GENETIC IMPROVEMENT

OF

EASTERN COTTONWOOD

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INTRODUCTION

Eastern cottonwood (*Populus deltoides* Bartr.) genetics research has moved during the past decade from formal statements of its promise to long-term formal tests of commercially promising material. Much of this research has been conducted in the Lower Mississippi Valley, where cottonwood has major commercial importance, but there have been significant contributions from other areas. Breeding progress in this region was last summarized by Farmer (1966). At this point we would like to review recent advances.

Initial improvement efforts in the Mississippi Valley were made during the 1950s by the U.S. Forest Service at the Delta Research Center (now Southern Hardwoods Laboratory), Stoneville, Mississippi. This work consisted of selecting phenotypically superior trees and testing them as clones after propagation by cuttings (Maisenhelder 1961). Some *Populus* hybrids of European and northeastern origin were also tested and found to be unsuitable for the Lower Mississippi Valley (Maisenhelder 1970). Encouraging early results and expanding industrial interest led to establishment of other breeding programs in the early 1960s. These include a broad cottonwood genetics project at the Southern Hardwoods Laboratory; major state and university programs in Illinois, Texas, and Oklahoma; and smaller scale applied breeding efforts by several other state and industrial groups.

The general goal of these breeding programs is development of planting stock with a genetic makeup which will result in increased financial returns to the planter. Such stock may have superior genetic potential for growth rate, wood properties, and pest resistance, or a combination of these and other advantageous traits. Specific goals may well vary with the current silvicultural system employed and management objectives. They may require future adjustment as a result of technological changes which influence utilization or harvesting and because of changes in cultural practices. Information obtained from genetics research may also have a direct influence on future breeding objectives. Therefore, programs should be designed with the flexibility necessary to respond to changes in specific goals and priorities.

GENETIC VARIATION

The first tasks in genetic improvement research are to determine what traits are important and to assess the variation patterns of these characteristics. This variation is the geneticists' raw material. Data acquired in such research are used in designing breeding programs. Genetic variation in wide-ranging tree species has usually been divided into that associated with major differences in geographical location and that found within local populations.

Within-population Variation

Within-population phenotypic variation in cottonwood was initially studied in surveys of stands. Wide variations in fiber length and specific gravity were observed in Illinois and adjacent states (Boyce and Kaeiser 1961, Wolters and Bruckmann 1965), and in the Lower Mississippi Valley (Farmer and Wilcox 1964, Wilcox and Farmer 1968). Results of these studies suggested that selection of individual trees with desirable wood properties would be effective. Strong genetic control of phenological variation was also noted in Mississippi (Farmer 1966), with trees within stands typically foliating in a highly predictable sequence over a period of several weeks.

These studies in natural stands soon led to clonal and open-pollinated progeny tests designed to evaluate the genetic and environmental components of variation. Characteristics of juvenile populations have been reported. Strong genetic control over wide variation in *Melampsora* rust resistance was found by Jokela (1966) in Illinois and by others in Mississippi (Farmer 1970, Wilcox and Farmer 1967). Data from these tests also indicated that much variation in wood properties (particularly specific gravity) and stem form was due to genetic differences (Farmer 1970, Farmer and Wilcox 1966 and 1968).

Genetic variation in juvenile growth has received the most experimental attention, because improvement of growth rate is a top priority goal in most breeding programs. While clonal and familial variations were not as great or under as much genetic control as some other characters, it was predicted on the basis of test data that a 5 to 20 percent increase in juvenile growth could be obtained by selecting the top 1 to 10 percent of the sampled populations (Jokela 1963, Wilcox and Farmer 1967, Farmer and Wilcox 1968). However, test rankings of clones and families changed from year to year. This fact, along with the demonstrated sensitivity of cottonwood to environment, suggested that juvenile growth data should not be patently extrapolated to mature performance. Phenological characteristics, which were highly heritable, were at least moderately correlated with juvenile growth; for example, early flushing clones and families grew faster than late flushing ones. Correlations between fiber length and juvenile growth were generally positive, but variation in specific gravity was unrelated to growth rate. These correlations between characters are important when selecting for several characters.

Genotype x environment interactions represent another class of genetic information which promises significant influence on breeding programs. In one of the first studies of this interaction, Curlin (1967) noted appreciable clonal variation in response to nitrogen fertilization. Genetic variation in nutrient content of cottonwood foliage has been subsequently observed (Broadfoot and Farmer 1969). Moisture stress has been shown to influence clonal variation in growth and shoot/root ratios (Farmer 1970). Studies of clone x site interactions indicate that changes in clone ranking with site may have considerable practical significance (Randall and Mohn 1969). So far, only genetic variation in growth has been shown to be greatly influenced by site.

