Breeding of American Chestnut

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ABSTRACT.— The low level of variation in blight resistance among native American chestnut trees has discouraged tree breeders from working with intraspecific hybridization in this species. If a less virulent fungus becomes established, chances are much better that the variation present will be sufficient to develop trees with adequate resistance. A recurrent selection breeding program is outlined and suggestions are made for cooperation in future breeding efforts.

The history of chestnut blight in America and the efforts to control the blight have been discussed in some detail by several speakers in the General Session. It may be concluded that we have been through two stages in history of the disease. The first stage was a "period of great concern" starting with the outbreak of the disease and ending with World War II. After WWII, interest in the American Chestnut *(Castanea dentata* [Marsh.) Borkh.) declined rapidly and by 1960, when the U.S. Forest Service dropped its research project, we reached the bottom of the second stage, which may be called "the period of resignation." This period lasted until about 1970 when conditions appeared more favorable and new research was started. The papers presented at this Conference give the background for this renewed interest in American chestnut, and the large number of participants give hope that we are now in the third and final stage. May this stage go down in history as "the period of solutions."

Biological control of the blight using hypovirulent strains is the main cause for renewed interest in the American chestnut. If further research with hypovirulence results in development of practical control methods in the field, there may be new opportunities for tree breeders interested in this species. Rather than having to breed for just a single characteristic, resistance to blight, the chestnut breeder may also consider characteristics such as nut and timber production. However, until such methods have been developed it is still prudent to concentrate on the single objective of increasing the amount of resistance in the American chestnut.

VARIATION IN BLIGHT RESISTANCE

The apparent lack of resistance to the blight fungus *(Endothia parasitica* [Mum] P. J. & H. W. And.) in the American chestnut made breeders look to other *Castanea* species for genes controlling resistance. A classic plant breeding program for disease resistance using interspecific hybridization and back crossing resulted in some trees with a high degree of resistance but poor growth form while other trees had good form but only intermediate resistance. Apparently, it is very difficult to combine high resistance and good growth form.

The lack of unqualified success in the hybrid breeding program made some tree breeders, professionals as well as amateurs, take a second look at the remaining population of American chestnuts. Although the picture in general was very discouraging there were numerous reports of large surviving native trees. These trees were not escapees; old cankers gave evidence that they had survived repeated attacks.

The limited amount of resistance in American chestnut may, at least theoretically, be enhanced by use of ionizing radiation. Some new varieties of agronomic species have resulted from radiation breeding, but the conditions conducive to success with small grains are not found in American chestnut. Seed of the American chestnut are limited in supply and very costly. Also, individual seedlings must be transplanted to large field plots where they must be maintained for several years before they start flowering. Since most mutants are recessive, large second-generation populations must be grown and tested to have a reasonable chance of finding a resistant mutant. Such large chestnut plantations would be extremely expensive to establish and maintain. While ionizing radiation breeding may be successful, work should be continued with the selection-hybridization program.

Considering the limited resistance in the American chestnut, selection would have to be carried out for a number of generations to obtain trees with a substantial amount of resistance to the present virulent strains. If, however, hypovirulent fungal strains can be established which will eliminate the virulent strains, it may be possible to breed trees with sufficient resistance for protection against these new strains. The new and hopefully much lower level of resistance needed in the future may not be known for several years. However, this time period will be relatively short compared to the time requirements of a selection breeding program. The present lack of a standard for the amount of resistance needed should not discourage an aggressive breeding program; it is indeed difficult to comprehend how American chestnut trees with an *excess* amount of resistance to the blight can be produced!

SELECTION OF SUPERIOR PHENOTYPES

The first step in a program of recurrent selection is the selection of the base population. Superior phenotypes of American chestnut are not common; large surviving trees are indeed so unusual that they are identified and talked about by landowners, foresters and hikers. Newspaper publicity regarding the breeding program will usually bring a number of letters with information on surviving trees. Most of them will lead to someone's backyard and an Oriental chestnut tree. However, occasionally American chestnut trees are found in forests and fields.

The breeder may not want to include any and all surviving American chestnut trees in his base population. He will want to select those showing promise of the largest amount of resistance. For that reason only relatively large trees, at least 10 to 12 inches in diameter, should be considered. Such trees have had ample opportunity to become infested through cracks and wounds in the bark. Also, they have been screened for resistance both as juvenile and mature trees. Evidence of old cankers on the stem does not disqualify a tree for use in a breeding program; on the contrary, a tree that has succeeded in stopping fungal growth and started healing over the wounds may have greater breeding value than one which has been successful in avoiding infection.

Further evaluation of a candidate tree, especially one with no signs of infection, may be obtained by artificial inoculation. This test may be made directly on the tree or on excised branches in the laboratory. Papers in the Technical Session discuss some of these methods.

CLONAL TEST AND BREEDING ORCHARD

In the University of Tennessee breeding program, the last step in selection of the base population and the first step toward production of progenies is combined in a clonal breeding orchard.

