TEN YEARS OF PROVENANCE RESEARCH AT MICHIGAN STATE UNIVERSITY AND THE NEXT STEPS IN TREE IMPROVEMENT

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Michigan State University's first provenance test was started in 1958, a little more than a decade ago. Tests in three more species were started in 1959. Others have been added until the list of species covered now totals 28. There are such experiments in eight species of pine, six of elm, three of spruce, two each of larch and the true firs, and one each of Douglas-fir, poplar, birch, cherry, walnut, arborvitae and oak. Some were started by Michigan State University. In other cases we received planting stock or seeds from outside the State. Almost all the experiments are part of the NC-51 regional tree improvement project and involve cooperation with others.

The decision to place major emphasis on provenance research was based on the supposition that the major portion of the genetic variability in any species is associated with geographic origin of the seed and that some superior nonlocal types could be found.

Genetic differences among trees originating from different parts of a species' range have been very large in Scotch pine, jack pine, ponderosa pine, southwestern white pine, Douglas-fir, white spruce, and white fir. In each of these species there have been two-fold or three-fold differences in growth rate between trees from different geographic areas. There were equally striking differences in other traits such as foliage color, hardiness, leaf length and terpene composition. In fact the list of variable traits is governed mostly by time available for study.

Important but less marked differences were found in another group of species. Eastern white pine trees from Tennessee and southern Ontario grew 10 to 20 percent faster than trees from more northern areas in southern Michigan plantations. (Southern Appalachian trees were not suited, however, to the northern Lake States.) Austrian pine from Greece outgrew the more commonly planted Austrian variety. Yellow birch from the southern Appalachians leafs out later than more northern types but so far in the Michigan tests all types have grown equally fast.[1] Differences in growth rate were minor in Japanese larch but trees from Mt. Fuji produced cones earliest and trees from the northeastern part of the range were slightly more hardy than others.

The provenance research has uncovered virtually no differences in two species only. Many years ago Paul Rudolf and Ashley Hough of the USDA Forest Service established red pine experiments in the Lake States and Pennsylvania. The trees are now more than 40 feet tall. According to the last measurements, the best and poorest origins were almost alike. We have a younger study which includes more origins but the results are the same. Northern white-cedar may fall into the same category. Scott Pauley sent seed from all parts of the range. The seed germinated well and produced an excellent nursery experiment. The origins were indistinguishable at age 3.

Most experiments include several different plantations, often in different States. When

1 *Results of a Wisconsin test of the same material is discussed in the paper by R. M. Jeffers on page 18.*

possible, the same seedlots were planted in each plantation. Generally speaking, an origin which grew well in one plantation grew well at many other test sites. For example, eastern white pine from Tennessee grew most rapidly when planted in North Carolina, Tennessee, southern Michigan, and Iowa; white pine from the southern parts of the Lake States grew well when planted in several parts of the northern Lake States. This tendency was much more pronounced than was the tendency for the local origin to be superior. Seed procurement rules must constantly be revised as the provenance experiments provide data.

Reliability of the Results

The following practical recommendations can be made for tree planters in southern and central Michigan. Similar lists can be made for other areas.

When planting this species	*Use seed collected from natural stands in these areas*
Eastern white pine	Tennessee, southern Ontario
Scotch pine	Spain (for Christmas trees) Belgium and northern France (for fast growth)
Red pine	Most parts of range
Jack pine	Michigan's Lower Peninsula
Southwestern white pine	Central parts of Arizona and New Mexico
Ponderosa pine	Eastern Washington and Oregon
Austrian pine	Parts of Greece
White spruce	E. Ontario, S. Manitoba, also parts of Wisconsin and Michigan
Douglas-fir	Northern Idaho or central parts of Arizona and New Mexico
White fir	Central parts of Arizona and New Mexico
Japanese larch	Almost any part of natural range

The red and jack pine recommendations are based on 18 to 30 years growth in plantations of the North Central Forest Experiment Station. The others are based on much younger experiments and further results can be expected soon from experiments which are now very young. How reliable are such data?

A student, Warren Nance, studied this question during the past year. He remeasured our oldest plantations of Scotch pine, ponderosa pine, and eastern white pine. The nursery data on growth and hardiness were excellent indicators of future growth rate. As it turned out, our tentative recommendations at age 2 were almost as good as our most recent ones. The jack and red pine stories have changed little with increasing age. Few surprises have been forthcoming in other experiments up to 8 years old.

Pest damage complicates the picture, however. Several insects are now active in 10-year-old Scotch pine plantations, and a wait will be necessary to learn the resistance of different varieties. A 15-year wait may be necessary when selecting elms for disease resistance.

Time has not helped cure mistakes made in the nursery. If uneven germination or uneven watering produced uneven seedbeds, the experiment is still uneven and relatively unproductive of results after a lapse of 5 to 10 years. Similarly, the results of poor weed control or poor planting are nearly as evident now as the year after planting. The moral is clear — do an excellent job from the start.

