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Role of genetics in tree improvement

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Abstract
If global warming materializes as projected, natural or artificial regeneration of forests with local seed sources will become increasingly difficult. However, global warming is far from a certainty and predictions of its magnitude and timing vary at least two fold, In the face of such uncertainty, reforestation strategies should emphasize conservation, diversification, and broader deployment of species, seed sources, and families. Planting programs may have to deploy non-local seed sources, imported from further south or from lower elevations, which necessitates a system for conserving native gene pools. Planting a diverse array of species or seed sources is a hedge against the uncertainty inherent in current projections of warming. Most tree improvement programs already stress genetic diversity and deployment of multi-progeny mixes, but may better prepare for climate change by testing selections in an even wider set of environments than is now the case. Gene conservation has three facets: (1) the maintenance of diversity in production plantations to buffer against vulnerability to pests and climatic extremes; (2) the preservation of genes for their future value in breeding; (3) the protection of species to promote ecosystem stability. In practice, economic forces tend to favour genetic monocultures to maximize short term gain. Genes are the raw material from which new strains will be constructed, but only if they are preserved. Tree improvement programs generally promote diversity in seedling plantations to a degree, perhaps, not attained even in natural stands. In high intensity programs, selections from scattered stands are brought together in seed orchards. The progeny, produced by cross pollination, have gene combinations that could never have occurred in nature, where their parents were widely separated. Production plantations established with seed from an orchard of several, say 40, different selections should be in little danger from reduced diversity, especially if the breeding program has been managed to control inbreeding and reduce the chance loss of genetic variability. Even in low intensity tree improvement programs, the genetic base is usually maintained.

Keywords: Diversity, conservation genes, global warming, progeny

Introduction
The primary objective of a breeding program is to increase the frequency of desirable alleles found in the breeding population. While breeders know the traits they wish to improve, they do not know which alleles (genes) favorably impact the traits or their distribution in the native population. Breeding programs must maintain sufficient genetic variation to allow for continued genetic gains over multiple generations. Complicating matters is the fact that traits of interest change over time in response to new pests or changes in markets. Population sizes needed to maintain gains in polygenic traits of current interest are much smaller than population sizes needed to find potentially rare traits that may be desired in the future. This paper considers the impact of breeding population size and structure on the maintenance of genetic variation and on continued genetic gain.
The breeder needs to consider both short- and long-term objectives when structuring a breeding program. Short-term objectives usually include obtaining substantial gains in current traits of interest in the first few generations of breeding while maintaining well-adapted trees. Long-term objectives include the maintenance of low frequency alleles and control of inbreeding. A major conflict arises between short- and long-term objectives. Selection intensity must be high to obtain substantial genetic gains, yet maintaining rare alleles requires keeping a large breeding population in subsequent generations. However, there are ways to structure the breeding population and make selections to reduce this conflict.
Foresters are concerned about gene conservation for three distinct reasons: (1) genetic uniformity increases vulnerability to pests and climatic extremes; (2) genetic variants are important for their potential breeding value sometime in the future; and (3) the loss of diversity by local or global extinction of a species may reduce the stability of entire ecosystems. These concerns give rise to three objectives: promote genetic diversity, preserve and evaluate

variability, and protect endangered species. Each objective demands its own strategy and, in fact, each concern is unique to entirely different types of forest stands, or populations: (1) the natural forest, or resource population, (2) the breeding population, and (3) the commercial, harvestable stand or plantation. The question of vulnerability is not a practical consideration applied to natural forest. Natural forest may prove vulnerable to new pathogens, like American chestnut *(Castanea dentata* (Marsh.), was to the introduced blight *(Endothea parasitica* (Murr.), but geneticists or foresters can do little or nothing if a species does not already have preadapted variants able to resist the new threat. Likewise, the preservation of genetic variants has little meaning in terms of commercial forest plantations. Whether rare variants are included in commercial plantations that are cut and replanted has no practical importance; such plantations are genetic dead ends. Gene conservation strategies in trees will differ from those employed in agricultural crops, or even other wild plants, primarily because of the great longevity of trees. Because trees are long-lived, genes can be stored "on the stump", with no change or loss, for very long periods of time. In annuals, in situ populations must be regenerated every year. However, a long life cycle can also be a disadvantage in commercial plantations because it compounds the problems of crop vulnerability.

