A review of tree improvement programmes in Ireland – historical developments, current situation and future perspective

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Abstract
Tree breeding or tree improvement programmes have been part of Irish forestry from its early days, but it is only since the 1950s that a significant effort was made. Tree improvement programmes, in addition to providing regular sources of quality seed, provide the means of achieving further genetic gains in the productivity and quality of forest tree species. The objective of this paper is to 1) explain how tree improvement is achieved, 2) to review past programmes in both coniferous and broadleaf species, 3) to discuss the current situation in Ireland and 4) to make a case for the continuance of this important work.

Keywords: *Breeding, plus-trees, seed stands, seed orchards and propagation.*

Introduction

It has long been recognised that to ensure the success of any planting programme, a regular and continuous supply of high quality seed is vital. Only the best and most suitable material currently available should be used. Poorly adapted or low quality seed sources can result in plantation failures or substantial losses in production and in Ireland there have been some experiences of such losses. Many times in the past it was the price of seed that determined which sources were purchased and subsequently used to produce material for planting. Once a crop is established, it is difficult to remedy these problems and it should always be borne in mind that seed costs constitute only a minute proportion of the total cost of establishment.

The first opportunity to improve timber production is to carefully consider what species can be successfully grown under the local climatic conditions. Next, the most suitable seed sources or provenances for the chosen species need to be identified. Further genetic improvements can be obtained by testing and selecting individuals of the most suitable sources and crossing them with other similarly selected individuals. Finally, the best individuals from the crosses of the best parents can be selected for further breeding work (Figure 1).

Breeding is however only part of the process. The production of commercial amounts of improved material is equally important if any real benefit is to be derived from tree improvement efforts. Different levels of improvement can be achieved through seed stands, seed orchards and also through the vegetative propagation of the improved material.

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The objectives of this paper are to first provide a brief introduction into how tree improvement is accomplished, then to summarise work on tree improvement that has taken place in Ireland over the last 50 years in both coniferous and broadleaf species and finally make some observations about the current and future direction of tree improvement efforts in Ireland.

Historical developments in tree improvement

Although the breeding of plants and animals for agricultural purposes started over 10,000 years ago, the idea of breeding trees is a relatively recent one. As early as 1717, Bradley in England suggested that seed origins were important to consider in the development of forestry and this aspect would only be re-discovered later. Duhammel Du Monceau in 1760 published observations on the inheritance of properties in forest trees, but this work also went largely unnoticed. Between 1820 and 1840, Vilmorin in France established trials that showed that species of forest trees could be subdivided into climatic races (provenances) and he also produced hybrids between species of fir (*Abies* spp.). It was Cieslar in Austria who in 1904 showed that clear climatically distinct races of Norway spruce (*Picea abies* (L.) H. Karst.) were identifiable, which stimulated a renewed interest in the importance of provenance. The first modern forest tree improvement programmes began with poplar (*Populus* spp.) in the U.S.A. in the 1920s. At about the same time, the use of seed stands and seed orchards to produce improved seed were also proposed. Work on controlled crosses (crosses between two known parents) in larch (*Larix* spp.) began in Denmark in the 1930s, which served as the inspiration for other programmes that were initiated after World War II.

Historical aspects of tree improvement programmes in Ireland

One of Ireland's earliest tree breeders was Augustine Henry who published the first scientific report proving that the "Dunkeld larch" was in fact a hybrid between Japanese and European larch (*Larix kaempferi* (Lamb.) Carr. and *L. decidua* Mill.). In 1912 he began experiments to produce poplar hybrids with potential for increased growth. The first Irish provenance trial was established at Avondale in Co. Wicklow in 1916 by A.C. Forbes. Coastal and interior sources of lodgepole pine (*Pinus contorta* Douglas) were included in this trial and the results clearly demonstrated the benefit of planting coastal seed sources of this species.

Documentation of the first plus-tree surveys in Ireland can be found in a file from the 1940s containing letters signed by M.L. Anderson, the then head of the Forestry Division, which authorised Prof. Thomas Clear of University College Dublin (UCD) to carry out such a survey in state forests. However, the exact outcome of that study was not reported.

In 1951, the "Cameron Report" on the then current situation of forestry in Ireland highlighted that procuring adequate supplies of seed was one of three major difficulties facing Irish afforestation. As a result of increased demand for quality forest tree seed following the end of World War II, the Forestry Division of the Department of Lands in the early 1950s started work on securing reliable sources of good quality tree seed. Early work in Nurseries Section of the Forestry Division included the identification of seed stands, the selection of plus-trees and the establishment of seed orchards for a range of species. This material mostly originated from old state forests and some private estates. While the intentions were laudable, the programme was never adequately funded to establish seed orchards of a sufficient size and with a satisfactory number of parents to produce commercial amounts of seed. This was typical of the situation in many other countries at the time, when the idea of tree improvement was first gaining popularity.

This early work concentrated on the use of seed stands and the establishment of seed orchards of Japanese and European larch as well as Scots pine (*Pinus sylvestris* L.). Efforts were later extended to Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), beech (*Fagus sylvatica* L.) and Corsican pine (*Pinus nigra* J.F. Arnold). This material was used to establish a total of about 15 ha (37 acres) of grafted seed orchards (Anon. 1964). However, most information on this programme, including the origin of the material in these seed orchards has since been lost. Only a few small isolated remnants of the orchards remain from this early work. Nevertheless, it was a start.

