The role of tree improvement in plant production and quality

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ABSTRACT

The four main objectives of this paper are:

1) to highlight the fact to the nurseryman and grower that there are certain inherent characteristics in each seed lot or clone that are controlled by genes which are foolhardy to ignore or attempt to over-ride by cultural treatments,
2) to show that traits vary genetically at the species, population (provenance), individual and even the clonal level,
3) to illustrate how tree improvement utilises this genetic variation to produce new improved individuals and varieties and
4) to explain how all this affects the work of the nurseryman.

INTRODUCTION

It is a basic tenant of biology that most major characteristics in living organisms are determined, at least in part, by genes inherited from their parents. By selecting parents with desirable traits and crossing them with others having different desired traits it is possible to produce a new combination of these desired traits in the offspring. This is the basis for genetic improvement in plants and animals that man has been doing for the last 8 to 10,000 years. Genetic improvement and specifically breeding of forest trees is a more recent development, starting in the 1920s, which really blossomed in the 1950s.

The question of how can you possibly expect to 'improve' on Mother Nature's handiwork with forest tree species in the lifetime of a tree breeder is a legitimate one. Nevertheless, Nature does not strive for optimisation or efficiency, she strives simply for survival. As a result the productivity of natural forests is only about 1/3 to $^1/_5$ of the theoretical yield that forest tree species should be capable of producing (Table 1).

By selecting individuals with superior traits and crossing them with other individuals with different desired traits, some of the offspring will be as good or even better than the parents. In this way the gap between actual and theoretical productivity can be narrowed. It is also important to recognise the fact that while cultural practices such as fertilisation, respacing, draining and other such practices may improve productivity temporarily, genetic changes result in permanent changes in die individual and all the offspring that it will produce.

For breeding to be effective it is necessary to first have some degree of natural genetic variation in the trait of interest and secondly this variation needs to be indeed genetic and thus heritable. If there is no genetic variation, there is nothing to improve and if there is variation but if it is not passed on to the offspring, breeding will be of little effect.

Any breeding programme has one or a series of objectives that it is attempting to achieve. initially most forest tree breeding programmes were mainly concerned about the 'adaptability' of the material they were producing. This means that the new material would survive and perform well under the new conditions where it is planted. Adaptive traits arc those directly related to survival, growth development and reproduction. These include such factors as seed weight, germination and stratification requirements, phenology (timing of bud break and bud set), photoperiodic (day length) responses, survival, height and diameter growth, stem and crown form, flowering and seed

Table 1. Theoretical versus actual productivity of forests (Farnum et al. 1983).

Theoretical Mean Annual Yield	16 Mg/ha/year
Actual Mean Annual Yield	
Douglas fir natural forest	5.7 Mg/ha/year
Loblolly pine natural forest	3.6 Mg/ha/year

production, resistance to insects and disease and many others. However, most commercial tree improvement programmes are not interested only in material that is well adapted to local climatic conditions, but also in material that produces more wood, with an improved stem form, perhaps with good strength properties (mainly wood density) and perhaps with greater resistance to major diseases and insects. Thus breeding objectives have changed over time.

While genes control most traits in forest trees such as growth rate. stem form, wood properties. date of bud break and bud set. branching habit, stress tolerance and insect and disease susceptibility and/or tolerance, genes do not entirely determine the entire performance of the offspring. A basic genetic tenant is expressed as the equation P = **G x E** or Phenotype = Genotype by Environment. This simply expresses the fact that when you look at an individual, be it a person, a race horse or a tree, you can only see the Phenotype which is the product of the Genetic information in that organism as expressed under the conditions of the Environment in which it is living. The same individual living under a different set of environmental conditions (more stressful or more optimal) might appear very different. So to look at the phenotype of an individual tells you very little about the genetic factors that make an individual they way it is. This problem will be discussed further in later sections.

SOURCES OF VARIATION

So where does all this genetic variation come from and how can it be utilised? Variations in most traits exist at almost all levels starting with the species, progressing to the provenances (material from geographic locations), on to families (offspring of selected individuals) and even to clones (vegetatively propagated selected individuals). In tree species, generally greater genetic variation can usually be found between individuals from the same population than can be found between different populations (provenances). Again, it is important that this variation is due mainly to genetic differences and not due only to environmental effects, hence the reason to test it in a range of different environments.

