GENETIC IMPROVEMENT OF HARDWOOD FIBER PRODUCTION IN THE NORTH-CENTRAL REGION: POTENTIALS AND BREEDING ALTERNATIVES

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In the Lake States, aspens are now growing towards senility faster than they are being harvested (Groff 1966). In the Central States, wood processing residues have recently supplied about one-half of the area's hardwood fiber requirement (Blyth 1970), thus allowing hardwood growing stock to continue its recuperation. In fact, the national hardwood fiber supply situation is improving (Hair and Spada 1970). However, a growth deficit is expected by the year 2000, given current management levels and "expected" demands. Josephson (1971) foresees about another decade of adequate fiber supply. Moreover, some of our economists tell us poor biologists that we've got to produce more and more fiber on less and less land. Somewhere between the unharvested senility of aspen and an unrealistic commitment to unrelenting growth, we must settle on a varied, productive forest to supply a stable, fiber-using industry.

Einspahr and Benson (1970) see three aspects to this forest: (1) certain lands for recreation and amenity with timber as a byproduct, (2) some areas for conventional timber management, and (3) good sites near mills for intensive short-rotation fiber production. Genetic improvement of fiber production has a role in all three of these settings. Despite the obvious intellectual and short-range economic attractions of research on intensive hardwood fiber production systems, geneticists, physiologists, and silviculturists must address themselves to the problems of all three levels of practice. Genetic improvement of hardwood fiber production must be considered within the framework of forest management's several regional goals, not as an isolated objective.

We can assume from previous analysis by Dawson and Pitcher (1970) that genetic improvement of hardwood fiber species in the North Central Region is a high priority research and development goal. They conclude that effort should be concentrated on aspen and cottonwood for which there are respectively about 8 and 4 million acres of highly productive sites in the region. Most of my discussion will thus center on probable first generation genetic gains in these species, especially aspen, which have not been subjects of recent review. However, data will also be noted for other northern species such as birch, maple, and oak, for which highly justifiable breeding programs are aimed mainly at improvement of lumber and veneer material; improvement of these species' growth capacity can ultimately add to our fiber supply. Finally, I will briefly review recent data for some southern hardwoods, because they suggest first generation gains that may be expected in north-central species. We will consider growth, wood properties, and pest resistance.

COTTONWOOD

Cottonwood breeding programs are aimed mostly at providing genetically improved material for intensive cultural systems. While these systems may produce lumber and veneer as well as pulpwood, they do so in fairly short rotations (20 to 30 years on excellent sites), at least in the lower Mississippi Valley. Conventional forestry techniques are presently used in pulpwood rotations, but cottonwood may be suitable for "silage" systems. Breeding programs should therefore produce material for both conventional intensive forest management and new methods of fiber production.

Mohn will discuss cottonwood breeding methods in a later paper at this meeting, and Schreiner (1971) has outlined a detailed cottonwood breeding system. My remarks will deal only with expected gains. Most of the data are for populations in the South and are not patently applicable to North-Central Region populations, but they represent a fair estimate of what may be expected farther north.

First, racial variation may be the source of considerable gain in the North-Central Region. Mohn and Pauley (1969) noted that while much material from 32° to 38° latitude was winter killed at a 44° planting site, surviving low-latitude plants exhibited much better second-year growth than local stock (6.0 feet vs. 4.4 feet). Further screening of 32° to 38° sources at higher latitudes should provide some valuable breeding populations for northern areas. A large provenance test now under way in Illinois may produce some of this material.

Most of the southern breeding effort has been concentrated at the USDA Forest Service's Southern Hardwoods Laboratory. The early work of Wilcox and Farmer (for review see Farmer and Mohn 1970) consisted mostly of field selection of good phenotypes followed by short-term (1 to 2 years) screening tests of clones and open-pollinated families grown under intensive culture. Genetic gains computed from test data were expressed as percentages of control populations, the means of which were equal to or slightly above a natural population. Expected genetic gains in height and diameter from selecting the top 10 percent of clonal populations were around 5 to 10 percent. Because of correlation between height and diameter, expected volume gains were 10 to 20 percent. Gains for specific gravity were estimated at 7 percent and for fiber length about 4 to 5 percent. Other characteristics related to growth, such as phenology and *Melampsora* rust resistance, were found to be more highly heritable in these and other (Jokela 1966) tests. Mohn and Randall (1972) have reexamined one of the Wilcox and Farmer (1967) tests at 6 years, and report slightly higher heritabilities than noted for first- and second-year growth, thus suggesting that early gain estimates for growth were probably conservative.

