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The Role of Forest Genetic Resources in Helping British Forests Respond to Climate Change

INFORMATION NOTE

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SUMMARY

This Note provides an overview of the issues surrounding the use of genetic resources in British forestry and presents possible strategies to help forests and woodlands adapt to the effects of climate change through the use of such resources. Ongoing discussions surround the choice of appropriate genetic resources for reducing the impacts of climate change on British forests and this uncertainty is leading to delays in the formulation of a definitive strategy. The objective here is to present the issues surrounding this debate by providing responses to the most commonly asked questions. The information in this Note is based on summaries of genetic population theory, recent research findings and current ideas on these topics circulating within the European research community. The Note does not provide a statement of policy.

INTRODUCTION

Both the Helsinki guidelines (MCPFE, 1993) and *The UK Forestry Standard* (Forestry Commission, 2004) encourage the use of local stock for planting native species, especially in existing and new native woodlands (Figure 1). The UK Woodland Assurance Standard (UKWAS) also encourages use of local provenance (UKWAS Steering Group, 2006). These guidelines are based on the principle that locally sourced planting stock is likely to represent the best-adapted material available for a site. The use of non-local planting material raises concerns that it is likely to be poorly adapted to local conditions. In addition, there are anxieties that the offspring resulting from interbreeding between local and introduced individuals will have reduced fitness compared with the truly local parents (Wilkinson, 2001).

Figure 1

Ancient semi-natural woodland in southeast England. Woodlands such as this will be increasingly affected by climate change.

The scale at which 'local' is meant is often poorly understood for tree species however, and some interpretations take it to mean that adaptation occurs over very short distances. Much of the supporting research for such narrow-scale adaptation is based on short-lived plant species, many of which are insect pollinated or predominately self pollinated. Under these conditions local populations can become genetically isolated and selection pressures can quickly lead to the development of an optimal range of genotypes. In some cases this can lead to very fine-scale population structures. For example, *Delphinium nelsonii*, a perennial herb pollinated by bees and humming birds in the mountains of western USA, appears to show adaptive variation over distances of as little as 50 m (Waser and Price, 1985). However, it has been suggested that the situation for long-lived, open pollinated species, such as many native British tree species, is different and the assumption that local is best has been questioned in these circumstances (Wilkinson, 2001) (Figure 2). Yet, there is a long history of provenance research in forestry that has demonstrated instances of failure due to movement of plant material over large distances (Figure 3). Such examples can also be found in commercial forestry, where failure has often occurred many years after establishment (Johnson *et al.*, 2004; Randall and Berrang, 2000). The key challenge is to define the spatial scale over which forest tree species can be moved without suffering maladaptation. The choice of suitable planting stock may be unnecessarily restricted if the safe transfer distance is larger than the existing seed zone. There is also a possibility that simple geographic proximity is a poorer predictor of success than ecological site matching. In addition, many of the guidelines that emphasise the use of local stock were developed before the likely rate and magnitude of climate change were fully appreciated.

Figure 2

A 10-year-old silver birch provenance trial in Perthshire showing contrasting provenance perfomances. (a) Sand Hutton (Yorks.), approximately 350 km from the trial, is one of the best performing provenances. (b) Newtyle Hill (Perthshire) is only 9 km from the trial, but is poor compared with the Sand Hutton material.

Figure 3

An oak provenance trial planted in 1990 at Fort Augustus, Scotland. The oak in the background is a Scottish provenance (Drummond Castle, Perthshire) and is now 3–4 m high. The grassy area in the foreground was planted with a French provenance (Charantes-Poitou) now virtually all dead due to frost damage.

Climate change now raises the following issues:

- The principle that 'local is best' is based on the assumption that natural selection has, over many generations, acted to optimise a population to its local environment. Since its local environment is now likely to change, the question arises of whether local is *still* best.

- Furthermore, there is the question of whether the local population has access to the necessary genetic variation to allow it to adapt to the magnitude of predicted change.

- Even if sufficient genetic variation is available, can a population at a site respond fast enough to match the rate of predicted change?

It is necessary to understand some of the concepts and recent research findings in forest genetics to appreciate the complexities of developing strategies which aim to minimise the impacts of climate change. This Note is therefore divided into two sections. The first provides a background to the principles of forest genetics, and this is followed by the application of these principles to the choices of appropriate planting stock, or the use of natural regeneration, as strategies for dealing with climate change. See the box on page 12 for definitions of key terms.

