

GEOGRAPHIC VARIATION IN FOREST TREES: ITS GENECOLOGICAL EVALUATION AND APPLICATION IN BREEDING AND SEED PRODUCTION

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SELOSTE:

METSÄPUIDEN MAANTIETEELLINEN VAIHTELU: SEN GENEKOLOGINEN
ARVIOINTI JA SOVELTAMINEN JALOSTUKSEEN JA SIEMENHUOLTOON

Geographic variation of genetic characteristics of forest species has drawn the attention of forest scientists for more than a hundred years. From the incidental experiments with provenances researchers gradually became more concerned with genecological studies on tree species. This work was later on pursued by more and more scientific enthusiasts and nowadays it is included in the national and international scientific research programmes. At present, research and practical utilization of the geographic variation of genetic characteristics of forest species is one of the basic lines in the strategy of forest tree breeding and seed production. This approach to tree breeding and seed production is followed in many countries of the world including the USSR. It is also connected with the growing intensification of forestry in these countries.

In the past, when artificial forest regeneration was carried out in small plots, scientists in the USSR traditionally used seed which was procured from local tree stands. Nowadays, when planting takes

place on millions of hectares but without permanent forest seed bases having yet been established in every region of the country, local seed is not enough and it is necessary to secure it from other geographical regions. In order to eliminate the possible negative consequences of this kind of seed transfer it is necessary to study the geographic variation of the genetic characteristics of forest trees and construct a scientifically based division into seed zones.

Until now, the basic task in making this kind of division has been the preservation of the productivity, quality and viability of the stands which have been raised from seed imported from other regions, when compared with local stands. Experimental information both from the Soviet Union and from abroad indicate that stands surpassing the local stands in some economically valuable characteristic, e.g. increment, may be raised from the seed of some geographic regions. Consequently, geographic transfer of seed must also be regarded as a breeding measure. In de-

limiting forest seed production zones the possibilities of raising the productivity of stands as a result of utilizing seed from other regions must also be taken into account.

Research along this line is especially promising in the Soviet Union, where the main forest species have extensive ranges, consisting of varying geographic conditions and creating a well defined differentiation of genetic characteristics within a given range.

Direct transfer of seed of the best ecotypes can become an important method in forest breeding, but for breeding and seed production it does not ensure the utilization of all the genetically valuable potential of a species. As the experience of agricultural plant breeding shows, a successful solution of this task is possible on the basis of geographically and ecologically distant intraspecific crossings of forest species and an elaboration of the methods of obtaining seed from the first hybrid generation on a massive scale.

These are the main premises on the basis of which the direction and contents of the research in the field of geographic variation of forest species have been determined. The utilization of tree breeding and seed production results has developed systematically in the USSR since the beginning of the 70's. The work is being carried out according to the unified programme and methods worked out in VNIILM and confirmed by the Council of Forest Genetics, Breeding and Seed Production. Almost all the leading scientific forest research institutes and forest experiment stations in the country take part in the research.

Under international scientific agreements, co-operation in related research was begun in 1976 with Hungary and with Finland. This allows not only the widening of the geographical range of genecological research of tree species, but also gives new opportunities for the solution of breeding and seed production tasks facing scientists in each of the co-operating countries (including exchange of seed and cuttings of the best ecotypes, selection of optimal varieties for intraspecific crossings and the joint establishment of seed orchards for mass-scale production of hybrid seed).

The research programme to be carried out in the USSR includes: 1) the inventory and study of all existing provenance trials, 2) explanation of the factors determining the geographic variation of forest trees, 3) improvement in the determination of seed production districts, 4) establishment of new provenance trials with the main forest tree species, 5) development of the methods of mass-scale production of seed from distant intraspecific crossings. We shall shortly examine the main results of the research made on the basis of this programme.

As we know, the task of research into the genecology of forest trees is to find out the genetic factors of the geographic variability of species and to evaluate the genotype-environment relationship. This task is achieved by the experiments with provenances (which in the USSR are called «geographic cultures»), to see if they are representative enough as far as sources of seed or plot sizes are concerned, if they have been established at the same time in several geographic places using seed from well-known stands and if they are characterized by uniform growth condition within the experimental area. The research has shown that we have quite a large stock of provenance trials (basically with Scots pine, and some with oak, larch etc.) in the Ukraine, Byelorussia and the Baltic republics as well as in the southern, central and northern districts of the Russian Federation, the Urals, Kazakhstan and in Siberia. A great part of the provenance trials were established in the post-war years, but there are also geographic cultures planted in the years before the revolution. Unfortunately, many of them fail to satisfy the above mentioned demands. An effective method of genecological research of forest trees has turned out to be the study of clones (grafts) of different geographic origins which is taking place in some institutes of the country (in VNIILM since 1959).