Forty clonal selections made from these screening studies were planted along with a control population of 40 clones in a larger test, and some 4- and 5-year growth data have been published by Mohn and Randall (1969), Randall and Mohn (1969), and Mohn *et al.* (1970). At 4 years, mean volume per tree for the 40 selections was 27 percent greater than for controls, indicating that preliminary selection in screening tests was effective. After the fifth growing season, when a second thinning (to 109 trees per acre) was made, 14 clones were selected from the study for further testing and pilot-scale commercial use. On a good cottonwood site, the mean volume of these 14 clones was 6.5 cubic feet per tree, compared with 3.7 cubic feet per tree for the control population. Three of the clones had mean volumes in excess of 100 percent over controls. The gain represented by these selected clones is realized gain on the test site, not predicted response computed from genetic parameters. Intensive clonal screening and testing should soon result in a number of clones with this sort of growth capability, because the initial breeding population represents only a minute portion of available material.

Exactly how much gain in growth was made in each of the various stages of selection noted above is difficult to determine from available data. Analysis by Mohn and Randall (1969) indicated some gain was made in field selection of phenotypically superior parent trees and at the other stages thereafter. In a 2-year, open-pollinated progeny evaluation using the same selected parents and a 52-family control population, Farmer (1970) observed identical means for juvenile growth of controls and selected families, and concluded that field selection had been ineffective. In this latter test, predicted response (genetic gain) to combined selection of the top *5* percent of the test population was 7 percent for height, 16 percent for diameter, 10 percent for specific gravity, and 5 percent for fiber length.

The Texas Forest Service breeding program includes clonal tests of local selection and material from throughout the eastern U.S. To date, local clones have proven superior in eastern Texas, and after preliminary testing, nine were recently compared with nursery-run material in a 4-year-old irrigated test.' The best clone, with an average tree volume of 4.0 cubic feet, is producing nearly twice the volume of controls and 45 percent more dry weight. Cottonwood twig borer *(Gypsonoma haimbachiana* Kearf.) damage, which is serious in Texas tests, has not varied appreciably among rapid growing local clones, but was found to be low in a hybrid poplar clone (Woessner and Payne 1971).

Woessner, R. A. Growth, volume, and dry weight differences among 4-year-old Populus *clones grown under irrigation. Pap. presented at First North Amer. For. Biol. Workshop. 1970.*

It thus appears that early estimates of genetic gain in southern cottonwood populations may be conservative and actual juvenile volume gains of up to 100 percent may be realized in first generation selection if enough clones are screened. Numerous tests and pilot plantings are now in progress throughout the Mississippi Valley, and the resulting data should shortly give a reliable estimate of realized gains on a per-acre as well as a per-tree basis. Data from these tests should substantially augment our scanty information on wood properties and pest resistance. Concurrent studies of growth relationships (Larson and Gordon 1969) may provide keys to effective screening for superiority in fiber production.

ASPENS

Genetic information on the aspens can be applied effectively at all three levels of silviculture noted above. The considerable amenity value of an aspen clone is not reduced if it is uncommonly healthy and rapid growing. A recreationally oriented silviculture aimed at a continuous supply of esthetically pleasing aspen will certainly produce fiber. The deer-aspen system of producing game and fiber pioneered by Westell (Graham *et al.* 1963) presents good opportunities for using genetically superior clones. Aspen's clonal habit and regeneration by root suckering enhance the potential long-range benefits of using genetically superior clones on lands managed with traditional techniques. Einspahr and Benson (1968) have already cited the important benefits of short-rotation aspen silviculture.

Early studies of phenotypic variation in growth and wood properties of Wisconsin quaking aspen were reported by Buijtenen *et al.* (1959), who took advantage of aspen's natural clonal habit to obtain rough estimates of broad-sense heritability. Expected gains from selecting the best 5 percent of the population were: height, 10 percent; diameter, 6 percent; specific gravity, 2 percent; and fiber length, 4 percent. Barnes (1969) used the same procedure to estimate broad-sense heritability for height and diameter of P. *tremuloides* and *P. grandidentata* in Michigan. His estimate for trembling aspen diameter was similar to that of Buijtenen *et al.* (1959), but his heritability for height was lower. Heritabilities for height and diameter ($h^2 = 0.34$) of *P. grandidentata* were higher than for trembling aspen. All of these estimates of heritability and gain are probably biased upward, since in studies of unreplicated clones, environment and genetic effects are confounded.

