The NC-51 Provenance Tests

by
JONATHAN W. WRIGHT

Department of Forestry
Michigan State University
East Lansing, Michigan

It is flattering to the NC-51 committee to be asked to play a large part in the program of this meeting of the Central States Forest Tree Improvement Conference. It is also appropriate to publicly summarize our progress at this time because this is the project's fifth year. The work needs careful appraisal, both publicly and privately, so that the next five years can be even more productive.

The NC-51 committee is composed of one forest researcher from each of ten state agricultural experiment stations in the North Central region. These members are: Illinois—J. J. Jokela; Indiana—Clair Merritt; Iowa—Gordon Gatherum; Kansas—Paul Roth; Michigan—J. W. Wright; Minnesota—Scott S. Pauley; Missouri—R. Brooks Polk; Nebraska—Ralph A. Read; Ohio—Howard B. Kriebel; and Wisconsin—Donald T. Lester. There is an administrative advisor—Robert W. Hougas of the Wisconsin Agricultural Experiment Station; a U.S. Forest Service representative—Hans Nienstaedt of the Northern Institute of Forest Genetics; and a Cooperative State Research Service representative—Philip N. Joranson of Washington, D. C. One can speak legally and say that the committee meets once a year to settle items on its agenda in an approved manner. One can also say that the committee is a friendly group which has functioned as a unit in promoting a sound provenance testing program which would have been beyond the reach of the individual states.

Regional projects such as this are organized under an amendment to the Hatch Act. That act, passed in 1886, provided federal support for agricultural research in experiment stations in each state. An approved regional project should tackle important problems. The problems should have significance to more than a single state and be of such a nature that they are handled best on a cooperative basis. Financing is meant to be adequate for cooperative phases of the work, but reliance is placed upon state funds to carry the work to a point of practical application within a state.

This, as the name implies, is the 51st regional non-marketing project in the North Central region. It is the first devoted to forestry science. It was activated July 1, 1960, although plans were formulated during a 3-year period prior to that.

Provenance testing was chosen as the main feature of the first 5 years' work for several reasons. Variety is characteristic of the region's planting program. A dozen species are planted in quantity in the Lake States, and a different dozen may be planted in the Corn Belt and Great Plains. From what little was known before 1960 it could be surmised that all species were geographically variable (red pine being a major exception). Data on that point would provide the easiest means of upgrading the general quality of planting stock. But the amount of such data would be many times greater than could be obtained from a series of independent studies. It was considered, too, that provenance tests would be basic to several other types of tree improvement work to develop later in the region. For example, a plus-tree selection program can be most effective if concentrated within the general population known to have the most favorable characters. And the tests might serve as breeding arboreta for later production of hybrids among selected races and selected species.

Another important consideration in the emphasis on provenance testing was its adaptability to the cooperative approach. A good test takes months to organize but only a few days to plant. Why not extend the applicability of the good tests by planting and measuring them in many different areas? Also, seed procurement is often costly in terms of goodwill and one should not impose year after year on the same seed collector's to organize essentially the same test for different areas.

This is not the place for a general summary of tree-breeding activities within the region. Agencies other than the members of this committee are doing important work. Also, several individual members have varied state programs, either implementing or separate from their NC-51 activities.

Species Covered

Range-wide provenance tests have been started in 12 species: Scotch, red, European black, and ponderosa pines (*Pinus sylvestris* L., *P. resinosa* Ait., *P. nigra* Am., *P. ponderosa* Laws.); tamarack and Japanese larch (*Larix laricina* [Du Roi] K. Koch, *L. leptolepis* Sieb. and Zucc.); balsam and white firs (*Abies balsamea* [L.] Mill., *A. concolor* [Gord and Glend.] Lindl); Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco); eastern cottonwood (*Populus* *deltoides* Bartr.); and northern red oak (*Quercus rubra* L.).

Horse-trading, using the NC-51 material for barter, brought other good provenance studies into the region. Thus, several members also participate in tests organized by others, particularly by the U.S. Forest Service, the University of Maryland, and the Petawa Forest Experiment Station. This is true for 10 additional species: jack, eastern white, Virginia, interior ponderosa, and limber pines (*Pines banksiana* Lamb., *P. strobus* L., *P. virginiana* Mill, *P. ponderosa scopulorum* Engelm., *P. flex ills* James and *P. strobiformis* Engelm.); white, red, and Norway spruces (*Picea glauca* [Moench] Voss, *P. rubens* Sarg., *P. abies* [L.] Karst); yellow birch (*Betula alleghaniensis* Britton); sugar maple (*Ater saccharum* Marsh.); and yellow-poplar (*Liriodendron tulipifera* L.).

