Betula pendula* and *B. pubescens*) in East Anglia using morphological and molecular (RAPD) techniques. Neither technique proved conclusive in distinguishing *B. pendula* (diploid) from *B. pubescens* (tetraploid), although the latter was less variable. Crossing appears to occur between these two cytotypes and introgression has resulted in numerous intermediate forms (Howland *et al.*, 1995), although this suggestion is not generally supported in studies of these species in Fennoscandia.

Rowan (*Sorbus aucuparia*)

In a study of isozyme variation in *Sorbus aucuparia* throughout Europe, decreased genetic diversity was found the more northerly the population. This pattern has been attributed to late-glacial spread from southern Europe, and loss of variability due to founding events during migration (Raspé, 1996). Unfortunately genetic information on *S. aucuparia* in Britain is sparse and the need for further research is recognised (Jackson and Flannagan, 1998).

Juniper (*Juniperus communis*)

A study of isolated populations of *Juniperus communis* in southern Scotland found considerable selectively neutral RAPD variation within them despite their very small size. Moreover only 7% of RAPD variation was found between populations (Borders Forest Trust, 1997). These results suggest that isolation and fragmentation of the populations has only occurred recently, and because of the long generation time of *J. communis* very little genetic variation has been lost by genetic drift.

Conclusions

Information on selectively neutral markers is not comprehensive and is unevenly distributed over taxa, with a strong bias to components of northern and upland forests. Nevertheless it has provided important clues about the post-glacial history of a number of our native species. Moreover it has reassured us that despite fragmentation of the range of many species, e.g. pine and juniper, the remnant populations still retain considerable selectively neutral variation and have not passed through extreme bottlenecks. This suggests that they are likely to retain a high proportion of the selectively important variation they possessed before the fragmentation events took place. Further work is in progress on selectively neutral variation of native species in both Britain and Europe and should yield fresh insights of the type outlined above for a wider range of species.

Studies of adaptive variation

As indicated in Chapter 1, studies of adaptive variation require the establishment of long-term field experiments in which populations or families of trees are grown and compared under common environmental conditions. Such studies are much harder to fund than those on selectively neutral genetic markers despite the fact that they yield more useful information for the development of genetic conservation policy. In this section we review the relatively few studies on adaptive genetic variation in our native tree species.

The majority of studies of adaptive genetic variation are concerned with genetic differences between populations or provenances, rather than with measuring the amount of adaptive genetic variation within populations. A number of factors influence the extent of adaptive genetic differences between populations. The first is the extent of the environmental differences between the sites from which populations are sampled. The greater the environmental differences, the larger the anticipated adaptive genetic differences.

The second factor is the time for which populations have occupied their present sites. The longer the number of generations they have spent in the site, the more opportunity there will have been for adaptation to that site. All of the native trees in Britain have arrived via colonisation after glaciation. Some species arrived very soon after the retreat of the glaciers, e.g. birch which arrived some 10 000 BP while others came much later, e.g. beech whose major expansion into Britain was about 3000 BP (Birks, 1989). Therefore there has been greater opportunity for adaptive differences to evolve between British and continental populations for birch than for beech (Worrell, 1992; Samuel, 1996).

A third factor which influences the degree of adaptive difference evolving between populations is the nature of the species concerned. Some species show high degrees of phenotypic plasticity and show little genetic differentiation over large environmental ranges. On the other hand, some species respond to small differences in environment by evolving very locally adapted populations. *Larix occidentalis* in North America, for example, can show genetic differentiation where populations are only 500 m apart (Rehfeldt, 1995). In contrast, areas of 2000 km² or much greater in North America have shown no significant differences for many traits in *Picea glauca* (white spruce) (Li *et al.*, 1997). The reasons for these differences in behaviour are not clear. The practical consequence, however, is that for any one species the extent of adaptive genetic differences shown is not predictable. There is therefore an absolute requirement to carry out

empirical provenance/progeny trials to quantify adaptive genetic variation.

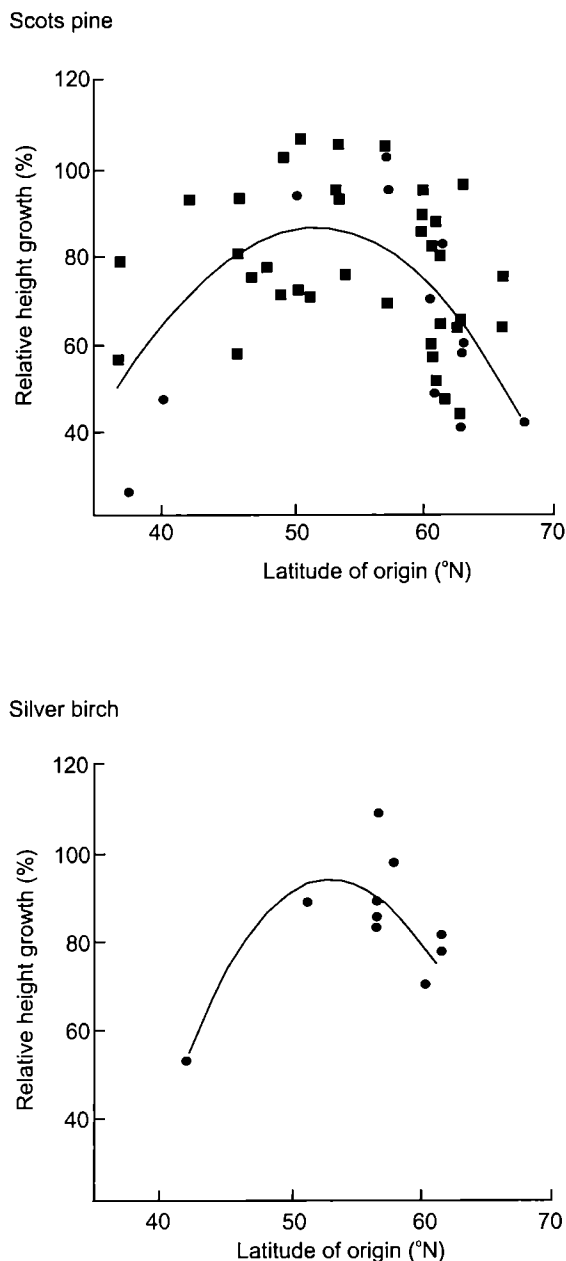
In this review of adaptive genetic variation, the studies are divided into three parts. The first looks at studies of adaptive genetic differences between British and continental European provenances of native species. Part two summarises information on adaptive genetic differentiation between provenances within Britain. The last part looks at studies which measure adaptive genetic variation within populations.

Variation between British and continental European populations

Pinus sylvestris is Britain's only native commercial conifer. This fact has led to considerable interest in examining potential increases in productivity from the introduction of continental European provenances. Studies of this nature provide a valuable insight into the extent of adaptive variation in this species. The results of many investigations suggest that *P. sylvestris* has undergone a fair degree of adaptation to environmental conditions in Britain. Native provenances consistently out-perform trees from mainland Europe, even where these have originated from similar latitudes (Worrell, 1992; Samuel, 1996; Figure 2.4). Mean height growth of *P. sylvestris*, for example, in continental provenances was only 72% of that of British trees on the same sites. Lowest values were obtained from more extreme locations, i.e. northern Scandinavia and southern Spain. Those in which growth was comparable to British provenances were from similar latitudes to the planting sites (Worrell, 1992). Survival was also much lower in the introduced trees, especially at the more extreme experimental sites where only 12% of those planted from continental origins were still alive at the time of recording (c. 20–30 years old).