With the establishment of Research Branch in the Forestry Division in 1957, a more formal series of research projects was initiated. Projects included work on eucalyptus, poplar as well as provenance trials of lodgepole pine, Scots pine, western hemlock (*Tsuga heterophyll*a (Raf.) Sarg.) and the first improvement work commenced on Sitka spruce (*Picea sitchensis* (Bong.) Carr.). Work on the development of seed orchards continued under the direction of the Nurseries Section up until 1977, when all tree improvement work was transferred to the new Genetics Section of Research Branch. Details of all this early work up until 1970 is documented in two "Forest Research Review" reports (Anon 1964, Anon 1970).

Most of the tree improvement work of the newly established Research Branch concentrated on conifers, particularly provenance studies of lodgepole pine, Sitka spruce and to a lesser extent Norway spruce, Scots pine, Douglas fir, grand fir (*Abies grandis* (Douglas ex D. Don) Lindley), noble fir (*A. procera* Rehder) and western hemlock. Seed stands of lodgepole pine, Scots pine and Corsican pine were also identified.

Soon after the establishment of a Genetics Section it was decided that a dedicated site was required to carry out the breeding and propagation work. In the 1960s, a research nursery together with a glasshouse was established at Shelton Abbey in Co. Wicklow, but pollution from the nearby fertiliser plant adversely affected the quality of plants. As a result, in the 1970s the work was first moved to Glenealy Nursery and finally to a new site at the old estate at Kilmacurra Park, Co. Wicklow. An office, potting shed, propagating tunnels and a nursery were established. Later a glasshouse, clone banks, an indoor Sitka spruce seed orchard and an outdoor Scots pine seed orchard were added. This site continues to serve as the centre of all the work in the Coillte Tree Improvement Programme.

Tree improvement work continued in the Forest Service until the establishment of Coillte Teoranta in 1989, when it was transferred to Coillte. Initially, funding for the tree improvement programme was provided by Coillte and the Forest Service, with additional funding from the European Union through a series of Research and Technology Development projects, whenever such funding was available. Over time, Forest Service funding became more limited and was directed only towards work on broadleaf species and eventually, even this funding ended. Since the mid-1990s all tree improvement work has been funded mainly by Coillte, supplemented by national (COFORD) and EU funds when available.

The establishment of the National Council for Forest Research and Development (COFORD) in 1994 emphasised the importance of forest reproductive material when it was identified as one of the five core sectoral areas, which were to be the main focus of COFORD's work (Anon. 1994). Many tree improvement projects have been funded by COFORD since its establishment.

In 2000, COFORD issued a discussion paper "Towards a strategy for gene conservation and tree improvement of broadleaved and indigenous coniferous species on the island of Ireland" which was based on the findings of a small working group comprising members from Northern Ireland and the Irish Republic (Fennessy et al. 2000). As a continuation of this work, COFORD published in 2007 "Sustaining and Developing Ireland's Forest Genetic Resources – An outline strategy" (Cahalane et al. 2007). This report was developed by a Working Group whose objective was to review the nation's forest genetic resources and it contained a number of recommendations, many of which still require implementation.

Tree improvement methods

Not all of the tree to tree variation that can be seen in a forest is due to genetic variation. Other sources of variation include environmental and developmental variation, neither of which is controlled by genes, and as a result this type of variation cannot be utilised in a breeding programme. The basis of genetic improvement lies in the fact that not all individuals within the same species are genetically identical. Most forest species are essentially wild populations, which have not been previously manipulated by man and as a result, they are genetically very variable. The best individual trees for one or more traits are chosen and used in a breeding programme to produce high quality planting stock.

Genetic improvement is permanent because the selected traits are passed on to the offspring of the selected trees. As a result genetic improvement is cumulative, so the improvements made in one generation form the basis of further improvements, which can be achieved in subsequent generations.

Tree improvement depends on utilising natural genetic variation in species and also selecting the best seed sources (provenances) of those species. In some cases, simply selecting the species or selecting the best seed source is all that is necessary to achieve the desired level of improvement. In other cases, particularly the commercially important species, it may be worthwhile to utilise additional sources of genetic variation. Additional sources of genetic variation can be utilised by:

- the selection of superior individuals (plus-trees) from the most suitable provenances;
- selection of the best families resulting from crosses between the plus-trees (superior families); and
- selection and propagation of the best individuals within these superior families (superior clones). This process is illustrated in Figure 1.