THE PRINCIPLES OF FOREST GENETICS

What is the genetic variation of a species?

Genetic variation is a result of differences in genetic sequence, as distinct from differences due to environmental influences. The genetic diversity of a species can be divided into 'inter-population' diversity and 'intra-population' diversity (see *What is local?* page 3). Genetic variation can be categorised into two types, neutral and adaptive. Neutral variation results from differences between genotypes which do not affect their ability to survive and reproduce, whereas adaptive variation represents those differences which do impact on the fitness of an individual.

What determines the genetic variation at a site?

The genetic variation of a given species present at a site depends on the following factors:

- **Natural colonisation**

  Natural colonisation is a chance event and the material that arrives at a particular location is not necessarily the best-adapted material that is present within the entire species. However, for sites with a long period (in terms of generations) of occupancy, the trees that are present should be considered the most optimal given the original colonising material.

- **Natural selection**

  Natural selection can only act on the material that is present at a particular location. It causes those traits that contribute to individual adaptedness to increase their frequency in a population. Any factor that prevents or reduces reproduction in certain individuals of a population represents a selection pressure. Since mortality is often highest when trees are at the seedling/sapling stage this is usually the point at which natural selection has its greatest influence. Natural selection acts on the adaptive variation at a site, but has no effect on neutral variation.

- **Gene flow**

  Gene flow via natural dispersal of seed, pollen or vegetative propagules acts to homogenise both neutral and adaptive variation between woodlands. This connectivity increases the capacity of a woodland to respond to changing selection pressures by providing a regular input of genetic material from trees adapted to different ecological conditions.

- **Genetic drift**

  Genetic drift is the random reduction in genetic variation in a population from one generation to the next enhanced by small population size. The loss of diversity is greater as isolated populations reduce in size.

- **Mutation**

  Mutation acts to create new genetic variation within a species. This is a random event that can alter either neutral or adaptive genetic variation. This latter type of mutation can either confer a selective advantage or disadvantage on the individual or have no effect at all.

Natural regeneration tends to reinforce the existing genetic structure at a site, whereas planting has the potential to introduce non-local genetic diversity. The impact of this introduced diversity will depend upon the scale of planting, relative to that of the local population, and the magnitude of the genetic difference between the populations.

How is genetic variation measured?

Provenance experiments have a long history in forestry and have been used to assess adaptive variation – the basis on which natural selection works. Molecular techniques, on the other hand, provide information on neutral variation. Natural selection does not act on neutral genetic variation and therefore studies of this kind of variation demonstrate founding effects and connectivity of populations (gene flow), but tell us nothing about natural selection. However, advances in molecular techniques are beginning to allow links to be made between adaptive traits and molecular variation.

What is local?

Environmental conditions vary between sites and therefore the selection pressures acting on populations at these sites will vary. This process leads to differentiation in adaptive variation between sites. Natural selection operates to remove the least suited genotypes at a site and this forms the basis of the 'local is best' principle. However, Gould (1997) argues that natural selection can only work on the material that is available. Therefore, the adult genotypes at a site are only better than the other local alternatives that were available at that site at the seedling stage, rather than being the best possible option for that site. Given Britain's history of glaciation, recolonisation and separation from mainland Europe it would not be surprising if there were better suited genotypes elsewhere.

Since the key evolutionary step is successful reproduction, a population, in genetic terms, can be considered as consisting of those trees of the same species that are within genetic contact and contribute to subsequent generations. As there is long distance gene flow this covers an area that is much greater than that of a single wood. It is also important to remember that this area is not fixed through time. In addition, terrain, population density, flowering intensity and the species of interest all influence the size of the local population. Gene flow from distant locations, even if extremely rare, can result in a meta-population, in which a number of populations are linked together.

Although it has been demonstrated that, for tree species, most gene flow occurs within a few hundred metres of the maternal parent, there is also a significant component from outside the woodland. Hence, gene flow in trees can occur over large distances, particularly for wind pollinated and/or wind dispersed species. Rare, long distance gene dispersal events are important but their frequency is

difficult to estimate. In more open, fragmented landscapes gene flow occurs over longer distances (White *et al*., 2002). Since there are already woodlands in existence in Britain that have been planted using non-local planting stock, natural populations are rarely isolated from the influence of introduced, non-local material. No data are yet available to determine whether material that is the product of mating between local and non-local material is less competitive and is therefore removed by natural selection.