Evidence of the specific nature of adaptation in *P. sylvestris* has been provided by Leionnen (1996). Comparisons between seedlings from five European origins revealed that Scottish material required the highest chilling requirement to bring about release of dormancy, while the chilling requirements of those from the continent were not so great (Leionnen, 1996). This genetic difference was associated with the need to prevent premature bud burst in response to temporary increases in winter temperature in the maritime climate of Scotland.

Further comparisons between British and Scandinavian *P. sylvestris* seedlings showed that the latter had greater frost resistance, earlier frost hardening and a longer period of frost hardiness (Perks and MacKay, 1997). Lower levels of overall



markedly between west and east coast provenances in Scotland (Lines and Mitchell, 1965). Ennos and Perks (1995) detected significant differences among native origins of *P. sylvestris* for survival, growth rate and flushing time in trees on a site in southern Scotland.

Adaptation in response to climate has also been seen in *Betula pubescens*. Leaf elongation was greatest in trees originating from south-east Scotland, and decreased with increasing distance towards the north-west (Billington and Pelham, 1991; Figure 2.5). Although clearly defined adaptations such as this have been observed, particularly in response to more extreme environmental conditions, patterns of adaptive variation are not always easily explicable. Blackburn and Brown (1988) found significant differences in growth and resistance to climatic damage in *Betula* spp. but no clear geographical pattern. Current research on provenance variation of native species in Britain is confined to birch, ash, oak and beech but these trials generally include only a small number of native provenances or, in the case of birch, have only recently been planted (Cundall, personal communication). Knowledge of adaptive genetic variation of our native tree species is woefully meagre.

These data from Britain are so limited that it is worth looking to continental European studies to determine whether genetic differentiation is likely to occur for unstudied species. Investigations in Europe have shown adaptive genetic differentiation

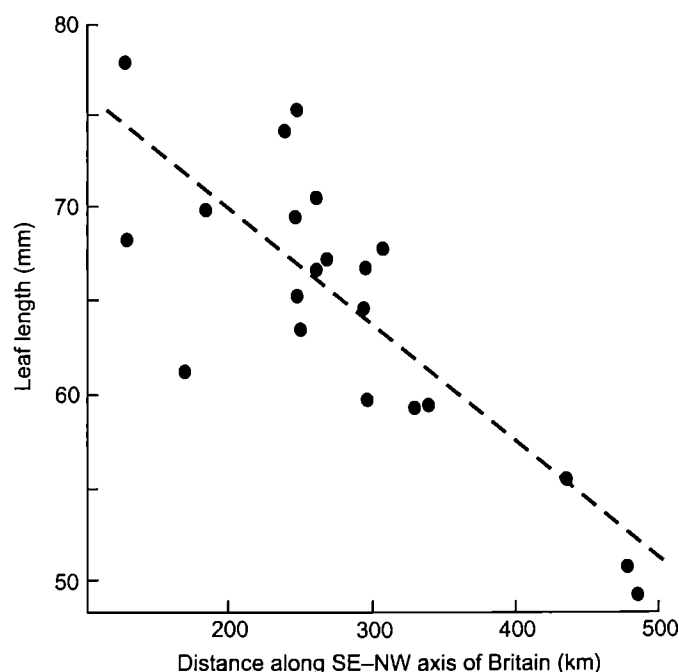


Figure 2.5 Variation in leaf length of *Betula pubescens* along a SE–NW transect across Britain. Reprinted from *Botanical Journal of the Linnean Society* 96: Pelham, J. *et al.*, Variation in *Betula pubescens* Ehrh. (Betulaceae) in Scotland: its nature and association with environmental factors, 217–234, 1988, by permission of Academic Press

in a diverse range of British native species, variation that is associated with environmental gradients. Examples where such differentiation has been found are for *Fagus sylvatica* (Loechelt and Franke, 1996), *Quercus petraea* (Ducousso *et al.*, 1996) and *Sorbus aucuparia* (Hillebrand and Rosenberg, 1996). Variation is usually greatest in relation to steep environmental gradients for factors such as soil, moisture, temperature and exposure. These occur in Britain over relatively short distances, especially in Scotland (Pyatt, 1995). Thus, sharply defined differentiation and adaptation is likely to be present in native British species. This may be most pronounced in northern and western regions of Britain since Sorensen (1983) and Campbell *et al.* (1989) demonstrated that the effects of elevation on differentiation in North America are more marked in areas with oceanic climates compared to those of a more continental nature.

Adaptive variation within populations

The capacity for a population to adapt to environmental change is determined by the extent of appropriate adaptive variation in the population (Ennos *et al.*, 1998). In order to measure such variation progeny trials are required. Very few such trials have been conducted in Britain for native tree species. The only taxa for which information is available are *Betula pubescens* (e.g. Blackburn and Brown, 1988; Billington and Pelham, 1991) and *Pinus sylvestris* (e.g. Perks, 1994). For both taxa significant adaptive genetic variation was detected within populations for a proportion of the characters measured. However for traits likely to be subject to stabilising selection such as date of bud burst, variation was often much larger between populations than within populations (Perks, 1994).

These types of studies have been undertaken more comprehensively in Europe (e.g. Eriksson and Jonsson, 1986; Giertych, 1979), where they have also found significant adaptive genetic variation within populations (Gosler *et al.*, 1994; Mattila *et al.*, 1994; Konnert, 1996; Larsen, 1996). Thus genetic variation within populations for phenology, frost hardiness, pathogen resistance and form have been recorded in species such as *Pinus*, *Betula*, *Populus* and *Quercus* in Europe. Adaptive variation within populations has also been examined in less well-known species. Jonsson *et al.* (1988) detected large family effects in *Carpinus betulus* for early height growth, bud burst and growth cessation, indicating significant within population variation. There is clearly the potential for these populations to respond to selection, though in times of rapid climate change the rate of response may be too slow to maintain adaptation to the environment if this takes place *in situ* (Billington and Pelham, 1991).

Human impact on genetic variation

The genetic structure of native trees and shrubs has been variously altered by mankind through disturbance and exploitation. Woodland developed in Britain from approximately 10 000 BP, when early colonisers included *Betula* spp., *Pinus sylvestris*, *Corylus avellana*, *Ulmus* and *Quercus* spp. By 5000 BP, during the Atlantic period, *Alnus glutinosa*, *Tilia cordata*, *Ilex aquifolium* and *Quercus* had expanded to dominate all but the northern area of Britain, where *P. sylvestris* and *Betula* spp. remained common (Godwin, 1975; Birks, 1989; Peterken, 1993). Since 5000 BP however, the woodlands, which were natural to most of Britain, have been subjected to substantial human impact, influencing their composition and distribution and hence their genetic diversity.

The first major human impact on the natural woodland of Britain was widescale clearance, predominantly to make way for agriculture. As the once continuous woodlands became increasingly fragmented, species previously linked by gene flow became much more genetically isolated (Ennos *et al.*, 1998). The anticipated effect of this genetic isolation is the development of genetic differences among populations by chance, and the loss of genetic variation within populations every generation. The extent to which these undesirable consequences occur is determined by the degree of genetic isolation of the woodland fragments, and the number of generations in which they remain in this state. Substantial loss of variation and large genetic differences between populations are only expected when fragments remain small (< 50 trees) and completely genetically isolated for tens of generations.

Another important effect of fragmenting populations is that the number of reproducing individuals in any one fragment may be so small that normally outcrossing species are forced to self-pollinate. This will lead to production of inbred offspring and the expression of inbreeding depression in these offspring whose fitness may be reduced by 50 % (Sorensen and Miles, 1982).

