A QUARTER CENTURY OF PROGRESS IN TREE IMPROVEMENT IN THE NORTHEAST

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ABSTRACT. Tree breeding started in the Northeast in 1923. The region has been the home of much of the pioneering research on hybrid poplars and other groups. Tree breeders everywhere owe a great deal to E. J. Schreiner, H.I. Baldwin, and others who set the stage for the research to come later. The hybrid poplar research has produced many valuable clones and is even more noted for the lessons it provides to breeders of other groups. Dave Cook's continued efforts with the larches produced a considerable body of information about their culture and set the stage for new variety development. Research on eastern white pine has produced faster growing trees for almost every part of the region as well as improvement in research technique. Work with balsam fir, white spruce and black cherry has resulted in new varieties ready for immediate planting. There have been some lost opportunities, however, and it is necessary for us to be sure we have no more such lost opportunities in the future.

It is a pleasure to return to Burlington for this 27th NEFTIC conference. Although gone from the region for 23 years, I still feel at home here and am deeply interested in NEFTIC. In this paper I shall try to cover some highlights of the past quarter century, confining my remarks to the Northeast.

It is desirable to preface the 25-year history with mention of some of those who set the stage by their work four and five decades ago. Ernst J. Schreiner who worked at the Northeastern Forest Experiment Station, and Carl Heimburger, who worked at Petawawa and Maple, Ontario, immediately come to mind. Both were optimists who told every one who would listen what tree breeders could accomplish, and thus made the later programs possible. Also, they taught us late comers how to do controlled pollinations, that poplars could be crossed, and many other things taken for granted now.

H.I. Baldwin of the Fox Forest and P.R. Gast of the Harvard Forest set up the region's first provenance tests in the late 1930's. They employed replication, which was a rather neglected concept at the time. They demonstrated the reality of geographic differences, showing that seed source could be important.

A special type of credit goes to some of the men working for state conservation departments, particularly to E.J. Eliason and E.L. Littlefied of New York, George Perry of Pennsylvania and H.C. Buckingham of Maryland. These men were practicing foresters with no research responsibilities but they were curious and like to try new things. In some respects they were the researchers of the day for they planted strange things in out of the way corners and were willing to try different planting methods. Special credit goes to Littlefield and Eliason for their record system. It was simple enough for people to use yet effective and still gives the state of New York a lead in the testing of exotics.

Dave Cook was another New Yorker who had great influence on later tree breeding activities. He hammered away at the larches and when he ran out of space on his own land talked others into planting them. As a result, New York already had a large body of information on larch silviculture and genetics a quarter century ago.

THEN AND NOW

In this section, I would like to make a few contrasts between the situation confronting a tree breeder then and now. Consider first the matter of education. Prior to 1950, most tree breeders were forestry undergraduates who did their graduate work in botany departments at either Berkeley or Harvard. They had generalized training, with little exposure to statistics or plant breeding and relied on books by Stebbins and Dobzhansky for bit of information about forest genetics. Most thesis problems were related only indirectly to tree improvement. Now, almost every state in the region offers undergraduate and graduate education in forest genetics. The training is much more specialized and there is an abundance of ongoing research from which a student can choose a thesis problem related to tree genetics.

As of 1946 the U.S. Forest Service was the only agency in the region with full time people devoted to forest genetics. Yale, Harvard, and the Boyce Thompson Institute joined the list in the next few years. All those making their living by tree breeding could easily fit at one small table. Only one or two people were actively working on any one subject such as hardwood genetics or experimental design. Inevitably, progress was slow although many of us were naive enough to believe that one or two people could solve the world's problems. There was little opportunity to exchange ideas or to confer with an expert about one's problems. Nowadays we take for granted the ability to call upon a colleague for advice on grafting pines, experimental design or hybridization possibilities in the maples. That ability was lacking 25 years ago, with the result that we often floundered in our research efforts.

For several years following the second world war, J.F. Martin of the old Bureau of Entomology and Plant Quarantine circulated a mimeographed newsletter to those interested in breeding white pines for resistance to blister rust. This consisted of brief progress reports and went to a score of poeple scattered across Canada and northern United States. It filled the same role now filled by Silvae Genetica and the various conference proceedings, being the only "publication" devoted to tree breeding. It also had to serve in the same way as this conference, offering tree breeders a chance to get together, if only by mail. As if that were not enough, this one newsletter had a third function. It was the principal way to promote cooperation, as there were no cooperative tree improvement programs or regional committees such as NE-27.