In order to achieve the largest amount of improvement it is essential to employ an improvement strategy that starts by selecting the species that provides the greatest likelihood of providing the improved material, followed by the use of the most suitable seed origin or provenance of that species, and filially the selection and testing of the individuals believed to have the traits of interest ('plus trees'). To start by randomly selecting individuals (without regard to their origin) that look good and to clone them will not result in the greatest level of genetic improvement achievable, as selection at the species, provenance and family level has been ignored. It is necessary to progress logically from species to clone in order to capture the genetic variation at each step. Tree improvement also takes time, especially if it is to result in valuable improvements in the species of interest. There are no shortcuts in tree improvement.

Sources of variation at the species level

Different species vary greatly in their genetic characteristics. It is also important to consider non-native species, because most species are native only as a result of past climatic conditions or geographic situations and thus may not necessarily be the most suitable species for the conditions. Most exotic species do not suffer from local insects and diseases, which generally makes them more productive than native species. In many eases non-native species occupy an ecological niche not occupied by native species. Some species, by their very nature, arc more adaptable to different conditions than others. For example, Monterey or radiata pine *(Pious radiala),* although not an important commercial timber species in its native locations (California and islands off the Mexican coast) has become an economically important species in Australia, New Zealand, South Africa and Spain. Similarly. other species such as red pine *(Pinus resinosa)* while an important species in their native species range, has not proven to be as successful in other parts of the world.

Species from regions with rather uniform climatic conditions may provide only limited genetic variation in certain adaptive trials. For example, Sitka spruce *(Picea sitchensis)* which has a long narrow coastal natural species range provides a very limited range in the date of bud break (7 to 10 days between provenances) and this provides essentially no protection against late spring frost. Other spruce species, such as Norway spruce (P *abies),* which ranges from high elevation to sea level, and covers a large north to south and cast to west range, can provide large differences in the date of bud break (months), because of the wide range of climatic conditions where it is found.

These genetic differences between species arc due to underlying physiological differences. In a comparison of Sitka spruce, Interior spruce *(Picea glauca x P engelmannii)* and the hybrid between these two species, it was found that the coastal Sitka had a higher gas exchange rate (greater net photosynthesis and stomata) conductance) than Interior spruce, and the hybrid between the two was intermediate between the parents, as would be expected if these traits were indeed under genetic control (Fan et al. 1999).

Sources of variation at the population or provenance level

Once the species has been selected, perhaps one of the largest and roost effective increases in productivity and quality can be achieved by selecting the most suitable seed origin or provenance for the local conditions. For native species the local provenance is not necessarily the best in terms of production and quality, asit is only the material that has consistently survived under local growing conditions in the relatively recent past.

At the provenance, or population level Burley (1965) reported that Sitka spruce provenances from Alaska and California showed little difference between the date of bud break (about two weeks) but showed about a one month difference in the date of bud scale formation. While this is important in the nursery, these factors are regulated by a combination of changing day length and temperature and cannot effectively be altered by cultural practices. In native northern European broadleaf species such as beech, oak and ash, it appears that eastern European origins break bud first while western European sources break bud later, thus providing some protection against late spring frosts which arc common in western Europe.

Ludlow and Jarvis (1971) reported that the slower growing northern seed origins of Sitka spruce (Alaska) showed increased photosynthesis rates and a reduced dark respiration rate compared to faster growing southern origins (Washington). It is likely that in spite of the more efficient photosynthetic rates of the northern material it is the longer growing season that makes the southern material more productive.

Murphy and Pfeifer (1995) found that southern provenances of Sitka spruce had fewer and small diameter branches which would result in fewer and smaller knots thus improving the strength properties of the timber.

Sources of variation at the individual or family level

Because, for the most part. forest tree species have been left undomesticated, they exist as tremendous sources of variation. Therefore superior individuals or 'plus trees' can be selected from either native stands or plantations and serve as the basis of a tree improvement programme. Because these superior individuals arc the result of a specific genetic by environment (0 X E) interaction, as discussed earlier, it is necessary to compare them in a common test environment. This is done by growing their offspring or 'progeny' in a range of different environments, together with a control or standard seed source to determine if they arc indeed superior across a range of site types where it will be grown. Testing takes time (typically $^1/_4$ to $^1/_3$ of the full species rotation length) to identify the superior individuals. It is also necessary to select only the top 10 to 15% of all plus trees tested, in order to achieve the greatest level of genetic improvement. If selection intensities arc not high enough, lower levels of improvement will result. This also means that a significant number of candidate plus trees must be selected and tested in order to have a large enough breeding population to support an improvement programme. Several hundred candidate plus trees arc needed if even a small breeding population of 20 to 50 individuals is to he available.

Proven superior 'plus trees' either serve as parents in the production of improved 'families' (offspring) or can serve as superior individuals for clonal propagation.