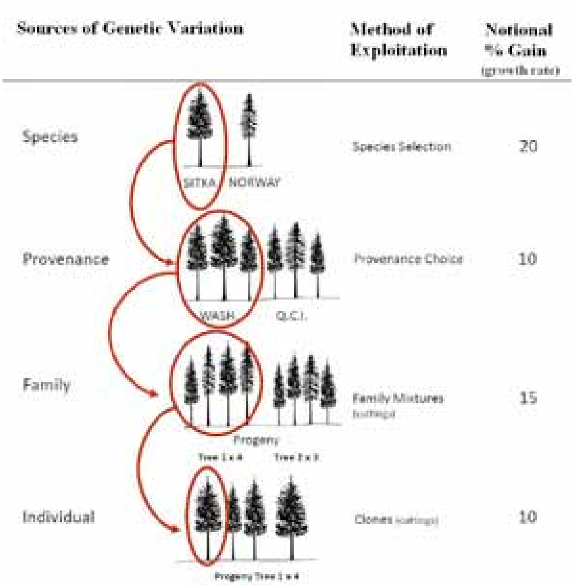

Figure 1: *Sources of variation and how they can be exploited in tree improvement.*

Whether an improvement programme stops at the selection of plus-trees or continues to selected superior clones, depends on the commercial importance of the species as well as available resource and how much time and effort is to be invested in the improvement of the species. Nevertheless, the economics for most conifer tree improvement programmes has been shown to be positive for a wide range of species. Similar results for broadleaf improvement programmes have not been established, as few evaluations have been completed. For example, Palmer et al. (1998) showed that broadleaf improvement in Britain was resulting in significant improvements, but concluded that only simple mass selection and simple recurrent selection methods could be justified. Simple mass selection yielded the highest net returns. In particular, they found that clonal techniques were difficult to justify for broadleaves, despite the higher genetic gains that can be achieved. Because of the lack of information on inheritance patterns for commercially important traits and their generally longer rotation lengths, it has been argued that appropriate silvicultural practices may provide a greater improvement in broadleaved species in a shorter period of time than classical conifer breeding techniques (Hubert and Lee, 2005).

It is also important to follow the sequence from species, to provenance, to plus-tree, to families, to clone in order to capture the greatest amount of improvement possible. Selecting what appear to be good phenotypes, regardless of parentage or provenance, will not provide maximal results from the improvement process.

In addition to selection, testing and breeding, methods for the large-scale propagation of the resulting material are important. If improved material is developed, but there is no way to produce sufficient quantities for commercial use, then the improvement work may have been wasted. Seed stands, seed orchards and vegetative propagation are critical steps which need to be considered in the production of improved material, which will be discussed in more detail below.

Species trials

Because of the limited number of native forest tree species in this country exotic species, particularly the early introductions,, played an important commercial role. Sycamore (*Acer pseudoplatanus* L.) and beech were among the first species to be introduced, although exactly when this happened is uncertain. Augustine Henry's submission to the 1908 Departmental Committee Report on Irish Forestry, made the case for considering introduced species to help re-establish forests in Ireland. A.C. Forbes, when establishing the trial/demonstration plots at Avondale, aimed to "….rightly or wrongly turn it (Avondale) into a forest experimental station along the lines of a continental forest garden…", "…as a demonstration and experimental area, which might prove of service not only for educational and training purposes, but as one which tree planters throughout Ireland could inspect at any time." In addition, species that survived and prospered in private gardens and arboreta, might also become potential forest species. The first Sitka spruce planted in Ireland was on the Curraghmore Estate in Co. Waterford in the early 1830s. Because this planting showed great promise, the first trial plantations were established in the 1870s and 1880s and by the 1920s it was already beginning to become an important commercial species in Ireland.

The Research Branch of the Forest and Wildlife Service established a series of species trials between 1958 and 1965 across a range of site types. However, the main conclusion from these trials was that Sitka spruce and lodgepole pine were the best suited and most adapted introduced species for the majority of site types available for afforestation in Ireland.

Provenance testing

Once a potential species has been identified, the question then becomes which are the most suitable sources of seed (provenances) to grow under Irish climatic conditions? Provenance testing is the initial phase of most tree improvement programmes. Seed is collected from known locations throughout the natural range of the species and tested in the new location on a variety of sites where it could be commercially planted. By their very nature, provenance trials tend to involve an extensive seed collection programme, followed by production of the plants, their establishment in scientifically designed field trials and their maintenance and assessment after a suitable period of time. For most species one quarter to one third of the rotation length of the species is required to provide meaningful performance results. For relatively fast growing coniferous species such as Sitka spruce, this means between 10 and 15 years, whereas for broadleaved species, this can require 17 to 33 years for species with a 70- to 100-year rotation length.

Most of the provenance trials of non-native conifers in Ireland were organised through the International Union of Forest Research Organisations (IUFRO). While this organisation does not fund provenance trial work, it facilitates international collaboration in the collection and distribution of reproductive material as well as the exchange of results. Without such an organisation, it is doubtful whether most of the large international provenance trials would have been possible. IUFRO provenance trials have been established in this country for a number of important species including Sitka spruce, lodgepole pine, Douglas fir, Norway spruce, grand fir, noble fir, Japanese larch, Japanese cedar (*Cryptomeria japonica* (L.f.) D. Don), Monterey pine (*Pinus radiata* D. Don), Bishop pine (*Pinus muricata* D. Don), Pacific silver fir (*A. amabilis* Douglas ex J. Forbes) and oak (*Quercus* spp.). In addition, several EU funded programmes have also allowed the exchange of material for provenance testing, particularly of broadleaved species.

Results from provenance trials identify the most suitable seed sources for this country and provided the basis of the "recommended seed sources" for the Forest Service grant aided planting programme (Pfeifer and Thompson 1994). However, it is perhaps also just as important to know which seed sources are unsuitable, so that they can be avoided.

In addition to international trials, in cases where native species are to be re-established, it may be worthwhile to try to identify the most suitable native seed sources. Specifically, in Ireland this has led to trials of Irish ash, oak and birch. In most cases, this material was also compared with international sources as controls.

