The Improvement of Forest Trees by Selection and Breeding

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THE first step in establishing a plantation is to select the species which is most suitable for the site and the future requirements of produce. Until recently selection ended at this stage.

Seed of the species decided upon was obtained from wherever it was cheapest or most convenient. Exotic species with very wide geographical and altitudinal ranges were planted on a large scale during the eighteenth and nineteenth centuries, but it was only towards the end of the nineteenth century that the importance of the actual area of origin began to be realised. For example European larch from high altitudes was recommended because of the northern latitude of Scotland where it was to be planted. Later still it was found that trees raised from these areas failed badly due to the late spring frosts, and lowland larch from farther east was found to grow better. Similarly the inland provenances of Douglas fir, the Blue or Colorado Douglas, were clearly inferior to the green or Coastal Douglas fir. It was realised that choice of species alone was insufficient; there must be a choice also of provenance of the species for the conditions where it was to be planted.

Within areas of similar climate there are tree populations which differ in quality and vigour. This is most marked where the trees occur in scattered groups too far apart to interbreed. A noted example is the Polish larch. The choice of provenance must then be narrowed down to the best stands within the chosen climatic or altitudinal zone, and the survey of populations to assess their quality is the first step in tree-breeding. This can be taken a stage further in certain cases, by removing all the inferior trees from the selected areas when the remaining high quality trees interpollinate. They also then have room to develop bigger crowns and carry more flowers, male and female, and so produce more and better seed.

The stage beyond that of selecting and thinning seed-sources is the selection of the finest individual trees, wherever they may be, and breeding from these alone. This requires the special techniques of vegetative propagation and the formation of seed-orchards.

Natural Selection.

The species and individual trees now growing in natural forests are the survivors of very long periods of natural selection. Any tree possessing an heritable difference rendering it capable of producing more offspring than the others will be represented in the succeeding generations by a greater number of offspring, until this favourable character is to be found throughout the population. Conversely an heritable disability to produce offspring is progressively swamped and disappears—in one generation, in the extreme case of sterility. Hence natural populations are composed of individuals inheriting primarily the ability to survive and flower in their environment. The features most important in a timber-tree may have been selected incidentally—a single straight stem is the most efficient way of carrying a crown high among other trees, for example—or they may, in other circumstances, have been selected against. For example, in an open stand, more flowers can be carried early in life on a low, spreading crown with strongly developed branches.

Artificial Selection.

The breeding of many plants and animals has been carried on almost unconsciously since man settled into pastoral ways. Cattle, dogs and horses were bred for different uses and conditions. Food crops have been gradually selected for increased production of the edible parts. The effects of selection are very powerful and even this unplanned selection has changed the food plants until they bear small resemblance to their wild ancestors. The same changes could have been made in very much fewer generations had they been planned. The first requirement is to decide the aim of the breeding programme. In each generation only the plants which are nearest the ideal are used to raise the next generation. Each generation is thus one step nearer the ideal. Carefully planned selection can have rapid and startling results as is shown for example, in Russell lupins, Excelsior foxgloves and Ballard Michaelmas daisies.

The response to selection depends on the amount of variation occurring in the original population and on the intensity of selection. Most forest tree species are very variable and cross-pollinate freely which maintains this variability. Thus selection can be an effective method of producing improved varieties.

Selection may be operating in undesired directions. One example is the way pests subjected to poisonous sprays produce varieties which are resistant to the poison, by the intense selection against susceptible individuals and in favour of any degree of resistance. A more subtle example is provided by the accidental production of Flax Darnel in the Netherlands. Darnel is a weed-grass growing in the flax fields. When the flax is cut for seed the flower-heads of darnel are normally below the level of the flax and unripe. An early individual plant occurred once, however, and at the flax harvesting time, its seeds were ripe and high enough to be cut. The seeds were mixed with the flax seed and were sown with it, and the process was repeated until this new variety of darnel became a regular contaminant of flax over a wide area.

It is evident that if the best individuals of any crop are removed before they have produced as many offspring as those left behind, a selection will operate in favour of the less desirable types. This is what happens in forests which are exploited in a primitive manner and it has degraded the natural forests of large parts of the world. In the course of time the better inherent factors or genes have been lost and such stands can no longer produce trees of good quality. Tree-breeding aims to reverse this process and raise stands possessing only the best factors.

The Objects of Tree-Breeding.

