Wood Wise

SEEDS OF HOPE

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WOODLAND TRUST

FOREST MANAGEMENT TO AID ADAPTATION

BUILDING RESILIENCE WITH HOME-GROWN TREES

CREATING A SEED BANK FOR THE FUTURE

BETTER TIMBER FROM NATIVE TREES

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Nature's library: it's all in the genes

Willow pollen

We associate autumn, the "season of mists and mellow fruitfulness", with nature's bounty of nuts, seeds and berries. Beloved of both human and animal foragers, this colourful harvest tides us through the dark days of winter.

But the seeds produced by native trees and shrubs do more than fill our larders. They could also be viewed as a giant library of genetic information, the blueprint for future generations of forests, and a vital resource which could hold some of the solutions to the environmental challenges we face. Many native trees and shrubs seed prolifically and every crop provides thousands of new combinations of genetic material, the potential for adaptation encapsulated in tasty bite-sized parcels.

Conserving biodiversity includes not just maintaining the widest variety of species, but also genetic diversity. For native woods and trees, safeguarding our genetic resources means understanding the genetic diversity in our native trees and shrubs, how this is impacted by environmental threats and also how it might help species adapt to environmental change.

Our genetic heritage

We have some understanding of the lineage of our native woods and trees. For example, it is thought oak colonised the British Isles after the last glaciation from a refugium in Iberia, in contrast to oaks in other parts of northern Europe which came from southern Italy. Scots pine is thought to have come to the UK from two sources – a distinct population in north-west Scotland having come across from south west Ireland and the remainder arriving from continental Europe via England.

However, there is still a great deal we don't know, and the need to find out is ever more pressing, given the challenges we face, particularly from climate change and pests and diseases. Today conservation focuses on the need for resilience – in ecological terms this could be defined as the ability of natural systems to absorb and respond to environmental change. Fundamental to this is the adaptability of individual organisms within those systems. In forests and woods, the adaptability of trees has implications for the whole woodland system.

Facing the future

Woodland managers face difficult decisions. In new woods, or when restocking, which species should be used, and of what provenance? When should natural regeneration be used? In existing woods, how can management help to build greater resilience? How should we respond to the impacts of pathogens likely to have a major impact on some of our most common species? Increasing our understanding of the genetic diversity within native tree species should help guide some of these decisions.

In this edition of Wood Wise we look at the mechanics of genetic variation in trees and shrubs, and consider their scope for adaptation. We look at the existing system used to delineate local provenance and consider how this could be improved. We also visit some projects currently under way which aim to conserve the UK's genetic resources through banking seed and promoting home-grown trees.

Adapt and survive

The origins of genetic variation in native trees and implications for practical management

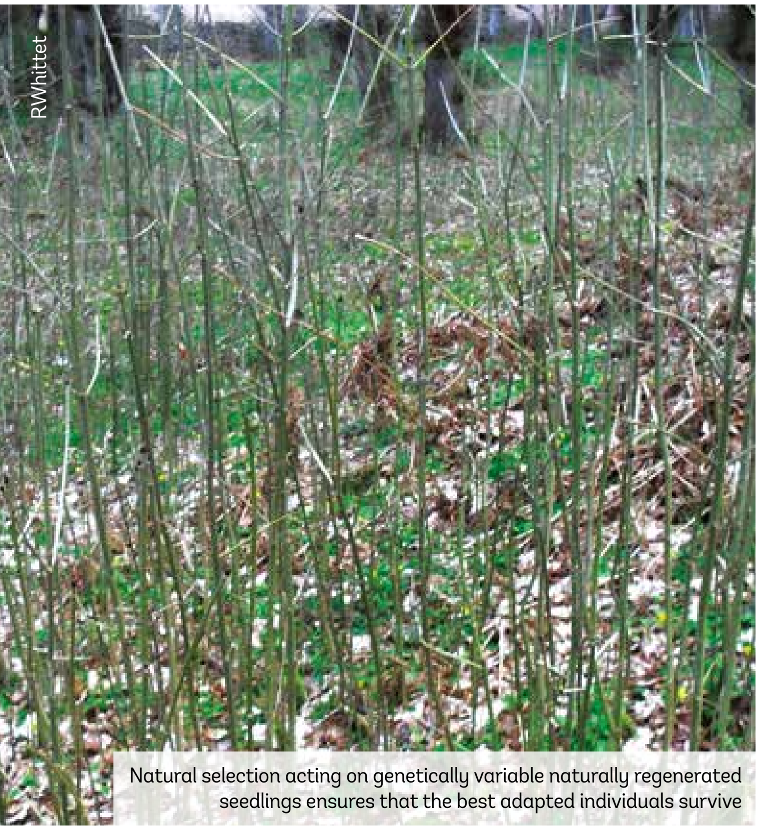
Richard Whittet, Richard Ennos, Stephen Cavers & Joan Cottrell

The combination of climate change and exotic pests and diseases poses serious challenges for trees and woodlands.

To meet these challenges we need to gain better knowledge of the native tree genetic resource in Britain to make more sustainable use of the naturally high levels of genetic diversity. Here we take a look at how evolutionary processes act to generate genetic variation and how knowledge of these processes can be incorporated into active woodland management.

Where does genetic variation come from?

The fundamental source of genetic variation is genetic mutation. Mutations are random changes in the sequences of DNA which occur due to errors during the DNA copying process. The majority of mutations have no discernible effect on the phenotype (observable characteristics of an organism) and are known as neutral variation. Those that do affect the phenotype tend to have a negative effect on fitness (the ability for the individual to survive and reproduce) under all environmental conditions and therefore are not passed on to subsequent generations.



RWhittet

Natural selection acting on genetically variable naturally regenerated seedlings ensures that the best adapted individuals survive

However, mutations can also occur that have small effects on the phenotype that may be favourable under some environmental conditions and unfavourable under others. The presence of these mutations forms the basis for adaptively significant genetic variation within tree populations.