Plus-tree selection and testing

In order to breed superior trees, it is necessary to have known superior parents in the breeding programme. This involves the selection of phenotypically superior individuals, which are known as plus-trees. An example of some of the traits used to select a phenotypically superior broadleaf are described in Figure 2. Because the appearance of an individual, or its phenotype, is the result of the interaction of the genes in the individual and the environment in which it is growing, it is necessary to ascertain that the superior phenotype is due to genetic rather than environmental factors. This is accomplished by collecting seed from the plus-tree, growing seedlings and planting them on a range of environmentally different sites, where they would be expected to be grown. These are known as progeny tests because the offspring or the progeny are being tested, rather than the plus-tree itself directly. After a suitable period of time (again about a quarter to one third of the species rotation length), individuals that are superior due to genetic rather than environmental factors can be identified based on the performance of their progeny across a range of different growing environments.

It is essential to reselect only the best plus-trees for a breeding programme, which typically means that only the top 10 to 15% of the selected plus-trees progress; the rest are usually discarded. As a result, a population of 200 or more plus-trees is necessary to provide a minimal breeding population of more than 20 selected plus-trees. Therefore, it is essential to select a sufficient number of plus-trees to begin a tree improvement programme. Relaxing the selection intensity at this early stage can only result in a lowering of the final level of genetic improvement achieved from the breeding programme.

Seed orchards may be established with phenotypically selected individuals but the

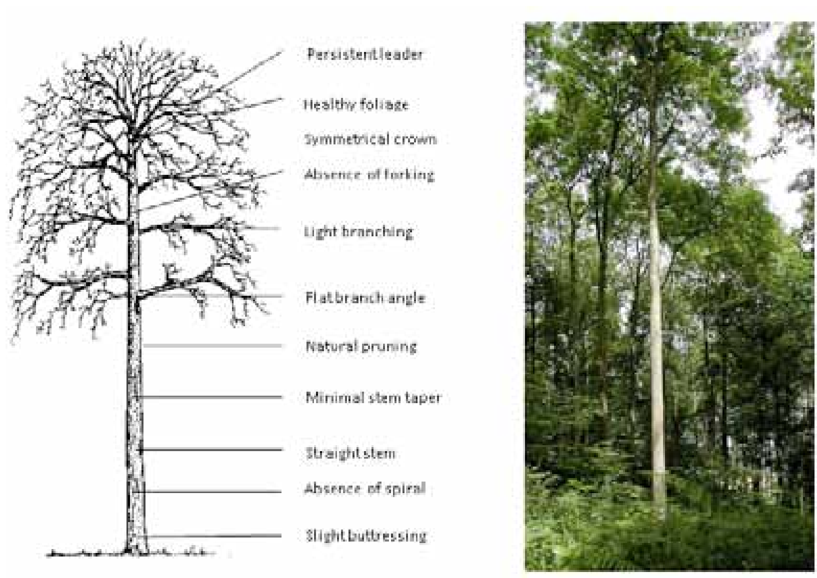

Figure 2: *Possible selection characteristics of a broadleaf plus-tree. Diagram from Future Trees Trust and photograph courtesy of Jo Clark.*

performance of the offspring is not evaluated, resulting in an untested seed orchard. Therefore, the improvement in productivity and quality achieved over seed collected from wild stands cannot be calculated. However, progeny testing the phenotypically selected individuals and the use of only the best in the seed orchard, results in a tested seed orchard which produces seed of a higher productivity and quality. Testing of material takes time, is costly and is usually only undertaken with already commercially important species.

Specific crosses and selection of superior individuals

Just as there are genetically superior parents, there are also certain specific combinations of genes that result in above average progeny. While these good crosses may occur randomly in seed orchards, they are usually lost when mixed with results of many other good, but variable, crosses. Results of crosses between two specific parents are known as full-sibling crosses because the offspring have both parents in common. The resulting individuals will be approximately equal to the average of the performance of their parents. The planting of this type of material is called family forestry or full-sib forestry because all the individuals in the plantation have the same two parents in common.

When two selected parents are crossed, the resulting offspring are not all genetically identical. As a result, some individuals are better than others within a cross and by selecting the best individual or a small number of individuals from a particular cross, further genetic improvement can be captured. These selected individuals can be propagated as clones because they exist as a single selected individual, which can then be reproduced using methods known as vegetative propagation (grafting, layering, rooting of cuttings or tissue culture).

Only for the most important species should selected crosses or clones be considered because of the time and costs involved. Nevertheless, the use of selected and tested clones can significantly increase the quality and productivity of the planting stock.

Propagation methods

Seed stands

Seed stands are a simple way to provide material from the most suitable seed sources. Once a suitable source of seed has been identified, the next step is to produce enough seed of this source for commercial use. Seed stands can either be specifically established new stands or they can be selected from existing stands of the most suitable sources. They are selected based on a set of criteria that include provenance, location, volume production, stand quality, health, size and age. Such stands are managed mainly for seed production and collection, with timber production a secondary objective (Fennessy 1994).

Since Ireland joined the EU in 1967, many stands have been registered under the National Catalogue of Seed Stands. However in most cases, when those stands reached maturity, they were clear-felled and replaced with new stands. This process continues and at the end of 2011, 344 stands covering 21 species, with a total area of 4,290 ha, are currently classified as seed stands (Table 1).