At the family level Tan et al. (1995) showed that in black spruce *(Picea banksiana)* a difference in the allocation of photosynthate could be seen between different families grown under stress conditions. The more vigorous families tended to allocate photosynthate to needles, with the less vigorous families allocating more to the roots. Under optimal growing conditions these differences between families were not observed. This again highlights the importance of testing individuals under a range of environments.

Differences in drought tolerance were also seen between families of black spruce (Major and Johnson 1999), as well as differences in photosynthetic characteristics (Major and Johnson 2001). Marshall et al. (2001) found that the taller families of Ponderosa pine *(Pinus ponderosa)* were the first to begin photosynthesis in the spring, and maintained it longer into the autumn than shorter families. They also reported that taller families of western white pine *(Pious monticola)* had higher rates of water use efficiency and lower photosynthetic rates than shorter families on warm, late summer days.

While as discussed above, there is very *limited* genetic variation in the date of bud break in Sitka spruce at the provenance level, it has been possible to identify individuals that may break bud 2 to 4 weeks later than average and yet still achieve above average annual height increments (Thompson, unpublished). Such individuals, if enough could be found, could serve as the basis for developing a late flushing variety for protection against late spring frost damage.

Sources of variation at the clonal level

As discussed in the preceding section there can be very large differences between individuals of the same provenance or even within individuals the same family. This individual variation can be best captured and utilised by clonal propagation where the resulting plants are exact genetic copies of the original. Cannell et al. (1983) reported differences in dry matter distribution between clones of Sitka spruce and lodgepole pine *(Pinus contorta).* Sparsely branched clones in both species were found to allocate the greatest proportion of their dry matter to the main stem. Sheppard and Cannell (1985) reported the identification of 'nutrient use efficient' clones of both Sitka and lodgepole which produced more biomass under conditions of reduced nutrient availability.

Coutts and Nicoll (1990) reported a difference in the mycorrhizal associations formed with different clones of Sitka spruce. Deans et al. (1992) found significant differences in the morphological quality and in the RGP (root growth potential) of different clones of Sitka spruce. Differences in the degree of frost hardiness between clones of Sitka were found by Nicoll et al. (1996) and differences in the susceptibility of Sitka clones to red deer damage was reported by Duncan et al. (2001).

The advantages of clonal material is that it reproduces exactly the genetic traits as the original individual (which might vary slightly under different environmental conditions). Clones will be much more uniform and predictable because of the reduced variation within the crop. Because vegetative propagation does not depend on flowering and seed production it can significantly reduce the time required to produce commercial amounts of improved material. Cloning depends on methods of vegetative propagation, as opposed to sexual propagation, and includes grafting, air-layering, rooting of cuttings and micropropagation (by both organogenesis or somatic embryogenesis). Typically, species vary in their ability to be vegetatively propagated and, in general, younger material is more responsive than older material. This causes problems because of the time needed to test individuals in order to identify the truly superior individuals, which by the time they have proven themselves it may no longer be possible to propagate them vegetatively.

It is also important to highlight the point that vegetative propagation provides no genetic improvement in the material it produces. Only by sexual propagation is there a recombining of selected traits from both parents to produce new individuals that combine the best of both parents. Thus, to be truly effective, material produced by vegetative propagation needs to have a breeding programme behind it to provide new and further improvements.

THE EFFECTIVENESS OF BREEDING

Plant breeding is based on the concept that by selecting good individuals and crossing them the resulting offspring will he as good or perhaps better than the parents. This is shown in the results of crossing different male and female parents in Sitka spruce as shown in Table 2.

It is important to note that in the Coillte Sitka spruce improvement programme only individuals that arc 10% or more taller than the unimproved Washington control seed source will be considered as candidates for the breeding programme. As can be seen from the performance data of the different parents used in these crosses, none of these parents would have been selected for inclusion in the breeding programme. Nevertheless, when certain poor parents are crossed with other poor parents, in some cases even poorer offspring are produced (e.g. parent 125 crossed with parent 61). In other cases some very good offspring resulting from specific unique combinations of genes can result (e.g. parent 2 crossed with parent 140). It can also be seen that certain parents such as parent 56 and 140 produce some very productive offspring in a number of specific crosses.

LIMITS OF TREE IMPROVEMENT

Having said all this, tree improvement cannot provide the solution to all problems. It requires a significant period of time to select, test and then breed new material and as the old saying goes 'time is money'. The level of improvement that is attainable is also important and varies with the species, so the question really becomes one of the 'amount of gain achieved per unit time'. Obviously the greatest gain in the shortest amount of time is the ideal situation.