In summary therefore, the genetic locality of a given species is largely the product of the original colonising material, natural selection and gene flow. The relative influence of these factors can be investigated using a combination of molecular markers and provenance trials to provide information on the geographic scale of local adaptation.

Estimating localness using neutral variation

- **Original colonising material**
  Most British tree populations originate from glacial refugia located in southern Europe. For example, maternally inherited chloroplast markers demonstrate that oak and ash recolonised from Iberian refugia (Petit *et al*., 2002; Heuertz *et al*., 2004) whereas beech and black poplar migrated from refugia in southeast Europe (Magri *et al*., 2006; Cottrell *et al*., 2005). This suggests that for any one of these species the populations in Britain, which are based on single lineages, are likely to have a more homogenous composition than populations in continental Europe where several colonisation routes have merged. In contrast, work on Scots pine suggests two refugial origins, one of which, from southwest Ireland, colonised northwest Scotland and the other, from continental Europe, colonised the rest of Scotland (Sinclair *et al*., 1998). Conservation geneticists generally aim to maintain the structure of these evolutionary lineages because they reflect the historic biogeography of a species, and these are used to define *evolutionary significant units* (units of conservation below the species level).

- **Gene flow**
  Molecular studies have demonstrated that long-distance gene flow maintains genetic contact between populations (Bacles *et al.,* 2004; 2005; 2006). This process reduces the chances of genetic isolation and associated loss of diversity if the size of a population were to be restricted (i.e. through genetic drift). In

terms of neutral markers, there is little differentiation of British populations of species such as oak or ash. Rare long-distance gene flow is sufficient to homogenise neutral genetic diversity between populations.

Estimating localness using adaptive variation

- **Provenance trials**
  A provenance trial brings together planting stock collected from different areas and grows them together in a trial site. Trials demonstrate that variation in many adaptive traits is clinal so that a phenotypic trait varies across a longitudinal, latitudinal, altitudinal or ecological gradient (Figure 4). The degree of change across the gradient demonstrates the sensitivity of a particular phenotypic trait to the changing feature of the environment. This provides a method of exploring the scale and degree of local adaptation. A rapid change in clinal variation suggests a causative process of natural selection across the environmental gradient. However, variation within provenances is often very high, and clear patterns of between-provenance variation can be difficult to detect at a British level. The impact of silvicultural management on provenance performance can be very important and provenances collected from registered seed stands (see www.forestry.gov.uk/frm for details) often perform well over a range of sites. This highlights the effects of consistent selection for fast-growing, vigorous individuals within a stand. A summary of provenance performance for different species can be found in Worrell (1992) and Hubert and Cundall (2006).

Figure 4

The clinal change in flushing date in relation to latitude of origin for different provenances of oak. The data were collected in 2004 at a trial established in Sussex (51° 06:53 N 0° 35:13 W) in 1990 (from Broadmeadow and Ray, 2005).
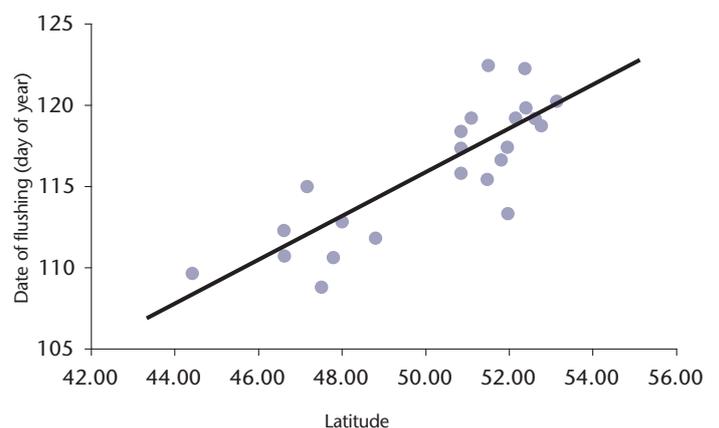
- **Reciprocal transfer experiments**
  Reciprocal transfer experiments transfer planting stock or seed between a series of sites so that each trial contains both the indigenous stock and stock from all the other sites. Those experiments that have been performed indicate that vigorous provenances provide seed which perform well on most sites. For example, no clear geographic pattern for seed source/site suitability has been detected for ash at the early stages using reciprocal transplant experiments (Boshier and Stewart, 2005; Stewart *et al.*, 2006). However, it should be noted that these experiments are restricted to Britain – a small part of the total geographic and climatic range of this species.