Seed orchards

Seed orchards, as discussed earlier, are plantations of selected superior (untested or tested) individuals, which are brought together to breed and produce seed, which combines the best selected traits of the parents. Seed orchards are expensive to establish, require more than normal maintenance, have a limited lifespan and are not easy to improve the genetic quality of the seed they produce once they have been established. In spite of this, for many species around the world, seed orchards provide the major source of improved seed.

Seed processing

While good sources of seed are required, it is also necessary to have facilities to extract, clean and store the seed. In the 1930s, a simple kiln was built at Avondale Co. Wicklow, for the extraction of seed from harvested cones. This facility was later updated, however, in latter years it was deemed more efficient to have all seed processed in the UK. In the 1980s, Ireland was the only country in the EU without its own forest tree seed processing facility. However, the rapid expansion of forestry in the early 1990s highlighted the need to have a national facility which led to the establishment of the National Seed Centre at Ballintemple Nursery in Co. Carlow. This modern seed processing facility was funded in part by the Forest Service. The objective was to meet Ireland’s needs regarding the provision of a continuous supply of the most suitable sources of reproductive material.

Table 1: *Total area of seed stands by species, correct as of 31st December 2011.*

	Number of stands	Area (ha)
Broadleaves		
Sessile oak	44	1381.3
Pedunculate oak	44	780.0
Ash	8	155.8
Alder	11	113.3
Beech	18	80.3
Birch	6	26.0
Sweet chestnut	3	8.6
Sycamore	4	7.0
Conifers		
Sitka spruce	74	610.9
Norway spruce	35	347.3
Douglas fir	19	203.6
Scots pine	19	158.2
Lodgepole pine	15	138.1
Japanese larch	16	68.7
Corsican pine	2	63.1
Yew	3	33.1
Monterey pine	9	21.7
European larch	4	19.7
Western red cedar	5	14.9
Lawson's cypress	1	3.3
Hybrid larch	1	2.9
Mixed species stands	3	52.8

Vegetative propagation

Among the several methods of vegetative propagation that are available for forest trees, only two have the potential for large-scale application: (i) rooted cuttings and (ii) a type of tissue culture propagation known as somatic embryogenesis. Both allow for the large-scale multiplication of selected individuals, but because both methods require significant amounts of handling, the costs associated with producing material is higher than that of seedling material. However, the higher per plant costs can be more than offset by the increased productivity of this highly selected material (Philips and Thompson 2010).

Somatic embryogenesis is a method of vegetative propagation, whereby a single selected individual is multiplied under laboratory conditions to produce a theoretically unlimited number of copies of the original individual. Material from full-sib crosses of tested parents are used to produce an embryogenic cell line, which is then used to produce a number of stock plants. These stock plants are planted as hedges, which produce cuttings (up to 50 cuttings per year for 5 to 7 years) that are rooted and the resulting plants are used to establish new plantations of improved material. In this way, the high cost of the somatic embryo stock plant is spread over several hundred rooted cuttings over time, thus greatly reducing unit costs.

Tree improvement programmes in Ireland - conifers

Lodgepole pine

State forestry commenced operations in 1904 but by the mid 1950s, a number of issues in relation to the performance of some species had arisen. Lodgepole pine had proved to be inconsistent in its performance due to variations in the genetic quality of the seed. As knowledge on suitable seed sources for Ireland was non-existent at the time, seed was procured on a tender basis, with the cheapest usually being purchased. As a result significant quantities of unsuitable origins were imported (e.g. Lulu Island), which subsequently formed poor and underperforming crops.

Provenance trials, however, were established in 1965, 1966, 1967, each consisting of a limited number of provenances. In 1972 the establishment of the IUFRO lodgepole pine provenance trial testing a total of 58 seed sources from Alaska to California, provided definitive information on the most suitable seed sources for Irish conditions. The dilemma with lodgepole pine was whether to select fast growing, unstable and poor stem form from south coastal sources (Washington and Oregon), or to select a slower growing, stable and better stem form from north coastal sources (British Columbia, Canada). Ultimately, the better vigour of south coastal sources was favoured over the superior stem form and stability of the North coastal sources. For a detailed summary of the results of provenance trials of lodgepole pine in Ireland, see Thompson et al. 2003.

Plus-tree selection of lodgepole began in 1961, with 332 plus-trees being selected in total. Most of these were progeny tested and a total of 171 were re-selected based on their performance in these trials. They were then included in four seed orchards.

Unfortunately, due to continuing problems with poor stem form and instability, the planting of lodgepole pine declined rapidly from peaks in the 1960s and 1970s to very low levels in the 1980s. As a result, the seed orchards were left unmanaged for so long that they now no longer produce any significant seed crops. However, with increased harvesting of lodgepole pine stands in the west in recent years, the demand for lodgepole pine seed has increased, but obtaining suitable seed has become very difficult. Work to regenerate these orchards has now commenced with the recent re-grafting of material from the former lodgepole pine seed orchards. This is also a way to conserve as many of the earlier selected parents as possible.

