Lessons from a One-parent Progeny Test in Scotch Pine

by

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I should like to discuss the lessons learned from a one-parent progeny test of Scotch pine (Pinus sylvestris L.) conducted recently. These lessons are from the first three years of the test and which is to run for a full generation.

From one standpoint the three-year data are weak. There have not been enough studies of juvenile-mature correlations to enable us to forecast with certainty that the tallest seedlings will make the tallest mature trees. There was no opportunity to study bole form because all the trees were straight in the nursery. Only time will tell which progenies are best for the long run.

From another standpoint the data are strong. They show the patterns by which genes are grouped in natural populations and are inherited. For many purposes it does not matter that these genes affect seedling stages. In fact, for many purposes it does not matter to which traits these patterns apply. It might be just as well to call them traits 1, 2, and 3, in stands A, B, and C.

EXPERIMENTAL PROCEDURE

In the autumn of 1958 Norwegian, Belgian, and East German researchers sent the Michigan State University Forestry Department open-pollinated seed from their countries from 140 different Scotch pine trees located in nine stands. Twenty East German and all 30 Belgian seedlots were from plantations. The 10 Norwegian and remaining 80 East German ones were from native stands. The same investigators sent large quantities of data about the growth rate, form, needle length, etc. of each parent.

The seed was sown in MSU's Forest Research Nursery in the spring of 1958. A modified randomized complete block design with four replicates was used. The modification consisted of keeping all 10 or 20 progenies from a single stand together within each replicate. This caused an apparent accentuation of within-stand as compared to between-stand variation. There was full randomization of the stand groups within replicates and of the single-tree progenies within stand groups.

Each plot consisted of a single 4-foot row containing about 40 trees. The rows were 6 inches apart and the average density was 20 trees per square foot. This was lowered to 10 trees per square foot at the start of the third year. The seedbeds were watered frequently and maintained in a weed-free condition. The soil is a fertile one. Growth was uniform and two to three times as great as in most commercial seedbeds.

Intermingled with the single-tree progeny test was a range-wide geographic origin study established at the same time. This is mentioned because it permits comparisons of the size differences found among single-tree progenies, among the offspring of different stands in the same region, and in the species as a whole.

At the start of the third year some trees were lifted and placed in five permanent outplantings in Minnesota, Illinois, and Michigan. These are to be followed until maturity.

A total of 43 complete sets of measurements was made. These could be grouped into data on a dozen different traits, of which six were found to be genetically variable within stands. Some sets applied to the same trait measured at different times or to different manifestations of the same trait. Each set was subjected to analysis of variance. Because of the very large differences between Norwegian, Belgian, and East German trees, the data for each country were analyzed separately. In these analyses plot means were used as items. All possible inter-character correlations were also calculated for each of the nine stands, using progeny totals or means as items.

BACKGROUND -- THE OVERALL GEOGRAPHIC VARIATION PATTERN

Scotch pine is a very widely ranging species, occurring naturally in most European countries as well as in most parts of Siberia. It is composed of a number of geographic ecotypes. These are of varying size. The Scottish one comprises a few stands in northern Scotland whereas the German-Czech one includes the populations native to Czechoslovakia, Rumania, and most of Germany.

These ecotypes are of varying distinctness. The populations from northern and southern France are so different that it is easy to identify single seedlings on the basis of any one of several traits; so also with the populations from southern Sweden and northern Germany, or with those from Greece and northern Italy. On the other hand, the genetic break between the German-Czech and the Pfalz-Vosges-Belgian populations is not sharp. On the average, the latter is the greenest, tallest, and longest-needled, but there is some overlapping between the two in all these traits.

These ecotypes are not miniatures of the species as a whole. The geographic trends and the inter-character correlations which one finds when studying progenies from all over Europe are not evident when one studies the progenies from a single region. For example, if one considers only the Scottish or only the German-Czech there are no significant inter-character correlations or correlations between characters and particular properties of the parental habitat.

In almost every trait there is a tremendous range of genetic variation from one end of the species' range to the other: a four-fold range in height; a two-fold range in needle length; a range from yellow-green to blue-green in autumnal color; and a 3-month range in time of first-year bud set. The range of genetic variation within an ecotype or within a single stand is much less, from 5 to 20 percent of the range in the species as a whole. It is this 5 to 20 percent which is applicable when discussing the improvement of an ecotype by selective breeding.