Mutation is a very slow process, occurring at a rate of 0.0001 per gene per generation. Over long periods of time, mutations accumulate across the genomes of individual trees within a population, producing a pool of variants which is referred to as the standing genetic variation of the population. A proportion of this genetic variation is lost from a population by chance every generation, by a process known as genetic drift.

However, a balance occurs between mutation increasing genetic variation and genetic drift leading to its loss. Large populations, where genetic drift is less important, retain higher levels of standing genetic variation than small populations. Realistically, faced with rapid climate change, new biological threats and a slow rate of mutation, tree species must rely on this existing gene pool to adapt.

The adaptive genetic variation in this gene pool is transmitted through generations by reproduction, which in plants can be sexual or asexual. When reproduction is sexual and mating is preferentially with other individuals (outcrossing), the combination of genes received by any offspring is determined by two processes. During meiosis (gamete production) parents generate non-identical gametes by re-assortment of their genes and during fertilisation these gametes are combined between parents.

Variation in adaptive traits is controlled by many genes, each having a small effect and so a single mother tree can produce offspring with many different combinations of adaptive genetic variation. This means offspring will display a range of variation for adaptive traits controlled by this genetic variation, e.g. time of budburst and resistance to pathogens.

Significance of genetic variation

Trees produce large quantities of seedlings each year and each individual is unique in terms of the genetic variation it contains. Environmental conditions at the time will determine which of the individuals are the fittest, i.e. have a greater chance of survival and ability to reproduce. Fitter individuals make a greater contribution to subsequent generations, thereby enabling adaptive evolution by natural selection, producing a range of phenotypes best able to cope with local conditions. Selective pressures differ between sites, causing populations to become adaptively differentiated from one another.

RWhittet

Pine pollen cones, or strobili. Scots pine pollen is produced abundantly and is capable of dispersal over tens or hundreds of kilometres

British native trees are generally outcrossing and adopt different strategies to discourage mating with closely related individuals, thereby avoiding inbreeding, which can result in a loss of fitness. Although trees are immobile and have very long generation times, their large stature means flowers are abundant, highly visible to animal pollinators or seed dispersers and are high above the ground, enabling efficient pollen and seed dispersal by wind. This ensures genetic variation is moved around the landscape and can be exchanged between populations. This exchange is known as gene flow.

When highly extensive, gene flow reduces the differences between populations but increases the diversity between individuals within the same population, as genetic variation is introduced from elsewhere. Even in very small populations (e.g. an isolated population of four ash, *Fraxinus excelsior*, in the Scottish Borders) inbreeding and loss of genetic variation by genetic drift are prevented by long distance gene flow.

To summarise, the fundamental source of genetic variation arises from mutation. This variation is then reshuffled during recombination and fertilisation, producing very large numbers of possible gene combinations. Natural selection can then act upon this variation, producing a range of phenotypes adapted to local conditions. This removes genetic variation from a population but ensures what is left over is best able to cope with local conditions. Gene flow reduces the variation between populations but increases that within single populations. Random genetic drift removes variation from a population but is constantly counteracted by gene flow when populations are sufficiently connected by pollen and seed dispersal.

These processes interact to produce populations of trees that contain high levels of genetic variation upon which natural selection can act, leading to continuous adaptation to changing conditions.

Evidence of adaptive genetic variation

Adaptive genetic variation can be assessed by growing trees from multiple seed origins in a common environment (common garden experiment). Under such conditions, each seed experiences similar environmental conditions which means observed differences between phenotypes are due to genetic differences between them. Such experiments with British trees have shown two key results.

Firstly, trees raised from seed from different parts of Britain show differences in traits such as timing of bud flush, growth increment, drought tolerance and disease resistance. The differences between populations are often related to continentality, which in Britain is determined by longitude. For instance, populations of downy birch from the north west of Britain have evolved smaller leaves than populations in the south east, which is thought to be an adaptation to windy conditions. In this case, local, natural selection has been sufficiently strong to counteract the homogenising effects of gene flow.

Secondly, despite the differentiation between populations, there is typically very high variation within single

JCottrell

Hazel

populations. For instance, under common garden conditions, individuals within Scottish populations of Scots pine show substantial differences in their susceptibility to *Dothistroma* needle blight. There is also greater variation within a single population than between populations for this trait. This reflects the effect of high gene flow rates but shows that if pathogen pressure increased, the population could potentially evolve by natural selection as more resistant genotypes were favoured.

Incorporating evolutionary principles into woodland management

Adaptive evolution occurs when natural selection acts upon genetic variation. In existing woodlands regeneration must be present for this to happen, providing the opportunity for new phenotypes to be recruited. Regeneration can be encouraged by protection from herbivores but periodic disturbance also promotes regeneration of new seedlings. This can be done through thinning, for example, as part of continuous cover forestry or other shelterwood forestry systems, or through opening gaps in the canopy, which could be part of a minimal intervention approach.

Protecting existing genetic resources is also a priority. A key step is establishing dynamic gene conservation units (DCUs): >500 mature trees of a given species, in effectively reproducing populations, representing known or probable genetic variation. DCUs are designed to maintain evolutionary processes and genetic diversity within large tree populations and to conserve adaptive or other traits in marginal or scattered populations. These may be particularly important in Britain because native populations are at the northern and western margin of the species range, so may contain unique components of variation not found elsewhere.

For species which are rare or have a scattered distribution, especially those reluctant to flower in Britain such as black poplar, establishing regional seed orchards may offer a practicable solution to conservation and deployment of genetic resources. The geographic scope of such orchards would not only greatly depend on the demand for seed, but also the scale at which populations are adaptively different from one another.