Ramets of the selected trees are established by grafting physiologically mature scion wood to potted Chinese chestnut seedlings. This operation is carried out in the greenhouse during the winter with dormant scion wood and actively growing understock. After one or two years in the shadehouse the grafted trees may be transplanted to the breeding orchard. This orchard will then serve two purposes; natural infection will screen out the less resistant clones and the remaining clones will be used for breeding purposes.

More efficient clonal tests can be established by using rooted cuttings. However, only juvenile cuttings will root easily; to date we have only obtained callus formation on mature wood (Fig. 1). The disadvantage of using juvenile shoots is that several years are needed before the surviving ramets start producing flowers. Ramets produced by grafting of mature shoots will start flower production within a couple of years and tend to have heavy annual nut crops (Fig. 2).

Figure 1. More research is needed to develop rooted cuttings of mature chestnuts.

Figure 2. Scion wood taken from American chestnut trees selected for apparent resistance to the blight are grafted on Chinese understock. This ten-year-old ramet has an abundant crop of chestnuts.

PROGENY TESTING

Two types of progenies are produced in the breeding orchards. They are the result of either open or controlled pollination (Fig. 3). Open pollination results in half-sib families while full-sib families can be obtained from controlled pollination. There are some important differences between them.

Half-sib families are comparatively inexpensive, but half-sib progeny tests will only give information on general combining ability. If the progenies of a given parent on the average have a high degree of resistance, this tree has good general combining ability for this trait. Due to the tedious task of control pollination in chestnut species the full-sib families are expensive to produce, but progeny tests with full-sib families will, in addition to general combining ability, give information on specific combining ability. If two parents produce progenies with more resistance than that expected based on their general combining ability they have good specific combining ability. Also, with controlled pollination, maternal effects can be assessed.

To obtain valid data of specific or general combining abilities it is necessary to use a suitable experimental design in the establishment of the progeny test. Several such designs are being used for other forest tree species and may be adapted to use in progeny tests of American chestnut. However, due to the variable number of progenies available and the expected high mortality the simpler designs offer greater flexibility.

Figure 3. Control-pollinated chestnuts are used in progeny tests to determine if any specific crosses produce trees with a high degree of resistance.

RECURRENT SELECTION

The main purpose of the progeny test may be to evaluate the parents in the breeding orchard. Parents with poor combining ability can then be removed from the orchard. However, the progeny test also provides material for second generation selection. Progenies of poor families will be avoided, while the best phenotypes within the best families are selected for further breeding.

Timing of this selection can be very important. Since the amount of resistance should increase with each generation of selection it is desirable to maintain a very short rotation age. Theoretically this rotation age should be equal to the time required for the trees to start flowering. In American chestnut this may be as little as five to six years. However, it is of little use to turn over generations if a meaningful selection differential is not maintained. By prolonging the rotations to about ten years natural selection will have reduced the task of further evaluation with artificial inoculation and the selected trees will be of sufficient size and age to provide all the flowers needed for production of the next generation.

Another problem encountered in a program of recurrent selection is that of inbreeding. This problem may appear very early in the breeding program if the number of parents used in the first generation is small (less than 15-20 surviving clones in the breeding orchard) and if second generation selection is carried out in open-pollinated progeny test plantations. Both mass selection and selection of individuals within open-pollinated families may result in a severe reduction of variation because most of the trees selected may have one parent in common, a tree with exceptionally good general combining ability. The use of full-sib family test plantations and selection of progenies with different pedigrees may be needed to maintain the variation necessary for recurrent selections.

CONCLUSIONS

A recurrent selection breeding program as outlined above may appear to be relatively simple. There are, however, several practical problems which have one thing in common—they require large investments of time and money.

Considering the large commitment of personnel and funds for a long period of time it is easy to understand why most forestry research organizations do not have breeding programs with American chestnut. At the University of Tennessee we have been engaged in this type of research for about 15 years, but limited funding has severely restricted the quantity of suitable breeding material.

It is curious that today an obscure fish or plant may stop projects worth hundreds of millions of dollars. The only requirement is that it be put on a list of endangered species. The American chestnut is, of course, too ubiquitous for such consideration;

it must be almost as common as the passenger pigeon was once.

To save the passenger pigeon would have required a regional effort and, likewise, the chestnut blight is not a problem of any specific state and should not be the responsibility of any one state to solve.

The resources needed to solve the problem require input from the federal government and cooperation among all participating institutions. In this respect, the renewed interest by the U.S. Forest Service in the American chestnut is very gratifying. A long-term commitment by the largest forestry research organization in the world should provide the leadership, coordination, and continuity needed to carry out a meaningful program.

For many years breeding efforts with American chestnut were carried out by enthusiastic amateurs at their own expense and often in their own backyards. Even though their efforts often were based more on faith than science and the reaction of professional breeders often was condescending they succeeded in establishing some plant material which should be of use in the future. If additional professional breeding programs with the American chestnut get started, it is essential that the amateur breeders be included; they can provide valuable services, particularly in selection and testing.