The FORESTRY CHRONICLE

Vol. XV.

SEPTEMBER, 1939

No. 3

THE BREEDING OF FOREST TREES¹

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INTRODUCTION

IN CULTIVATED agricultural plants selection and breeding have been practised for many centuries and have resulted in the production of types which are highly superior to the original, wild forms. Forest trees, however, were not concurrently subjected to this process of improvement since to a very great extent forest products were obtained by purely extractive means without recourse to cultural methods.

Uncontrolled commercial exploitation of vast forest areas, a process of extraction without replacement, has created, however, serious problems involving both private and public interests. The depletion of readily accessible stands, with steadily increasing distances from timber supply to mill, has created a pressure on commercial forestry which forces serious consideration of reproductive and cultural practices. The denudation of natural forest areas has created the further problems of soil conservation, flood control, land utilization, wild-life conservation, and others which demand the attention of public agencies.

Forest operators are beginning to realize that they must make provisions for the regeneration of the areas they are cutting over, and in many cases are adopting methods which appear to be both successful and in harmony with the degree of management practicable in their region. But this does not affect the large tracts of cut-over forest which have been so devastated that they can be properly regenerated only by planting or artificial seeding. If private reforestation is not possible on these areas, they should, in the public interest, be reforested and managed as national forests.

Various types of afforestation are also receiving increased attention, both private and public. Only one example, prairie shelterbelts, need be mentioned.

The above should serve to show that the forest problem is one of great importance, that, born of necessity, there is coming into being a new and more intelligent attitude toward this problem as a whole, and that cultural

¹ Paper presented before the Science Association, National Research Council, Ottawa, March 8, 1939.

Contribution from the Division of Biology and Agriculture, National Research Council, Ottawa, Canada.

forestry¹ will play no small part in the practical, and probably far-reaching expression of that attitude.

When the forester adopts cultural methods he acquires, with some limitations, a control over the type of tree to be grown. It follows, since existing types of forest trees leave much to be desired, that cultural forestry should logically embrace efforts to improve upon the wild forms.

The increasing need for improvement in forest-trees, and the belief that this could be accomplished by breeding research, has led the National Research Council of Canada and the Dominion Forest Service to undertake a co-operative program of forest-tree breeding having the following objectives: the development of inherently superior forest-tree types capable of producing high quality products over a wide range of environment and in the shortest possible time, a corresponding improvement of naturally regenerated forests by derived genetical knowledge, and the development of superior, rapid-growing types particularly adapted to shelterbelt and other afforestation purposes.

THE TIME ELEMENT IN FOREST-TREE BREEDING

With the coming of cultural forestry and the need for forest-tree breeding, the forest geneticist is confronted with the problem of dealing with material having relatively long periods between generations. This obstacle has undoubtedly contributed greatly to the tendency to neglect tree breeding, and it is also undoubtedly true that certain recent developments indicating possibilities of removing or substantially reducing this time factor have had a great deal to do with the present increased interest in forest-tree breeding. It was, in fact, the possibility of developing suitable methods of vegetative propagation, which was brought in by recent discoveries in connection with plant hormones, that gave much of the impetus which led to the establishment of the forest-tree breeding program in Canada.

1. Utilization of the First Generation

In dealing with the time factor, introduced by the long period between generations, a logical step lies in the utilization of the first generation hybrid, (F_1).

First let us consider such a procedure from the point of view of theoretical genetics. The characteristics of the F_1 are determined by the dominance and interactions expressed by the genes brought into combination by hybridization of the parents. Depending on these expressions, the F_1 may or may not

1. The term "cultural forestry," for want of a better, is used to denote forestry practices in which new forests are established by planting or by direct seeding. In its broadest sense this term is extended to include regeneration by seed from selected natural trees left standing at time of cutting.

possess the characters in which the breeder is interested. Thus, it might be found that the F_1 possesses the desired characteristics and could to advantage be utilized directly by vegetative or other means; or, the characteristics might be unfavorable, in which case it would be necessary to grow the second or segregating generation (F_2) in order to obtain the desired types.

An outstanding characteristic of the F_1 is the phenomenon known as heterosis or hybrid vigor. This may be expressed in various ways, in plants usually as a greater rate or extent of growth, or both, than is possessed by either parent. Where not conducive to poor quality, hybrid vigor should be a very valuable property in forest trees. There are a number of examples of marked hybrid vigor in forest trees.