In this scenario, it may also be important to assess whether there is any maternal effect on phenotypes, i.e. are seedling phenotypes influenced by the phenotype of their mother or the environment in which seed is formed? It is a common misconception that combining individuals from different populations in seed orchards will necessarily maximise genetic diversity, as there can be similar levels of genetic diversity within a single population.

When establishing new native woodlands, where natural regeneration is not possible, the choice of planting stock should recognise the extensive variation that exists within native tree species. Current policies related to choice of planting stock for native trees and shrubs recommend sourcing seed which is local to the planting site, on the basis it should be adapted to the local environment.

Using currently adapted planting stock, based on seed collections from as many parent trees as possible, is likely to promote higher survival to maturity under current conditions, not least because locally sourced stock should be conservatively adapted to extreme but infrequent events. Maximising survival in newly established woodlands will promote larger population sizes and maintain genetic diversity levels.

Provided ongoing management of the newly established population encourages regeneration, an evolutionary response to changes in the environment via the continued delivery of genetic variation by gene flow and the actions of natural selection upon this variation, is a realistic expectation in the long term.

Breathing new life into timber woods

David Boshier & Tim Rowland

Timber is an important natural resource that must be managed sustainably. As scientific understanding increases it may be possible to grow more genetically superior, native timber trees.

Future Trees Trust (FTT) is a registered charity dedicated to the improvement of broadleaved timber trees by conventional selective breeding, to improve their growth rate and form while maintaining a broad genetic base to maximise disease resilience and adaptability to climate change. This work is needed because current broadleaf woodlands are of insufficient quality to provide an economically viable domestic timber resource, meaning the UK currently imports 95% of the hardwood timber it uses.

In a country with such good growing conditions for many important timber tree species, it is unfortunate so few landowners wish to plant them for timber as their genetic form is so poor and the economic returns consequently so low.

FTT's work aims to increase disease resistance, timber yield and carbon dioxide sequestration in seven species of broadleaf trees by up to 40%. By making their planting more economically attractive, it is hoped more and better trees will be planted in the future. This also contributes to all the associated benefits and advantages trees will bring to society, our environment, our economy and our countryside.

Future Trees Trust

Ash graft

Tree improvement and genetic diversity of British broadleaves

The respective roles of planting and natural regeneration of trees in the British and Irish landscape have varied over time, reflecting changes in the perceived role of trees and forests. The last 25 years have been marked by an increase in both the planting of broadleaf species and their management, principally for social, environmental and conservation benefits. It is widely acknowledged that over the next 10 to 20 years the scale of broadleaf tree establishment will increase. This will be due largely to the conversion of large areas of non-native conifer plantations to broadleaved woodland and the restoration of plantations on ancient woodland sites.

Sourcing material to re-establish such woods will potentially have a large impact on both the productivity of these woods and the gene pool of native tree species. At the same time, the spectre of climate change raises the question of whether trees adapted to current conditions will continue to flourish in another 50 to 100 years.

Forest policy in Britain currently favours the use of local stock as the central principle to establishing or restocking woodland areas. Various parts of the revised UK Woodland Assurance Standard state: *"Where appropriate and possible, use natural regeneration or planting stock from parental material growing in the local native seed zone (native species) or region of provenance (non-native species)."*

At the same time, the use of genetically improved material attracts attention related to a number of perceptions about its impact on levels of genetic diversity and the conservation of native gene pools. It should be stressed the term genetically improved refers to trees selected through traditional breeding processes and does not cover genetically modified organisms.

Effective management of tree genetic resources is a key element for both forest conservation and management.

Genetic variation is the raw material upon which selection, natural or human, acts and therefore the basis for evolutionary change and adaptability. Genetic diversity is essential for both the long-term stability and the short-term productivity of trees, whether planted or from natural regeneration.

Ash seed orchard

However, a species' gene pool and associated genetic structure is not a fixed entity that can be preserved. Rather it reflects a continually fluctuating process through chance events (called genetic drift) and as a response to changes in the environment that consequently determine adaptation and survival.

The conservation of evolutionary processes is regarded as the most desirable goal, above the preservation of a particular genetic structure and status which is largely unachievable. Therefore, any genetic conservation policy of native British trees should aim to conserve the evolutionary potential of the species and their populations.

Key features of trees

While trees share much of their basic biology with other plants, certain features mark them as distinct, with consequent impacts on their genetics and any genetic conservation strategy. Trees are characteristically long lived, reaching sexual maturity at a relatively late age, with overlapping generations. In contrast to many herbaceous plants, they have been shown to be generally out-crossed, maintaining high levels of genetic diversity that may buffer them against the range of environments they experience during their long lives.

However, they also accumulate mutations over time and consequently carry a high genetic load. This means they are susceptible to inbreeding depression (e.g. reduced vigour and fertility) when atypical levels of inbreeding, from selfing or mating between relatives, lead to the expression of such deleterious alleles.

Similarly, loss of genetic diversity through reduced population size poses a threat to fitness. Maintenance of genetic diversity in tree populations is therefore a key component of any conservation or management programme.

Tree improvement and genetic diversity

Tree improvement programmes typically start with mass selection of phenotypically superior trees, as judged by silvicultural characteristics. These 'plus trees' are selected on the basis of superior form and growth, as compared to other trees in the same stand/wood. Seed collected from these trees is then grown in progeny trials, which provide information on the extent to which parent trees' superior characteristics are genetically heritable (i.e. transmitted from parents to offspring). At a later date (e.g. a third or half of the rotation age) the progeny trial may be thinned to leave the best trees in the best families as a seed orchard for the supply of improved seed.

Improvements in yield provided by seed harvested from such seed orchards depend on the selection intensity (i.e. the proportion of trees originally selected, the proportion of trees left after thinning the orchard and the degree to which the trait of interest is genetically heritable). Similarly the levels of genetic variation maintained in these selected populations depend on the numbers of trees maintained in the breeding population, the production population and indeed the number and geographic spread of the originally selected trees. These factors apply equally to the levels of genetic variation maintained in tree improvement programmes that emphasise clonal propagation. Economic forces may increase pressure for the rapid culling of genotypes to attain higher genetic gain.

