

RECENT PROVENANCE TESTS IN SWEDEN

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Why do we continue provenance studies when so much progress has been made in other fields of tree improvement? Is it not because such trials are among the best and simplest methods of uncovering forms of intra-specific diversity as determined by habitat diversity. Once populations have been identified in a broad way by provenance experiments, plus-tree selection and other refinements such as inter-provenance hybridization can be followed for further development.

Why has provenance research been so active and productive in Sweden? Partly because the two native tree species exhibit great variability and extended habitat range, and partly because seeding and planting came into practice very early, following the German influence, and because natural regeneration was slow and uncertain.

Attention was first drawn to Scotch pine (Pinus sylvestris L.), from the beginning the more important species commercially, when direct seeding with German seed resulted in crooked trees and greater susceptibility to needlecast (Palmcrantz 1855; Sjögreen 1877). The First International Union Provenance Tests of 1907 have been followed by numerous others right down to this day, recently concentrated on correlations between adaptive variability and climatic conditions and phenology. That interest in this field which has continued and intensified is also partly due to the increase in clear-cutting and planting in Sweden, as well as other parts of Europe, and, indeed, the USA, and partly from the determination of industry to improve the productivity of trees.

From the beginning of this century the question has been: how far can seed collected in one place, be moved, north or south, or up and down a slope with impunity, i.e. without decrease in frost and disease resistance, rate of growth, etc. At one time it was assumed that local seed was always the best and safest because local populations were supposed to be best adapted to the site through thousands of years. However, there was always the intriguing possibility that some other than the local provenance might be superior in growth (as the German pines often were, though poor in quality). Furthermore, seed crops are irregular and when a local crop fails, can seed from another region be used? This was studied and argued for decades by Wibeck '31, Schotte, Eneroth '26, Langlet '36, '57, '68 and others, and many schemes of zones and patterns proposed. Merely to enumerate them would be a lengthy matter; suffice it so say that provenance tests formed the basis for these studies. What of the present situation?

First as regards Scotch pine---emphasis on zones for moving seed have now given way to intensified provenance research in the north of Sweden, and attention to seed orchards and progeny testing in the south. Phenological observations in provenance trials are considered of equal or greater importance than measurements of growth. The annual rhythm of growth, when and how it starts in the spring, and when the plant goes into dormancy can be of critical importance. This rhythm is strongly genetically controlled. However, the rate of growth can be very

different in plants with the same growing period. Variation within a provenance can result in a certain group of trees having the same phenology as the average of another provenance either south or north of the one in question. This insures that some individuals will survive during extremely unusual climatic conditions.

Recent tests in Southern Sweden (south of Lat. 59°) showed no significant difference in mortality among 20 provenances, but rather great differences in rate of growth and quality between the best and the worst provenances planted in 6 different locations (Remröd '72). A large part of the difference could be attributed to clinal and/or latitudinal tendencies. Not infrequently movement to the north gave taller plants compared to the local provenances---the movement not being great enough to involve problems of frost-hardiness.

Departure from the mean of a latitudinal regression expressed the individual character of a provenance (Eiche '66). Thus the progeny of the "best provenance"...an average of all the different test locations, exhibited a greater height than it should have produced from the influence of latitude alone. The conclusions from these and other investigations are that movement of Scotch pine seed within Southern Sweden leads to no untoward consequences, and secondly that the soundness of the other facets of the tree betterment program---selection of plus trees, progeny testing and seed orchards is confirmed. This program seems to be well on its way to improve quality and productivity.

An entirely different picture is presented in Northern Sweden (north of the above-mentioned parallel). The essential problem here is to find trees that will survive at all, especially on the large clear-cut areas that have rendered the already harsh environment all the more severe. Formerly, reliance was placed on natural regeneration of northern forests; indeed, the high mortality of planted seedlings discouraged anything else. Partial cuttings failed to produce the hoped-for pine, and spruce took its place. Spruce was less desirable for timber, and it was believed to shade the ground too much, retard decomposition of humus and nutrient cycling. Furthermore, mechanization and labor shortages and costs favored large clear cuttings especially on company lands. Why wait 20 to 50 years for an infrequent seed year to restock a clearing when planting could accomplish it immediately? But plant with what? The old zones for safe movement of seed were not always reliable. The provenance question became a matter of survival---for the companies as well as for the trees.