Geographic Variation

Because of the wide range and natural hybridization and introgression of eastern cottonwood with other species of *Populus*, considerable taxonomic confusion has existed in the species (Schreiner 1970). Genetic studies of geographical variation in cottonwood will be helpful in both taxonomic definition and in extending our knowledge of the "raw material."

Pauley and Perry's (1954) early study of photoperiodic ecotypes in *Populus* was one of the first investigations of geographic variation in this genus. Variation in leaf morphology was described by Marcet (1961), and in the 1960s efforts were begun at more complete delineation of geographic variation patterns. J. J. Jokela of the University of Illinois, who has been a leader in this work, organized a regional study in which material from throughout the range of eastern cottonwood is being tested at diverse locations. Some early results are now available. In Minnesota, trees from southern latitudes (30–38° N) have had poor survival after two seasons because of winter kill. However, some trees from seed sources as far south as 38° N survived at 45° N and exhibited juvenile growth rates greater than the local source (Mohn and Pauley 1969). A larger test of trees from sources along the Mississippi River (Louisiana to Minnesota) has been established at Stoneville, Mississippi (33° N), and first-year growth has been evaluated (Rockwood 1968). Trees from central sources (southern Illinois and Missouri) were tallest at the end of the first growing season. Southern trees are branchier than northern ones. There is also considerable genetic variation in growth, form, and phenology within all sources. Growth rate and form are under moderate genetic control, while phenology is under strong control.

In another recent study, Posey *et al.* (1969) sampled cottonwood found on several east-west river systems in the Southwest. Their early results indicate that trees from eastern Oklahoma have longer fibers, lower specific gravity, faster growth, straighter stems, and greater drought susceptibility than those from western Oklahoma.

There has long been international interest in Mississippi Valley cottonwood. In 1967 this interest prompted the American Poplar Council to sponsor an extensive seed collection aimed at providing foreign breeders with source-identified cottonwood seed. Seeds were collected throughout the Mississippi Valley and sent to research institutes in sixteen countries. We are already receiving information from these stations that will supplement data from tests in the Mississippi Valley (Avanzo 1968, 1969).

CULTURAL AND PROPAGATION TECHNIQUES

Successful planting and cultural techniques have been developed over several decades and are being rapidly improved (Williamson 1913, Bull and Muntz 1943, Maisenhelder 1960, McKnight and Biesterfeldt 1968). Vegetative propagation on an experimental scale is relatively easy (Allen and McComb 1956, Briscoe 1963). This is true even with mature trees, if rooting hormones are used (Farmer 1966). Sekawin's (1963) review of *Populus* propagation covers cottonwood rooting considerations in detail. There is variation in rooting capability associated with genetic and physiological factors (Cunningham 1953, Avanzo 1968, Giordano 1968, Koster 1968, Wilcox and Farmer 1968). When unrooted cuttings are to be used commercially, selection must provide easily propagated materials, or refinement of vegetative propagation procedures for field use will be needed for difficult-to-root clones.

Adaptations of greenhouse crossing techniques used with European poplars have been moderately successful (Farmer and Nance 1968). It now appears that controlled crossing in plantations will be more efficient than greenhouse crossing procedures; bagging and pollination techniques are being developed at the Southern Hardwoods Laboratory. Seed have been stored successfully for as long as one year (McComb and Lovestead 1954, Farmer and Bonner 1967).

BREEDING METHODS AND RESULTS

Origin of Materials

Schreiner (1970) has correctly emphasized that the whole genus *Populus* is a potential source of genetic material for cottonwood breeding. We should ultimately take advantage of this valuable diversity, but considerable research will necessarily precede exploitation of this potential. Results from existing provenance tests (Rockwood 1968, Posey 1969, Posey *et al.*, 1969) and other trials of potentially useful materials will help us to anticipate valuable combinations. In evaluating these tests we should remember that general performance does not always reflect potential value as a source of germ plasm. For example, some wild cotton species with little economic value have contributed important genetic material to the cultivated varieties.

At present, improvement research in the Lower Mississippi Valley deals almost exclusively with cottonwood native to this region. This choice was made because of the urgent need for improved materials in expanding commercial planting operations. The native population exhibits wide variation in important traits, and improvement can be made quickly with assurance that selected materials will be well adapted to local conditions.