As result of the research into provenance trials and geographic grafts, intraspecific variation has been established for all the studied species, in growth, quality of stem and wood, morphological characteristics, resistance to unfavourable environmental factors (e.g. low temperature, diseases), phenological development and other bio-

logical and economical characteristics. These differences are connected with the geographical origin of the seed and scions. They are manifested in a similar way in all districts covered by the experiment. This allows us to speak about the existence of geographical ecotypes as genetically determined units. At the same time, it has been shown that the establishment of geographical ecotypes as intraspecific taxons is a difficult task still to be solved. Clinal (gradual) variation in genetic characteristics within the bounds of a range is typical for all forest species. This fact excludes the possibility of having clearly expressed boundaries between geographical ecotypes (larch is somewhat an exception). The deciding role of climate is evident (especially the quantity of heat and moisture) in the formation of geographical genetic variability within forest tree species. For this reason, the populations of different geographical origin can be called climatic ecotypes, but it is better to confine oneself to the term «provenance», thereby deferring the question of the taxonomical classification of these populations.

The more favourable the climatic conditions for a given species in a seed and cutting production district and the higher the average site class of the stands in the district, the more intensive is the growth of progeny in provenance trials and in clone archives. It is evident that for the purpose of breeding and seed production, a transfer of seed from districts of optimal geographic conditions is desirable, and in general from districts where planted stands surpass the local ecotype in growth and quality. The extent of such transfers is determined by the climatic resistance of the ecotype under new environmental conditions.

The possibility of breeding on the basis of selecting the best ecotypes is confirmed by experiments. It has been established that stands can be raised from local seed which are among the best with regard to growth and quality. But as a rule, in all the studied provenance trials, there are some provenances from other districts which are superior compared with good (or superior) growth and quality. A practical solution of this problem is dependent on the development of methods for the rapid evaluation

of the resistance of climatic ecotypes, especially to low temperatures. At present, prolonged observations are needed in such work (in the range of 15–20 years).

Genotypic adaptation of woody plants to climatic factors, i.e. their micro-evolution, apparently cannot be explained only by natural selection. Suffice it to call attention to the fact that genotypic adaptation of, for example, Scots pine took place in a relatively short period after the last glacial period. Limited genetic variability of the original populations, low frequency and spontaneousness of mutations, polyphyletic origin of ecotypes, clinal variability of their characteristics, adaptability of natural populations and morphologically identical forms to the conditions of their current environment (temperature, moisture, seasonal variations) and other circumstances allow us to suppose that the rate and character of micro-evolution are conditioned not only by natural selection, but also by prolonged modifications. The study of the factors of microevolution should be one of the tasks of international experimentation with provenances.

In accordance with the results of the study of existing provenance trials the division of seed production districts has been defined more exactly. The starting point was that the division into seed production districts should, first of all, solve the task of organizing forest seed production on a genetic basis. Secondly, it should regulate the geographic transfer of forest seed for silvicultural purposes. According to these principles, a uniform division into seed production districts has been prepared for the whole territory of the country. Recommendations have also been made for the use of seed from other regions in the absence of local one (for pine and spruce). By seed production district we mean a certain area (usually within the administrative boundaries of regions, territories, autonomous and soviet republics of the USSR) with well defined natural and forestry characteristics. A regional standard is thereby set for the main organizational measures of modern forest seed production which include planning and project designing, material and technical provision, establishment and maintenance of an economically

valuable genetic pool, establishment of a permanent forest seed centre on a genetic basis; handling, storage and evaluation of seed; use of seed for afforestation and geographic transfers. The division into seed production districts has been made with due regard to local forestry administration. For each district and subdistrict there is a fixed number of species, which are included in forest seed production.

Recommendation for the use of seed from other regions have been made as a result of the clinal variation in genetic characteristics of woody species. These recommendations are summarized in a list of seed consumers (districts, territories and autonomous soviet republics or their administrative regions) and a list of districts, territories and autonomous soviet republics or their administrative regions from which it is possible to procure seed. This kind of structure in the recommendations contributes to planning the transfer of seed and the control of its execution.