The limited opportunities for cooperation made certain types of research difficult. I remember attempting interracial crosses in white pine. As there were no provenance tests, pollen had to be obtained by mail. I failed at the outset because I could not locate enough friends who had access to native white pines and who also knew how to collect male catkins and extract pollen. Large progeny or provenance tests involving many plantations would have been a major undertaking but are common place today.

Plantation establishment was a challenge 30 years ago. We lacked experience and found it difficult to do such simple things as nursery mapping, lifting and labelling stock, achieving randomization, or keeping straight lines. Today we can do most of those things better and in one-third to one-half the time. However, chemical weed control has resulted in the biggest changes. A quarter century ago weed competition could be eliminated only by mulching or cultivating several times the first 2-3 years. That was expensive and put a limit on the amount of field testing which could be done. From 1940 to 1955 the poplar breeding project was one of the main thrusts of the Northeastern Forest Experiment Station. Planting and cultivating the F_1 clonal tests probably accounted for 75% of the effort devoted to that project. Frequent attempts to improve other hardwoods also hit a snag at planting time. Fortunately, this situation has changed and we no longer need to avoid studies which involve planting more than a few hundred trees.

Much of the research planning in the 40's and 50's was unrealistic. Progeny tests were believed to be difficult to establish. People thought many years would be required for seed production. Inheritance data on which to base judgments were lacking. As a result, we who were doing the research often looked for quick, easy solutions instead of tackling more important problems which promised to be difficult. As an example, considerable effort was spent on the rooting of cuttings of such things as oak and pine because vegetative propagation of a single exceptional individual seemed to offer a much quicker solution than selection and the development of seed orchards. As another example, I cite my own skirting around the problem of weevil resistance in white pine. I realized there was one sure way to learn the possibilities of breeding for resistance, and that was to make selections in heavily weeviled stands and progeny test them. That approach seemed too difficult, so I dodged the issue by attempting statistical manipulation of data gathered from wild stands.

Today's research planning seems much more realistic to me. For one thing, there are more basic data on which to make a choice between different improvement methods. Also, experience has taught that such so-called difficult things as plus-tree selection and progeny testing are not really so difficult after all. Modern researchers are not so likely as their predecessors to avoid a productive plan of action just because it involves 15-20 years of hard work.

Forest genetic research in this region was oriented more toward than practice in the 1930's and 1940's. That was so for three - Only New York had a large planting program. In other states little interest in improved varieties. The few tree breeders liked an audience clamoring for practical accomplishments. Second, Columbia, Harvard and Yale were the first academic institutions to under take forest genetic research and trained all the region's breeders prior to 1960. Those institutions are Ivy League and inevitably put a theoretical stamp on the research. The third factor affected the Forest Service mainly. Its work was concentrated in Philadelphia and Beltsville, both places close to the Washington office. The genetic project was a convenient place to shunt foreign visitors who wanted a day's exposure to theoretical tree breeding. The function as a showcase played a role in the research planning.

That has changed considerably, for the better. There is more tree planting and more need for improved varieties. Also, in eight northeastern states the state universities support tree breeding research, most of them hoping for practical results. Inevitably the applied research is funded more adequately than theoretical research, so is apt to produce more results, both theoretical and applied.

EASTERN WHITE PINE

At this point I would like to mention accomplishments in specific trees. Eastern white pine immediately comes to mind. Next to the poplars it has received the most attention. The largest experiments are the cooperative provenance tests started by the Forest Service in 1957 and by the University of Maryland a decade later. The Forest Service results have been summarized by Garrett et al (1973) and by Demerritt and Kettlewood (1976), the Maryland results by Genys (1968).

In these experiments certain seedlots grew well wherever planted over a wide range of test conditions. Trees from Pennsylvania and Massachusetts were among the leaders in northern plantations; trees from the southern Appalachians were among the leaders in all southern and mid-latitude plantations. These results are of great practical importance. In every part of the region growth rate increases of 10 to 25% can be obtained by using something other than the native seed most commonly planted in the past.

The results are especially important for Virginia. Trees from that state grow less rapidly than trees from farther north or farther south. Virginia foresters can make especially great progress by using out-of-state seed.