However, for forest tree species, breeding with too genetically narrow populations is seen as particularly dangerous for two reasons:

1. Each tree plantation must endure more variable environments than traditional agricultural crops

2. Breeding cycles are long, forcing an extended response time for the incorporation of new genetic material

In second and further generations of improvement, breeding programmes become more complex but are managed to maximise gain, while at the same time minimising inbreeding and consequently maintaining levels of genetic diversity. The frequently observed reduction of genetic diversity seen as a result of breeding in agricultural crop plants is therefore not expected, nor has it been observed in forest trees.

Breathing new life into timber woods

For 25 years, the Future Trees Trust has been improving broadleaved trees and has amassed huge knowledge of woodland genetics. We are currently working with the Woodland Trust on a major project to identify sustainable seed sources for many species with future timber potential. In partnership with Earth Trust, Forest Research and Sylva Foundation, we are working together on the Defra-funded Living Ash Project to ensure ash remains a viable timber species for the future by identifying resilient trees. You can help with this work by looking for healthy ash trees, especially in areas where Chalara dieback of ash is prevalent, tagging them and letting us know. Tags are free and available, with full guidance and instructions, from www.livingashproject.org.uk

If you have an enthusiasm for the FTT's work or a specialist interest in any of the species we are currently improving (ash, birch, cherry, oak, sycamore, sweet chestnut and walnut), please get in touch. Membership is free and members are drawn from across the forestry and ecology sectors, including forest managers, researchers, landowners, saw-millers and nursery managers. Our co-chairs are Graham Taylor (Director at Pryor & Rickett Silviculture) and Geraint Richards (Head Forester, Duchy of Cornwall).

Birch clonal orchard

To find out more and get involved in the FTT's work to ensure the survival and growth of broadleaf forestry in Britain and Ireland contact Development Officer Tim Rowland at tim.rowland@futuretrees.org.

Birch clones at Teagasc

Banking on the future

Clare Trivedi

Millennium Seed Bank

Kew's Millennium Seed Bank Partnership is the largest *ex situ* plant conservation programme in the world and is at the forefront of safeguarding the future of the planet's flora. In the UK, Kew is ensuring we safeguard our forest genetic resource with its National Tree Seed Project.

A range of reports in recent years have recognised the many benefits of the UK's native trees and woodlands, and the need to protect and restore them. The importance of increasing the area of wood cover is also well recognised. For example, the Independent Panel on Forestry has suggested English woodland habitats should be enhanced through sustainable management, restoring ancient woodlands and expanding tree cover with appropriate species. These ambitions are made more challenging by the significant rise in pest and disease outbreaks in the last decade and potential impact of future climate change scenarios on our natural environment.

Reports frequently refer to the need to develop resilient woodlands, able to withstand these varied pressures. However, there is debate over what this means in terms of the benefits of planting different species, and of using local provenance versus non-local planting material. Certainly the arrival of Chalara dieback of ash, *Fraxinus excelsior*, in 2012, has highlighted the benefits of homegrown planting material but supply is still limited.

At the heart of these complex issues is the need to maintain and utilise the full genetic diversity of our woodland resources. Gene conservation programmes can address such challenges by conserving genetically diverse, locally-adapted material, which can be used to help resist and manage disease, and help enable the supply of appropriate native planting material.

UK National Tree Seed Project

The Royal Botanic Gardens, Kew's Millennium Seed Bank (MSB) is the largest seed bank for native plants in the world and is at the forefront of safeguarding the future of the planet's flora. In light of the issues outlined above, Kew began its UK National Tree Seed Project (UKNTSP) in 2013. The aim is to establish multi-provenance seed collections that will represent the majority of the adaptive genetic diversity present in each species. These collections will be stored at the MSB and are intended to provide a resource for research and woodland conservation and management.

The current five-year plan for the project is focused on a target list of 70 priority native species of trees and shrubs. This list was developed through a scoring and ranking system which included conservation status (based on the GB Red List), pest and disease risk (based on Defra's Plant Health Risk Register) and prevalence in the landscape (based on the Plant Atlas). The list includes 38 *Sorbus* micro-species and 30 other native species.

This ambitious initiative is too much for one organisation to do alone. Therefore, Kew has established partnerships with more than 30 other organisations across the UK to help source and gather the target seed collections. The Woodland Trust is a key partner, contributing significantly in terms of access to its woodlands and providing staff and volunteer resource to the collecting programme. We are also working towards better collaboration for sustainable seed sourcing for tree seeds in the UK.

'Genetically representative' collections

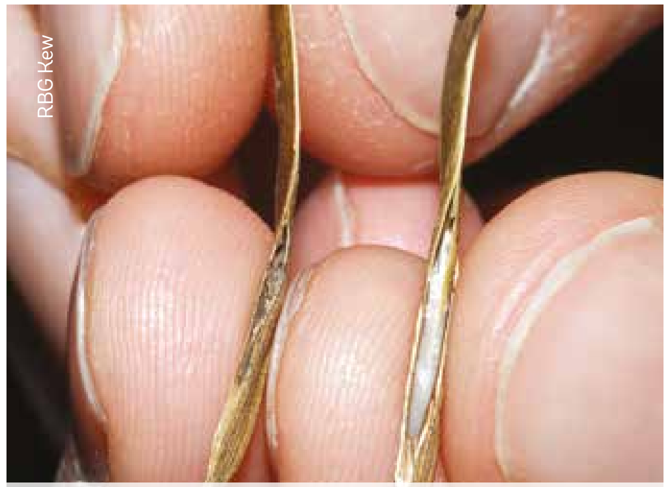
In common with most countries, the UK does not know enough about the population genetics of its native trees and shrubs to ensure seed collections are genetically representative of the national flora. However, the Forestry Commission has divided Great Britain into 24 biogeographic areas, termed native seed zones, for the purposes of commercial tree seed collecting and supply. This provides a proxy of likely areas of locally-adapted genetic diversity. Through the Botanical Society of Britain and Ireland (BSBI) there are also good species distribution records – though it can be hard to tell whether botanical records are for native populations or planted ones (or indeed the number of individuals linked to a single record).