(a) *Vegetative Propagation*¹.

In plant material which possesses a degree of inherent capacity to root vegetatively, there is a possibility that plant-hormone treatment and improved horticultural methods may stimulate and promote this natural tendency to the point where vegetative propagation becomes possible on a practical scale. Norway spruce (*Picea excelsa*) and black spruce (*P. mariana*) are examples of species possessing relatively small degrees of inherent rooting capacity, but which may upon the discovery of appropriate treatment be propagated vegetatively without difficulty.

Through hybridization between such species as *P. excelsa* and *P. mariana* there is, theoretically, a good possibility of producing a hybrid with a greater natural capacity to root than that possessed by either parent. This possibility is dependent upon the bringing together in the hybrid, genes for rooting which will interact in a complementary or cumulative manner.

The demonstrated efficiency of plant hormones and improved propagation methods to promote rooting and the possibility of increasing the inherent rooting capacity in many species, supports the belief that vegetative propagation holds good possibilities as a convenient, efficient, and commercially-adaptable means of increasing F_1 hybrids in certain forest-tree genera not ordinarily propagated vegetatively. In materials which naturally root to a high degree, vegetative propagation is, of course, the most efficient method of utilizing the F_1 .

(b) *Large-scale Hybrid Seed Production*.

There are, however, certain forest trees in which it will probably never be possible to utilize vegetative methods of propagation. In these cases the solution to the problem of utilizing the F_1 lies in the practice of cross fertilization on a sufficiently large scale to meet the demand for F_1 plants.

1. A more detailed discussion of some of the points raised in this section may be found in the paper by J. L. Farrar, which follows. For Chron. 15, 152-163.

There are several possible attacks upon the problem of large-scale hybrid seed production, any one of which might provide a practical solution. The more promising possibilities are as follows:

1. Certain individual trees among the conifers have been observed to show a definite tendency toward being exclusively female. (This variation may prove to be environmental rather than inherent.) It would be possible to increase such individuals by cuttings or grafts, growing them in an isolated area where a given hybrid could be produced by open-pollination. The pollen could be brought as dust from a distant source or, in some cases, pollen trees could be interspersed among the female trees. In 1938 two Norway spruce trees and one white pine on the Petawawa Forest Experiment Station were observed to be exclusively female. A normally dioecious genus, such as *Populus*, would be perfectly adapted to this form of large-scale hybrid seed production.

2. Self-sterility may be found to be absolute, or nearly so, in certain species or varieties. Vegetative propagation of a superior, self-sterile individual could probably be extended to produce a large clone of trees which would be inter-sterile. Under isolation, controlled, large-scale, cross-pollination would be possible in spite of an abundance of self-pollen.

3. Differences in time of flowering among male and female flowers (dichogamy) may be such that early-opening female flowers (protogyny) may be fertilized by controlled, open, cross-pollination before anthesis of corresponding male flowers. The utility of this phenomenon in large-scale hybrid seed production is obvious. Definite protandry (male maturing before female) has been observed in Scotch and red pines, and a definite tendency toward protogyny (female maturing before male) has been observed in white pine and to a lesser extent in spruces.

4. The removal of male flowers from trees grown under isolation, though laborious, would make controlled pollination possible on a reasonably large scale. In pine and spruce, it is possible that severe pruning or spraying of the lower branches, which bear the male flowers, might result in complete suppression of male-flower development for a period of years.

In any of the above methods the problem of isolation may give some difficulty. Possible means of isolation are: (1) growing of seed trees in a region remote from sources of pollen (prairies, small windward islands, etc.); (2) use, as females, of introduced species which are lone representatives in the region; and (3) tree coverings (necessarily on a relatively small scale).

2. Shortening the Period between Generations

In cases where undesirable expressions of character are obtained in the F_1 , it becomes necessary to grow the second generation in order to produce

the desired types; and, if these types are to be propagated by seeds, it will be necessary to isolate true-breeding forms, which will require probably two to four further generations. Since forest-trees normally require perhaps fifteen years on the average to reach the flowering condition, the seriousness of the time element in such a procedure is obvious. The problem is also complicated by the fact that at the stage of sexual maturity (flowering) it may be too early to select for certain characters which can be evaluated directly only in older trees.