Tree Improvement

Tree improvement, or as it is often referred to as genetic improvement, is the process of improving the genetic quality of a tree species. Our forest trees are still genetically close to their wild state in their natural range. However, considerable variation exits in economic traits such as growth rate, stem form and wood quality between different populations within a species, and also between individual trees within populations. Opportunities, therefore, exit to improve the silvicultural value of a species by identifying the best wild seed sources; and also to select individuals within these to develop varieties that are considerably better than the wild material.

Two different methods of improvement are generally used:

- Provenance studies – to identify the best wild populations
- Tree breeding programmes – to select and breed from the best individuals within the best populations.

Provenance Studies

Many of the tree species common to our forests have wide natural ranges which cover many different habitats and climatic zones. Trees have adapted to these conditions and as a result they can have very different characteristics depending on the origin of the seed source. For example, Douglas fir and lodge pole pine have natural ranges that cover large areas of western North America, from moist coastal regions to high altitude dry interior mountain ranges, and from northern to mid-latitudes. They have developed characteristics that allow them to survive and grow in these conditions, and depending on which region the seed is collected from, the performance of these seed sources can be very different when grown in Ireland. To determine the best sources, seed origin or provenance studies, have been carried out by the Forest Service since the early 1960s. These have subsequently been continued by Coillte and Teagasc with funding from Coford.

To date, provenance studies have been carried out on all the main species planted in Irish forests and also many of the minor species. Field trials of each species have been established across a range of sites types and observations on survival, growth rate, stem form, resistance to damaging agents such as insect pests and diseases, frost, etc have been made over many years. This has allowed foresters to identify the best adapted and most productive tree seed sources for Ireland.

Generally, with some exceptions, the best seed sources are those from areas of similar climate and latitude to this country. It is therefore no accident that most of our main non-native species come from the coastal regions of Washington and Oregon in North West America which, like Ireland, are also on the western edge of a continent and experience cool temperate climatic conditions.

Tree Breeding

The wide variation in traits such as growth rate, stem form and wood quality that exists in many of our tree species provide tree breeders with the opportunity to develop improved varieties. These have the potential to produce larger volumes of better quality wood than can be achieved from wild material.

Breeding activity has expanded over the years to include both conifer and broadleaved species. Techniques being used by tree breeders are:

- Plus tree selection
- Controlled crossings
- Progeny testing
- Clonal testing

Plus tree selection

Superior trees (Plus trees) are selected in the best forest stands as breeding stock for the improved varieties. These trees display superior characteristics to the surrounding trees in the stand e.g. straighter stem, larger volume etc. Shoots from these trees are taken and grafted onto seedling rootstock in the nursery. These grafts are clones and are therefore genetically identical to the original plus tree. They are planted out in a clonal archive or clone bank to preserve the genes of the original tree and to be used as breeding material. Plus trees are generally selected on the basis of their appearance (phenotype) in the forest but their breeding value cannot reliably be assessed by the trees outward appearance alone. Their breeding value must therefore be determined by testing their offspring or progeny.

Controlled crossings

Controlled crossings are carried out on flowers produced by the grafts of the original plus trees in the clone banks. Their purpose is to produce seed from selected parents to test their breeding value and/or to combine the best traits of the selected trees for the next generation.

Controlled crossings are carried out in spring when the flowers first emerge. In conifers the male and female flowers are separate and the female flowers are isolated using plastic tubes or pollen proof bags. Pollen is then gathered from the donor tree and injected onto the isolated female flowers when they become receptive. This process requires great attention to detail both in record keeping and observing when the females reach their optimum receptivity and also in collecting and maintaining hundreds of separate seed lots.

The seed from controlled crossings is collected, kept separate by mother tree and sown to produce offspring which are then planted out in progeny tests on typical forest sites.

Progeny testing

In developing improved varieties it is important to test the offspring or progeny of plus trees to determine their breeding value. Only those plus trees that produce superior progeny are used as breeding stock for the next generation. The progeny from a particular plus tree or controlled crossing is known as a family.

The performance of families are determined in progeny tests established on forest sites typical for the species. The families are planted in replicated plots and their growth and development assessed at periodic intervals. It can take many years before reliable information on the performance of the progeny is known – approx 10 for Sitka spruce and many more years for slow growing species such as oak.