Using this information, the distribution records across the country were overlaid with the seed zones map to develop a database of target collections. The aim is to make at least one collection from every seed zone in which an autochthonous (locally native) population of a species naturally occurs. Where populations are found both above and below 300m in altitude in a zone, attempts will be made to collect from both altitude zones.

However, developing a list of target collections is only the start. It is equally important the collections adequately represent the populations (or sub-populations) from which they are made. This means collecting from as many genetically distinct trees as possible. Teams are asked to gather seed from at least 15 separate trees for each collection. However, UK woodland is highly fragmented and for some species it is not possible to find this number of individuals on one site; in this case collectors must find several sites in the same seed zone. At the individual tree level it is vital seed is sampled from across the canopy to catch the progeny pollinated by different father trees.

Having worked so hard to capture the maximum diversity in each collection, it is important not to lose access to this once seeds go into storage. Therefore, mother trees are tagged and georeferenced, and seeds stored separately. This allows users of the collections to study traits, such as disease resistance, for families as well as at the population level.

Working with geneticists, the sampling strategy is improving as the project evolves. A desk-based decision tree approach, first developed at Royal Botanic Gardens, Edinburgh, has helped identify what is already known about the UK genetic diversity of our target species, and set priorities for further studies. Geneticists are also being engaged in an attempt to develop a model to assess how effective the collections are at capturing the genetic diversity available in the wild. This is being piloted using some of the UKNTSP's first priority collections of ash.



Ash seed cut test. Left - empty seed; Right - full seed (firm & white)

The seed research component of the project seeks to better understand germination and seed storage requirements of the UK's trees and shrubs.

Spindle seed collection

Kew staff and Suffolk Wildlife Trust volunteer collecting Lime from Bradfield Woods

Using the UKNTSP collections

The primary advantage of the UKNTSP is conservation of the genetic diversity of a range of native trees and shrubs for the long term. The longevity of seed bank collections is species specific, but most will last for many decades in storage. Collections made today will provide a baseline against which genetic change, for example due to climate change, can be measured in the future. Most target species have a range that extends across Europe, but the UK is at the limit of the natural distribution range for a number of species. Therefore, it may contain unique elements of natural variation particularly worthy of conservation.

The collections may also have many immediate uses, particularly in studies that would benefit from the assessment or comparison of traits from geographically dispersed populations or from different maternal lines. Samples of seed collections will be available for scientific research via the MSB seed list.

They are an ideal source of experimental material for provenance trials to measure the performance of materials from different seed sources across different parts of the UK, particularly in light of adaptive traits such as drought resistance. Seed collections of known provenance from across the UK could also be useful to assess gradients in seed viability and varying requirements for cold stratification before germination, which may impact the ability of different populations to adapt to climate change.

They can also be used as an ideal source of material to screen for differential susceptibility/resistance to a range of pests and diseases, as well as in studies to better understand the interactions of trees with pests and diseases and the development of potential management solutions. For example, the collections may be used to assess the efficacy of new treatments or preventative measures, and the impact of these on related and associated species.

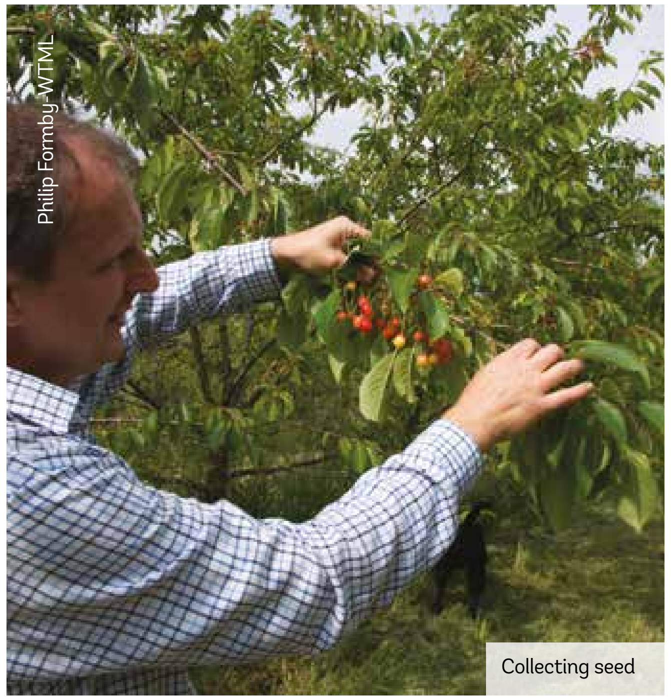
The UKNTSP should contribute to the identified need to develop UK-sourced and grown planting material. Kew is exploring ways to appropriately share site data with others to help identify potential new registered seed sources for native species in the UK. This could help facilitate an improved supply of known provenance planting material of native species for afforestation and reforestation. For several species, collecting directly from seed sources is unlikely to be efficient, either because sufficiently large native stands simply do not exist or they rarely produce seed. In these cases, it could be possible for the UKNTSP collections to provide the founder stock for establishing seed orchards which could be tailored to meet a variety of needs.

Through the various partnerships, the UKNTSP is enhancing skills and knowledge in tree seed collecting and storage across a range of organisations, as well as raising awareness of issues such as genetic diversity and seed quality. Seed banking can play a significant role in understanding, conserving and wisely using the UK's forest genetic resources. As the project matures, Kew is engaging with others to consider how this tool could fit with others to develop a wider process for tree gene conservation, which should ensure a resilient woodland resource is available for many years to come.