A novel way to combine the fast growth of the South coastal material with the good stem form and stability of the North coastal sources was to hybridize these two sources in what are known as interprovenance hybrids (Thompson et al. 2003). Some of these hybrids do in fact combine the rapid growth of the South coastal material, with the improved stem form and stability of the North coastal sources. In the UK, seed orchards designed to produce this material were established, but at about the same time demand for lodgepole pine also declined in the UK and these orchards were also allowed to go unmanaged, so they no longer produce seed crops either. However, scion material was obtained from Forest Research in Scotland and has been grafted to establish a new series of interprovenance hybrid seed orchards in this country, but it will take a number of years before this material will be available in commercial amounts.

Sitka spruce

With the decline of the lodgepole pine planting programme, demand switched to Sitka spruce and in the early 1970s an improvement programme commenced. The first Sitka spruce provenance trial was planted in 1960 with a limited number of provenances. Nevertheless, early results suggested that the more southern sources (Washington and Oregon) were more suitable than from northerly sources (Queen Charlotte Islands). This was confirmed by the results of the IUFRO Sitka spruce provenance trial series planted in 1975. The results of the provenance work on Sitka spruce is discussed in Thompson et al. 2005.

The original objective of the Sitka Spruce Improvement Programme was to select and test 1,000 superior trees (plus-trees) with the objective of identifying approximately 100 selected individuals, which would form the basis of a Sitka Spruce breeding programme. Only about 750 plus-trees were selected for a variety of reasons, and the progeny of about 550 of these plus-trees were tested. Selecting parents that would provide a 15% or more increase in height growth relative to unimproved material, combined with a similar improvement in stem form, resulted in the re-selection of 86 plus-trees (16% of the original 550 parents). Then wood quality was considered; parent trees were maintained in the programme only if the result showed no significant loss in wood density, which resulted in the selection of a total of 40 plus-trees from the original 550 plus-trees (7%). This formed the first stage of the selection and breeding programme.

Sitka spruce is not a regular seed producer under Irish climatic conditions, so seed orchards were not considered to be a feasible production strategy. As a result, alternative plant production methods were explored. Fortunately, branch cuttings from young Sitka spruce plants root well, so a vegetative propagation programme was initiated. In this way, small amounts of seed (or plants produced by somatic embryogenesis) resulting from superior crosses can be used to grow stock plants, which produce cuttings for rooting which are eventually planted in the field. This is carried out commercially at the Coillte nursery at Clone near Aughrim in Co. Wicklow. This facility produces a "bulk mix" of material representing a very diverse range of genetic material.

The objective of the current breeding programme is to identify the best full-sib crosses and to use this material to generate stock plants for the vegetative propagation programme. The first full-sib progeny trials have been established and the first results are now becoming available. Preliminary results demonstrate that further improvements are possible by planting the best full-sib crosses. In addition, trials have also been established to determine the level of further improvement possible from selecting the best individuals within the best full-sib crosses.

Monterey pine

A third conifer species, Monterey pine, gained some prominence in the late 1970s and was the subject of an improvement programme starting in 1979. This species has shown promise in plantations, but it tended to suffer from what is known as the "yellows," which is a fungal needle disease. This disease caused the loss of all but the current year needles, thus reducing the photosynthetic area and consequently productivity. Individuals can be selected with resistance to this disease and the improvement programme was designed to select fast growing healthy individuals, which did not suffer from the yellows problem.

In total, 456 plus-trees were selected and several progeny and clonal tests were established before the programme was terminated in 1985. A provenance trail with mainland and island populations showed that material from Guadalupe showed good resistance to the "yellows" under Irish conditions.

Other coniferous species

Over the years there has always been a high level of cooperation between Irish and British scientists working in the area of tree improvement. Material selected by the Tree Improvement Branch of the British Forestry Commission was made available to Ireland in the 1980s. This included tested Scots pine and a hybrid larch clones which were used to establish seed orchards. The hybrid larch orchard has never been very productive, but the Scots pine orchard continues to be very productive, even after 30 years. In addition, a seed orchard based on selected individuals from a high quality Irish Scots pine stand at Killballyboy in Clogheen forest is also currently in production. Currently, all Scots pine planted in Ireland originates from these two seed orchards.

Provenance testing work with noble fir was originally designed to select material for timber production, but later it was expanded to include the identification of seed sources suitable for Christmas tree production. In 1996, a particularly good cone crop in Irish stands of noble fir was exploited to provide material for the establishment of a provenance trial, funded by COFORD. Several imported seed sources were also included in this trial. Differences were found between provenances in survival rates, height growth, stem form, leader status, crown symmetry, crown density, foliage colour and several other traits important in the production of quality Christmas trees (Thompson 2005). In 2004, seed was obtained from what are considered some of the best Danish seed sources of noble fir seed. The seed was used to establish a provenance trial in Ireland. The results of the assessments carried out after five years in the field are currently being evaluated.

For most of the conifer species, with the exception of Sitka spruce and lodgepole pine, work beyond the identification of the most suitable seed sources has not been considered necessary. The low number of seedlings of these species currently being planted makes the long-term investment in further breeding work (e.g. the selection of superior parents and individuals) uneconomic for these species. In addition, for some species tree improvement programmes in other parts of the world may have already developed improved material based on the provenances best suited to Irish conditions. Douglas fir from ongoing breeding programmes in Oregon and Washington and hybrid larch breeding programmes in Europe are examples of this kind of material. It is more cost-effective to purchase material from these programmes, rather than duplicating these efforts.