The problem as stated suggests two lines of attack: (1) the induction of abnormally early flowering by grafting hybrid scions (from young seedlings) on suitable sexually-mature stocks, and (2) correlative studies on related immature and mature trees to establish criteria for the evaluation of mature expressions on the basis of immature characteristics.

Fortunately, the problem of shortening the period between generations relates only to breeding materials in the hands of the breeder. This permits the use of refined methods on an experimental scale and under experimental conditions. It remains to be seen how effective the ingenuity of the breeder may be in attacking this problem.

3. Production of New Forms Through Chromosomal Doubling

By doubling the number of chromosomes in a material, new forms are produced which may be fertile and true-breeding. The new colchicine method of inducing chromosomal doubling makes the production of such forms relatively easy in many species. This advance in the production of immediately stable forms is particularly significant in forest-tree breeding since it reduces the time element to a minimum by complete elimination of the need for growing hybrid generations.

THE POSSIBILITY OF IMPROVING EXISTING TYPES OF FOREST TREES

In the forest, natural selection has operated on the basis of ability to grow, reproduce, and persist under the stresses of the natural environment. This ability represents a superiority only in the sense of capacity to survive. Since points of superiority from the viewpoint of man's economic requirements do not necessarily have a survival value in natural selection, it follows that deliberate selection based on economic requirements will lead, in general, to the isolation of types which will be superior to wild forms in meeting those requirements.

It is perhaps safe to say that there is not a single forest-tree species which, in its natural state, approximates an economically ideal composite of desirable characteristics found in the range of related species intercrossable with it. Granting this, a breeding program involving interspecific hybridization, in any group of intercrossable species, must afford the means of producing new types, economically superior to wild forms.

Deliberate selection in the natural range of variation, and in the range of variation arising from artificial hybridization, will lead to the isolation of these economically superior types, which may then be increased as new races. Comparable selection along these lines is responsible for the special capacities to meet man's requirements which make cultivated plants and domesticated animals superior to their wild relatives.

A TENTATIVE PROGRAM FOR THE IMPROVEMENT OF FOREST TREES

The following outlines of a tentative program for the improvement of forest trees is very briefly stated. Only the main features are touched upon, and these are discussed only in their general aspects and as interrelating factors in the program as a whole. The order in which the different parts of the program is taken up may, to a limited extent, be considered as a chronological sequence in the progress of the program, although most of the work would be done concurrently.

1. Evaluation and Selection of Superior Natural Types

The evaluation and selection of superior types from the range of existing natural variations must be the first step in the breeding of any material. This necessary preliminary phase, while not entirely neglected by foresters, has, nevertheless, not been given its due consideration. C. G. Bates, a prominent American forester, made in 1927 the assertion that, "... between 25 per cent. and 50 per cent. of all forest planting in the United States to date represents wasted effort ... because of the use of poorly adapted species and races of trees." The lack of appreciation of heredity aspects in selecting seed trees whether for natural regeneration or for seed collection, represents not only the loss of an opportunity to improve the succeeding stand but also the introduction of a pronounced tendency toward lowering the heredity quality in the succeeding generation. In the case of natural regeneration, a common practice has been to leave for reseeding the area trees which, because of poor form, disease, or other reasons, are unmerchantable. In the case of seed collections, trees are commonly selected which are low, scrubby and branchy because they are easily climbed and yield good quantities of seed. Thus, while in the virgin forest natural regeneration has maintained well-adapted types by natural selection, man in his short-sighted economics bequeaths to the future the progeny of culls.

The first step in breeding, then, is the evaluation and selection for parentage of those existing types which may be expected, on the basis of genetic principles, to produce superior progeny. This phase deals in part with native forms and in part with introduced, exotic forms. In the case of native forms evaluation and selection may be carried out on the basis of a knowledge of what constitutes heredity variation as opposed to environmental variation.

In the case of exotics the additional factor of adaptation must be considered. The source of seed should be stock which has developed under environmental conditions similar to those of the new habitat. Even with this precaution the forest investor should first make small preliminary plantings for testing the adaptation and general suitability of the introduced material.