MSB staff collecting Spindle from a Suffolk Wildlife Trust site

Home-grown trees: a sustainable future

Sian Atkinson and Christine Reid



Collecting seed

Identifying new sustainable seed sources for some of our less common trees will help build resilience by reducing the need for imports.

The Sustainable Seed Sourcing Project is an initiative to identify sustainable sources of seed for less common broadleaved trees (and yew) grown in British woodland. It was set up by a partnership including the Woodland Trust, Future Trees Trust, Millennium Seed Bank, Forest Research, Forestry Commission and Royal Forestry Society.

Demand for trees to create new woodland for timber, conservation or provision of wider ecosystem services, to diversify existing woodland and to replace trees lost from the wider landscape is likely to increase in future.

For the more common broadleaved trees such as oak, birch and beech, there are already reliable registered seed stands within the UK, from which planting stock can be grown. However none of the less commonly planted broadleaved trees have registered seed stands in the UK, leading to a need for imports. We know from experience importing plants can introduce new tree pests or pathogens, and also risks importing stock that is not well adapted to UK conditions.

Making full use of our diverse genetic resources is a key strategy to building resilience in our forests and wooded landscapes. Long term resilience is likely to be greatest where there is good, intraspecific genetic diversity with potential for adaptive responses to change – however, this need not be at the expense of selection for traits which favour timber production or other desirable characteristics.

UK sourced and grown

Since 2013, the Woodland Trust has used only UK-sourced and grown trees in its planting schemes. Most of its seed is collected by Shropshire-based seed supplier Forestart and grown on by a small number of nurseries selected for their standards of biosecurity and traceability.

However, the Trust also wants to make it easier for others planting trees to do the same, with access to UK-sourced and grown material of a much wider range of tree and shrub species. Working with Defra and Grown-in-Britain, the Trust is developing an assurance scheme for nurseries so buyers can be confident they are buying UK-sourced and grown trees and shrubs.

Growing on seed collected from native tree stands

Sourcing seeds

Control of seed, cuttings and planting stock for forestry and conservation purposes is through the Forest Reproductive Material (FRM) (Great Britain) Regulations, which ensure planting stock is traceable to a registered source, and provides information on the genetic quality of the stock. These regulations are the expression of a European Directive controlling marketing of FRM within the EU.

Britain is divided into four Regions of Provenance, which provide a framework for specifying sources of FRM. These are defined areas within which similar ecological and climatic characteristics are found.

The FRM register details selected seed sources for a relatively limited list of broadleaved species – including the native oaks, silver birch, beech, sycamore, sweet chestnut and small-leaved lime. The Sustainable Seed Sourcing Project aims to identify domestic seed sources for 14 broadleaf species, plus yew, which are not included in the existing register, and for small-leaved lime, for which there are insufficient registered seed stands.

Identifying future stock

In 2014, Forestart, funded by the Forestry Commission, assessed the selected stands for broadleaved tree species currently on the register. This determined the stands' suitability as commercial seed sources and identified options to increase productivity and to make collection easier. It highlighted a need for more selected stands of sweet chestnut and small-leaved lime to be identified.

In the second phase of the project, a report by Future Trees Trust, commissioned by the Woodland Trust, investigated the availability of seed sources for the species listed below. These were species for which there is likely to be a future timber demand but for which no seed source was currently registered (other than small-leaved lime for which there is only one registered selected stand). However, consideration was also given to the conservation needs of each species and the need to foster genetic diversity.

Species covered in the Sustainable Seed Sourcing Project

Aspen	Small-leaved lime
Black walnut	London plane
Black poplar	Norway maple
Common alder	Wild apple
Common walnut	Wild pear
English elm	Wild service
Field maple	Wych elm
Hornbeam	Yew

Demand for UK sourced and grown trees is likely to increase

Home grown stock helps reduce the risk of importing pests and diseases

Information supplied by the project partners and other organisations (e.g. Wildlife Trusts, National Trust, and Natural England) was reviewed to identify candidate population sites for the target species, and a strategy recommended for all 16 species considering seed demand, seed viability, genetic diversity, appropriate seed production unit type and prioritisation. Research has shown there is enough information for most of the species to identify likely populations, seed stands and individual trees to improve seed supply. The Woodland Trust is working with the Future Trees Trust and others to develop a more detailed seed sourcing strategy for the species of most interest: aspen, black walnut, common alder, field maple, hornbeam, small-leaved lime, wild service, wild apple (crab), and yew. We also hope to develop strategies for the shrub species blackthorn, hawthorn, hazel, and privet.

Developing a strategy for each species will involve visiting and assessing potential suitability of the sites identified in each seed zone. Recommendations will be made around registration as seed stands, or development of seed orchards or clonal orchards, depending on the needs of each species. The best strategy for each species will depend on a wide range of factors. These include market demand for seed, natural range of the species, pollination mechanism, location of stands and their suitability for regular wild collections, longevity and viability of seed and propagation success, and the genetic variation within stands and across seed zones.

There has been a lot of interest in this work from many organisations, tree species interest groups and woodland owners. Existing collaborations, for example with the UK Tree Seed Project at Kew's Millennium Seed Bank, will be strengthened around individual species.

The Woodland Trust sees this as an important project which is using information about the genetic diversity of trees in the UK to develop a practical application for woodland conservation.

Deploying our genetic resources: local provenance in practice

Richard Whittet, Richard Ennos, Stephen Cavers & Joan Cottrell

If we are going to use our genetic resources to build ecological resilience, we must address some of the fundamental difficulties found in the current system of provenance and seed origin for new planting in Great Britain.

Seed zones for native trees and shrubs

It is generally agreed there is a need to expand the UK's woodland resource, and there is also a demand for planting stock for restocking or restoration. So how do we go about getting the right trees in the right place?