In assessing species priority we were governed first of all by current importance. Thus, most conifers planted in quantity are now covered. Plans are underway to remedy a few deficiencies such as eastern redcedar (for Great Plains windbreaks) and blue spruce (increasingly used as a Christmas tree). Another factor was ease of working. Tests such as these demand good planting success, so that the hardwoods have not received as much emphasis as their importance warrants. The first 5 years was too short to consider another important factor. Use of the material in future species hybridization would be much enhanced if collections of nearly related crossable species were also available. Thus, for the future, we also hope to cover Himalayan and western white pines (to be crossed with eastern), lodgepole pine (to be crossed with jack), etc.

Each state followed its own self interest and proposed work on species of interest to it. Those finally chosen were of interest to at least three other states; and some are being tested by 9 of our 10 members.

Lessons in Planning Provenance Tests

The NC-51 provenance studies are similar in having range-wide coverage, relatively intense sampling, and field tests scattered over a wide variety of site conditions. All three features proved desirable. Origins from unlikely localities frequently are promising—too promising to limit sampling to a narrow belt around the probable place of use. Also, the first thinning promises to be easier if a few "automatic failures" are included in the form of origins from far-away places. Collections from 100 areas• scattered over a species' range has been the goal for each species. That goal was achieved in three cases but not in others because of poor seed years. Where range sampling was that intense, the experiments have given the most results. The Japanese larch experiment shows best the value of having many test plantations. Of 20 established in 1960, some failed because of poor choice. Nevertheless there are enough successful ones that the experiment is productive. Already Wisconsin, Michigan, and Nebraska data are different, showing that one or two plantations would not have been sufficient.

From 2 to 6 months work over a 2- to 3-year period were required to initiate each large test. This included letter writing, thank you notes, seed extraction, and putting the origin data in good form. These origin data were placed in an accession record, of which 125 copies were mimeographed and widely distributed to all who might have future use for the data. Distribution of the accession record has already proved itself by furnishing every cooperator full data before he planted the trees.

From 1960 to 1963 planting stock for each experiment was raised in a single nursery, then distributed by express to cooperators in other states. Shipment by surface carrier was often unsatisfactory. Now, long-distance telephone calls and air shipment are used at surprisingly low cost and uniformly favorable results.

At first, stock was raised to plantable size, then distributed for immediate planting. There were timing difficulties and seedlings which did well under some conditions did not do well under others. Hence, we currently recommend that stock be lined out for one year prior to field planting.

Growing of the seed in two or more nurseries from seed to transplant size has proved relatively costly and not greatly advantageous. Most of the NC-51 nurseries are located far from the tree breeder's office, and the planned duplicate nursery studies have not materialized.

Experimental standards have been raised since 1960. At that time it was felt that any provenance data might be useful—almost any test plantation would give results. That no longer seems to be a legitimate goal. We know that most species are geographically variable and must find the details of the variability pattern. This requires survivals of 90 to 95 percent and making all trees start uniformly under weed-free conditions. With good choice of site and modern weed-control techniques that proved possible—even easy. As a matter of fact, extra care to promote good growth has usually paid for itself by reductions in measurement time and statistical analysis.

Small-plot, many-replicated designs characterize the NC-51 experiments. Otherwise it would have been impossible to test as many origins or as many localities as seemed desirable. The small plots are more efficient than very large ones but we do not know whether they give information applicable to stand conditions. As it turns out, this is relatively unimportant because a large percentage of the data from each experiment will accrue by age 15, before competition becomes severe. That appears to be the case in eastern white pine where, as Dave Funk will report, southern Appalachian origins show exceptional promise at age 8. Thus, a more intensive study of southern Appalachian material will quickly supersede the initial, range-wide experiment.

Although most of the useful information will come by age 15, it was desirable to plan that each test plantation be permanent. This meant planting on publicly owned land, wide enough spacing (slightly wider than the best commercial practice) to avoid too-early thinning, and a record system designed for permanence. In cases where those precautions were not followed, the useful life of the plantations promises to be even less than the desired 15 years.

Traditionally, provenance tests have been regarded as ends in themselves. They would show which origins grew best in a given locality, and then have little more use. Could they also serve as breeding arboreta; reservoirs of material for detailed chemical, physiological, or resistance studies; or as seed orchards? This is feasible, but only if planned beforehand. For example, flowering is required in a breeding arboretum. This means wide spacing and provision for adequate cultural and fertilizer treatments. Testing for wood quality means increment borings and perhaps cutting trees. Special plantings dedicated to such study provide the best solutions.

Possible Solutions to Measurement and Analysis Problems

From two to six months were spent planning and initiating each provenance test. The outplantings required two to four weeks on the part of each cooperator. Those are reasonable times but do not produce results, which come only when the plantations are laboriously measured.

An immediate boon to record keeping was the realization that only plot means need be recorded. In the past, individual-tree measurements were written down. This necessitated much extra writing and office work before the meaningful part of the analyses could be started. By recording only the plot means and partially summarizing the data while still in the field, the worth of each set of measurements could be judged while there was still time to make new ones.