Tree improvement programmes in Ireland - broadleaves

Work with broadleaf improvement began with the establishment of the Avondale plots in the early 1900s. Improvement work by the Nursery Section of the Forestry Division in the 1950s began with beech and was later extended to silver and downy birch (*Betula pendula* Roth and *B. pubescens* Ehrh.), ash (*Fraxinus excelsior* L.), sycamore and aspen (*Populus tremula* L.). Initially Research Branch work was undertaken with poplar clones and red oak (*Quercus borealis* Michx.), as well as continuing work on *Eucalyptus* spp. that had begun in the 1930s (Mooney 1960). Improvement work was later extended to southern beech (*Nothofagus* spp.).

Interest in oak improvement was stimulated by a good acorn crop in 1987. Work was undertaken to test different native Irish oak stands (Felton et al. 2006, Felton and Thompson 2008). At about the same time, an IUFRO provenance collection of oak including material from Ireland, the UK, France, the Netherlands and Germany was established in Clonegal Forest in Co. Wexford (Lally and Thompson 2000). Subsequently, trials were established to test further sources of oak, as well as ash and cherry.

In 1991, Coillte participated in an EU funded project under the ÉCLAIR programme to collect and propagate valuable broadleaf material. This programme allowed for the selection and propagation of phenotypically selected oak, ash, sycamore and cherry in the Coillte estate, along with an exchange of material with other partner countries. The work continued after the project ended in 1994 with funding from the Forest Service. In total about 100 selected individuals of oak, ash and sycamore and about 50 of cherry, were selected and used to establish a series of gene banks (Figure 3).

As a result of these selections, a number of untested clonal seed orchards were established in a former nursery site near Ballyhea, Co. Cork (Figure 4). To date, an area of approximately 20 ha is dedicated to a National Broadleaf Seed Orchard. This dedicated orchard area now includes an untested ash clonal orchard, planted in 2003 and based on material selected under the ÉCLAIR Programme, as well as a further similarly untested ash clonal seed orchard of 3.5 ha that was established in 2006. In 2003, a small (0.5 ha) untested sycamore clonal seed orchard was established at the site, also using material selected under the ÉCLAIR programme.

In 1995 and 1997, Coillte participated in a project to establish a set of provenance trials with beech across Europe. In total 21 trials were established consisting of 34 provenances collected from the UK and Ireland in the west, to Romania in the east, Sweden in the north and as far as Italy in the south. This trial will provide information on the best Irish or UK beech seed sources for use in Ireland, as well as information

Figure 3: *An ash clone bank at Kilmacurra, Co. Wicklow.*

Figure 4: *A broadleaf seed orchard at Rathluirc, Co. Cork.*

on unsuitable seed sources that should be avoided during years in which there is insufficient seed available from Irish or UK stands (Thompson 2007).

In 2001, an EU project (RAP; Realising Ash's Potential) provided funding for the collection and exchange of material to establish a series of ash provenance trials at European level. Coillte established one trial of this material consisting of 48 seed sources from Britain and Ireland in the west to Poland in the east and Italy to the south. A detailed assessment was carried out in 2011 (after six years growth), but this is only a preliminary assessment of performance. More meaningful results are expected to emerge after about 15 to 20 years.

Teagasc commenced work on birch in 2004, with a pilot study for the improvement of Irish birch funded by COFORD (O'Dowd 2004). An outcome of this programme was the development of a small (0.5 ha.) untested seedling seed orchard in Rathluirc and an indoor seed orchard in the Teagasc Research Station at Kinsealy. In 2009/10 the first commercial quantity of improved birch seed became available from this indoor seed orchard and was sown in 2011. This seed will produce the first commercial crop of plants from the programme in autumn 2012.

In 2004 a small untested alder seedling seed orchard composed of selected Irish material and 0.5 ha in extent was establish in Rathluirc and this orchard was thinned in 2011 (Figure 5).

More recently interest in *Eucalyptus* has redeveloped due to the species rapid growth rates and its ability to provide both fibre and fuel for biomass projects (Nielan and Thompson 2008). Work at present is mainly aimed at the identification of the most suitable species for use under Irish conditions and where they can be successfully grown.

Figure 5: *An alder seed stand at Rathluirc following a first thinning.*

Future Trees Trust
As the broadleaf element of our afforestation programme expands, the need to improve quality becomes paramount. Over the past 21 years, a similar move has taken place in Britain with the establishment of the British Hardwoods Improvement Programme (BHIP) to improve the quality and productivity of broadleaved woodlands. Since 1998, BHIP fully incorporated Ireland into its activities as the British and Irish Hardwoods Improvement Programme (BIHIP), now known as the Future Trees Trust. This programme is a voluntary association of landowners, research workers and professional foresters, who have an interest and determination to improve the quality and productivity of seven broadleaf species with the potential to produce valuable commercial timber crops, namely oak, ash, birch, cherry, sweet chestnut, sycamore and walnut. Separate sub-programmes are in progress for each of the seven species and these are expected to increase the proportion of timber volume recoverable through practical selection and breeding programmes. This includes an oak seedling seed orchard of approximately 2.5 ha, which was established in 2003 in Rathluirc and is one of a series of eight such orchards established throughout the UK and Ireland and coordinated by Future Trees Trust.