The existing seed zones for native trees and shrubs in Britain divide the country into 24 geographical regions (Figure 1a). These are intended to describe areas containing populations adapted to similar conditions. The regions are roughly similar in size and are applied uniformly to all native species – with the exception of Scots pine, *Pinus sylvestris*, which has a separate set of seed zones within its native range based on variation in selectively neutral genetic markers.

The seed zones were established when little was known about the pattern of distribution of adaptive variation in our native British tree species. Therefore, the seed zones were set out using proxies; major geomorphological landforms and watersheds. A major achievement of the seed zones is that, provided honesty prevails throughout the supply chain, a certification standard adds assurances to British origin seed. This gives British seed suppliers and nursery producers a competitive advantage over businesses elsewhere. However, there are several important shortcomings in the application of fixed-boundary seed zones in Britain.

Are the seed zones biologically relevant?

Seed zones are defined by lines on maps on the basis of geographic proximity. However, in rugged terrain, such as the British uplands, sites within seed zones which are geographically close will not necessarily experience similar climatic conditions. Indeed it may be the case that the most climatically similar source of planting material to a planting site is actually a population in another seed zone (Figure 2).

Another issue is the relative uniformity in the size of seed zones, which implies environment varies at the same geographic scale across Britain. Because of the heterogeneity of environment in upland landscapes, greater subdivision of geographic areas may be required than in lowland regions, such as in southern and eastern England where topography is relatively homogeneous.

Better understanding is needed of the adaptive genetic variation in native tree species across the landscape

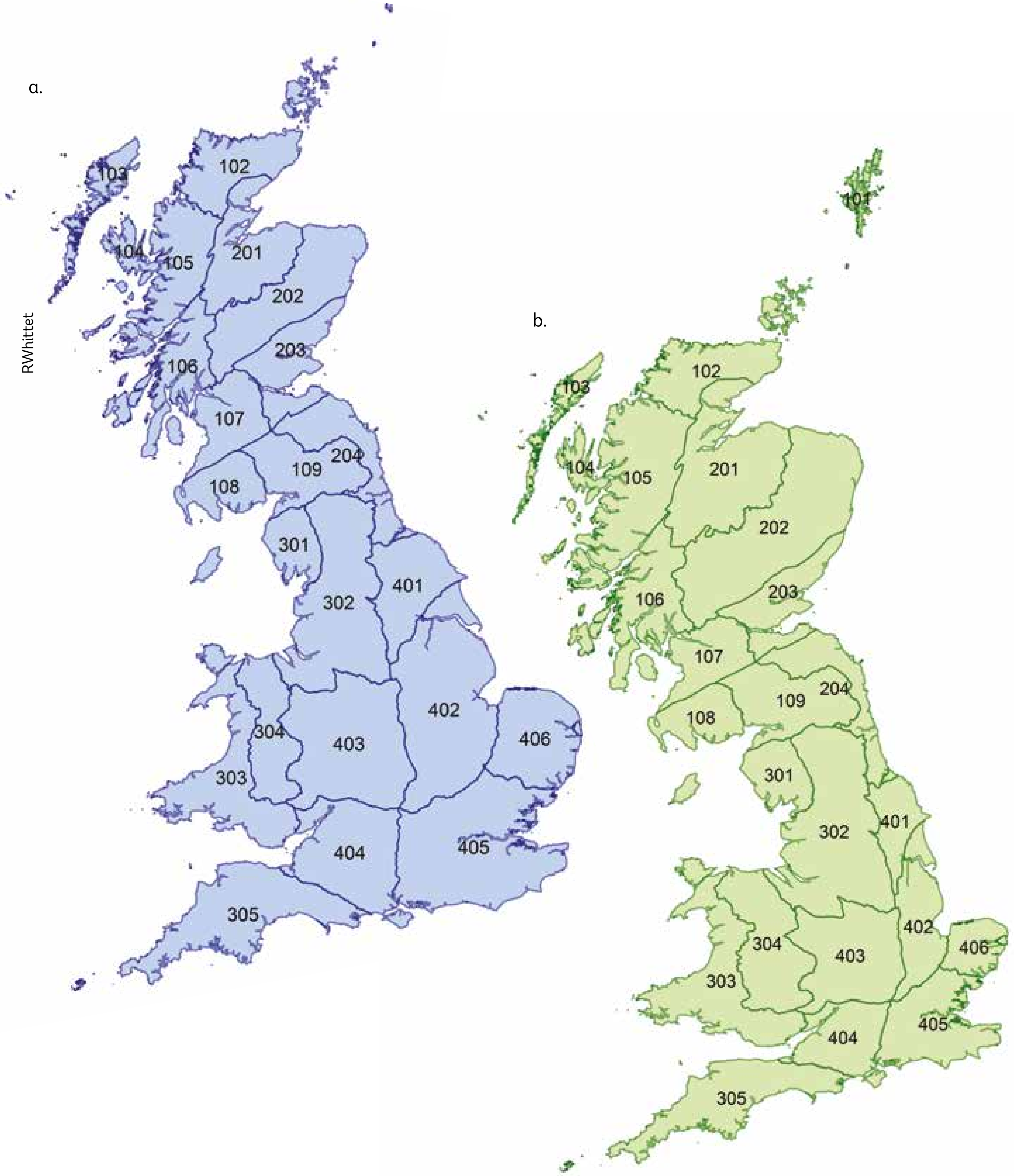


Figure 1. a) Map of the UK native tree seed zones. b) Cartogram of the UK native tree seed zones scaled by the volume of land within each zone.

This is demonstrated in Figure 1b, which shows a cartogram of Britain in which the volume of land above sea level rescales the area within the seed zones – as though the land within the seed zones was rolled out flat and stuck together again. The north of Scotland expands while central and southern England appears much smaller. There may be more seed zones than are strictly necessary for most species in England.