Survival of seedlings after planting was found to decrease as one moves north, and differences among provenances become wider. Survival became the dominant factor in provenance testing. It was found that early results could be deceptive, and that mortality continued to increase for 20 or more years after planting. A high survival rate was not so important with the old, close spacing that used to be practiced, but now, to reduce plantation costs and eliminate the need for thinning, it has become fashionable to set trees at a far wider spacing. This means that one cannot afford to lose trees and come up with a fully stocked stand, which alone can raise productivity on these near-marginal northern lands.

Local provenances were believed to be the best adapted and safest to use; but these local provenances varied in survival after 20 years from

71% near the 59th parallel of latitude to 50% in central Norrland and in the northernmost station for commercial forestry 25% (Remröd op. cit.)
Surely this will not do, and some better provenance must be found.

The most northern provenances, that survived best in this experiment had an increasing proportion of plants with a growth period enabling them to survive in severe climates; but if this growth period is too short, actual growth may be so poor that the trees are worthless economically. The problem is to weigh the requirement for hardiness against that for good growth per tree. Some provenances slightly north of each test site have produced 20% more volume than the local provenance (just the reverse of the case in Southern Sweden) and also in Northern Sweden. When provenances slightly south of the test site were tried they produced less than the northern ones. As Eiche and Gustafsson ('70) have concluded, length of growing season is the criterion for survival capacity, and transfers from harsh to slightly milder climates give better survival. But there are cases where local populations seem to be hardier than any others. Exceptions do exist.

To summarize the situation for Scotch pines: in Southern Sweden the objective is to select the most productive provenances, and then refine them with all the genetic techniques; while in Northern Sweden survival is the critical factor, and the way to increase forest production is to get fully stocked stands 20 years after planting, and not be misled by first-year survival.

Norway spruce (Picea abies (L.) Karst.) presents a totally different picture. It survives better than pine in the north (although pine is found farther north than spruce at the tree limit) and southern seed can be moved north and lowland seed to higher elevations with less risk of mortality; frequently southern sources produce better growth than local ones. Twenty-three different sets of provenance studies confirm this (Remröd et al., '72).

It is well to digress a bit in order to better understand this behavior. As the Pleistocene ice sheet withdrew from Southern Sweden, pine was among the earlier pioneer trees and it advanced slowly all the way up the Scandinavian peninsula, developing into progressively hardier and slower-growing ecotypes, the average of each population better adapted to its own habitat than its neighbors. This differentiation was typically clinal as Langlet has shown.

Spruce on the contrary, invaded from the east and north through Finland, and the progeny of exceptionally hardy northern races slowly made its way south in the period following glaciation. By the time of human settlement, which had moved northward behind the ice, and by the time the country became cultivated, spruce had reached a point little south of Stockholm by natural spread. These invasion routes have been confirmed by pollen studies, so that the advance of each species can be roughly dated (Moe '70). Accordingly, as long known, spruce in Southern Sweden has been solely of planted origin, and since most of the seed was collected in the northern and central part, it was of relatively slow-growing type. The result of this type of migration route is that Swedish spruce is "over-hardy" at the expense of growth rate. Not only does

northward movement of southern provenances within the country improve growth where frost-hardiness is maintained, but spruce from the Hartz Mountains in Germany, and from Poland and Czechoslovakia has outstripped Swedish spruce in growth and maintained this superiority in stands as old as 60 years (Langlet '60).

Kiellander ('70) has recently summarized 30 years of provenance tests of spruce in Southern Sweden, with special attention to frost-hardiness. He concluded that spruce also has a clinal type of variation, but a discontinuous variation as well because of its adaptability to extreme conditions locally. The superiority of central European sources to Swedish ones was confirmed. In an average of 7 different series of tests, 21 years old, Swedish trees had 91% of the height and 86% of the diameter of progenies of "continental spruce" planted on the same sites.

These recent revelations from provenance tests pose some important questions for practical forestry. As Remröd (op. cit. 72) remarked at the close of his lecture: "Perhaps the solution to the pine provenance problem in Northern Sweden is spruce."

What lessons for us can be drawn from all these experiments, and experiences? Our commercial species have no doubt less variability, reflecting the less pronounced habitat differences in their ranges, but how well do we know the more subtle variations that are not apparent? It would appear prudent to reexamine them in greater detail. Provenance tests should continue to be a basic starting point in a tree improvement program.

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