Broad variation in growth of naturally occurring clones of both aspens has also been reported by Einspahr and Benson (1967), Koenig (1960), and Romeril (1961). Einspahr and Benson used growth data for trembling aspen in Wisconsin to establish base lines for judging potential field selections. In Koenig's study of bigtooth aspen in Michigan, 28 clones were selected for their phenotypic superiority in growth, and were paired with randomly selected adjacent clones. Selected clones had trees that averaged 12 percent taller, were 19 percent greater in diameter, and contained 53 percent more volume than random clones. Six selected clones on the best site sampled had 166 percent more volume than random clones. Romeril extended this sort of selection study to a wider area in Michigan and designated 16 phenotypically superior clones that contained trees 15 percent greater in diameter, 13 percent taller, and with *51* percent more volume. Zahner and Crawford (1965) have shown the importance of considering clonal variation in aspen site evaluation; their data on phenotypic differences are in agreement with those above. Because of aspen's natural replication, these variation data are more meaningful in terms of potential gain than similar phenotypic variation information for other species. They suggest good progress may be had through clonal selection and testing.

Variation in aspen wood properties has been most recently reviewed by Kennedy (1968) and Pronin and Lassen (1970). It is sufficient to note here that most phenotypic variation studies suggest that prospects for improving fiber properties and specific gravity through breeding are good, but specific estimates of genetic gain from clonal selection are lacking except for those of Buijtenen *et al.* (1959).

While the insects and diseases of aspen are well known (Graham *et al.* 1963), and there is some information on variation and inheritance of pest resistance (Schreiner 1963), data that might be used to estimate gains are rare. A study by Copany (1969) of clonal variation in susceptibility of trembling aspen to *Hypoxylon pruinatum* (Klotsche) Cke. represents the kind of work that will be prerequisite to breeding efforts. This pathogen causes an estimated annual loss of 1 to 2 percent of standing volume (Anderson 1964). Copany surveyed 88 clones on five sites in Michigan, and reported that on a poor site infection ranged from 10 to 83 percent. Study conditions suggested that much of this interclonal variation has a genetic basis. Preliminary observations by Einspahr[2] indicate that hybrids

[2] *Personal communication with D. W. Einspahr, Institute of Paper Chemistry, Appleton, Wisconsin.*

involving *P. alba, P. canescens,* and *P. grandidentata* parentage may be more resistant to *Hypoxylon* than quaking aspen.

The discovery of triploid quaking aspen clones in Michigan and Wisconsin (Buijtenen *et al.* 1957, 1958) led to interest in their fiber-producing merits relative to diploids. Comparison with adjacent diploid trees indicated that triploids were significantly faster growing in one area but not in another. Wood properties were studied in one area; triploids had significantly longer fibers, but there was no difference in specific gravity. A study of phenotypic variation among 20 trees from four triploid clones suggested that differences in growth and wood properties were under moderate to strong genetic control (Einspahr *et al.* 1963). Subsequently, a formal 10-year comparison of two triploid clones with two diploid full-sib families (Benson and Einspahr 1967, Einspahr *et al.* 1968) revealed no significant triploid superiority in growth, form, and specific gravity; triploid fibers were no longer than diploid. In another test, the mean 5-year growth of three triploid clones was about 20 percent greater than that of nine diploid, full-sib families (Einspahr and Benson 1964); the report did not include a statistical comparison, however.

Aspen hybrids of *P. tremuloides* x *P. tremula* have been tested in Europe for several decades and are believed to be distinctly superior to the local *P. tremula.* Larsen (1970) has reviewed the numerous reports of this work; my comments will cover American tests. Ten-year results from the New England screening tests of Pauley *et al.* (1963) indicated that crosses involving Massachusetts *P. tremuloides* females and *P. tremula* males from mid-latitudes of Europe or from Italy performed best, with height growth of 2 to 3 feet per year.