A number of studies have addressed the question of whether these undesirable genetic effects can be detected in native British trees. Selectively neutral genetic variation in fragmented *Juniperus communis* populations in southern Scotland was found to be comparable with that of species with large effective population sizes and substantial gene flow between populations (Borders Forest Trust, 1997). This was despite the small size and isolation of the remnant *J. communis* populations. Similar results have been recorded for *Taxus baccata* in Europe (Lewandowski *et al.*, 1995). Maintenance of genetic variation was

attributed to the longevity of *T. baccata*, its dioecy, and wind pollination, promoting gene flow over considerable distances (Lewandowski *et al.*, 1995).

In a study of derelict *Pinus sylvestris* in Glen Falloch, Scotland, Kinloch *et al.* (1986) did not detect a significant loss in genetic variation despite an effective population size of only 50 breeding trees. However, the effects of inbreeding depression in seed progeny due to increased self-fertilisation in this population have previously been observed (Boyle and Malcolm, 1985).

The impact of wholesale forest clearance can also lead to restrictions in the distributions of native species to more marginal site types. This can be further confounded by the effects of grazing pressure, and many populations are often limited to inaccessible sites. This has occurred in populations of *Sorbus aucuparia* (hybrids) on the Isle of Arran (Vickery *et al.*, 1998) and *Tilia cordata* in the Lake District (Piggot and Huntly, 1980). Restriction of populations to certain site types will inevitably tend to reduce adaptive genetic variation to only a proportion of that originally present in the species (Ennos *et al.*, 1998).

In addition to the effects of large-scale reductions in the distribution of native species, management of the remaining woodland area is also likely to have had a significant influence on genetic variation. The main impact is likely to come from the widespread introduction of foreign planting material of native species. When this occurs outcrossing can take place between native stands and plantations of the same species established from foreign genetic material (Graudal *et al.*, 1995). The result will be a change in the original distribution of selectively neutral markers, and hence a loss of the information on post-glacial history that is stored in the genes. Offspring inheriting half their genes from the native and half from the exotic source will be produced. These may well have lower fitness compared with pure native offspring. The regenerative capacity of the native population will therefore be reduced, compared with its value in the absence of the exotic stand, as a consequence of the 'migrational load' from the exotic stand. However, in the long term, there may be relatively little genetic impact if the extent of pollen flow is low and selection eliminates the less fit hybrid progeny from the site.

These problems are likely to be met with in trees that have received intensive management such as oak, beech, gean and to a lesser extent Scots pine. Scots pine seed has been transferred throughout many parts of Scotland for several centuries, including the use of some foreign material at least since the eighteenth century (Anderson, 1968).

Widespread use of a few popular seed sources may have decreased genetic variation over the geographic distribution of this species (Soutar and Spencer, 1991). However, the vast majority of *P. sylvestris* in the natural range of the species planted during this century is of local provenance (Steven and Carlisle, 1959). Nevertheless, it is likely that genetic exchange may have taken place where introduced stands were planted adjacent to native woodlands (Forrest and Fletcher, 1995). The problem of genetic interaction between native and planted stands is likely to increase in the future with the use of genetically improved Scots pine from a small number of tested seed orchards.

Extensive planting of non-indigenous *Quercus* spp. has continued for a very long period and, as a result, many populations will no longer retain significant natural adaptation (Ferris *et al.*, 1997). Translocations and introductions of foreign genotypes were frequently used in large-scale landscaping (Ferris *et al.*, 1997). Studies of genetic variation in *Quercus* spp. populations in East Anglia have revealed anomalies among indigenous populations due to the planting of non-native trees in roadside boundaries and estate grounds for example (Ferris *et al.*, 1995).

Recent use of commercial stock for landscaping has resulted in introductions of *Crataegus monogyna* from Europe. However, the introduced material proved to be inferior to native stock (Jones and Evans, 1994). Problems associated with the use of maladapted material from foreign stock are well known in continental Europe. Major decline in *Alnus glutinosa* in Germany in the past has been attributed to planting frost-sensitive provenances from Belgium (Franke, 1994). Concern has arisen in Britain over the possibility of gene flow from introduced cultivars into native *Salix viminalis* (osiers) (White *et al.*, 1994).

In heavily managed species where vegetative propagation is the main means of multiplication, there is the potential for very rapid reductions in genetic diversity through use of only a small sample of clones. Past selection of cuttings from a few 'prime' male *Populus nigra*, a dioecious native tree, has virtually eliminated females (which were considered a nuisance because of their production of large quantities of seed fluff) and has narrowed the genetic base of this species (Tabbush, 1996a). *P. nigra* var. *betulifolia* is now considered to be severely threatened (Tabbush, 1996b). Where vegetative propagation through tissue culture is incorporated into future tree improvement programmes this danger of dramatic reductions in genetic diversity is also an issue (Nicoll, 1993; Palmer *et al.*, 1996).

As well as this effect of conscious selection of

desirable genotypes by man, the past selective harvesting of phenotypes of better form may have led to dysgenic selection in native tree populations. This would occur if the proportion of offspring arising from trees of poor form was enhanced by the harvesting operations, and if the phenotypic variation for form had a genetic basis.

In the future, one of the most significant potential impacts that man may have on the genetic variation of native trees and shrubs is through selection exerted by atmospheric pollution and global climate change. Variations in responses between species suggest that their competitive balance may be altered as a consequence of climate change due to differences in effective growing season, and selection for adaptation to the new climatic regime will occur (Kramer, 1995). However, Billington and Pelham (1991), measuring genetic variation within populations, found that levels of adaptive variation for date of bud burst were insufficient within Scottish populations of *B. pubescens* and *B. pendula* to allow rates of adaptation in line with predicted rates of climatic warming. This has implications for the movement, natural and artificial, of genetic material to provide insurance against the deleterious effects of rapid environmental change (Ennos *et al.*, 1998).

Overall conclusions

This review of our knowledge of genetic variation within native tree species reveals a number of very important points. The first is that we possess a relatively large body of work on selectively neutral variation that is either completed or ongoing (Table 2.1). This work has been useful in revealing information about the biology of these species (mating systems, clonal spread and diversity), post-glacial migration routes, the location of their glacial refugia, and their mechanisms of colonisation. It suggests that at least for cpDNA markers levels of genetic variation may be lower in Britain than in southern Europe. On the other hand, studies of selectively neutral variation also tend to suggest that fragmentation of populations by man has not yet led to significant loss of genetic variation from remnant populations, since the fragmentation event has been too recent.

In contrast to the large body of work on selectively neutral variation, there is a dearth of studies on adaptive variation in our native trees. This is well illustrated by Table 2.1 which summarises published work in these two areas. The information actually available highlights the differential adaptation of British and continental material.