In many parts of the region damage from the white-pine weevil is a greater problem than slow growth. Unfortunately, little progress has been made in selecting and breeding eastern white pine resistant to this pest. There were statistically significant but nevertheless unimportant differences in resistance in the Forest Service provenance test. Similar results were obtained in half-sib progeny tests conducted in Michigan.

There is hope, however, as Ron Wilkinson is reporting at this meeting. He located western white pines (seemingly from northern Idaho) with acceptable growth rate and a high degree of weevil resistance. They offer a satisfactory resistant variety for immediate planting in the heavily infested areas such as New York's southern tier of countries.

While this research has produced practical results in the form of faster growth, it has also changed our way of thinking. When the Forest Service experiment was being planned in the summer of 1955, most of us thought that the results would fall into neat little mathematical packages. We assumed that by testing trees from 31 different parts of the natural range in a network of 12 test plantations we would obtain a set of data which could be analyzed in such a way as to show the probable performance of any particular seedlot in any particular locality. The aberrant performance of the Virginia trees came as a complete surprise. They did not conform to the general north-south clines and could not be explained in terms of climate or inbreeding. They showed that there was no substitute for empirical experimental data.

As already mentioned, there was a notable tendency for certain seedlots to grow well wherever planted over a wide range of test conditions and for others to grow poorly at all places. This lack of interaction also came as quite a surprise, and gives us new insights into the process of natural selection.

A quarter century ago it was standard practice to use large plots containing 121 to 200 trees and to have a few replications. That practice was expensive and scared many researchers off any form of field testing. It was decided that the Forest Service plantations should follow three different designs, all using small plots. Success of these designs had a profound effect on field testing procedure throughout the world and on the role of provenance and progeny tests in tree improvement. They were found to be simple enough to be considered as an integral part of the selection process.

THE LARCHES

Dave Cook of New York pushed Japanese and European larches. He planted them on his own property at Cooxrox and converted all who would listen into larch enthusiasts. As a result, the annual planting rate has exceeded the million level for many years in New York. Considerable 4
numbers have been planted in Pennsylvania, also. Few of these plantations were established with seeds of the best races, and none were established with the offspring of selected and progeny tests trees. At this point in time, those lacks are not so important as the fact that thousandE of acres of larch were planted on a variety of sites in the two states The network of plantations provides New York and Pennsylvania with a large amount of data on site preferences, pests, yield tables, thinning regimes, etc.

Japanese and European larches grow faster than any of our native conifers. They are valuable as sources of poles and pulpwood. The ability to use them in a rational manner is a big step forward. The next steps, leading to genetic improvement within the species, are underway. There is the Fox Forest provenance test of European larch, reported upon by John Genys. That experiment showed the best seed to come from a portion of Czechoslovakia. There is a limited amount of provenance to ing of Japanese larch. The state of Pennsylvania has made an excellent start on developing Japanese larch seed orchards.

These starts on genetic improvement are not enough, however. Just as Dave Cook was dedicated to pushing larch regardless of difficulties, a program devoted to larch improvement regardless of difficulties is needed to produce the next giant step. European foresters have shown the way for European-Japanese larch hybrids and Japanese foresters have demonstrated the value of Korean-Japanese larch hybrids for northern areas. A full-scale followup of that hybrid work in this region could not help but produce large gains. Individual tree selection and progeny testing deserve more than token effort. The factors affecting seed production must be studied if the seed orchards are to become as productive as we would like them.

HYBRID POPLARS

The year 1923 saw the start of the Oxford Paper Company hybrid poplar project in Maine and the Eddy Tree Breeding Institute at Placerville, California. These were the first two places in the United States to undertake tree improvement as a full-time activity. As firsts, they had great influence on tree breeding activity throughout the world in the next 30 years. Therefore I want to mentions some of the ways in which the poplar work influenced other research.

A few years after the start of the hybrid poplar project, A.B. Stout and E.J. Schreiner established a large test plantation near Rumford, Maine. Other test plantations followed in the late 1930's, and a comprehensive series of clonal tests was established from 1947 to 1951. Establishment of those test plantations was a difficult and expensive task and took time away from the study of poplar genetics. At the time those field tests were spoken of as Ernie's poplars, but I think it well to consider them as among the pioneer hardwood plantations in the region. I would guess that two-thirds of our pre-1960 information about successful hardwood planting came from the poplars.