A further purpose for which the evaluation and selection of natural forms are prerequisite has to do with providing the best possible parental forms for hybridization. Selection of parental types should be particularly close where the F_1 is to be utilized, for example, if it is desired to combine the disease resistance of an exotic with the general characteristics of a native form, it would greatly increase the possibility of obtaining a suitable F_1 if the exotic were well adapted and of good type than if the contrary were true.

2. Production of New Types

Heritable variability is the very essence of potential improvement. Without such variability both natural and artificial selection would be futile and improvement, therefore, impossible. The natural variability existing in a given material may in range or quality be inadequate for certain breeding objectives. In such cases new and, with limitations, predetermined types may be induced by hybridization. New inherent characteristics may be produced also by experimentally induced chromosomal changes.

(a) Hybridization of Selected Natural Types

Selection within the range of natural variability occurring in a material is commonly limited to choice among distinct well-established forms, (species) or among small variations centering about these forms (biotypes, varieties). Hybridization between these forms, on the other hand, provides a relatively wide range of variability covering intermediate classes between the parental forms; and, since it admits of crosses between forms that nature has never brought together (e.g. native species crossed with exotic species), these intermediate forms may be dissimilar (and thus inferior or superior) to any previously existing type.

Another advantage of inducing variability by artificial hybridization is that the direction or quality of the variability may, with limitations, be controlled. To a degree it is possible for a breeder to produce an F_1 hybrid which combines the desired expressions of a number of characters. The degree to which this is possible depends upon the dominance, inter-action and chromosomal location of the genes involved. The extent to which the F_1 characteristics may be predictable in advance depends, of course, upon the breeder's knowledge of these genetic phenomena for the material in question.

Let us take an example of interspecific hybridization in *Pinus* (pine) and trace it through a number of possible courses in the breeding program. *Pinus*

strobis L. (Eastern white pine) is a valuable native tree, but highly susceptible to blister rust, while *P. peuce* Griseb. (Macedonian white pine) is a native of the Balkan Mountains, adapted to severe climates, and possesses strains highly resistant to blister rust. These species belong to the five-needle group of pines and are probable intercrossable. Assume that F_1 hybrids are obtained.

First, we shall assume that the F_1 proves, upon testing, to possess the general characteristics of *P. strobis* and the rust resistance of *P. peuce* coupled with a degree of hybrid vigor. This is a highly favorable combination of characteristics. In order to utilize the hybrids as quickly as possible and to retain the hybrid vigor, the F_1 would, if possible, be produced in commercial amounts by vegetative propagation or by some method of large-scale hybrid seed production as suggested above.

Second, assume that the F_1 proved to have the rust susceptibility of *P. strobis*. In this case it would be necessary to grow the F_2 in order to obtain types having the desired resistance. The disadvantages of this procedure lie in the amount of time involved, the possibility of a degree of sterility, and in the fact that hybrid vigor is lost. If the selected F_2 type cannot be propagated vegetatively, it will be necessary to grow probably two to four additional generations to procure true breeding types, which will require many years, unless some expedient for shortening the time between generations can be applied.

In many cases the F_1 will be found to have a mixture of both desirable and undesirable characteristics. Here a compromise would be made. To save time and to retain hybrid vigor the F_1 would be propagated and, since there is a probability of obtaining superior segregates, it would perhaps be worthwhile also to undertake the longer method of breeding.

(b) Induced Chromosomal Doubling

In many genera of cultivated plants the species with polyploid chromosome numbers, e.g., tetraploid (4x) and hexaploid (6x), appear to be of greater economic value than diploid species (2x). Since most of our important forest-tree species are diploid, it would appear that chromosomal doubling holds good possibilities as a means of producing new, superior forms.

A recent development in the experimental technique of inducing chromosome doubling particularly in dicotyledonous plants, has greatly stimulated the interest in this method of producing new forms. The new technique involves treatment of seeds or plant parts with the alkaloid, colchicine, which, through its effect on cell division, is highly efficient in producing chromosome doubling.

It is important to note the fact that new forms produced by chromosome doubling may possess a high degree of fertility and stability from the start. In the case of forest-tree breeding this is particularly important since it holds

the possibility of reducing the time element to a minimum by completely eliminating the need for growing hybrid generations.