Broadly, the object of tree-breeding is to produce varieties of trees which are the most desirable for both grower and user. Fortunately the qualities required by silviculturists and timber-merchants are largely compatible.

The silviculturist or forester requires rapid germination and growth in the nursery; rapid establishment of a crop of disease-free trees and rapid growth to timber-size. The trees should also have compact crowns with dense foliage and small, nearly horizontal branches which prune easily or fall naturally.

The timber users require a straight, nearly cylindrical stem, free from fluting and spiral grain, and wood of uniform quality and of the necessary density, fibre-dimensions and so on, with few or small knots, perpendicular to the grain.

The two qualities of rate of growth and size of branches can be altered by silvicultural practice, but only within the limits inherent in the population. If the crop is inherently very vigorous, growth can be retarded if necessary by close spacing or delayed thinning but if the population is not inherently vigorous, no silvicultural treatment can make it grow very fast should this be required. Hence selection of the parents should be in favour of maximum vigour. Again, it is difficult to foresee the requirements of the timber-trade sixty years ahead of the date of planting so the safest plan is the production of the maximum possible yield of wood per unit area of land.

Thus the aim is to produce trees of great potential vigour, healthy, with straight, persistent stems which are as nearly cylindrical as possible and possess regular, numerous, small and level branches cleanly set in the stem.

The Selection of Parent Trees.

It will be evident that only those characters which are inherited can be improved by breeding. It is fortunate that the greater number of the important characteristics of trees have been found to be heritable in varying degrees. It would seem simple, therefore, to find trees in the forest which approach the ideal and breed from these. This is the general plan, but there are complications in assessing the trees for use. No characteristics are inherited in the manner of goods—the same entities belonging to successive generations. The most that can be inherited is the ability to show a character given the required environment. For example, although gorse plants are said to inherit spiny leaves, a gorse seedling grown in high humidity will develop trifoliate leaves and not spines. Trees are long-lived and may be conditioned to their environment to a greater degree than other organisms. The tree in the forest is the result of the interaction between the potentials inherited and the effects of the environment. This important concept is expressed in the terms *genotype,* or inherent make up of the tree and the *phenotype,* the actual appearance of the tree modified by its environment. The selection of trees for breeding is dependent on the estimation of the relative importance of genotype and environment in forming the tree. Three methods are used in selecting trees by which this is done. These are:—

(1) For single trees, straightforward assessment of the environmental effects from topography and soil and the condition of other trees and plants in the area.

(2) In plantations the potential plus trees are surrounded by other trees in very nearly the same environment and their relative performance can be seen. If conditions were completely uniform the differences among trees would be solely those due to their genotypes.

(3) On very favourable sites every tree will be almost as good as its genotype is capable of making it i.e. genotype almost equals phenotype. Such sites do in fact produce a great variation among trees of the same species and the outstanding trees can be selected and the rest safely ignored.

Further difficulties arise from trees which would be selected but have some defect which may be due to damage of a random nature i.e. loss of the leader some years previously. This could have been caused by wind, snow, another tree blowing against it or by birds. Sometimes many trees in one area show such damage at similar heights and from the date when it occurred it can be attributed to an ice-storm known to have happened at that time. This kind of defect might occur in any tree, but on the other hand, there may be trees which are more susceptible to it than others and these would not be desirable. The safest course is to discard such trees unless certain desired characteristics are really exceptionally well developed.

Selection of trees in very unfavourable conditions, as for example at high altitudes or severe exposure is a special case. It may be that the best trees selected on favourable sites would produce the best plants for extreme sites too, but this hypothesis needs testing. Meantime trees are selected on such sites and should be used separately because their use may be limited. For example in severe exposure the only trees which can show good stem form and crown-shape are those able to withstand the wind. Any other trees which might on a favourable site, have been of excellent form, will be mis-shapen on the site where it is growing. Plants raised from trees selected on these sites may be the best for growing on such sites but not on others.

The selection of broadleaved trees raises the problem of the lack of persistence of the main stem, which even in the best oak for example is seldom longer than fifty feet. This is so even in plantations, whereas open grown oak frequently fork much lower. Nearly all the value of an oak stem lies in the bottom thirty feet and it might be thought sufficient to select trees which fork at or above this height. But there is no guarantee that progenies of such oak will not fork below thirty feet whereas this is less likely if all the parent trees have grown fifty feet with a single stem. In beech it is possible to select trees with stems persistent through the crown to the top at over 100 feet, although this is rare. Good boles of seventy feet are, however, found less rarely.