Another immediate boon to record keeping was the design of a record system which would be complete and yet relatively easy to maintain. The fundamental principles were that a bound record folder would be prepared in advance for each plantation, every plot would be given a line, empty columns would be used as needed to keep the data on single traits, all data would be recorded in numbers such as could be analyzed directly by computer, all summaries and analyses would be bound within the folder, and there would be easy means of duplicating all pertinent results within a few days of their being gathered. Every cooperator's record system differs slightly in detail, but those who have used care in planning have found their measurement and analysis time can be reduced by 50 to 90 percent.

The tests have been studied comprehensively while in the nursery, and several have been measured since outplanting. The primary purpose was to obtain information on the trees' biology. However, another type of analysis is also being made, the purpose being to eliminate routine measurements which do not produce their quota of worthwhile information. James P. King found that three or four Scotch pine plantations gave 95 percent as much information as nine plantations in three states. Results from four low-mortality European black pine plantations were easy to analyze and included nearly 100 percent of the information. that could be obtained from some additional plantations in which mortality had been heavy. Some sets of data are used only to show which origins are the tallest (or greenest); that could be told just as well by noting the tallest (or greenest) plots in a few replicates in each test. Work in this general area can point the way toward the elimination of 75 percent of the data gathering which has been considered essential in the past.

Time saved on routine work can be spent on new problems of fundamental importance. The desire to analyze foliar chemistry of Scotch pine brought a new look at experimental procedure. Each 13-element analysis costs $4.20, and there was enough money for 222 such analyses. There were 108 origins, up to 10 replicates per plantation, and 20 test plantations. It was obviously impossible to make 108 x 10 x 20 = 21,600 analyses. The problem was solved by judicious bulking of the sample material to give reliable estimates of origin means, plantation means, and error term needed to test the significance of origin x plantation interaction. Perhaps only 90 to 95 percent of the possible information will be recovered, but that seems a good trade.

Concrete Results to Date

I will confine these remarks to a few species not covered by others on the program. One is Scotch pine, in which seed procurement started in 1958, nursery study took place from 1959 through 1962, and permanent test plantations were made in 1961 and 1962. First stock distribution included 108 origins, each representing several trees in a native European or Asiatic stand. That was supplemented by late distribution of an additional 62 native-stand progenies. Successful NC-5l outplantings were made in seven North Central states from Indiana and Michigan westward to Missouri and Minnesota.

The nursery study indicated the presence of 14 more or less distinct races or ecotypes. The degree of their genetic separation was correlated with the degree of their geographic isolation within the native range. A concomitant taxonomic study by John L. Ruby showed that the geographic distribution of the races could be learned by study of the climates and phenotypes of the native Eurasian stands, but most of their growth characteristics in America could not be learned by such study. Also, within a race, Ruby found it difficult to forecast genetic characteristics from study of the parental phenotypes. All of which indicates that the provenance-testing approach is the most direct way to obtain genetic data on geographic variation patterns.

The Belgian-north French-west German collections are of special interest to Scotch pine timber growers. These trees were the fastest growing in the nursery, and continue to excel at age 6. That accords with observations made in earlier IUFRO tests in New Hampshire and Europe. However, Belgian material was very crooked in the IUFRO tests whereas it is still straight in much of our area. The probable explanation lies not in inherent crookedness but in inherent response to leader or bud damage. Where the external agents causing leader or bud damage are not present, the trees are straight.

The Spanish race is of special interest to Christmas tree growers. It is short needled, of relatively slow growth, and without winter discoloration. Also, although tap-rooted, it survived best in all test areas, indicating superior ability to regenerate damaged roots. This is the only race which has suffered winter damage, in central Michigan, northern Wisconsin, and northern Minnesota.

Previously the Greek-Bulgarian-Turkish population of Scotch pine was scarcely known in America. It has a medium growth rate, dark green winter foliage, and coarse branches. Trees from these places appear hardy and a useful addition to the Christmas tree growers' planting plans.

Inadvertent inclusion of material from two English plantations shows the possibility of interracial hybridization. According to British plant geographers, Scotch pine is not native there; so the original seed must have come from elsewhere. The characteristics of the progeny and British thought both point to a hybrid origin between Scottish and German types. The two progenies are uniform and quite vigorous. They are either F_1's (unlikely) or a stabilized third-or fourth-generation segregate.

Along with the provenance stand and its stand-progenies, 140 open-pollinated progenies from single trees (mostly Belgian an d German) were grown. The variability shows that, once we decide on the best race, considerable improvement is still possible. The data also give many useful hints as to how to go about that next stage of improvement.