Experiments underway indicate that the colchicine method is highly effective on forest-tree seeds, and there is every reason to expect ultimate success in inducing polyploid forms in many forest-tree species.

3. Evaluation, Selection and Multiplication of Superior New Types

The mere production of new types represents only a new and potentially valuable range of variability upon which selection may be practised.

In the case of hybridized material the variability will have been produced deliberately with a more or less definite objective. If the objective were disease resistance, the hybrids would be subjected to the attack of the disease, and evaluated and selected on the basis of their reaction. Among types which resist the disease, further selection must be made on the basis of quality, vigor, adaptation, etc. Here again the time element enters in. It is to be hoped that juvenile expressions will be so correlated with mature expressions of characters that selections may be made at an early stage of development.

Since forest trees are in most cases open pollinated and may therefore tend to be heterozygous, it is thought best to consider the F_1 as a variable generation in discussing selection.

In the case of material in which chromosomal doubling has been induced, the characteristics will probably resemble the original forms qualitatively, but may be very different quantitatively, e. g., size of organs, rate of growth, etc. Selection should be simple, since there should be little variation within the material and since the quantitative characters should be definitely expressed at an early age.

4. Practical and Economic Utilization of New Selections

The breeding program should, in the interests of the practical utilization of the new selections, be concerned with methods of reforestation in relation to these selections. To be useful in commercial forestry, a new production must be adaptable to commercial methods of propagation. The fact that the new productions will be, in most cases, appreciably more valuable than wild forms, will permit a higher cost per acre for establishment. But since there is a definite limit to the extent of their greater value over wild forms, there must be a corresponding limit to their greater cost of growing. We must, therefore, consider proposed methods of propagation (vegetative, large-scale hybrid seed production, etc.) not merely as expedients necessitated by the nature of the breeding material, but as methods which must be developed to meet the practical and economic requirements of commercial forestry.

If there is to be any assurance that the breeder's selections will exceed natural types in commercial value to the extent that increased returns will

yield a reasonable profit after compensating for increased costs of production, direct and indirect, the breeder's objectives must be sound from the points of view of the requirements of both the grower and the wood using industries. This condition calls for a good deal of foresight on the part of the breeder since, because of the long-term nature of both the tree-breeding program and the crop rotation, he must anticipate trends in both wood production and wood utilization.

Much of the interest created by forest-tree breeding has centered around the possibilities of producing rapid-growing trees (through the utilization of hybrid vigor, etc.). On the one hand, rapid growth means quicker returns and, thus, a more profitable investment. It has been estimated by Professor Walter Mulford, University of California, that "... to cut ten years off the growing time, at any stage, will reduce the growing cost approximately 40 per cent. ...". On the other hand, there is the question of rapid growth as it relates to wood quality. In deciduous trees, rapid growth is usually correlated with higher density, greater strength, and higher yield per unit volume in chemical utilization. In conifers the reverse—lower density, less strength, and lower chemical yield—is often the case.

While rapidity of growth in terms of annual increment of wood volume may, even in conifers, be expected to compensate for any adverse wood quality that may result, it remains true, nevertheless, that the question of growth rate in relation to quality must receive serious consideration from the breeder.

JUSTIFICATION OF FOREST-TREE BREEDING IN CANADA

It has been stated that forestry in Canada has not reached a degree of intensification where widespread planting is practicable, and that a program of forest-tree breeding was, therefore, not warranted. Against this argument the forest-tree breeder may raise a number of facts:

- (1). Forest-tree breeding must in most cases precede by ten to twenty or more years the actual need for improved types. The breeding program may, therefore, be justified to a considerable extent on future needs.
- (2). There are in Canada over twenty-six million acres devoted to farm woodlots which may be managed with sufficient intensity to include planting, especially when improved stock becomes available.
- (3). There are needs for improved types of trees, entirely apart from strictly commercial forestry. Examples are plantations for conservation purposes, flood control, shelterbelts, etc. Such planting may be done by private or public interests and may or may not be primarily for wood production.
- (4). In the selection of seed trees for natural regeneration, accurate information on inherent characteristics and their mode of inheritance would be of great value. Such information can be obtained only through experimental breeding.

Collectively, these facts are considered to provide ample justification for the present program of forest-tree breeding in Canada.