Where it has been investigated, differential adaptation among British populations has been found for growth, survival, phenology, morphology

Table 2.1 Bibliography of native British tree and shrub species literature

Tree/shrub species	Research information and number of publications available by species (UK and foreign sources)									
	Selectively neutral		Adaptive		Performance and provenance		Genetic conservation		Other taxonomy	
	UK	For	UK	For	UK	For	UK	For	UK	For
Large-medium sized trees										
<i>Alnus glutinosa</i>						2		2		
<i>Malus sylvestris</i> ssp. <i>syvestris</i>						1				
<i>Fraxinus excelsior</i>		2				2		2		
<i>Populus tremula</i>		1			1	3	1	2		
<i>Fagus sylvatica</i>		7		1		2		3	1	
<i>Betula pubescens</i>	1		2			2			1	
<i>Betula pendula</i>	2		1	2		2			2	
<i>Prunus padus</i>	1									
<i>Prunus avium</i>		3				2	1			
<i>Ulmus glabra</i>	1	2						1	1	1
<i>Carpinus betulus</i>						1				
<i>Tilia cordata</i>				1		1		1	1	
<i>Tilia platyphyllos</i>								1		
<i>Acer campestre</i>										
<i>Quercus robur</i>	2	6		2		2	1	2		1
<i>Quercus petraea</i>	1	7		2		2	2	4		
<i>Pinus sylvestris</i>	2		1	1		3			1	
<i>Populus nigra</i> var. <i>betulifolia</i>	1	2					2	1		
<i>Populus canescens</i>				1						
<i>Sorbus aucuparia</i>	1					1			1	
<i>Sorbus torminalis</i>						1				
<i>Sorbus aria sensu lato</i>										
<i>Salix fragilis</i>							1	1		
<i>Salix caprea</i>							1	1		
<i>Salix alba</i>							1	1		
<i>Taxus baccata</i>		3					1	3		

and physiology. Patterns of variation depend upon the species and character involved. Some of this variability is associated with environment of origin. Extrapolation from knowledge of studies elsewhere, and from analysis of climatic variation, suggests that adaptive variation may change over shorter distances in the north and west of Britain than in the south and east. The few measurements that have been made reveal that substantial adaptive variation remains within native populations.

Although these studies on adaptive variation have provided a broad overview, it is clear that the patterns of adaptive differentiation found are very different among species, and difficult to predict. We remain very ignorant of the extent of local adaptive variation in our native tree species. Appropriate provenance and progeny trials with British populations of native tree species are a necessity for understanding patterns and extents of local

adaptation, and estimating the risks of transfer of material within Britain.

The final point to emerge from this review is that the original genetic structure of native tree species in Britain has been profoundly altered by human activity. Fragmentation of populations has reduced gene flow and population size. There is the potential for loss of genetic variation from populations and the expression of inbreeding depression if population size is kept below 50 over many generations. Evidence for inbreeding depression has already been reported. Where species have been restricted to certain site types, adaptive genetic variation associated with alternative site types has been lost.

Transport of material and its planting close to native woodland within the range of gene flow may have altered genetic structure for selectively neutral

Table 2.1 continued

Tree/shrub species	Research information and number of publications available by species (UK and foreign sources)									
	Selectively neutral		Adaptive		Performance and provenance		Genetic conservation		Other taxonomy	
	UK	For	UK	For	UK	For	UK	For	UK	For
Small trees and shrubs										
<i>Prunus spinosa</i>									1	1
<i>Buxus sempervirens</i>										
<i>Cytisus scoparius</i>										
<i>Frangula alnus</i>										
<i>Rhamnus catharticus</i>									1	
<i>Ruscus aculeatus</i>										
<i>Cornus sanguinea</i>									1	
<i>Sambucus nigra</i>										
<i>Ulex europeus</i>										
<i>Viburnum opulus</i>									1	
<i>Crataegus monogyna</i>					1		1		3	
<i>Crataegus laevigata</i>										
<i>Corylus avellana</i>							1			
<i>Ilex aquifolium</i>							1			
<i>Juniperus communis</i>							2			
<i>Ligustrum vulgare</i>									1	
<i>Rosa canina</i>									1	
<i>Rosa arvensis</i>										
<i>Euonymus europaeus</i>									1	
<i>Daphne laureola</i>										
<i>Viburnum lantana</i>									1	
<i>Salix triandra</i>										
<i>Salix pentandra</i>										
<i>Salix aurita</i>										
<i>Salix cinerea</i>										
<i>Salix viminalis</i>		1				1	1			
<i>Salix purpurea</i>										

Key The column headings represent the type of information contained in the relevant research papers. Selectively neutral: selectively neutral traits. Adaptive: adaptive traits. Performance and provenance: performance and provenance information on each species. Genetic conservation: information on genetic conservation of the species. Other taxonomy: other information relevant to the review of genetic conservation of native tree and shrub species.

variation. For adaptive variation, gene flow between native and exotic populations could lead to the formation of less well-adapted offspring, but the extent to which this leads to long-term alterations will depend on the power of natural selection to remove these less well-adapted genotypes from the population. Changes in adaptive variation are likely to have occurred in the past as a consequence of dysgenic selection and the preferential planting of desirable genotypes. The increasing intensification of tree breeding operations, and the more widespread use of clonal propagation, may mean that native populations, in future, interact

genetically with less well-adapted populations of low genetic variability. This could lead to a significant reduction in the adaptedness of the native populations.

In the future, climate change will be genetically altering populations. There is considerable debate about whether the genetic variability of populations will be sufficient to allow them to adapt to such rapid climate change *in situ*, or whether measures such as long-distance transfer of genotypes from elsewhere will be needed to facilitate rapid adaptation in native populations.

Developing a genetic conservation strategy

Need for genetic conservation

A number of broad issues can be identified for which genetic conservation policy is needed in order to improve decision-making.

Issue 1: choice of seed origin for planting stock

Planting stock needs to be well adapted and contain adequate genetic diversity. It appears that some two-thirds of broadleaves currently planted in Britain (i.e. in forestry and landscaping) are imported from continental Europe and are unlikely to be properly adapted to British environments. There is a lack of appreciation of the importance of seed origin and genetic diversity, especially in the nursery sector. Planting material which is of British origin, from a similar region or locality and from similar site type, is often the best choice. There are exceptions to this for some species (e.g. beech) especially when the planting sites are in southern and eastern England. Choice of seed origin is particularly important in the planting of new native woodland.

Adaptation

Good adaptation is a key aspect of choosing seed origins, irrespective of type of planting scheme (e.g. Lines, 1987). There are a number of different indices of adaptation. Growth rate and survival are used for tree crops and ability to reproduce (fitness) for natural populations. A broad approach to defining adaptability is needed which includes resistance to climatic damage, pests and disease, and looks at long-term performance, thereby assessing adaptability to climatic incidents with long return periods. There is a particular need to assess the appropriateness of using growth rate as the main or sole indicator of good provenance choice, as this may encourage the use of material with long growing periods, which as a rule is more susceptible to frost damage. Frost damage to leading shoots in broadleaves is thought to be an important cause of poor form, and the form of broadleaved trees is of more concern in timber production than overall growth rate.

Transfer rules

No scientifically based guidance is currently

available on how far seed sources can be moved within Britain without loss of adaptation. Geographic patterns of genetic variation in any species may vary:

- between adaptive and selectively neutral variation;
- for different characteristics in the case of adaptive variation (e.g. growth rates cf. survival); and for different markers in the case of selectively neutral variation.

This potentially complicates the drawing up of transfer rules. It is accepted that greater weight should be attached to conserving adaptive rather than selectively neutral variation. However it is likely that any provisions designed to conserve adaptive variation will usually be of a type and scale which also would conserve patterns of selectively neutral variation.

Current moves to restrict choice of planting material for native woodlands by the use of seed zones is an important step. These provisions need to be backed up by improved scientific evidence. For vegetatively propagated species, such as aspen, guidance is also needed on the appropriate number of clones to plant within woodlands to prevent future genetic problems associated with lack of genetic variability.

Genetic conservation policy is needed to help to ensure the use of planting stock from appropriate origins and to provide guidance on the planting of vegetatively propagated material. Policy should aim to provide guidance on how to assess adaptation and maladaptation and should ensure that both adaptive and selectively neutral variation needs are taken into account in developing regulations.