What do we mean by 'fitted' and 'best'?

Three criteria must be met in order for a natural population to be considered as 'fitted'.

- an ability to cope with a changing environment;

- an ability to compete successfully with other species;

- an ability to reproduce.

It is impossible to test fully whether one population is more fitted to a site than to another due to the many variables involved in such an experiment. However, provenance trials provide an estimate by using a 'focal trait', such as height, that reflects the fitness of the whole organism. Height is a good choice of character for the following reasons: (i) within-site variation in height is largely under genetic control; (ii) taller trees are generally better able to compete and reproduce; and (iii) height growth is one of the first parameters to reflect a warmer climate (Ying and Yanchuk, 2006).

If height is used as the focal trait, results indicate that provenances from 2° south of the growing site generally outperform the local provenances and this is considered a safe distance over which to transfer material (Worrell, 1992; Ying and Yanchuk, 2006). However, the adaptedness of a population has to be considered over the entire life cycle and rare, extreme events may represent the key selection pressures that test true adaptedness to a site. Thus, short-term provenance trials may not be able to provide a true measure of lifelong local adaptedness.

The 'best' provenance does not need to be the most 'fitted' and can be judged using other criteria. For example, the best timber-producing population does not need to meet the criterion of reproductive capability. Similarly, for woodland creation grant schemes, the best population could be considered to be the one that establishes itself effectively and grows well in the first few years so that it qualifies for grant aid.

What is the difference between adaptedness, adaptability and phenotypic plasticity?

There is some confusion over terms relating to the ability of populations and individuals to respond to climate change. The definitions of these terms are as follows:

- **Adaptedness**
  The state of being adapted that allows a population to survive, reproduce and permanently exist under the prevailing environmental conditions.

- **Adaptability**
  The potential or ability of a population to adapt to changes in environmental conditions through changes in its genetic structure.

- **Phenotypic plasticity**
  Non-genetic variation in an organism in response to environmental factors, or the capacity of a genotype to develop any of several phenotypic states in response to environmental conditions; usually, this capacity is considered to be adaptive.

At a population level, tree species found in Britain today are only present because of their capacity to adapt and migrate from southern refugia after repeated ice ages. Those species and populations that were not highly adaptable failed to reach northern latitudes. Mating studies based on neutral markers demonstrate that most of our tree species are generally outcrossing, which maintains high levels of genetic variation, thereby conferring high levels of adaptability within populations.

At an individual level, trees vary in their ability to tolerate changes in the environment through phenotypic plasticity. For example, a plastic individual may have the ability to change its flushing date to reflect a change in climate. The plasticity of individuals varies with species (Kramer, 1995). There is currently interest in Europe in testing the plasticity of individuals of native species by growing cloned representatives of genotypes at a range of climatically contrasting sites. Trials of this type will help to predict what capacity individuals have to respond to climate change.

How do we identify seed zones?

Seed zones are areas which have defined geographic boundaries and altitudinal limits, within which soil and climate are sufficiently uniform that it is expected that seed can be freely moved without problems of maladaptation. They are important because uncontrolled seed transfer can lead to failures due to climate, insect attack or disease – sometimes occurring many years after seemingly successful establishment.