Stout and Schreiner quickly found that different species of poplar could be crossed rather easily and that some of the hybrids grew very well. Their hybridizations were the forerunners of others to come by poplar breeders in Canada, Austria, Italy, Korea and Argentina, to name a few places. The vigor and the ease with which the hybrids could be produced focused attention on species hybridization as an improvement method in other genera such as pine, spruce, ample and eucalypt.

When Schreiner started his big clonal testing program in 1947 he used a randomized complete block design with 16-tree plots and four replications. That was an innovation at the time. To those involved in establishing the plantations, this was the first exposure to a recognized, statistically adequate design.

The hybrid poplars grow rapidly, root easily from cuttings and sprout prolifically. The easiest way to reproduce them in large numbers is to plant young trees, cut them back to the ground annually, harvest the sprout growth and cut it into suitable lengths, and use those cuttings to establish plantations. That has been the practice for 50 years. Change a few of the phrases to "cut every 3-4 years" and "use the sprout growth for pulp or fuel" and one has the description of short-rotation forestry. As a matter of fact, nearly all the short-rotation forestry now being considered for the northeastern quarter of the country is basically an extension of the hybrid poplar research.

With a few seasons crossing work, Stout and Schreiner produced thousands of hybrids belonging to 99 different species combinations. They did the crossing work in New York, producing hybrids for use in Maine, and made the original selections in the latter state. Some of the hybrids, particularly those having P. deltoides, P. caudina and P. charkoviensis as parents are very satisfactory in Maine and other parts of the Northeast. On the other hand, the hybrids have not grown as well as native non-hybrid poplars when tested at other places such as Stoneville, Mississippi. I can think of three lessons to be learned from those facts: (1) Hybrid poplars can be produced easily, (2) some are useful if produced from well adapted parents, and (3) poplar breeding should be more than the testing of one set of clones produced a half century ago. Perhaps the poplar breeder might want to concentrate on selecting well adapted parents and crossing them, then turn to testing the hybrids.

The research has taught us other things about poplar breeding. The clones are uniform enough that inexpensive small-plot experimental designs can be used for field testing. The cottonwoods and balsam poplars are generally propagated clonally and have traditionally been subjected to clonal selection. However, family selection has a place as well and could reduce the cost of testing by 90%. Nearly all the promising hybrids belong to two or three of the 99 families included in the original test plantations; the rest of the families might as well be dispensed with. There are strong enough age-age correlations that considerable gain can result from selections made as early as age 5, but not at age 1.

The first half century of poplar breeding has produced many valuable clones. I run into them even in Michigan. However, I have the feeling that we are only on the threshhold of success and that we should use the lessons from the past to make even more rapid progress.

WHITE SPRUCE AND BALSAM FIR

Most of the work on white spruce has been done cooperatively with agencies in Canada and the Lake States. The results have benefited all taking part in the research. Chief among the experiments is the range-wide provenance test started by the Institute of Forest Genetics at Rhinelander and reported on by Nienstaedt (1969) and by Genys and Ninestaedt (1979). This is a classic example of an experiment showing almost no interaction. The same seedlot, No. 1633 from the Ottawa Valley, of Ontario, grew best wherever planted in the Northeast, Canada or the Lake States. This is an important advance for Maine, one of the states with the most active reforestation programs.

Balsam fir is another species in which the cooperative approach paid big dividends. The provenance test originally started by Don Lester of the University of Wisconsin includes plantations in Vermont. Unlike the situation in white spruce, there was a great deal of interaction, the best seedlots in Vermont differing from those which were best in other places. For Vermont conditions, two Vermont stands, near Granville and Ripton, produced the best offspring. That result, combined with the Vermont work on fir culture, gives that state a good start on the production of balsam fir for Christmas trees.

BLACK CHERRY

Among the quality hardwoods, black cherry has received the most attention in this region. Most of the genetic work has taken place during the past 15 years in West Virginia, Maryland and Pennsylvania. Considering the short time span, the results have been good. One of the largest experiments is a 25-origin provenance test. In this test there were important growth rate differences and indications that considerable increase in productivity could result from the use of non-local seed in some localities. There were also easily recognized and important differences in branchiness, particularly at early ages.