Selection—General

The central feature of any breeding program is selection for the improvement of overall economic value. If, as in cottonwood, economic value depends upon several traits, this selection can be a complicated procedure. Although there are a number of possible approaches, use of a selection index is apt to be the most effective. Stonecypher (1969) reviewed the development of selection indices and pointed out the need for reliable information on inheritance, correlation among traits, and economic values. For cottonwood we do not yet have all of this information. The development of good economic data will depend upon industrial cooperation and efforts. Much of the necessary genetic information will be obtained as existing tests become older.

Selection, of course, has already been performed in natural stands and in screening tests. Field selection of breeding material has been based mostly on the method of independent culling levels; for example, individuals falling below a certain standard in any considered trait are not selected. In other cases, selection has been restricted to a single trait, most often juvenile growth rate.

Clonal testing is emerging as the basic tool in selection. Clonal selection is theoretically effective (Libby 1964) and tests are relatively easy to establish. This ease of testing and the adaptation of cottonwood to short rotations will permit high selection differentials which are critical to progress.

Genotype x environment interactions are potentially important in selection. Site, spacing, and cultural techniques all may affect clonal performance. If these interactions are large, then adjustments in testing and selection procedures will be required. Significant clone-site interactions have been found in Stoneville tests (Randall and Mohn 1969), and plantings of partially tested clones from the Stoneville program are being established on a variety of sites throughout the mid-South. These tests will provide some of the information needed to refine selection procedures. Spacing and cultural techniques which may influence clonal performance are also under investigation (van Buijtenen 1970).

First Generation Selection

The simplest approach is that described by Schreiner (1970) as "plus tree clonal propagation," in which phenotypic selections from local populations are vegetatively propagated, then directly tested as clones. Farmer and Wilcox (1964) outlined the method in detail. If rejuvenation procedures (e.g., pollarding) can be relied upon to produce cutting material with good rooting capacity (and experimental data are needed to verify this for Mississippi Valley cottonwood), mature trees may be selected. If not, selection must be confined to juvenile trees.

Estimates of genetic improvement in early growth rate resulting from selecting the top 10 percent of a test population in this system were about 5 to 10 percent (Wilcox and Farmer 1967, Farmer and Wilcox

1968). However, results from a similar but older (4-year) clonal test at Stoneville indicated that actual growth gains with this selection intensity (10 percent) may be between 10 and 20 percent (Randall and Mohn 1969). For some other characters (flushing date, specific gravity, *Melampsora* rust resistance), an equivalent selection intensity will produce much higher gains. In a Texas test (van Buijtenen 1970), three-year data are available on growth of fifty clones from local and more northeastern sources. The ten best clones, which mostly originated in the Brazos River Valley, have an average dbh 70 percent greater (4.4 in. *vs* 2.6 in.) than that of the ten poorest clones, most of which came from outside the Gulf States.

A slight variation of the above system might consist of phenotypic selection of mature trees followed by tests of their open-pollinated progeny. Seedlings in these tests would then be selected and tested as clones. In early breeding, this system is advantageous only if gains accrued from testing progeny as well as clones produce greater total gain than simply proceeding from field selection to clonal tests. Farmer (1970) reported that early growth of progeny from randomly selected and phenotypically superior parents in natural stands was about the same. Further, genetic control over familial variation in the test was relatively low. Mohn and Randall (1969) reviewed genetic gains in growth rate made at various stages of the system. They concluded that although some gains had been made in field selection of parents, as well as in preliminary progeny and clonal tests, major emphasis in the future should be placed on testing large numbers of clones.

It appears that to obtain the quickest, greatest gain in an applied breeding program, one should select a large number of juvenile seedlings, test them thoroughly as clones and select intensively. It would be best if these seedlings came from well-formed, dominant parent trees and were grown in plantations, but the expense of family separation and evaluation can probably be avoided without great loss.

Subsequent Generations

Extensive mass selection in a natural population will produce rapid early improvement. However, the longer it is continued, the slower progress will become. Other procedures will be needed to create populations in which the frequency of desirable genotypes is higher than in nature so that selection will be more rewarding.

Long-term, open-pollinated progeny tests may serve as gene pools of genetically diverse but partly pedigreed materials (Schreiner 1970). Some kinds of needed genetic information will be obtained from these tests. However, full-sib tests resulting from various controlled crossing programs will provide the detailed inheritance data essential to selecting the best breeding approach. This may take the form of recurrent selection for general combining ability or perhaps breeding for specific combining ability. There are as yet no full-sib tests in the ground in the Mississippi Valley, but the Stoneville group has completed crosses leading to them. In some programs it may be profitable to delay this more expensive phase of testing until some data and partially tested parents are available from clonal and open-pollinated progeny tests (Schreiner 1970).