Given sufficient genetic data it would be possible to define any number of seed zones ranging from European-wide zones, reflecting common post-glacial lineages, to family or even clonal groups within a wood. Hence, the number of seed zones is a balance between cost and benefit and a compromise between a restrictive and an open approach to seed sourcing. Britain is divided into four regions of provenance and 24 native seed zones. These seed zones, which are applied uniformly across all tree species (with the sole exception of Scots pine) are an attempt to delineate broad biogeographic zones on the basis of geological and landform boundaries and major watersheds. This subjective approach has given rise to seed zones of roughly equal sized areas (Herbert *et al*., 1999; Forestry Commission, 2007). The zones are not based on genetic scale information. The seed zone system for Scots pine does not follow the same delineation and is based on biochemical and molecular marker information. Seed zones in Britain are therefore best viewed as an administrative tool rather than something that is grounded in genetic science. Current knowledge would suggest that the 24 native seed zones are rather conservative in their scale and operate in a risk averse way. However, they provide a very useful system of provenance identification that allows clear, informative labelling of planting stock. Provenance trials can inform the scale over which maladaptedness is likely to occur and recently planted local provenance trials for silver birch, ash and rowan should help to provide firm data to test the appropriateness of this zonation.

In British Columbia, for example, there are also 24 seed zones but with an average area of $39\,492$ km^2, compared with an average native seed zone in Britain of 9582 km^2. British Columbia initially had a larger number of seed zones (67) until the 1980s when, in contrast to Britain, a quantitative modelling approach was introduced. This was based on a combination of biogeographic classification and provenance trial results (Ying and Yanchuk, 2006). This has given rise to fewer zones of very different sizes along with a less restrictive 'floating

seed transfer' system reflecting the ecological and adaptive significance of the zones (Ying and Yanchuk, 2006). Similarly, in the Pacific northwest of the USA, seed zonation was broadened, redesigned and made species-specific as more information became available from common-garden studies and genetic field trials in the late 1990s (Johnson *et al*., 2004). Likewise, in France, seed zones for common species can be very large. For example, for *Quercus petraea* there are 19 seed zones with an average size of $25\,903$ km^2 and a size range from 8100 to $62\,000$ km^2. Interestingly, the second choice of planting material is not necessarily from the nearest neighbouring zone, as ecological matching is also used as a criterion (Cemagref, 2003). The zonation in France is also different for different species.

Some form of seed zonation is useful because an overly lax approach to seed sourcing involving transfer of seed over very long distances is detrimental. Previous large-scale importation of seed material from southern Europe has resulted in examples of poor adaptedness (Hubert and Cundall, 2006; Cundall *et al.*, 2003), including anecdotal evidence of ash in Ireland and cherry in Britain.

Modern methods of seed zonation based on ecological site matching using Geographical Information Systems offer an alternative tool for matching seed source to site, as geographic distance may be less important than site ecology. This method of matching provenance performance to site conditions has been applied to Sitka spruce, the most important non-native timber species in Britain (Samuel *et al.*, 2007), and could be more widely applied to our native tree species.

What other factors could influence the choice of planting stock?

The priorities and objectives for the new woodland should guide the choice of source material for planting. If the main objective were to conserve the genetic integrity of the woodlands then a strict policy of seed control would make sense if appropriate seed could be sourced. If the creation of functional woodland for biodiversity, amenity or timber production were a higher priority, then a more flexible approach to local seed collection could be justified. It is perfectly possible to create an ecologically functional woodland with non-local provenances. The process of creating new woodland under strict genetic conservation principles is likely to be slow because of difficulties associated with seed sourcing and establishment. Many of the common tree species have irregular mast years and an insistence on locally-sourced seed may restrict the area that can be planted in certain

years. This problem is worst in northern regions of Britain. In areas where there are few seeding trees, seed may have to be collected from inferior genotypes and this could result in poor quality seedlings. Similarly, lack of seeding trees may mean that seed has to be collected from geographically close but poorly-matched ecological sites. Hence, conservation of tree genetic resources needs to be balanced against the broader range of benefits achieved from a more rapid woodland expansion based on less strict criteria for sourcing local material. Furthermore, many woodland-associated species are poor dispersers, so their conservation may be aided by the creation of an interlinked series of woodlands within the landscape.

What are the potential impacts of non-local tree material on associated plant and animal species?

The issues raised in this section expand the concept of 'fitted' to the ecosystem level. The differences between tree populations may influence the organisms which depend on them. Since it is impossible to test fully the fittedness of a population to a site, it is even more complex to examine the interaction between different tree populations and associated flora and fauna. However, although hard evidence is lacking, differences between certain key traits have been cited as possible examples of where imported material may have such an impact. For example, imported hawthorn has been shown to flower up to five weeks earlier than native hawthorn, potentially threatening the insects and birds whose reproductive cycles are timed to coincide with this event (Jones *et al*., 2001). The impact of non-local material will depend on how different it is from local material, the relative proportion of local and non-local material at a site, and the rate of migration and degree of phenotypic plasticity of the associated wildlife.