Some defects debar a tree from selection completely. These are susceptibility to disease, possession of spiral grain and excessive fluting or bending.

Selection of plus trees along the lines outlined above does, in fact, produce progenies much superior to the normal seed. In Australia, trees raised from normal and selected Loblolly pines have been compared, also those raised by controlled pollination of selected trees as would occur in a seed-orchard. The results, with the trees at 800 to the acre are tabulated below:—

	Good trees/acre	Plus trees/acre
Average seed (normal collection) ...	112	1
Selected parents (open pollination) ...	200	10
Three best selected parents	277	47
Controlled pollination	412	80

Controlled pollination of larches in Britain has shown that at four years of age the progenies are outstanding. At two years assessments showed that vigour is heritable to a small degree and only the most vigorous trees produced progenies significantly more vigorous than normal. Later assessments may well show a greater inheritance of vigour but selection should be very rigorous and only outstanding trees should be selected.

Once sufficient plus trees have been selected to make graphs of the height and girth reached at different ages by this kind of tree, the figures can be used as a basis for selection as far as vigour is concerned. The fastest growing plus trees of larch at various ages lie on curves up to three quality classes above Quality Class I in the Yield Tables.

The Use of Hybrids.

Progress in breeding by selection depends on the natural variation available. One way to increase variation is to cross trees of different species and select among the hybrids. Only species which are closely related will cross, but even so their genotypes are usually very different and the second generation of their hybrids (i.e. F_2 plants raised by crossing the first generation, F_1) will segregate to produce new variants. In other branches of plant-breeding it is possible to work through generations rapidly and great progress is made by this method. In forest trees the time needed for raising and seeding a generation makes it desirable in practice to use the first generation hybrids for planting in the forest. But while these are being raised in quantity, a few of the most desirable are selected and planted together for raising an improved second generation. Selection here must be rigorous, for in raising a second generation from hybrids, there is normally a loss of a phenomenon known as hybrid vigour, or heterosis. Heterosis occurs where plants raised from dissimilar parents are superior for any characteristic to either parent, and is therefore confined to the F_1 cross. Heterosis in some qualities—for example vigour in some western American pines —has been shown to occur only in climates intermediate between those of the parent species. It may have a number of genetic causes but in some cases a simple explanation may be sufficient. For example, natural crosses between Nootka cypress, *Chamaecyparis nootkatensis* and the Monterey Cypress, *Cupressus macrocarpa* arose in Wales in 1888 and 1911. The Nootka cypress inhabits the cool moist regions of western North America and the Monterey Cypress comes from a hotter, drier peninsula in California. The former is of slow growth and the latter is fast. The hybrid, known as Leyland's cypress *x Cupressocyparis leylandii,* on all sites so far used, easily outgrows the Nootka cypress, and on many sites outgrows the Monterey cypress as well. This could be due to inherited ability to grow well in both the cool moist periods in which the Monterey does not do so well, and in hot dry periods, in which the Nootka is slow, so that in our climate with both kinds of weather, the hybrid can grow well at all times.

Species which have a wide natural distribution may consist of a number of geographic races or even subspecies. Crosses between the geographic races are intra-specific but since their parents are of different non-interbreeding populations, these crosses may show hybrid vigour. Crosses between the Blue or Colorado Douglas fir and the Green or coastal Douglas fir; and between the Polish European larch and Western alpine European larch are such intra-specific hybrids and may prove to be of value.

Tree Seed-Orchards.

The seed-orchard is the means of selective breeding and cross-breeding in trees. The selected "plus" parent trees are propagated by grafting and clones of these grafts are planted in balanced mixtures in such a way that the female flowers of a given clone can be pollinated equally by all the other clones in the orchard. The individual grafts of each clone are separated from each other to prevent self-pollination for this inbreeding causes a loss of vigour and the production of many aberrant forms. The minimum number of clones in any one seed-orchard is usually 20, and 30 is better but a few small orchards of 10 clones are made for special purposes. The higher numbers are preferable for large scale forest use, to avoid the harmful effects of inbreeding among progenies from the stands which will be raised from seed-orchard seed, where natural regeneration may be required.