A start has been made on plus-tree selection and progeny testing. The selections were made in Pennsylvania and West Virginia. At age 12 it looks as if the gains from selecting good parents within a stand are about the same as from choosing the better of the two geographic origins. Admittedly, this initial work was on a small scale, but it sets the stage for rapid progress in the next few years. It shows that definite progress will result from a combination of individual-tree selection and stand-progeny testing.

Hardwood planting is in its infancy and the black cherry test plan tations are among the first hardwood plantations in the region. Most were successful from the planting standpoint. I think that is equally as important as the genetic data themselves because it means that cherry planting and improvement can go forward together.

HYBRID PINES

I would like to say a few words about hybrid pines, having been associated with them for so long. From 1937 to 1955 a great deal of crossing work was done in the region. That and the work at Placerville laid a good theoretical foundation about crossability patterns and genetic relationships among species. Enough crosses were attempted to give a very good idea as to the possibility of success from any particular species combination.

The hybrids have been tested during the past quarter century. The results have been disappointing from the practical standpoint. Most hybrids have turned out to be intermediate in growth characters and cases of usable hybrid vigor have been rare. Of the several dozen combinations under test, most are of scientific interest only. The three with some promise are the pitch loblolly, Austrian-Japanese red and eastern-western white pine combination.

There has been progress, however, in the way we look at species hybridization as an improvement tool. For many years we followed the corn model, looking for heterotic F_1 hybrids which could be mass produced. That view is changing because relatively few F_1's are worth planting and because F_1 mass production is rarely realistic. Attention is now turning to the F_2 and later generations. Many of the hybrids have flowered, producing fertile seed. Limited work with the F_2 and backcross generations shows that segregation is not so great as was expected. It now seems as though we should get from the F_1's to the F_2 and later generations as quickly as possible. As of point of interest, Pennsylvania state nurseries are now selling F_2 Austrian X Japanese red pine hybrids in limited numbers to the public.

Slim Gerhold at Penn State has done considerable work with interracial hybridization in Scotch pine the past 15 years. As was the case with the species hybrids, most combinations showed intermediacy, none having useful hybrid vigor. Growth rate of hybrids was influenced almost as much by the individual parent tree as by the racial combination. This work gives us a new look at racial hybridization as in improvement too. It should be used primarily as a method to generate variability, from among which selections can be made in the F_2 and later generations.

LOST OPPORTUNITIES

It is not good to pretend that everything has gone along as it should. There have been lost opportunities. The most obvious ones concern trees with pest problems.

The chestnuts furnish an example. Breeding work has been going on for nearly a century, ever since Van Fleet's first crosses. American chestnut is a rapid grower with desirable wood properties and the ability to attain large sizes on infertile ridge tops, but it lacks resistance to the chestnut blight. The Japanese and Chinese chestnuts are orchard-type trees which produce good nuts but are of little value for timber; they are resistant to the blight. Most species can be crossed with each other and the hybrids are fertile enough to use in crossing programs.

Given those facts, it is reasonable to assume that 90 years of breeding could have produced a blight resistant timber type tree capable of replacing American chestnut in our forests. That is not the case and the prognostication for the future is not good. Some hybrids and varieties of the Asiatic species are available for those who want to grow nuts but there is no satisfactory replacement for timber-type chestnuts and little work toward that goal is now underway. There is little hope that we can once again grow chestnut for lumber unless the disease dies out.

Turning to conifers, it has been 25 years since the discovery that western white pine is more resistant to the white-pine weevil that is eastern white pine. The two can be crossed easily. The western species is susceptible to blister rust damage and starts off slowly but can grow rapidly in later life. There are rust-free localities well suited to the western species in the Northeast. Nevertheless we do not have a weevil resistant white pine variety ready for planting although the possibility is there.

Why were such opportunities lost? I can think of two principal reasons. There was a failure at the outset to take a good hard look at the problem and design a course of action capable of reaching the goal. For the chestnuts there was no one to say, "Even if it takes 10 generations, I will keep selecting and testing until I get hybrids combining blight resistance with the desired growth characters." Also, we were often not critical enough. There was a tendency to hope that the occasional slight evidences of progress would some time change to world shaking conclusions.

I mention these lost opportunities not so much to be critical as to make a challenge for the future. Twenty five years hence will we say,"Unfortunately there is no replacement for the thousands of acres of red pine lost to the New York strain of Scleroderris," or "The trees replacing red pine in New York are growing even better than it did?" Many other questions of a similar nature can be asked. I hope we will get positive answers to all of them.

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