USING GENETIC APPROACHES TO MANAGE FORESTS IN A CHANGING CLIMATE

Climate change implies that the environment is changing and this will result in different selection pressures and potentially different rates of gene flow. Therefore, current tree populations are heading towards a non-equilibrium state with respect to their environment. Although there may be sufficient diversity within existing populations to prevent local extinction of a species, there is the potential risk of high levels of tree mortality as a result of climate change in some regions. For example, 90% mortality at a

population level would be evolutionarily tolerable if the 10% of that population that survived were eventually able to reproduce to replace the losses. However, it is likely that such high levels of mortality would be unacceptable to both woodland owners and the public. These levels of mortality would also have negative impacts on other woodland species. In contrast, for some areas of Britain climate change will potentially provide a better environment for tree growth. More southerly provenances and, possibly, different species may be better adapted to benefit from these predicted milder conditions.

Possibly the most difficult issue surrounding climate change is that it implies increased uncertainty for the future. Predictions of future climates are based on global climate models with different strengths and weaknesses and often a range of scenarios are provided (Broadmeadow, 2002; Broadmeadow and Ray, 2005) (Figure 5). In addition, most climate change scenarios present trends in the mean values for temperature and rainfall, whereas it is the extreme events that often have the greatest impact on forests and woodlands and these are the least predictable. Forecasting the effect of climate change on woodlands therefore implies an increased uncertainty for the future and hence increased risk.

At a recent European meeting of tree conservation scientists the following points were identified as being key with regard to genetic resources and climate change (Koskela *et al*., 2007).

1. Genetic diversity has an important role in maintaining the resilience of forest ecosystems to threats associated with climate change, as well as opportunities such as longer growing seasons in the north. Therefore, the first priority is to maintain high levels of within-species diversity across Europe. (Genetic) Conservation Units need to be established.

2. The appropriate use of genetic diversity provides flexibility with respect to forest management and helps to reduce the risks associated with climate change.

3. Widely distributed species in Europe are unlikely to face extinction at the species level but local tree populations are likely to decline, especially at the margins of the distribution ranges.

4. Tree species with scattered or limited distributions are more vulnerable to climate change than widely distributed tree species and they may face serious threats at the species level.

Figure 5

Climate matching for Kelty in Fife, Scotland, under different climate change scenarios (a–d). Climate matching is based on monthly temperature, monthly diurnal temperature range and monthly rainfall (see Broadmeadow *et al.*, 2005). The red and the yellow areas are the best-matched 0.1% and 0.5% of grid squares in Europe to the current or predicted future climate of Kelty.

a. Areas matching the current climate for Kelty.

b. Areas currently having climates predicted to be similar to the climate of Kelty in 2050 (low CO_2 emissions)

c. Areas currently having climates predicted to be similar to the climate of Kelty in 2050 (high CO_2 emissions). This is virtually identical to the 2080 low CO_2 scenario.

d. Areas currently having climates predicted to be similar to the climate of Kelty in 2080 (high CO_2 emissions)
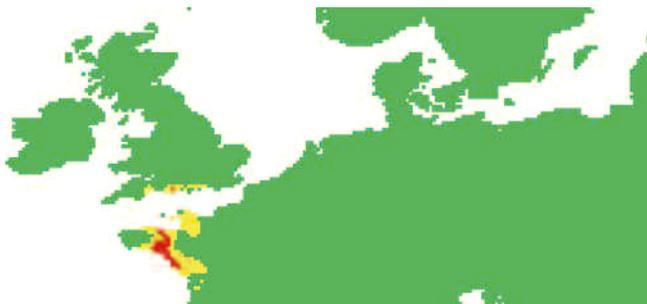
5. Climate change may alter the competition between tree and other plant species and this may adversely affect the tree species.