THE PRESENT STATUS OF BREEDING RESEARCH IN FOREST TREES

Forest-tree improvement, as a definite research program, had its inception in Canada early in 1938 with the establishment of co-operative investigations by the National Research Council and the Dominion Forest Service. To date hybrids have been produced between various species in *Populus* and in *Picea*, and cross pollinations have been made extensively in *Pinus* species and to a lesser extent in *Tilia*. Colchicine treatment of seeds involving twelve genera and twenty-seven species of forest trees, indicate that this technique is highly effective in producing characteristic polyploid effects in nearly all species. Investigations on the use of plant hormones in the vegetative propagation of forest trees are being carried out on an extensive scale.

Other institutions known to have established definite programs of forest-tree breeding are as follows:

In the United States: Northeastern Forest Experiment Station, New Haven, Conn. (This station has taken over the pioneer work on the breeding of *Populus*, which was originally a co-operative project of the New York Botanical Garden and the Oxford Paper Company); Institute of Forest Genetics, Placerville, Cal. (Which has developed out of the original Eddy Tree Breeding Station, founded 1925); Arnold Arboretum, Jamaica Plains, Mass.; Forestry Division, Tennessee Valley Authority, Norris, Tenn.; Division of Forest Pathology, Bureau of Plant Industry, Washington, D.C.; and the Brooklyn Botanic Garden, Brooklyn, N.Y.

In Sweden: Association for the Breeding of Forest Trees (founded 1937).

In Denmark: Forstbotanisk Have, Charlottenlund.

In Germany: Erwin Baur Institut für Züchtungsforschung, Müncheberg.

The breeding of forest trees is in its infancy, but it is expanding rapidly in many important timber-producing countries. Breeding results are meagre as yet; but when, as is confidently expected, tangible proof of the importance of forest-tree improvement to private and public forestry is produced, there is little doubt that expansion will continue with increasing momentum.

The problems confronting the forest-tree breeder are many and great. There are first the difficulties arising out of the nature of the material—the relative lack of botanical information, the time element in breeding, etc. Secondly, there are the questions of trends and developments in the industry which must, if possible, be anticipated, since the present breeding objective can be proved and justified only with the maturity of the first crop, perhaps forty years from now. Thirdly, there are the problems which arise out of

the very early stage which the present represents in the development of cultural forestry—the forest-tree breeder must justify his existence by argument, must change an old order for the support of his program, must prove to the grower that it pays to make an investment which will bring its first returns forty years hence.

There is a plea, here, for patient understanding and adequate support, in order that an organization with prospects of a long-time existence might find a way to cope successfully with these problems as they apply in Canada.

SUMMARY

The increasing needs for greater accessibility of forest stands, and for reforestation and afforestation in conservation, flood control, shelterbelts, etc., have resulted in increased attention to cultural forestry. The coming of cultural forestry removes the necessity of utilizing wild types, many of which leave much to be desired. Thus, cultural forestry naturally embraces attempts to improve forest trees.

The time element in forest-tree breeding, introduced by the long period between generations, may best be reduced by utilizing F_1 hybrids, by shortening the time required to reach the flowering stage, and possibly by the production of immediately stable types through induced chromosomal doubling.

A tentative breeding program is outlined. Selection among natural types is a preliminary step toward improved types both for direct use and for parental material in hybridization. The inadequacy of natural types to meet certain requirements makes it desirable to produce new types with special characteristics. This may be done by hybridization or by induced chromosomal doubling.

The practical utilization of the new productions must be considered from the economic standpoint and objectives and methods made to conform accordingly.

It is shown that, while the more extensive type of Canadian forestry still remains preponderantly non-cultural, forest-tree breeding is amply justified for other reasons, particularly in connection with farm woodlots and conservation plantations.

ACKNOWLEDGMENTS

The available literature relating directly or indirectly to forest-tree breeding has been freely used, particularly the work of Dr. E. J. Schreiner of the Northeastern Forest Experiment Station, New Haven, Conn., U.S.A. The author is greatly indebted to Doctors R. Newton, F. H. Peto, C. Heimburger and E. J. Schreiner, and to Messrs. W. M. Robertson, E. Druce, J. W. B. Sisam and J. L. Farrar for editing the manuscript.

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