Issue 2: foreign material in existing woodland

The existence of foreign origin material (or material transferred long distances within the UK) in existing woodland has the potential to introduce maladapted genes into native populations, reducing the fitness of offspring. Recent studies suggest that historical planting of native trees and shrubs may have occurred over a longer period, and

been more widespread and involved a wider range of species than previously thought (e.g. Smout, 1997). However the scant evidence available also points to the bulk of seed sources used in such historic planting usually being British (Ennos *et al.*, 1998). A key question is whether historical planting of translocated material has been on a significant scale compared to local origin and autochthonous material. This is certainly the case in some regions for some species (e.g. oak and beech).

A genetic conservation policy is needed to provide guidance on how serious such effects are, and what options there are for overcoming any risks.

Issue 3: conservation of small, isolated and rare populations

Small remnant populations pose a number of potential problems. While they appear to retain relatively high levels of genetic variation, they may face problems regenerating (or acting as seed sources) due to inbreeding. They also face potential losses of genetic variation in the long term as a result of the inability to acquire genetic variation by gene flow from neighbouring populations. This means that they are particularly poorly placed to respond to climatic change.

Some species/subspecies are naturally rare in Britain (e.g. some *Sorbus* species). In addition some species and populations have become particularly rare as a result of deforestation (e.g. aspen, treeline woodlands). Some of these species encounter difficulties in seed production due to reproductive isolation (e.g. Worrell *et al.*, 1999) and are particularly vulnerable to further losses. Another concern is that widespread planting of naturally rare species may not be appropriate. A further complication is that some conservation professionals regard small remnants as unique examples which must be conserved and remain 'pure' without invasion by genes from elsewhere.

A genetic conservation policy is needed to provide guidance on identifying populations most at risk and to develop appropriate management practices.

Issue 4: influence of past exploitation and management

Past management and exploitation of woodland may have altered populations by:

- dysgenic selection as a result of removal of the more desirable trees from populations, the restriction of woodland to poorer sites types and

a shift away from high forest conditions towards trees existing in non-woodland situations (scrub, wood pasture, hedges etc.);

- selection in favour of desirable types of tree where woodland has been managed for timber production.

Dysgenic selection is sometimes cited as a potential problem in using British origin planting material. Some conservationists are concerned about possible implications of using material from populations which have undergone selection in favour of timber producing genotypes.

A genetic conservation policy is needed to assess the scale and influence of such effects and to recommend which measures might be taken to counter any undesirable results.

Issue 5: in situ conservation: the role of designated genetic reserves

The conservation of maximum genetic diversity *in situ* is a desirable objective. This can take place in both the forest resource in general and in specially designated areas. One option is to identify genetic reserve areas in regions where there are high concentrations of autochthonous woodland. In such areas sufficiently large populations exist, genetic exchange with other populations occurs and undesirable gene flow from plantations of foreign origin is minimised. Reserves could also be considered for uniquely adapted or particularly rare genotypes worthy of conservation on genetic resource grounds.

Designated areas (including woodland SSSIs, NNRs, FC forest nature/Caledonian reserves and SWT reserves) can make an important contribution to genetic conservation. However they have usually not been selected with this in mind and it would be useful to evaluate their potential contribution to genetic conservation.

As a rule, genetic conservation value will be closely related to indicators of nature conservation value such as site occupancy (ancientness), naturalness, species diversity, scale, representativeness and rarity (Ratcliffe, 1977).

Genetic conservation policy is needed to evaluate the desirability of, and approaches towards, designating genetic reserves. Criteria for assessing the genetic conservation value / potential of different woodland types are needed, to clarify which woodlands should be prioritised for genetic conservation.

Issue 6: ex situ conservation

Ex situ genetic conservation is needed to safeguard some rare and valuable genotypes adapted to particular environmental conditions, which may be threatened in the wild (e.g. rare *Sorbus* species). A major impediment to our understanding of variability in our native forest species has been a lack of adequate collections of native material on which to carry out research, and from which readily accessible and adapted seed sources could be developed. Properly established *ex situ* gene banks could fulfill this role.

Genetic conservation policy is needed to provide guidance for the design and establishment of gene banks.

Issue 7: forest design

Spatial arrangement of trees both at a stand scale and at a landscape scale may have a significant influence on the patterns of gene flow, interconnectedness and adaptive potential of populations. Forest design could therefore be extended to include genetic aspects. Where broadleaf/native components of plantation forests are seen as being long term and contributing to connectivity, more attention should be paid to their genetics.

Genetic policy is needed to provide guidance on how genetic issues could be incorporated into forest design practices.

Issue 8: regeneration of species-poor secondary woodland

There is often a degree of historical accident in the species composition and the genotypes represented in secondary woodland, and basing their restoration and expansion purely on natural regeneration limits both the species and genotypes available. Where secondary woodland is clearly species poor, with limited likelihood of colonisation from nearby seed sources, a case can be made for introducing both missing species and genotypes from populations in the same region.

A genetic conservation policy is needed to give guidance on best practice in this respect.

Issue 9: use of genetically improved material and non-local material

The development and use of genetically improved material of native species raises the question of

possible impacts of gene flow from plantations into native tree populations (and vice versa). This has already led to the withdrawal from use of improved Scots pine in new native pinewoods. An argument can be made for some level of selection being a useful means of countering any past dysgenic selection and expanding the proportions of genotypes which are adapted to growing in high forest conditions (cf. scrub, wood pasture and hedges). Selection of improved material on a regional rather than country-wide basis has been proposed to help overcome possible problems of adaptation to regional conditions.

Many conservation professionals oppose the use of improved material. There is a need to establish a dialogue with conservationists to explain that sensible use of regionalised improved material of native species does not constitute a threat to genetic conservation. In addition there will be situations when using non-local material may be appropriate, for example specific provenances thought to be particularly suitable for timber production.

A genetic conservation policy is needed to address the use of improved material or non-local material, especially providing guidance on minimising any undesirable effects arising from its use in the proximity of important semi-natural woodlands.

Issue 10: response to environmental change

Genetic resources are constantly changing and evolving in response to ecosystem dynamics, edaphic and climatic changes. A genetic conservation policy would need to promote this primarily by encouraging conditions necessary for gene flow and natural selection.

The unprecedented rates of climate change which are predicted present forest tree populations with problems in adapting to future conditions. Two general approaches have been suggested:

- sourcing material potentially adapted to future climates in existing woodland in Britain;
- introducing and planting genetic material from other climatic regions adapted not to current environment, but to anticipated conditions later in the rotation.

Introductions from the near Continent to southern Britain or movement of material northwards within Britain may be an option for some species. However, for many upland areas, no climates exist abroad which are good analogues for projected future climates in Britain.

A genetic conservation policy is needed to address the consequences of climate change and suggest research priorities and management options for enhancing the degree of adaptation of forests in the future. This requires assessment of the ability of indigenous populations to adapt naturally to new climatic conditions and the desirability of transferring material to anticipate climatic change.

Issue 11: species differences and woodland types

Different species have different genetic structures and will ultimately require some distinctive provisions. It may be possible to group species into those with similar characteristics, in order to simplify genetic conservation measures. This could be done on the basis of their mating systems, ecology and post-glacial history. For example: catkin-bearing, early successional species in the Saliceae such as willows, birches and aspen could potentially form one such group; and late successional, shade bearing species such as beech and hornbeam could form another.

It is useful to distinguish between main woodland types when developing genetic conservation measures as some may require more stringent provisions than others. The categories in the Forestry Standard could form a basis for this. A key question is whether planted woodland *other than* 'new native woodland' should have less stringent requirements regarding choice of origin of planting material.