Pest Resistance and Special Breeding Techniques

Breeding for pest resistance requires special comment because of its potential importance as we discontinue strong reliance on chemical pesticides, and because it may be considerably more complicated than breeding for other traits. With the exception of selection for *Melampsora* rust resistance, more lip service than investigative attention has been given to improving pest resistance. This is especially true with respect to insect resistance. Schreiner (1963) has reviewed breeding for disease resistance in *Populus*, and most of his conclusions on breeding needs and methods are applicable to cottonwood. Steenackers (1969) has summarized recent breeding progress. As Schreiner noted, maximum gains in disease resistance will depend upon interdisciplinary research in (1) variation and inheritance of resistance in the host, (2) biology of the pathogen, (3) establishment and progress of parasitism, (4) effect of total environment on host-pathogen relationships, and (5) disease resistance improvement methods, particularly testing. These considerations are probably equally applicable to insect resistance. In short, a considerable research investment will be required.

Effective manipulation of genetic material may ultimately require procedures which are not presently in the population geneticists' bag of standard tricks. There are now research programs which are formally investigating some of these techniques. Production of haploid *Populus* plants is one of them (Winton and Einspahr 1968). Stettler *et al.* (1969) have commented on the possible use of haploids in, for example, heterosis breeding and interspecific hybridization. Induction and use of polyploidy is also being considered (Zufa 1968). Although we will not review the details of these and other efforts, it is notable that these lines of investigation may eventually lead to dramatic new breeding methods for cottonwood.

DISTRIBUTION AND USE OF IMPROVED STOCK

After formal tree improvement programs are established, the breeder is immediately faced with the persistent question: When will genetically superior stock be available? This eagerness to use the products of research that is characteristic of modern forest practice is good, but a professional responsibility exists that calls for guarantees to insure that techniques and/or material will work before they are used on a large scale. This responsibility is foundation for the geneticists' sometimes conservative attitude about releasing stock. We would like to note several points which will be of concern as some cottonwood breeding products begin to be available.

Schreiner (1970) has warned of the "eager beaver fever" and recommends on the basis of long personal experience that "selection of new clones for commercial use be delayed to at least half rotation age." Actually, any selection of material short of rotation age will involve assumptions about future performance. Wright (1962) pointed out that both breeders and commercial planters will make these assumptions because the delay involved in completely testing material is unacceptable. It should be recognized, however, that the performance of these materials is uncertain and that the shorter the testing period, the greater this uncertainty.

Commercial use of partially tested selected clones is not particularly hazardous when reasonable care is taken. The risks are reduced considerably if materials are drawn from a population adapted to local conditions. In contrast, they are relatively high for materials whose adaptability is questionable—that is, trees of nonlocal origin and/or hybrids which are nonexistent or unsuccessful in nature. Mixtures of clones (at least ten and preferably twenty to thirty) should be used to provide insurance against selection errors or conditions which might adversely affect a small percentage of the clones.

Clones in the Stoneville program have reached small pulpwood size on good sites. Some of these clones have been selected, primarily for growth rate, and will be described soon. In the test where selection was performed, their diameters exceeded the control group by 20 percent and on a marginal site this superiority was 15 percent. These clones, along with others showing promise in improvement programs, will be used in commercial plantings; however, they represent only an initial step in genetically upgrading planting stock. Individual clones should be dropped from the mixture and new ones added as a result of continued testing and selection. The useful life of any particular mixture may be relatively short, especially during these early stages of our work. Continued improvement of planting stock will require maintaining the identity of clones in the nursery and close cooperation between the geneticist, nurseryman, and planter.

As clones are distributed for further testing and commercial use, it will become increasingly important that we have an adequate labeling and certification procedure. Barber (1969) has described the essential features of such a control system. At present in most states anyone can market "genetically superior" cuttings, following little or no selection and testing, because there are no specific legal standards for certification or identification of cottonwood. Many cottonwood clones can be easily identified on the basis of highly heritable morphological traits, and the clonal breeding method lends itself to simple testing standards. Thus, a workable set of regulations could be easily formed. Perhaps the American Poplar Council would be the logical organization to formulate them and promote their use.

SUMMARY

Eastern cottonwood breeding programs in the Lower Mississippi Valley have expanded during the last ten years. Considerable data on phenotypic variation in natural stands and early genetic information from field tests are now available. Clonal testing has emerged as a basic breeding tool and some early clonal selections are being released for commercial use.

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