Probable differences in resistance to insect pests are now evident. During the past two years four southern Michigan Scotch pine plantations were infested with European pine sawfly. Incidence of attack varied from 0 to 50 percent (the differences are highly significant). Supplementary feeding tests showed that the preference was at the oviposition rather than the larval feeding stage. Growth rate has something to do with the preferences—the taller origins were attacked most. There were significant exceptions to this general trend, however. Those exceptions indicate the presence of a chemical or anatomical preference factor and also indicate the possibility of breeding a fast-growing resistant variety. A heavy white-pine weevil attack on a central Michigan plantation led to similar conclusions for that insect. Attack varied from 0 to 75 percent and there were significant exceptions to the general height-attack trend.

The foliar chemistry work on Scotch pine is being done by Klaus Steinbeck. The relationships uncovered are not simple. There are geographic trends for most elements but the trends are not in accord with known growth data. For example, high nitrogen and low nitrogen are found respectively in the Scandinavian and Spanish races. Both have equal growth rates and the latter are by far the greener. Thus this work will have to be continued to delve more deeply into the interrelationships between mineral nutrition and growth responses.

Prior to 1960 there was little seed-source information to guide the very large Scotch pine planting program within the North Central region. The NC-51 data are better than none at all and are already being used to guide planting practice. As a matter of fact, there have been few changes in relative performance between age 2 in the nursery and age 6 in the outplantings. Hence, it seems possible to place relatively great confidence in data gathered during the first decade and proceed rapidly with further improvement measures.

The high correlation between the earliest nursery data and later performance is evident in some other species. It suggests a worthwhile improvement in experimental procedure. Relatively little effort is required to test hundreds of thousands of progenies in the nursery but outplanting is another problem. Why not test very many things, and outplant the 10 or 20 percent showing the most promise?

The Japanese larch experiment includes 7 origins distributed in 1961 and 22 (including the above 7) distributed in 1962. The same experiment was conducted simultaneously in Germany. German-American correlations were low as regards growth rate, high as regards date of growth cessation and associated traits. The species' natural range is small and the total range of genetic variation was much smaller than in Scotch pine. In the Wisconsin and Nebraska test plantations significant growth differences are present whereas in other areas the growth differences are too small to be significant. Because of the small range of genetic differences the percentage of the total variance attributable to plantation X genotype interaction is relatively high.

The Japanese larch test plantations have special promise as breeding arboreta for the production of Japanese-European hybrids, which are so promising in Europe. In 1963 one origin bloomed well in Nebraska and in the following year another one in Wisconsin. It appears that the production of test hybrids can start quickly.

The third species distributed in 1961 was European black pine. The material was intensively studied in the nursery and shipped as 2-0 stock. Only a few of the 14 test plantations are successful because of deficiencies in packing and delays in planting. Also, the experiment includes fewer origins (27) than is desirable in view of the large natural range (Spain to Turkey and southern Russia). Even so, one outstanding practical fact emerges. Of the hardy sources, Austrian pine is among the slowest growing. That shows what can be done by introducing new types because Austrian seed had hitherto been used almost exclusively in this country.

In the nursery only two types of European black pine could be recognized with any certainty—Corsican (curly-needled, winter-tender) and non-Corsican. Now, by age 6, a third type can be distinguished—the Spanish trees have different foliage color and different foliar arrangement than those from farther east.

An anatomical study of the species is underway by Carl Lee, using foliage and twigs collected from the test plantations. This supplements earlier anatomical studies based upon wild European phenotypes. It may also straighten out the confused taxonomy. Over 100 Latin epithets have been applied to all or parts of European black pine during the past two centuries and a thorough look at that synonymy is overdue.

As with Japanese larch, use of the European black pine test plantations as breeding arboreta is eagerly awaited. Interspecific hybrids with Japanese red or possibly Scotch pines will be among the first crosses tried, using selected known-origin trees for both female and male parents. In 1964 30 female flowers were found on trees of 6 origins in Ohio. During the past season two trees on every 4-tree plot in one test plantation were given a fertilizer-weed control treatment with the object of hastening flowering.

Simultaneous experimentation with a number of species is bringing to light facts not apparent within a single species. That is true as regards European black and Scotch pines. They parallel each other north of the Mediterranean, the Scotch pine occurring at the higher altitudes. Strangely, few parallel trends are evident in the provenance tests. For example, the Spain to Greece to Turkey trends in foliage color and leaf length are reversed between the two species, indicating that it is necessary to have a long new look at the evolutionary factors responsible for genetic differentiation.

The Future of the Project

June 30, 1965 will mark the end of the first five years of NC-51, and a renewal or new project. The most urgent needs as regards initiation of range-wide provenance tests will have been met although trees now in nurseries will be planted and cared for just as during the first five years. Routine work has been simplified, and there will be opportunity to study our collections more intensively. Thus there will be a change in emphasis away from recording of obvious growth differences toward learning the meaning of the differences.