A genetic conservation measure should aim to distinguish between different species or groups of species and develop measures appropriate for the range of woodland types.

Issue 12: influence of tree genotype on woodland fungi and fauna

Some species of woodland fungi and fauna may be influenced by the genotypes of the trees they are associated with. Trees which are well adapted to site conditions are likely in general to provide the most appropriate woodland habitat for associated species. In particular, some species of woodland flora and fauna may be adapted to specific patterns of phenology and seasonal development (flushing, flowering, seasonal growth, seed production, etc.) in their host trees. These phenological traits are largely genetically determined. This subject appears to be virtually unresearched.

A genetic conservation policy should aim to initiate research in this field and ensure that genetic issues are integrated into wide conservation policy.

Elements of a genetic conservation policy

Policy statements

Genetic conservation has been raised at a general level in international policy statements and to a lesser degree in national policy (see Appendix 1). Policy statements relating to genetic conservation, while disjunct and somewhat superficial, cover most of the main issues. Most thorough treatment is given in biodiversity policy rather than forestry policy.

The following improvements could be considered:

- Clearer articulation of desirability, objectives and scope of genetic conservation in national forestry policy.
- A policy document which specifically addresses genetic conservation.

Regulation and guidance

A number of regulations are already in place which address aspects of genetic conservation (see Appendix 1), particularly:

- conserving genetic character of semi-natural woodlands through encouragement of natural regeneration, the use of local origin planting of Scots pine and use of buffer zones;
- inventory and registration of seed sources for Scots pine.

Plans are also being developed to introduce regulations on the choice of seed sources for all native tree and shrub species when planted in new native woodlands (Forestry Authority, undated). For this purpose a system of seed zones (Figure 3.1) which subdivide the existing four 'Regions of Provenance' is being developed. EC rules on seed sources are currently being redrafted to allow use of locally collected 'source identified' seed and to extend the number of species under regulations (currently only beech, oak and Scots pine). In addition to formal regulations, guidance on good practice, some of which is effectively required in order to receive grant aid, is also given in a number of fields relevant to genetic conservation (see Appendix 1). The following opportunities to build on existing regulations and develop guidance could be considered (main headings ordered according to priority).

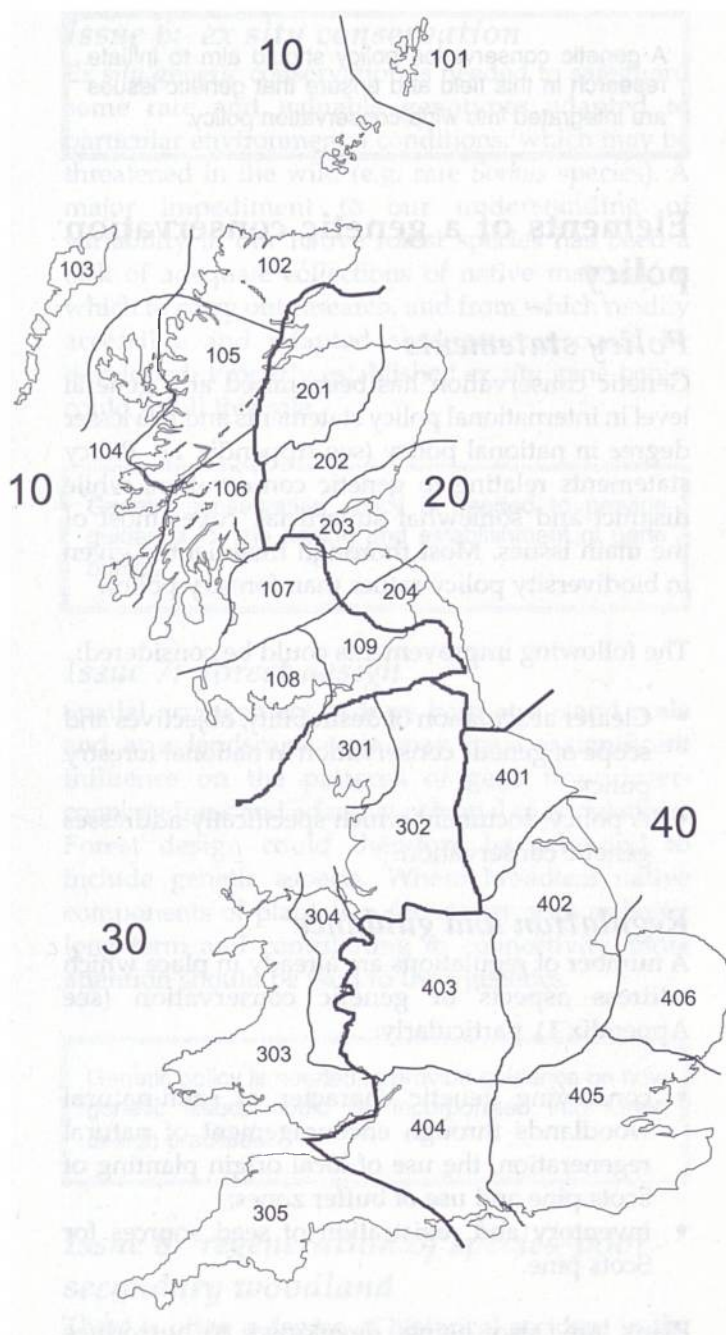


Figure 3.1 Map of local seed zones. There are four broad Regions of Provenance. These divide the country into eastern and western zones within northern and southern divisions, and are identified as Regions 10, 20, 30 and 40, delineated by the bolder lines

Choice of origin for planting stock

1. Continue to develop guidance as to what constitutes appropriate choice of seed origins.
2. Institute transfer rules stating the acceptable distance for moving planting stock.
3. Appropriate regulation of the seed and nursery sector including certification of seed collections and lots of plants derived from them. Certification of seed collectors and forest nurseries agreeing to apply such a system could also be considered.

4. Encourage owners and agents to consider early in the planning of planting schemes where to obtain seed/stock of appropriate origin.
5. Guidance on the appropriate numbers/sxes of clones when planting vegetatively propagated material.
6. Guidance on good practice in domestic seed collection.
7. Guidance on what constitutes adapted and maladapted material.

Foreign material in existing woodland

1. Guidance on priorities for removal of inappropriate species and genotypes.
2. Use of felling licences and grants to promote removal of undesirable genetic material, especially in privately owned forestry.

Small isolated and rare populations

1. Guidance in identifying populations particularly at risk and how best to restore them, including deliberate introduction of genotypes from other populations.
2. Guidance on how to encourage gene flow by linking populations. Options for maximising connectivity, as in the Forest Habitat Network, could be assessed.
3. Guidance on the planting of naturally rare species on to new sites.

Genetic reserves

1. Guidance on assessing the genetic conservation value/potential of different woodland types to clarify which woodlands have priority for genetic conservation.
2. Possible designation of genetic reserves.

Forest design

1. Guidance on how to incorporate genetic considerations into forest design practices particularly by considering connectivity of areas of native woodland in areas of plantation forest.

Regeneration of species-poor secondary woodland

1. Guidance on the circumstances where it is desirable to introduce 'missing' species and genotypes into species-poor secondary woodland.

Use of genetically improved material and non-local material

1. Guidance on the use of genetically improved and non-local material in the proximity of important areas of semi-natural woodland, including the potential use of buffer zones.
2. Guidance on the possible regional use of improved Scots pine.

Non-forestry planting

1. There is need to increase dialogue between the forestry and landscaping professions to ensure that provisions for regulation and guidance are coordinated.

A publication on genetic practice giving guidance on these issues would be useful. It could also be incorporated into forest practice publications as they are revised.