Current developments in tree improvement
In 2007, COFORD assembled a small group of experts to prepare a strategy for managing Ireland's forest genetic resources (Cahalane et al. 2007). This report provided a series of recommendations which include:

- adoption of the proposed strategy as the basis for a national programme;
- the establishment of a National Forest Genetics Advisory Group to manage this resource; and
- the establishment of a prioritised long-term funded research and development programme for forest genetic resources.

In late 2010, a number of calls for proposals were launched by the Department of Agriculture, Fisheries and Food under the COFORD programme, which included work on Forest Genetic Resources. This call was directly based on the list of research priorities presented in the 2007 strategy. A new four-year programme, "ForGen" was awarded to a team co-ordinated by UCD Forestry of the School of Agriculture and Food Science in late 2011, which also includes the UCD School of Biology and Environmental Science, the Botanic Gardens, and Teagasc, with Coillte as a subcontractor to UCD. The programme will include work on the following subjects:

- Broadleaves
  - Setting priorities for species improvement programmes;
  - Completing provenance work;
  - Development of improved material.
- Sitka spruce
  - Continued development of the breeding programme;
  - Developing improved material for mass production;
  - Developing clonal varieties;

Demonstrating the potential of family block (full-sib) plantings;
Commencement of the second and further generation improvement programmes.

- Vegetative Propagation
  Further development of micropropagation systems.
- Developing Breeding Tools
  Improving flower induction techniques;
  Improving cryogenic storage systems;
  Developing early selection and testing methods;
  Improving methods to predict seed crops;
  Consideration of the effect of climate change on forest genetic resources;
  Prioritisation of species in breeding programmes though a cost-benefit analysis.
- Developing a National Gene Conservation Strategy
  Conduct a critical review of existing forest genetic resources;
  Prioritise species for conservation;
  Identify infrastructural gaps;
  Provide recommendations on how this strategy could be implemented.

The ForGen programme is a welcome stimulus to tree improvement efforts in this country. However, it is uncertain as to what will happen to the area after the project ends in 2015.

Conclusions

Significant progress has been made in the genetic improvement of many of the species used in Irish forestry over the last 50 years. Information from provenance trials has been used as the basis of seed source recommendations and tree breeding work has produced genetically improved planting stock for certain species. However, it is essential that the valuable genetic material from this effort be protected, especially during these current difficult economic times. Considerable resources have gone into the development of this material and it would be costly to have to duplicate these efforts again. An example of this is evident from experience in the lodgepole pine improvement programme, which was discontinued in the 1980s. While some valuable material was lost, enough survived to provide the basis for a series of new seed orchards.

It is relatively simple to identify phenotypically selected plus-trees, but this is only the start of any improvement work. It needs to be appreciated that a considerable amount of time and money must be invested to achieve significant genetic improvements in a species. Without progeny testing of an adequate number of individuals from which to select the best parent trees (discarding 80 to 90% of selections), the level of improvement will be very limited. Progeny testing requires an investment of both time and money, particularly for broadleaved species.

As has been suggested by Hubert and Lee (2005), applying the conifer tree improvement model of plus-tree selection, progeny testing followed by the establishment of grafted seed orchards, while successful with commercially important conifer species, may not be as successful with broadleaf species. With broadleaf species, conventional silvicultural practices can have just as much effect on quality as breeding, but without the investment in time and money required in a tree breeding programme. Therefore, before a tree improvement programme is undertaken, a realistic review of the time, resources and level of commitment is required.

A long-term commitment to a national tree improvement programme needs to be made as highlighted by Savill et al. (2005). Tree improvement programmes, especially those for broadleaves, have suffered from inadequate and sporadic investment. There has been a lack of target setting, long term commitment and sometimes use of inappropriate methodologies. Most funding opportunities for tree improvement programmes depend on short (three- to five-year) funding periods, during which it is very difficult to make any significant progress unless work is already underway. Even so, frequently work on a particular species ends, or at least becomes dormant, when funding ends. To overcome this dilemma, some countries have established successful cooperative tree improvement programmes. Unfortunately in Ireland, the number of potential members would be quite small. Nevertheless, if tree improvement work is to continue and make significant progress, some form of stable long-term funding commitment is needed which is best provided at national level. This would include the maintenance of facilities, genetic collections, the ability to establish, maintain and assess field trials (as well as the presence of trained personnel to carry out this work) are all essential for such work to continue. Unless this is recognised, together with an acknowledgement of the importance of the protection of the forest genetic resource, as presented in the 2007 COFORD forest genetic resources strategy, considerable investment in time, effort and resources will have been wasted, with potentially serious consequences for forestry in Ireland.

Practical considerations

The following is a list of actions that need to be undertaken to ensure that tree improvement work continues in this country:

1. The proposed national strategy for forest genetic resources (Cahalane et al. 2007) needs to be adopted, including the establishment of a National Forest Genetic Resources Advisory Group.
2. A national long-term commitment to tree improvement requirements is needed to maintain the infrastructure and provide trained personnel to carry out this work.
3. A programme to promote the use of the most suitable genetic material needs to be developed and implemented.
4. A programme of prioritisation of species for tree improvement (which will be developed in the COFORD funded *ForGen* project) needs to be implemented.
5. The influence of climate change on species and provenance selection (which will be explored under the *ForGen* project) needs to be implemented.

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