Upsets in Theory

Theory also received a great deal of attention. A decade ago I hoped that the provenance research would lead to a very clear understanding of the processes of genetic formation of races and clines, and that with such an understanding we would be able to forecast what would happen under any set of circumstances. The answers are still far from good.

As of 10 years ago there were theoretical generalizations that races from warm climates grew fastest and that races from cold climates were hardiest. Both generalizations proved true in general, but there are some very embarassing exceptions. Eastern white pine from warm Virginia grows more slowly than does the same species

from colder Pennsylvania and New York. The parental stands in Virginia were not selfed, were not on particularly cold microsites, or on poor soils. In the grand-white fir complex of the Rockies, grand fir from high elevations in northern Idaho suffered extreme winter injury (in southern Michigan) whereas there was no such injury on white fir from Arizona or on Douglas-fir and ponderosa pine from lower elevations in Idaho.

In each of four Rocky Mountain species an Arizona-New Mexico race grew rapidly and was distinct from races to the north. Migration between these races was inhibited by a wide treeless barrier. And in each of the four species the slowest growing trees came from Utah. But there the similarity in patterns ended. Selection pressure operated to produce a large amount of genetic variability within the Colorado population of Douglas-fir whereas there is little difference between Colorado and Alberta limber pine. Different responses to the same selection gradient were also evident in two European species. Spain produces Scotch pine with exceptionally short and dark green needles; Spain produces Austrian pine with exceptionally long and yellow-green needles.

Theoretically, 24 origins of white spruce, well scattered over the entire natural range, should cover the gamut of genetic variability in the species. Not so. We planted Hans Nienstaedt's white spruce experiment at Kellogg Forest in southern Michigan and used border stock of unknown origin (probably some place in Wisconsin or Michigan). The border trees have been unique in producing many cones and suffering heavy attack by a gall aphid although the crowns have not yet closed.

Progress on cause-and-effect relationships has been slow. There is as yet no good explanation for the resistance of the Ural Mountain variety of Scotch pine to the black-headed pine sawfly, for the earliest flower production on slow-growing sources of eastern white pine but fast-growing sources of Scotch pine, or for the high content of four different elements in the foliage of the coastal variety of ponderosa pine.

These problems are challenging, not frustrating. Evolution has been complex. Much more work is required before we can forecast whether a genetically unknown species will behave like eastern white pine (considerable geographic variation) or red pine (almost no geographic variation), the effect on height growth of a genetic increase in nitrogen assimilation rate, or whether the genetic variation in a particular region will be continuous or discontinuous.

Many of these theoretical questions have important practical implications and need solution. In general the solutions will come only from further experimental work because there are too many gaps in existing population genetic theory.

The Future

Insofar as Michigan is concerned, the job of starting large range-wide provenance tests is nearly completed. Maintenance and measurement will continue on those now in the ground, but I believe that most of the important results will be forthcoming in the first 10 to 15 years of each experiment.

An interdisciplinary approach promises to be successful in the solution of some of the theoretical problems mentioned earlier. Dr. Hanover is bringing his physiological talents to bear in some of the provenance experiments and is studying differences in terpene chemistry, photosynthetic rates, and other internal characteristics. He hopes to learn why some of the trees are fast growing. This would help when attempting to breed new trees for specific purposes.

The provenance experiments were preliminary and were meant to point to best regions from which to obtain trees for more intensive breeding work. Two followup experiments have been started in eastern white pine. Seeds were collected in 1960 from 125 single trees located in various parts of Michigan; seeds were collected in 1964 from 170 single trees or stands in the southern Appalachians. Similar progeny tests have also been started in jack, red, and Scotch pines.

These followup experiments have already yielded some information on local variation patterns and on the amount of genetic variability in important growth traits. Differences among stands have generally been more pronounced than differences among trees within stands. The correlations between characteristics of the parents and of their offspring have been disappointingly low. Thus, the practicing forester interested in

good seed for the immediate future need not practice stringent selection in his cone collection work. And the tree breeder interested in a better strain for the future needs to progeny-test his selections.

For the past 3 years Dr. H. D. Gerhold of Pennsylvania State University and I have been using one plantation of the Scotch pine provenance experiment as a breeding arboretum. We have made crosses between distinct varieties, hoping to produce hybrids with hybrid vigor or with a combination of the best characteristics of different varieties. The crosses are easily made but we still have to wait for the results. Much more of this work will be done as other species flower.

The provenance experiments also offer new opportunities in hybridization between species. Many successful hybrid combinations are now known. Among them are Japanese red pine X Austrian pine, Japanese red pine X Scotch pine, eastern white pine X western white pine, Japanese larch X European larch, Japanese larch X Korean larch and white spruce X Engelmann spruce. Average parents were used to make most of the hybrids available now. Even so, many exhibit desirable growth characteristics. It is virtually certain that even better hybrids can be produced by crossing selected types of the parental species.