LESSONS APPLICABLE TO SELECTIVE BREEDING

In selective breeding I shall include all those phases of tree improvement having to do with selection, grafting, progeny testing, or crossing of individual trees within an ecotype. It is assumed that there has been a previous provenance test to outline ecotypic boundaries and to permit selection of the proper ecotype to use as a basis for further improvement work.

The lessons learned from these progeny tests apply directly to seed production areas, grafted seed orchards, or one-parent progeny-test seed orchards. The lessons have limited applicability to the problem of one-parent (using open-pollinated seed) versus two-parent (using control-pollinated seed) progeny tests or to the problem of genetic improvement in succeeding generations.

Feasibility of practicing selective breeding within a local population. -- Is there enough genetic variability within a single stand or small group of stands to justify starting a selective breeding program within a geographic ecotype? The answer is a definite yes. Among the 20 single-tree progenies from a stand near Nedlitz, East Germany there were statistically significant differences (5 or 1 percent levels) in growth rate (not attributable to differences in seed size), first—year foliage color, time of bud set, bud diameter, percentage of trees with branched buds, and time of formation of secondary leaves. Among the 20 single-tree progenies from a stand near Gu-trow , East Germany there were significant differences in four of the same traits. In every one of the nine stands three or more traits were proven to be genetically variable. It is fair to assume that differences in wood quality, branch size, or needle chemistry would also be found if those traits were to be studied.

When differences were found, they were large enough to be economically important. For example, the seedlings from tree 279 in southern Norway were 26 percent taller than the mean of all seedlings from that stand.

Desirability of testing progenies from single trees or bulked stand progenies. -- In both the East German and Belgian populations there were significant differences in height among single-tree progenies from the same stand. However, the within-stand variation was relatively small compared to the between-stand variation. A forest near Pijnven, Belgium yielded the three tallest half-sib families in the experiment. They were 7 percent taller than the average for all Belgian seedlings. A stand near Nedlitz, East Germany yielded 20 half-sib families, every one of which was taller than any of the 20 families from a stand near Neustrelitz, East Germany. The Nedlitz stand yielded the four tallest East German families. They were 8 percent taller than the stand average and 16 percent taller than the all-German average.

When attempting to breed for increased growth rate it would be much better to start with tests of bulked progenies from a large number of different stands than to concentrate at first on testing progenies from single trees within one or a few stands.

The pattern was not the same for all traits. There was considerably more between-stand than within-stand variation in the East German population whereas the reverse was true for the Belgian one. In both populations there was considerable within-stand variation in time of secondary needle formation whereas the differences between stands were negligible. Improvement in the latter trait could come only from the testing of single-tree progenies, which might equally well be derived from one or from several stands.

Phenotypic selection of parents or stands before progeny testing. -- The East Germans sent us tables containing 14 columns of information about every seed parent.

The Norwegians and Belgians also sent us abundant parental data. However, this information proved to be of no use in forecasting the relative performances of the progenies in southern Michigan. The fastest growing progenies were not from the tallest parents, nor were the long-needled progenies necessarily from long-needled parents. The stands which exhibited the greatest amount of genetic variability in height growth were not those with the greatest amount of phenotypic variability among parents.

This lack of parent-progeny correlation means that attempts to establish seed production areas or grafted seed orchards for the production of seed to be used in Michigan would have failed to result in an appreciable amount of genetic improvement. The results of progeny tests in Michigan would have been the only satisfactory means of determining progeny performance in Michigan.

The lack of parent-progeny correlations can be partially explained by three factors: growth of the parents and progenies under different conditions; mature data for the parents and juvenile data for the progenies; and the great amount of environmentally induced variablity found in most older stands. Possibly higher correlations could be expected if the parents and progenies were grown under the same conditions, as would be the case when working with most native species. However, the lack of correlation cannot be ignored because it points up the fact that parental selection is not a guaranteed method of starting a seed orchard or breeding program.

Selection for one, two, three, or more traits. -- Considering the 10 Norwegian progenies, family 279 was 26 percent above average in height growth, slightly superior in first-year winter foliage color retention, and average in other respects. Family 277 was 9 percent above average in growth rate and had significantly longer needles. Simultaneous improvement in height and first-year color by the selection of family 279 is possible. Simultaneous improvement in height and leaf length by the selection of family 277 is also possible but would mean a reduction of 17 percent in the selection differential for height. Simultaneous selection for three traits would fail.