Any successful strategy to deal with climate change will need to be one that reduces risk of, for example, poor performance or mass mortality leading to a loss of woodland cover and its associated benefits. From a genetic point of view, risk of local extinction is minimised in nature by maintaining a wide variety of genotypes. A high diversity of genotypes increases the probability that some genotypes will survive into the future. This genetic diversity is maintained and re-randomised each time that regeneration occurs. Woodland managers might therefore consider options that will at least maintain the current levels of genetic diversity within their woodlands or even increase it.

There are three potential strategies to accommodate climate change and each has a different mix of risks and benefits. It is therefore important that woodland managers are aware of these when adopting any one particular approach.

1. Maintain genetic variation and promote natural regeneration

This strategy relies on the use of natural regeneration to restock woodland. If natural regeneration has been successful the initial stocking densities will be very high (>5000 ha^{-1}), which allows for high levels of mortality (i.e. high selection pressure) while enabling reasonable final stocking levels to be achieved. This strategy assumes that there is sufficient natural variation within the wood, or available to it via gene flow, to produce individuals that are fitted to the new conditions. There is a risk that this may not be true or that there will be very few fitted individuals. If this is the case, there is the danger of complete failure of the woodland, or at least a period of low tree cover until the few fitted individuals produce seed to recolonise the area. There is also the practical challenge for the woodland manager of promoting natural regeneration through silvicultural interventions such as gap creation. This approach has other implications, as the increased rate of felling would alter the traditional structure of many woodlands.

This approach has the greatest chance of success if the woodland manager can create circumstances whereby regeneration occurs on a regular basis. This provides a continuous supply of material on which natural selection can act throughout a period of climate change.

2. Adopt a portfolio approach and plant a mix of provenances alongside the current population

Planting at the standard density of 2500 stems ha^{-1} means that approximately 1 in 6 to 1 in 8 of the trees will go on to be a final crop tree. This is in contrast to the approach using natural regeneration where the survival rate is less than 1 in 20. Therefore, the lower selection intensity in planted woodlands should be deliberately offset by higher initial diversity. This can be achieved by planting a mixture of provenances within a site, using the best climate change predictions to guide the choice of provenances for the future. It would always be worth using a proportion of local stock to act as a safeguard. This is generally a strategy that would be effective for tackling possible crop failure but, since some of the provenances are likely to be sub-optimal, it is accepting the trade-off between guaranteed establishment and potentially lower than maximal returns.

3. Use assisted migration by planting a different provenance or species

Uncertainty over the rate and magnitude of climate change may narrow with time, and genetic understanding will improve, thereby allowing more precise matching of provenance to site. In addition, a woodland manager might choose to accept higher risks for higher potential rewards by planting a single provenance from a location with a climate similar to that predicted for the site. This may be the best option for locations that are predicted to experience high rates of climate change, or where the current species is predicted to become unsuitable, and hence where strategies 1 and 2 are unrealistic. This is, however, a high-risk strategy with no insurance to counter the uncertainty in climate change predictions at this time.

Within Europe there is an acceptance amongst the research community that assisted migration of provenances and a portfolio approach are legitimate strategies for accommodating climate change and that provenance rules, where they exist, may need to be relaxed to reflect this. The fact that Britain is separated from mainland Europe is likely to hinder or prevent the natural movement of gene-complexes better adapted to our future climate. Hence, assisted migration may become an important strategy, particularly for southern England. The strategy adopted will depend on the perception, or acceptability, of risk and the balance between the desire to maintain evolutionary processes and the desire to maintain functioning woodland. Additionally, emphasis in the scientific debate seems to be moving away from a conservation of specific genetic populations towards maintenance of the evolutionary processes at a site. For example, encouraging regeneration for natural selection to work on is perceived to be more important than conservation of those genotypes currently occupying that site.

CONCLUSIONS

- There is now little doubt that the British climate will change. The impacts of this change on forests and woodlands are predicted to be felt more strongly in the southeast of Britain than in northern Britain. The fact that the English Channel acts as a significant barrier to the natural processes of migration could exacerbate the challenges faced by woodlands in southern England. Predictions of climate change are based on trends in the mean values of temperature and rainfall, but it is the extreme events that are usually the most influential, given the timescales involved in forestry. In addition, the rate of change is as much of an issue as the magnitude of change.

- The uncertain nature of climate change and the long-term nature of forestry makes decision making for the woodland manager difficult but, because trees planted now will be maturing in 50–200 years time, action is required now to deal with the anticipated impacts of climate change.