A further problem is the application of the same seed zones to many species, as it assumes variation in adaptive traits for different species show the same geographical pattern, which may not be the case.

To improve the biological relevance of seed zones, or seed transfer guidelines in Britain, a deeper understanding is required of how adaptive genetic variation is distributed across the landscape. As it suggests, this is the variation that determines variation in phenotype (physical characteristics and performance) upon which natural selection operates.

This would involve establishing replicated common garden experiments, to investigate and predict variation in phenotypic traits when different seed sources are deployed in different environments. The locations of field trials should include mixtures of challenging and benign sites, those at varying altitudes and with varying degrees of oceanicity.

Problems implementing the seed zones

An important bottleneck in the supply chain is a natural one. The size of seed crops varies naturally from year to year and place to place. For some species, like the oaks, seed does not retain viability for extended periods in storage. This means there will be times when it is very difficult to supply domestically-grown trees from locally-sourced seed. The perception is this natural bottleneck is not always taken into account in woodland creation plans, despite the fact it can entirely stop planting schemes from going ahead.[1]

The vast majority of trees and shrubs grown commercially by nurseries for native woodland creation, expansion and restoration are grown speculatively. The reasons for this are complex and mostly related to the way grant schemes are designed, which place a limit on the time allowed for planting work following grant approval. As it can take up to three years for a tree grown from seed to be ready for planting, nursery producers are rarely able to predict demand in advance of sowing.

Authorities responsible for processing and approving grant applications will typically stipulate seed of local origin is used. Although this is appropriate from a genetic conservation point of view, it creates problems in the supply chain.

Without this advance notice of demand, nurseries have to try to predict the seed origins of planting stock that will be required by the time they are ready for sale. Most nurseries stock a wide range of species and supply them in various sizes. Therefore, there are limits to the number of seed origins/provenances a nursery can sow and a nursery must compromise between growing a large volume of few seed origins (high risk/high reward), in the hope that they will be in demand two or three years later, and growing smaller quantities of many seed origins (lower risk/lower reward), which would be more costly to produce but increase the likelihood of making a sale.

When demand is underestimated and a nursery cannot supply orders, they have the ability to trade between one another or to import planting stock (with the risk of bringing in pests and diseases) from large nurseries in other countries in western Europe. If demand is overestimated or a moratorium is placed on a species due to a health risk, the unwanted trees will have to be destroyed (burnt) on the nursery site.

In times of shortage it is sometimes considered acceptable to plant trees raised from seed collected in adjacent seed zones, creating an interesting loophole in the supply chain that helps nurseries retain their competitiveness. With this knowledge, a shrewd nursery might make the decision to sow seed originating from seed zones with many borders. This means seed collected from a single population in each of zones 201, 107 and 403 can be used to supply 17 out of 24 seed zones (see Figure 1a).

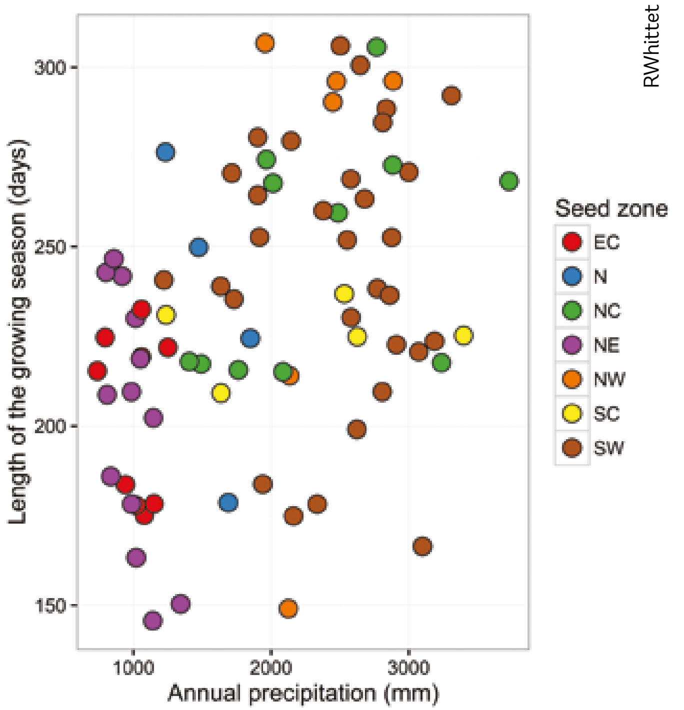


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Figure 2. Mean annual precipitation plotted against mean growing season length for the 84 'Caledonian' pinewoods, with colours indicating site membership of the seven 'biochemical regions'. Populations from the individual biochemical regions do not form discrete clusters indicating that populations within a seed zone do not necessarily experience similar climatic conditions.

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Nursery stock

Guidelines for seed collections recommend they are based on a minimum of 20 open pollinated progeny from unrelated mother trees in order to provide sufficient genetic diversity. If this is the case, a shrewd nursery supplying trees from the three seed zones with many borders would be able to supply most of the country with the offspring of only 60 individual trees. The extent to which this is a problem will depend very much on the species and the planting sites.

Moving forward

The main problems in the seed supply chain are caused by natural variability in seed availability and the configuration of grant schemes and regulations. With stronger evidence based on the results of common garden experiments across a range of sites, it will be possible to design more biologically relevant seed zones or seed transfer guidelines for Britain. However, the ability for tree planters to provide nurseries with more notice will be crucial to securing a more sustainable supply chain for native trees and shrubs. Paying attention to the availability of seed and planting stock, as well as arranging contract growing or at least advance consultation with a local nursery, is strongly encouraged.

1. Whittet, R., Cottrell, J., Cavers, S., Pecurul, M. & Ennos, R. (2016). Supplying trees in an era of environmental uncertainty: Identifying challenges faced by the forest nursery sector in Great Britain. *Land Use Policy*, 58, 415-426.

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