The results of progeny tests are used to select the plus trees with the best breeding value. These can be either the original plus trees or superior individuals selected within the progeny test itself. Material (grafts or seed) from these trees is then used create a seed orchards for the production of improved planting stock.

Clonal testing

Within populations (unimproved stands, seed stands or families) individuals are often found with outstanding characteristics which are far superior to the rest. Tree breeders select and vegetatively propagate these individuals to produce superior clonal varieties with the same traits as the parent trees. In developing these varieties it is necessary to test the performance of the clones to ensure that they are indeed superior and will perform consistently over a range of site types. Clonal testing is similar to progeny testing in having the objective of screening the best material for the production of improved planting stock.

Matching tree genetics principles to silvicultural systems

Tree improvement refers to the application of forest genetics principles within a given silvicultural system for the purpose of improving the genetic quality of the forest. Its goal is to improve the genetic value of the population while maintaining genetic diversity. Meeting this goal means that genetic improvement is aimed at the population level, rather than improvement of breeds or inbred lines.

Tree improvement programs provide a known source of seed, seedlings or propagules for forest establishment. Worldwide, tree improvement programs are linked to a range of silvicultural systems but they are most commonly integrated with plantation silviculture (Zobel and Talbert 1984) [6]. As such, each tree improvement program must be designed to fit not only the life history and natural range of the species but also the organization's planting schedule, annual budget and harvest goals. For example, the least intensive tree improvement programs provide a known seed source for a specific period of time. More intensive tree improvement programs typically have enough profit incentive to invest on a full-scale breeding program for generations to come. Today's tree improvement programs vary widely as a result but they do share some components and concepts. To understand this, one must first find the historical roots behind the idea.

Tree improvement, as the application of genetic principles to silvilculture, is considered a 20th century idea but few realize that the concept of planting trees is ancient, harking back as far as the origins of Neolithic agriculture. The first records for planted tree farms date to the Ptolemy kingdom in Egypt circa 3rd century, B.C. Perlin 1989 [3]. Written records exist because Ptolemy's administrators, faced with a dwindling timber supply, wrote orders on papyrus for forest tree species to be planted along the rich flood plains of the Nile Valley. Forest plantings came from seedlings grown in gardens or nurseries. Unlike Fertile Crescent agriculture, this early concept of planted forests languished for centuries as a consequence of timber oversupply. Subsequent civilizations had unending sources of old-growth forests as a result of colonial expansion and native forest discovery until 19th and 20th centuries (Williams 1989 pp. 238-285) [5].

With the rediscovery of Mendel's principles at the start of the 20th century, crop breeders integrated genetic principles into agricultural systems. The tree improvement concept first surfaced in Nordic countries then it was adopted on an industrial scale along with plantation silviculture in the U.S. as expanding uses of southern yellow pine for pulp, paper and later rayon prompted widespread plantation forestry after World War II (Williams 1989 pp. 238-285) [5]. Reliable sources of known seed sources were in short supply. Establishing tree improvement programs became the U.S. timber industry's answer.

Parts of an advanced-generation tree improvement program

Tree improvement rests on the reservoir of genetic variation inherent to a species (Zobel and Talbert 1984) [6]. This means that understanding the patterns of genetic variation is the cornerstone to matching a well-adapted seed source to the right physiographic region. Early tree breeders quantified patterns of genetic variation across the natural range of species using common garden trials. These trials, composed of a common set of provenances or seed sources planted across many different physiographic locations, often showed profound adaptive differences within a species. With knowledge of genetic variation patterns within a species, provenances could now be matched to a region, ensuring well-adapted forests in the future.

How to supply the right seeds or seedlings was the next challenge. Breeders began by selecting the best trees from natural stands or even from existing plantations (Figure 1). Some breeders collected seeds from their selections and other collected branches for grafting. These initial selections or founders were established into seed orchards (and breeding populations) either as seedlings or grafts. As the selections in the seed orchards reached reproductive onset, they supplied a known source of seeds for planting programs.

In many parts of the world, this initial seed orchard was the start and the end of tree improvement programs. As the least-intensive tree improvement programs, they meet the planting needs for many low-cost agroforestry species, species with limited planting demand, species which are poorly adapted to plantation silviculture or programs dedicated solely to gene-conservation.