A breeder working with the 30 Belgian half-sib families would achieve a selection differential of 8 percent in height by using all progenies from stand 531 - 540 (located near Pijnven) or of 15 percent by selecting families 532, 538, and 539. Simultaneous improvement in two traits could be obtained by selecting progeny 539, which was 13 percent above the Belgian average in height and slightly greener (one-half the least recognizable color difference) than average on 28 October 1959. The remainder of the outstandingly tall trees were average in other respects.

A breeder working with the 100 East German half-sib families would achieve a selection differential of 8 percent in height by using all progenies from stand 381-400 (located neat Nedlitz), or of 16 percent by selecting families 385, 390, 392, and 395 from that stand. The progenies from that stand also had outstandingly long needles. It would be possible to achieve a significant amount of improvement in height and needle length but not in height and other traits or in needle length and other traits.

Much the same story can be told for other combinations of traits.

Number of progenies on which selection should be based. -- Among the 10 Norwegian families, family 279 was markedly superior in height growth and average in leaf length. Family 283 had the longest needles but was far below average in height. Selection of one of these families would have assured improvement in one character or the other, but not in both. If a breeder demanded improvement in both these characters (not in any two), it would be necessary to raise approximately 10^2 (or 100) half-sib families to achieve the same amount of superiority in both as was achieved in either one individually. Similarly, concentrating on three traits would require the testing of about 10^3 (or 1000) families.

In these Norwegian calculations the danger of inbreeding was not taken into account. Theoretically one should start a several-generation improvement program with about five superior progenies. Otherwise inbreeding can become so severe after three or four generations as to result in serious inbreeding depression. Hence, if the work is to serve as the basis for a several-generation project, the 10, 100, or 1000 families quoted in the above example should be multiplied by 5 to become 50, 500, or 5000 families needed for 1-, 2-, or 3-character selection, respectively.

There were four outstandingly tall progenies among the 100 tested from East Germany. This is almost enough to form the basis for a several-generation height improvement project. Several hundred would have to be raised to obtain the same amount of improvement in height and another trait as was obtained with height only from the present sample.

Trustworthiness of heritability calculations. -- Family heritabilities were calculated from the expectation mean squares by the formula

$$\text{Family heritability} = h^2_f = \frac{s^2_F}{s^2_F + s^2_S + s^2_e/4}$$

in which s^2_e, s^2F, and s^2_5 are the variance components for error, between-family (within stand), and between-stand variations, respectively. These estimates apply to data from progeny tests replicated four times; they do not apply to single trees.

The family heritabilities for 2-year height were 0.315 and 0.255 for the East German and Belgian populations, respectively; for second-year winter color they were 0.633 and 0.362, respectively; for leaf length they were 0.000 and 0.675, respectively. In other words, a heritability calculated for one population was not necessarily true for another population. This was especially true of estimates made for progenies from single stands. In that case they varied from zero to very high in every trait.

These calculations illustrate the fact that heritability estimates must be made and used with caution. They apply strictly to the populations and test conditions for which they were made. Estimates based on analyses of the progenies of a few trees in limited areas apply to those areas but bear no relation to the picture in a large region or in the entire species.

Ease of establishing progeny tests. -- Progeny testing has long been recognized as desirable but has been avoided because of the supposedly large amount of work involved. Our experience with this test indicates that the work can easily be done by a station with good nursery and outplanting facilities. Of course, this experience was limited to a one-parent test in a species in which successful plantations are easy to establish.

Inthis test the time chargeable to seed procurement was negligible. A few man-days sufficed for sowing of the seed and care of the stock. With machine-planting at the rate of 4000 to 5000 trees per tractor day, the permanent test plantations could be established in a few days. So far measurement and analysis have represented a few-manweeks. Of course,the measurement time would have to be increased if one were interested in internal properties such as wood density.

This particular species fruits rather early. Nine seedlings produced male flowers at the start of the second year, and several flowered in their fourth year, 1962. It is estimated that there will be sufficient fruiting by 1963 or the year after to start controlled pollinating work in earnest. If so, a second-generation, two-parent test could be started, using the present test as a foundation.

The relative ease of establishment is mentioned because it affects the possibility of doing similar work with other species. This test, like any other single one, gives partial answers, but the answers are real, not hypothetical. And these real answers can lead to real improvement at a very reasonable cost.