Hybrids of German *P. tremula* and Massachusetts *P. tremuloides* have been compared with local *P. tremuloides* stock in an unreplicated Wisconsin test (Church 1963). At 12 years, the hybrids averaged 24 feet in height and local stock 21 feet. In a 5-year replicated test, Benson and Einspahr (1967) noted that two families of triploid hybrids *(P. tremula* x *P. tremuloides)* grew 3 and 4 feet per year while two local diploid families grew 2.5 and 3 feet. Specific gravity of the triploid families as about 0.4, compared to 0.36 and 0.38 for the diploid. Other reports (Barnes 1961, Pauley 1956) note existence of natural hybrids and suggest their breeding possibilities. In short, hybrids have been successfully grown in the North-Central Region, but large-scale screening and testing will be required before estimates of gain can be made. Some of this work is in progress at the Institute of Paper Chemistry (Einspahr and Benson 1964).

While no replicated progeny tests in aspen have been reported, Einspahr *et al.* (1967) studied variation in growth and wood properties among 25 full-sib families planted in single blocks on a uniform site. Narrow-sense heritability estimates, based on progeny-parent regression information, indicated moderate possibilities for genetic improvement of growth and moderate to good genetic control over fiber length and specific gravity. Einspahr (1968) has brought together the limited published heritability data, then assumed parent trees were to be two standard deviations better than the population mean, and predicted average genetic gain that might be obtained from full-sib families of these parents. Some of these estimates are presented below:

Improvement characteristics	*Estimated means**	*Average expected genetic gain (Percent)*	*Absolute gain*
Height growth, ft./yr.	3.00	10	0.300
Diameter growth, in./yr.	.25	11	.030
Volume growth, cu. ft./A./yr.	100.00	20	20.000
Specific gravity, g./cc.	.38	4	.015
Fiber length, mm. (age 10)	.80	6	.050

Systems for genetically improving aspen fiber production could take several forms. Selection of a breeding system and investment level should be hinged on a formal analysis of the relationship between improved material and management, as proposed by Namkoong *et al.* (1971). Perhaps the simplest procedure might consist of roguing existing stands in appropriate situations, a silvicultural measure recommended by Graham *et al.* (1963). Recent information on the nature and development of natural clones (Barnes 1966, DeByle 1964, Garrett and Zahner 1964, Tew *et al.* 1969) suggest techniques for such roguing. Rogued clones might

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* *Estimated means for 8- to 10-year-old diploid quaking aspen plantations growing at a moderate rate of growth.*

be replaced with genetically improved material, or existing phenotypically good clones might be expanded. The results would be a genetically variable and superior stand obtained without the high cost of complete conversion.

I see no major barriers to development to commercial vegetative propagation procedures based on known techniques (Farmer 1963, Benson and Schwalbach 1970); thus selection and testing of naturally occurring clones appear feasible. Because of natural replication, field selection in aspen is probably more effective than in other hardwood species. A clonal selection program might gradually -evolve into one aimed at development and commercial use of parents with high specific combining ability. Schreiner (1971) has outlined such a breeding system for cottonwood; it is equally applicable to aspen. Given any of several possible systems, however, it will be important that (1) some large, well-designed tests be established to give badly needed genetic information, (2) field selection be extensive enough to obtain a genetically diverse breeding population, and (3) control populations used in breeding tests be large enough to truly represent natural population means.

OTHER HARDWOODS

Northern breeding programs in birch, oak, and maple, and southern efforts in sweetgum, sycamore, and yellow-poplar have been under way for several years. The impact of these programs on fiber production in the' North-Central Region will be variable and will depend on the manner in which improved stock is used. Analyses of the relationships between tree improvement research and action programs and establishment and management plans are particularly important for the fine hardwoods with their relatively long rotation. Improved stock of some sawtimber and veneer species may not be planted at traditional spacings in single species plantations. Rather, this material may be "inserted" in regenerating natural stands at crop-tree densities (i.e., 50 to 100 stems per acre), and cultural methods during establishment may center on these individual trees rather than on the whole stand. Recreational and esthetic benefits may be major management goals in these forests. In such a system, improved growth potential would not be reflected in pulpwood production for at least one rotation. On the other hand, breeding in species such as sycamore and sweetgum is aimed at intensive plantation culture of pulpwood and sawtimber, and genetic gains can be immediately realized.