The seed-orchard is planted on a site isolated by distance from other trees of the same or related species to avoid contamination from unselected trees. The minimum distance from a stand of other related trees is a quarter of a mile. Scattered individual trees at half this distance will have a negligible effect. The best areas are those of a good but light soil of high nutrient status, preferably with a southward slope and in a part of the country receiving much sunlight and high June and July temperatures. These factors increase the flowering and hasten the first crops of seed. Air-drainage is of great importance to minimise damage from late frosts.

Seed-orchards intended for the production of inter-specific hybrids are planted with the grafts of the two species alternately in the column and the rows. Thus each graft of one species has four plants of the other species adjacent to it. Conifers are wind-pollinated and it has been found that all but a small fraction of the pollen comes from adjacent trees. The proportion of hybrid seed produced, however, depends also on the relative flowering times at each orchard of the two species and of the clones of those species being used. The parent trees may be growing in any area of Britain or abroad and their times of flowering observed where they are growing does not show their relative times of flowering when all are in one area in an orchard. These can be found only from the seed-orchards themselves or from the collection of grafts, called "tree-banks" which are built up by the breeder. Tree banks are discussed below.

From observations on flowering times in tree banks, of all plus trees, early and late clones may be used to exercise some control over the output of seed and in hybrid larch orchards the outgoing seed can be sorted at picking, if the right trees are used. The Japanese larch sheds pollen two weeks before most European larch but the cones of the European are receptive when the Japanese pollen is shed. Hence by ensuring that the orchard does not contain any unusually early pollinating or late coning European larches, all the cones collected from the European larch clones will contain hybrid larch seed and the cones from the Japanese larch will produce pure Japanese larch seed. To produce pure European larch from a hybrid orchard, late coning European larches could be used with early pollinating Japanese but in practice it is better to have pure European larch orchards separately. Pure Japanese larch orchards will be unnecessary as this seed will be produced by the Japanese larch cones in a hybrid orchard if there are no early pollinating European larch. From these findings it is also apparent that the output of hybrid larch seed is proportional to the number of European larch grafts. Since the Japanese larch cones used have mostly proved copious pollinators, hybrid larch orchards can now be made with only one Japanese larch graft to every four European larch grafts.

The onset of flowering in grafted plants is usually earlier than in trees of seedling origin, especially in pines, spruces and beech. The flowers are first borne within easy reach of the ground making controlled crossing work easy. The trees may be pruned to increase or encourage early flowering—the shapes of the grafts cannot affect the genotype of the seed they produce. If the grafts are allowed to grow tall, climbing for seed-collection is concentrated and special methods may be developed to make cone-collection easier.

The Tree-Bank.

As has been said above, for observation small numbers of grafts of every plus tree selected are put in tree-banks. These are also used to build up supplies of grafting material. Ideally seed-orchards would be made after these observations in tree-banks had been made, but in order to save time and to have seed-orchards from the earliest possible time, so that their management can be learned, the best of the first plus trees found are put straight into seed-orchards. The grafts in the tree-bank ensure that if the parent tree is blown, or felled, or dies, there is still material available from it to make more grafts. It enables scion-collection to be done rapidly from the ground within a few acres, from parent trees which may be scattered all over the country. The grafting material taken from grafts is frequently much superior to that from the parent tree and makes better grafts.

Botanical and cytological work and small scale experimental crosses can also be carried out in tree-banks and to some extent the forms of growth of the parent trees can be compared under the same conditions of soil and climate etc.

General Conclusions.

Although at first sight, the long time-gap between generations might make tree-breeding seem impracticable, there are now techniques which make possible the production of improved cultivars within a few years. Eight years after establishment, the first larch seed-orchard has produced two crops totalling about ten pounds of seed. More recent seed-orchards are getting established more quickly and have been planted at twice the density. The estimated annual production after ten years should be 10 lbs. of seed per acre and at twenty years perhaps 50 lbs. per acre. Thus 20 acres of larch seed-orchard can contribute substantially to national requirements. Seed-orchards are expensive to establish but even if their products give only a one per cent. increase in the crop value, the outlay yields a big return, for it must be noted that one pound of larch seed for example, of normal germination, provides plants for 15 acres of forest. With the improved germination a good seed-orchard should provide and the wider spacing which may be adopted with high quality plants, one pound of seed may plant 30 acres. A small increase in value of timber on 30 acres of land would allow a very great increase in the economic price of a pound of seed needed to plant it.

The establishment of seed-orchards enables the few really outstanding trees growing in any country to be used as the progenitors of all the crops planted, and provides the material for raising a succession of improved cultivars.