Research

Research in Britain into the genetics of native trees and shrubs has only begun to address four species: Scots pine, oak, silver birch and black poplar (see

Chapter 2). Even for these species information is very limited: for instance variation in growth and form among Scottish populations of Caledonian Scots pine is still unknown. Recent work has concentrated on genetic markers at the expense of work on adaptive variation. Information on other species is virtually non-existent. This is one of the most neglected research topics in British forestry.

There is a need to increase significantly research on genetic variation and its conservation. Box 3.1 provides a summary of topics on which work is required. Main headings are listed by priority but could be pursued concurrently.

Box 3.1 Research requirements on genetic variation and conservation: priority topics

1. Adaptive variation and choice of seed origins

Research is required into adaptive variation in native tree and shrub species (based on different 'species groups' defined by their mating systems and ecology). This would provide information :

- to verify genetic conservation provisions, particularly provenance choice, transfer rules, and maps of seed collection areas;
- on choice of the best material for timber production and other objectives of management;
- on the possible effects of climate change on tree populations and the consequences for provenance choice;
- for developing definitions of 'maladapted' for different species and circumstances;
- on the extent of past introductions of foreign material;
- on the post-glacial history of different species (using molecular methods on provenance collections);
- on links between genetic variation in trees and their value as habitat for associated plants, fungi and fauna.

Such research would include (in order):

- The location of representative autochthonous populations of broadleaved trees and shrubs, or other populations of high genetic value and assessing their relative importance for genetic conservation.
- Establishment and assessment of provenance trials.
- Analysis to interpret provenance variation, and relate it to environmental conditions of the seed sources; and to model the consequences of transfer of material along environmental gradients.
- Studies of material in provenance trials using molecular techniques to determine patterns of post-glacial migration etc.
- Physiological studies of adaptation/maladaptation and causes of damage to stock.
- Possibilities of progeny testing for recurrent selection in tree improvement.

Information can be made available in the shorter term from nursery and early growth studies (3–5 years) following methodologies developed during the last decade in the USA (e.g. Rehfeldt, 1995). Such studies need not be as expensive as traditional large scale provenance programmes in introduced species.

2. Small, isolated and rare populations

The characteristics of genetic variation and gene flow in tree populations could be examined for different 'species groups' (based on their mating systems and ecology). This would provide information on:

- the best approaches for reinstating woodland at a landscape scale in order that genetic processes (i.e. gene flow and natural selection) are safeguarded;
- the ability of linked tree populations to respond to climate change.

The work could build on the principles of landscape ecology and utilise work carried out at the species level during recent years, for example the Forest Habitat Network concept.

3. Seed supply potential in Britain

Collation of reliable statistics on historical and recent patterns of use of seed and stock from domestic and foreign origins. A review of the factors affecting seed supply of native species in the UK.

4. *In situ* conservation

The need for and approaches towards designating genetic reserves.

5. *Ex situ* conservation

Development of collections of living material of all the main and endangered species, as a source of genetic material for scientific studies and possible seed production.

6. Dysgenic selection

Investigation of the occurrence and nature of possible past dysgenic selection.

Table 3.1 An outline strategy for developing genetic conservation

Theme	Milestone	Fulfilling aims	Priority	Timeframe for action
General	Development of a programme of awareness-raising of the basic concepts in genetic conservation	All	High	Short/medium
	Development of a policy statement	All	High	Short
	Production of publications describing policy and giving guidance to practitioners	All	High	Short/medium
Adaptation and choice of seed origins	Develop guidance on seed origins and removal of inappropriate genetic material	All	High	Short/medium
	Institute regulations on seed origins and removal of inappropriate genetic material	All	High	Short/medium
	Initiate research on genetic variation and seed origins and adaptation	All	High	Short/medium/long
	Refine guidance and regulations in light of research findings	1,2,3	High	Long
	Initiate programme of promotion and training on choice of seed origin and domestic seed collection	1,2,3	High	Short
	Develop guidance on use of genetically improved and non-local material	All	Medium	Medium
Small, isolated and rare populations	Initiate research into identification of and management of these populations (including <i>in situ</i> and <i>ex situ</i> conservation)	All	High	Short/medium/long
	Issue guidance on management of these populations	All	High	Medium/long
Designation of genetic reserves	Initiate research on the desirability of and approaches towards genetic reserves	All	Medium	Short/medium/long
	Possible designation of genetic reserves	All	Medium	Medium
<i>Ex situ</i> conservation	Initiate research into the need for and approaches to <i>ex situ</i> conservation	All	Medium	Short/medium
	Institute programme of <i>ex situ</i> conservation	All	Medium	Medium/long
Adaptation to climatic change	Initiate research on adaptation of populations to local environment	1,2,3	Medium	Short/medium/long
	Issue guidance on measures to counter climate change	1,2,3	Medium	Long
Forest design and management	Initiate research on incorporating genetics into forest design	1,2,5	Medium	Medium/long
	Develop guidance on management of species-poor secondary woodland	2,3	Low	Short/medium

Funding

There is particular scope for partnership working with conservation agencies (SNH, EN, CCW), universities, plant breeding institutes, Royal Botanic Gardens, and other European countries (EU funds). The nursery industry can provide SME (small and medium sized enterprise) members in research teams where this enhances funding possibilities.

Promotion, training and awareness-raising

Promotional events and training for practitioners could be considered both for genetic issues in general and for a small number of specific topics. A major aim would be to raise awareness of genetic concepts and issues and to encourage the correct use of terms.

Outline strategy for developing genetic conservation

The issues outlined at the beginning of this chapter can be grouped into six main themes:

1. Adaptation and choice of seed origins
2. Small, isolated and rare populations
3. Genetic reserves
4. *Ex situ* conservation
5. Response of populations to climatic change
6. Other forest design and management issues

In addition, a general problem of a low level of understanding of many of the basic concepts and issues is apparent among practitioners. To address these the following main elements of policy are available:

- Development of a policy statement in national forestry policy.
- Development of guidance on a range of policy and technical issues.
- Development of a small number of key regulations.
- A major and sustained research input.
- A programme of promotional events, training and awareness-raising.
- Production of documents describing genetic conservation policy and providing technical guidance for practitioners.

An outline strategy for developing genetic conservation is given in Table 3.1.

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UK policies and forest practice relating to genetic conservation

Policy

Aspects of genetic conservation appear in international and national policy statements on both forestry (Anon., 1994) and biodiversity (Department of the Environment, 1994). The main issues covered are summarised below.

1. **Protection of genetic resources in natural forests** (Rio Principles article 4; Biodiversity Convention article 8; Helsinki Guidelines resolution 1 articles 1 and 3; *Sustainable forestry: the UK programme* 3.34; *Biodiversity: the UK action plan* 1.20, 1.22, 1.2, 6.43)

Both UK forest policy and biodiversity policy include commitments to protect, restore and extend ancient and semi-natural woodland. UK biodiversity policy also refers to the *'need to conserve gene pools as a reserve to use as a resource for future needs'*.

2. **Adaptation of native species** (Helsinki Guidelines resolution 1 articles 7,8; *Sustainable forestry: the UK programme* 3.34, 3.67, 3.69. *Biodiversity: the UK action plan* 1.14)

The Helsinki Guidelines state that *'forest management practices should aim at maintaining the adaptive capability of forest ecosystems'* and that *'chosen tree species should be well suited to local conditions and capable of tolerating climatic and other stresses such as insects and diseases and potential climatic change'*.

UK forest policy states that *'woodlands established using native species have potentially the largest benefits for biodiversity as native trees are well adapted to particular ecological niches'*. UK biodiversity policy also states that *'genetic diversity provides the variability within which a species can adapt to changing condition'*.