Information on yellow birch, northern red oak, sugar maple, and white ash is available from provenance tests. In a 3-year-old rangewide birch test in Wisconsin (Clausen and Garrett 1969), there is wide, but apparently random, variation in growth. Seedlings from the best source were twice as tall as those from the poorest one and 32 percent taller than the local Wisconsin stock. First-year heights of northern red oak from southern sources (e.g., Tennessee, southern Indiana, Arkansas) grown in northern Ohio were 30 to 100 percent greater than those of oak from more northern sources (Kriebel 1965). Family (open-pollinated) differences were also prominent, and Kriebel concluded that selection of individual seed parents will be important in improving growth we. Fourteen-year data from the sugar maple study (Kriebel and Gabriel 1969) also indicated that, in northern Ohio, trees from the central portion of the distribution of the species complex grew better than trees from other sources. Low juvenile 11-year correlations in other tests suggested, however, that early selection for growth is not practical, though juvenile narrow-sense heritability was moderate (h^2 = 0.28, 0.30). While no major breeding programs in ash are now in progress, results of Wright's (1962) early provenance tests indicate the existence of southern ecotypes that may outgrow local stock in some portions of the North-Central Region. In brief, information to date suggests that some major improvements in northern hardwood growth may ultimately be based on provenance test results confirming non-optimality of local races (Namkoong 1969).

Sycamore *(Platanus occidentalis* L.) has received most attention in the South as a candidate for "silage" culture (Herrick and Brown 1967). Webb (1970T has analyzed 2- and 3-year data from an evaluation of 64 randomly selected open-pollinated families growing on a good site at 4- by 4-foot spacing. Genetic gain in height from combined selection of the best 5 percent of the population was estimated to be 6 percent. Heritability estimates for third-year growth parameters in this test, which have not been published, suggest that gain will be considerably more than 6 percent.'

A number of well-designed and potentially valuable sweetgum progeny tests have been established, and some reliable estimates of gain in juvenile growth will soon be available. The only heritability estimates published to date are those of Wilcox (1970), based on a population of 40 open-pollinated families from southern

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3 Personal communication with C. D. Webb, U.S. Plywood-Champion, Inc., Athens, Ga.

Mississippi. Narrow-sense heritability was 0.25 for 3-year height on a site in central Mississippi, and 0.40 for height on a Gulf Coast site. While Wilcox did not publish data essential to estimating genetic gains, means and family ranges suggest that at least 10 percent genetic gain in growth could be obtained with a selection intensity of 5 or 10 percent. A larger (81 open-pollinated families) test of material from throughout the lower Mississippi Valley is planted on two contrasting sites in central Mississippi, and Schmitt and Webb (1970) have briefly noted some 6-year results. These data indicate the possibility of major gains in growth through a combination of source and family selection in the test plantation. The data so far do not make an encouraging case for mass selection in the field.

Yellow-poplar which should provide some fiber in the southern portion of the North-Central Region, has been subjected to some provenance testing with varied results (for review see Wilcox and Taft 1970), and it is as yet uncertain what sort of gain may be expected from source selection. At least one open-pollinated progeny test has, to date, produced no evidence of significant familial variation.[4] At present it is apparent that early estimates of gain must await full-sib tests now in progress.

One further comment on breeding in this group of species is appropriate. As Schmitt and Webb (1970) have noted, early data from a number of tests suggest that mass selection in natural stands of most hardwoods will probably not lead to good first generation gains in juvenile growth potential. They recommend that "more effort be devoted to establishing sizable breeding populations rather than refining phenotypic selection in wild populations.'.; I believe this recommendation is particularly pertinent to rapid progress in genetic improvement of fiber production.

CONCLUSIONS

Review of existing published data on variation and inheritance of growth and wood properties in hardwoods suggests that at least 10 to 20 percent improvement in fiber production can be realized in first generation selection. Prospects of indirect improvement through pest-resistance breeding appears good, though based on little data. Because aspens are the predominant pulping species in the North-Central Region, and because they possess silvical characteristics that are assets to breeding, a major investment in their genetic improvement would be profitable in the long run. Realization of possible genetic gains in aspens and other species will depend on early implementation of judiciously selected applied breeding programs and on increasing improvement-oriented regeneration investments. To ensure wise investment in research and development, early analytical attention must be given to the relationship between improvement programs and the establishment and management of genetically superior stock.

Personal communication with E. Thor, University of Tennessee.

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