Typically, it is the fast growing conifers that have received the most attention, mainly because they arc the major commercial species. The time required to test and accurately select superior individuals differs greatly between conifers and broadleaves, due to differences in the rotation lengths (recall the $^{1}/_{4}$ to $^{1}/_{3}$ of the rotation length required for testing). Conifers, with rotation lengths of 40 to 80 years require 20 to 30 years to produce improved material. In `shorter' rotation length broadleaf species such as ash or sycamore 30 to 40 years would be required for a cycle of breeding. In the 'longer' rotation broadleaf species such as oak and beech probably 40 to 50 years or more would be required to produce improved material.

By its very nature improved material will always cost more than unimproved material. This is mainly due to the methods required to produce improved material. and not usually as a result of an attempt to recover some of the R&D costs incurred in developing it. Improved seed is typically produced in managed seed orchards, and costs more to produce than wild collected seed, but of course the improved material provides growth rate, stem form and wood property improvements not available in wild material. Controlled crosses between two specific individuals arc more expensive yet. Vegetatively propagated material produced either by 'maeropropagation (rooted cuttings, grafting, air-layering) or `micropropagation' (axillary of adventitious shoots formation. somatic embryogenesis) all require significant amounts of handling. which increases production costs. Propagation costs can eliminate certain technologies from commercial consideration because propagule costs must be kept as low as possible. However, the level of improvement possible with controlled crosses or vegetative propagation arc greater than those provided by conventional seed orchards.

Fable 2. Performance of controlled crosses in Sitka spruce (height as a percentage above the control seed lot).

	Male Parents	2	56	125
Female Parents		5.7	7.4	8.3
48	5.5	0.3	11.9	0.0
61	6.3	1.2	16.0	-1.4
140	5.5	21.4	18.4	7.4

Second row from top shows open-pollinated performance of male parents and second column from left shows open-pollinated performance of female parents.

Finally, the 'best' improved material will always be in short supply. Multiple propagation system (e.g. micropropagation to produce stock plants that provide cuttings for rooting) may be necessary to produce commercial amounts of improved material as quickly as possible production). The planting of mixtures of improved with unimproved material (which will be removed in Winnings to leave the improved material as the final crop trees) may also need to be considered to maximise the number of hectares planted with limited amounts of improved material.

WHERE IS THE FUTURE DIRECTION FOR TREE IMPROVEMENT?

For tree improvement to continue to provide the type of improvements required by the industry it needs to be in touch with the end users. The change in emphasis from adaptability, to increased production, to wood quality is evidence of this reaction to industrial needs. However, exactly what properties of wood are most important for the future is not clear. There also needs to be a good connection with forest managers and nurserymen who will manage and produce the improved material.

Perhaps more importantly, breeders currently select individuals which phenotypically have the traits they want, with little or no understanding of how these desired traits are produced. For example, increased growth can results from a number of reasons, including early bud break or late bud set, however, this may be at the expense of damage or loss due to late spring or early autumn frosts. Thus a better understanding of the physiological basis for improved traits could play a more critical role in a tree improvement programme in the future and might also help make the identification of superior individuals more efficient than phenotypic selection alone.

WHAT DOES ALL THIS MEAN TO THE NURSERYMAN?

The genetic variation between species, provenances, families and even clones has a large effect on their production in the nursery. Differences in the date of seed maturation, seed stratification requirements, germination rate and length of the growing season vary by species, provenance, family and clone. Differences in the date of bud break, date of bud set, length of the growing season, number of branches and other such morphological differences can easily be seen between different materials in the nursery bed. What may be less apparent, and perhaps more important, is the fact that there are underlying differences in the physiology of different species, provenances, families and clones as well.

This has implications for the production of plant material in the nursery. For example in Sitka spruce plants derived from more northerly sources, such as the Queen Charlotte Islands off the coast of British Columbia, tend to stop shoot elongation and set bud by late August or early September, become dormant by early to mid October, and are ready for lifting by early November. More southerly sources from Washington continue to grow into early October and set bud by early to mid November and become dormant in late November so they are ready for lifting by early to mid December, or about one month later than QCI plants. Thus, if the nurseryman lifts both QCI and Washington Sitka at the same time, even though it is the same species, there will be inherent differences in the hardiness and thus survival potential of the plants even though the may have come from adjacent beds in the nursery and were grown under the same cultural regime.

As a result it is important to understand these inherent genetic differences in different species, provenances, families and clones that cannot be manipulated by cultural practices. It is better to understand these differences and work with them rather than to try and work against them.

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