3. **Genetic variation and provenance choice** (Helsinki Guidelines resolution 1 article 9; *Sustainable forestry: the UK programme* 3.69; *Biodiversity: the UK action plan* 3.21, 6.43)

The Helsinki Guidelines state that *'native species and local provenances should be preferred where appropriate. The use of species, provenances, varieties or ecotypes outside their natural range should be discouraged where their introduction would endanger important/valuable indigenous flora and fauna'*.

UK forest policy states that *'the choice of species for new woodlands is further complicated by the fact that trees of native species may be cultivated from the seed of non-native strains. There is also genetic variation on a regional basis. There is some reason to suppose that local strains may be better adapted and at least may be worth preserving. In many cases, though, neither wildlife nor human beings are likely to be able to distinguish native from imported strains and this distinction can therefore be difficult to translate into generally applicable policies'*.

UK biodiversity policy states that biodiversity is defined as encompassing three levels, including *'genetic variation within species'*. It goes on to detail the importance of variation within populations and the effects of isolation of populations. Recommendations are made to *'encourage the use of native species of local provenance'* and to promote the use of *'good quality local genetic hardwood stock where native broad-leaved tree species are being planted'*. It is noted that *'careful selection of seed sources will help to ensure that local genotypes are preserved and that trees being planted are well suited to local environments'*.

Issues of provenance choice also arise in local authority policies as a result of Agenda 21, in respect of tree planting in landscaping, e.g. along roads.

4. Genetic selection and improvement (Helsinki Guidelines resolution 1 article 8; *Sustainable forestry: the UK programme* 3.28)

The Helsinki Guidelines state that '*genetic selection should not favour performance traits at the expense of adaptive ones (except in particular cultures where intensive care may protect them against damage)*'.

UK forest policy includes a commitment '*promote the development and use of improved genetic stock*'.

5. Development of a strategy (*Biodiversity: the UK action plan* action point 37)

The biodiversity action plan suggests the need to '*review genetic resources and consider whether to develop a formalized strategy for future en-site conservation across all genetic resources...*'.

6. Research (*Sustainable forestry: the UK programme* 3.19; *Biodiversity: the UK action plan* (principles).

UK forest policy includes a commitment '*to carry out research into climate change and the adaptation of trees to it*'. Importantly UK biodiversity policy states that '*conservation practice and policy should be based on a sound knowledge base*'.

Regulation and guidance

Several aspects of genetic conservation are already incorporated into forest regulation and practice, and these are summarised below. These are detailed in Forestry Practice Guides (Forestry Commission, 1994), *The UK forestry standard* (Forestry Commission, 1998a), Forestry Authority (undated), Habitat Action Plans (e.g. Forestry Commission, 1998b) and *The forest reproductive material regulations* (Forestry Commission, 1987).

1. Maintenance of patterns of genetic variation

There is a recognition of the need to maintain patterns of genetic variation (genetic integrity) in existing semi-natural woodland.

2. Inventory and registration of seed stands

An inventory has been developed of autochthonous pine woodland and a large number of seed stands have been registered. Surveys of broadleaved native woodland are currently taking place from which it may be possible to develop similar inventories for other woodland types. At present only a small number of seed stands of broadleaved native species exist (see aspect 5).

3. Use of natural regeneration and colonisation

Natural regeneration is usually required when restocking or expanding ancient semi-natural woodlands. Natural colonisation is preferred to planting when encouraging diversification of woodland; however exceptions are made which allow enrichment of species to meet wood production objectives or where natural colonisation is unlikely to occur.

4. Choice of seed source

Use of local stock adapted to the site is usually required when planting in the vicinity of ancient and long established semi-natural woodlands and is encouraged in new native woodlands. For native Caledonian pinewoods a buffer zone of 500 m is enforced within which no non-local Scots pine can be planted. Such specific regulation is not in place for other native species.

For new native woodlands of Scots pine, use of local stock is a condition of grant (based on the seven biochemical zones) and is regulated by the use of seed certificates. Such regulation is not currently in place for other native species, but is under active development (Forestry Authority, undated). For broadleaved planting in the vicinity of semi-natural woodlands seed sources from local autochthonous stands are preferred. For planting in areas *not* in the vicinity of semi-natural woodland, British origin material is preferred, but supplies of stock mean that this requirement is often not met.

For Scots pine, oak and beech EU regulations are applied through *The forest reproductive material regulations* which specify that seed can only be collected from registered seed stands selected on the basis of their (species) purity and timber form. Derogation from these regulations is available for Caledonian Scots pine on scientific grounds and for the other species by request to the Forestry Commission. Current legislation (EC Directives, FRMR) covering marketing of seed/stock does little to promote genetic conservation; and by specifying suitable material largely in terms of timber quality has tended to work against it. Revisions are now being put in place (by 2000) which:

- make it easier to collect from British sources by allowing collection of 'source identified' material;
- provide EC member states with more control over the use of reproductive material which it considers is not suitably adapted for its territory. Material can be prevented from being imported into the UK if there is long-term experience suggesting that it is poorly adapted.

The scope of EC regulations is to be extended to include a wider range of species. This should assist in developing regulation of marketing and use of seed within Britain. In addition member states can set up their own schemes for non-EC species. Ongoing revision of the EU regulations to allow use of source identified material should improve the potential for home collection of seed from autochthonous stands.

5. Removal of undesirable genetic material

There is general encouragement to remove underplanted material of introduced conifer from native woodlands. Forest Enterprise have carried this out on a considerable scale, but little such work has been carried out in private woodlands.

Some non-local material of native species has also been removed from key areas of native woodland, mainly on land managed by Forest Enterprise and conservation organisations.

6. Connectivity

There is general encouragement to increase the size of individual native woodland and to link small woods to others.

7. Use of improved material

Use of improved Scots pine is not permitted in new native pinewoods.

8. Rare species

Rare species are generally not recommended for planting in new native woodland.

Consultation with experts

List of respondents whose views have been incorporated into the report

I.R.Brown	University of Aberdeen (retd.)
R.M.M.Crawford	University of St Andrews
A.J.Davy	University of East Anglia
D.Deans	Centre for Ecology and Hydrology (formerly Institute of Terrestrial Ecology), Bush
R.Harmer	Forest Research, Alice Holt, Farnham
C.Hughes	Oxford Forestry Institute
A.C.Newton	University of Edinburgh
K.Kirby	English Nature, Peterborough
K.Russell	Horticulture Research International, East Malling
P.Savill	Oxford Forestry Institute

In addition a round-table discussion was held with the Tree Improvement Branch of Forest Research at Roslin attended by C.J.A. Samuel, G.I. Forrest, E.P. Cundall together with A.F. Fletcher and J.R. Aldhous.

Since the Rio Earth Summit in 1992, there has been growing international recognition of the importance of genetic resources as the basis for biological diversity of all kinds. In forestry we have seen a growth of interest in the genetic conservation of our native trees and shrubs over the past few years, as the amount of planting of native species has increased.

This Technical Paper results from a review commissioned by the Forestry Commission in 1998 and is the first attempt at setting a comprehensive framework for the development of knowledge and policies for the genetic conservation of our native trees and shrubs. The main objectives are:

- To provide an accessible account of genetic variation and its behaviour in forest tree species.
- To review knowledge of the genetic resources of native tree and shrub species.
- To highlight the issues which need to be addressed when developing a genetic conservation policy for British forestry.

This is important information for foresters and all other practitioners interested in the future of our native trees and shrubs.