Recurrent or advanced-generation tree improvement programs continued with additional breeding cycles (Zobel and Talbert 1984) [6]. Here the initial selections were intermated to provide offspring. The offspring were planted into replicated field tests then measured for traits of interest. The value of the parent was assessed on the basis of its offspring's mean trait value. If a parent's offspring were subject to disease or characterized by slow growth or malformation then the parent was removed from the seed orchard.

Selection

Most forest tree species chosen for tree improvement programs have high levels of inherent genetic variation. Observed characteristics for a single tree is defined as the phenotype. An individual phenotype is determined both by its genetic constitution or genotype and its environment as described in the following equation:

P=G+E (Equation1)
where,
P=Phenotype
G=Genotype
E=Environment

This equation provides the rationale behind testing offspring from initial selections even for the least intensive tree improvement program. From Equation 1, one can see how a desirable phenotype (P) could have low genetic value if it grows in a favorable micro-site relative to surrounding trees. Conversely, one might overlook a genetically superior tree because it is growing in an unfavorable micro-site relative to surrounding trees. How to sort the genotypic value from the confounded environmental value? Make the initial selections then collect their seeds and test their offspring. If the offspring are also superior then the parent's genetic value is also high. Testing the offspring is a critical step in any tree improvement program because this is the method for removing genetically inferior parents from the production population.

Breeding

Branch tips or scions from each selection are grafted onto seedling rootstock. Another option is to start with seeds from each selection. In either case, the initial selections are established into a seed orchard. In many programs, controlled-pollinations are made among the select group of parents. Control-pollination starts with isolating female reproductive structures (female flowers for angiosperms and female strobili for conifers and other gymnosperms) with bags. Pollen from the selected paternal parent is injected into the bag. The choice of the paternal parent depends on the type of mating design. At the end of the pollination season, the bag is removed and the seeds mature. The resulting seeds from a controlled-pollination has a pedigree complete with a known mother and a known father. This is the start of the breeding population.

Testing

The breeding cycle within a tree improvement program is a succession of breeding, selection and testing activities in order to upgrade the genetic value of the breeding population. Only the very best of the breeding population are selected for the production population or the trees which provide the seeds, seedlings or propagules for planting. Tree improvement is only one of many silvilcultural tools available for forest management but its benefits are among the most enduring.

Safeguarding genetic diversity

Tree improvement programs improve the genetic value of the population while maintaining genetic diversity (Namkoong *et al*., 1988) [2]. How to maintain genetic diversity given selective breeding is narrowing the population size?

Early generations of recurrent genetic improvement maintained high levels of genetic diversity by keeping large population sizes and by maintaining a high degree of unrelatedness among the selections (Williams *et al*., 1995) [4] 1984. This could change in the future as more intensive breeding programs face a trade-off between enhanced genetic gains and decreased genetic diversity. One solution is to safeguard genetic diversity using grafted archives. Conservation archives protect the original selections, a type of insurance against widespread loss due to pests, pathogens, extreme weather events, climate change and encroaching demands for arable land. Monitoring genetic diversity after large shifts in breeding or production population size becomes important particularly in light of climate change, reductions in wild forest populations and use of fewer genotypes in forest plantations.

The best trees are selected from natural stands or plantations. Breeding or intermating this select group of trees is followed by testing their offspring. The next set of selections are made among the tested offspring (forward selections) although some of the best parents might also be included here (backward selection). This select group of selected trees is the breeding population. The three-step process or breeding cycle is repeated for each successive generation. The goal of recurrent breeding is to raise the average value of the breeding population with respect to a desired trait. Examples of traits include disease resistance, growth, form or wood quality.

The seed orchard serves as the production population. Its purpose is to meet demands for seed, seedlings or propagules. Production populations are upgraded as better selections become available from the breeding population. With completion of a breeding cycle, new selections from breeding population become available for the next production population.

Summary

Tree improvement programs, aimed at genetic improvement at the population level, require large amounts of land, highly skilled labour and annual expenditure on a long timeframe. In the short term, forest managers are rewarded with a reliable supply of seed from a known source. In some cases this is adequate. But with patience, breeders of recurrent tree improvement reap substantial genetic rewards which increase through time. In these programs, molecular domestication places a premium on maintaining genetic diversity because genetic diversity measures the reservoir for future adaptive variation.

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