- Risk minimisation is now the best approach in view of current uncertainty. High levels of genetic diversity enable a species to cope with a range of environmental conditions and this allows many European tree species to have such large natural ranges covering very different environments. This genetic variation is a resource that woodland managers can use to minimise the risks associated with climate change. By increasing the adaptive genetic variation within a woodland there is a greater probability that the woodland will survive and thrive in the face of any changes. Three strategies have been outlined using either natural regeneration or planting that aim to achieve higher levels of genetic diversity. They have different risks associated with them and woodland managers will need to consider the likely impacts of climate change in their area, and their attitude towards the management of risk, when choosing a particular approach. A fuller discussion of the management of risk in forestry can be found in Gardiner and Quine (2000).

- There is a general need to accept that there is no single answer and that the situation is a dynamic one which requires potentially different approaches through time. The fact that the environment is changing implies that the relationship between current genotypes (i.e. provenances and even species) and the environment is no longer at equilibrium. The use of static concepts, such as seed zones and possibly habitat types, will need to be reviewed to ensure that woodland managers have access to sufficient genetic variation in their planting stock. The British native seed zones system is a valuable tool for labelling and traceability of planting material. However, this relatively fine-scale system of zonation, if rigorously imposed to control the use of planting material, may be overly restrictive in the face of predicted climate change.

- Research is being undertaken to gain a better understanding of the phenotypic plasticity of our current provenances and of survival and growth rates of non-local provenances. However, to evaluate a provenance sufficiently to ensure that it can reproduce successfully is a long term project.

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Definitions

Adaptive genetic variation Differences between individuals in the DNA sequence that have an effect on the ability of the plant to grow and reproduce. These are differences that occur in the coding regions of the genome and may affect a group of genes or only a single gene. It is easier to observe the differences in adaptive variation using field trials than to detect the specific changes in the DNA sequence, although laboratory techniques are rapidly advancing in this area.

Clinal A steady rate of change of an observed trait (e.g. flushing dates) over an environmental gradient, as opposed to a step change or an abrupt discontinuity.

Fitted Those individuals or populations which, through the process of natural selection, are best able to reproduce and pass their genes on to subsequent generations.

Genetic diversity The variety of genetic information contained in all of the individual plants, animals and microorganisms. Many studies commonly measure genetic diversity within a single species at the population level. At this level, total genetic diversity can be split into within (intra-) and between (inter-) population diversity.

Genotype The genetic constitution of an organism. This interacts with the environment to produce the phenotype.

Maladaptation Populations of forest trees become adapted to their native environments through natural selection by synchronising their seasonal growth patterns with the average timing of their local growing season conditions. When trees are transferred beyond a certain distance injury or death may occur and in such cases trees would be termed maladapted to the new environment. During periods of climate change, such as global warming or cooling, species that were well adapted in the original climate may be maladapted to the new climate and die out.

Neutral genetic variation Differences between individuals in the DNA sequence that have no detectable effect on the plant. Many regions of the genome are termed non-coding since they do not seem to play any role over the lifetime of the plant. Differences between individuals in these regions result in neutral variation and can only be detected by laboratory methods.

Open pollination Natural pollination occurring due to wind or insects. The seed produced by an open pollinated mother tree are typically a mixture of selfs, full-siblings from a few adjacent trees, crosses from more or less distant relatives and pollen parents situated very far away.

Origin This is used to define the location where the material was growing before any transfer, i.e. the seed from the German oak will always be German in origin even if the provenance is now GB.

Outcrossing Matings (controlled or natural) among unrelated individuals. May also refer to a species that has specific barriers to selfing, or exhibits such inbreeding depression that inbred individuals never reach maturity.

Phenotype The visible appearance or set of traits of an organism, e.g. morphological, physiological, biochemical, etc., that develop through the interaction of the genotype with the environment.

Population A defined group of interbreeding trees of the same species growing in a given geographical area at the same time.

Provenance The location where seed or cuttings were collected from. Through human intervention this can change with each generation, for example, a German provenance of oak grown in a GB trial will produce seed that would then be considered of British provenance.

Refugia (refugium sing.) locations of isolated or relict populations of once widespread species. Isolation can occur due to natural phenomenon such as ice ages.