The maximum distances of the geographic transfer of seed have been determined on the basis of an assured maintenance of the productivity and quality of stands when they are raised from seed from another region.

The existing provenance trials did not allow the recommendation of the use of ecotypes of other regions as a selective measure, although they did confirm its possibility. The existing provenance trials did not expose well enough the general regularities of the variability of genetic characteristics of forest tree species in the territory of the country. This is because they have been established in relatively few places, in different years, by different methods and they are represented by various and small collections of provenances.

Research has shown the necessity of establishing, in the USSR, a network of provenance trials of all the main forest tree species, as well as the definition of a standard procedure for this work.

In order to avoid the mistakes of earlier experiments it has been decided to work along the following principles in the establishment of a national network of provenance trials:

- 1) The places of seed production for provenance trials must reflect the variability of silvicultural and biological characteristics of woody species within the bounds of the whole range. Similarly, the places of the establishment of provenance trials must reflect the variability of forest growth conditions in all regions of its cultivation.
- 2) In all the places where provenance trials are to be established, the same population of a given provenance must be represented. Seed has to be produced in specially selected mature stands of the most common, economically valuable type of forest.
- 3) In the establishment of provenance trials the experiment must be repeated three times and the plot size has to be large enough (0.10—0.25 ha) in order to ensure the raising of at least 100 trees of each climatic region up to mature age.
- 4) A control culture from seed of the local climatic region should be established in every place where provenance trials are to be established and in every place where seed is produced.

The State Committee on Forestry has decided to establish provenance trials of *Pinus sylvestris*, *Picea abies*, *Larix spp.*, *Pinus cembra sibirica*, *Abies sibirica* and *Quercus robur* according to these principles on a total area of more than 2 000 ha. The trials include 800 ha of Scots pine in 37 places in the country with a representation of 126 provenances and 350 ha of spruce in 21 places with a representation of 58 provenances. At present, the programme of establishing provenance trials of pine and spruce has largely been completed and work is continuing regarding the establishment of provenance trials of the remaining tree species.

Unfortunately, due to unevenness of seed-bearing, the planned programme of pine and spruce provenance trials could not be fully completed. Seed of all the produced provenances are only represented in some places. Elsewhere, cultures are established on a regional basis. Samples of the pine seed and spruce seed used for the establishment of the national network of provenance trials in the USSR have been

sent for genealogical experiments to researchers in Hungary, Finland and the USA.

At present, tending is taking place in the established provenance trials. It should be noted that one of the basic factors determining the survival of cultures of different geographic provenance has proved to be resistance to needle cast disease.

Research on seedlings in simultaneous provenance trials over the area from the Murmansk region in the north to Azerbaijan in the south, and from the Baltic republics in the west to Khabarovsk territory in the east, showed a well defined differentiation in the phenological development, growth and condition of seedlings which was observed at all places of the seeding and in all the species in the experiment. Regardless of the experimental site certain provenance are found which secure better results in comparison with local seed, though usually (but certainly not always) local seedlings also turn out to be among the best ones. In the provenance trials it was clearly noticed that a deterioration of the growth of seedlings occurred as the place of seed production moved to the north or to the east. This corresponds with the character of geographic variability of the productivity of most of the woody species in the territory of the Soviet Union. Exceptions of this geographic rule are connected with a localization of high productive stands (for instance the Ob region pine forests in the Altai territory and in the Novosibirsk district). Dependence of the growth of seedlings on such factors as seed quality, geographic origin and the characteristics of seed collection stands has been analyzed. The dependence of seedling growth on genotype, whether being raised in one place or in several places, has been established. Of great interest for genealogical research is the exchange of experimental results from raising seedlings of pine and spruce of the same provenances in a number of places in the USSR and also in Hungary and in Finland.

Of equal importance for such an evaluation is the study of 100 clones of pine of 20 provenances (Altai Territory, Amur and Arkhangelsk districts, the Bachkir ASSR, Bryansk, Volynsk, Vladimir, Voronezh and

Koktshetavski districtes, Krasnoyarsk Territory, the Latvian SSR, Minsk, Murmansk, Orenburg, Penza and Sverdlov districts, the Tatar ASSR, Khabarovsk Territory, Cherkass district and the Yakut ASSR), which have been given to Hungarian and Finnish forest researchers and which also have been grafted in five regions of the European part of the USSR.

A simultaneous experiment with seedling and vegetative progenies facilitate the selection of the best ecotypes of pine for Hungarian and Finnish conditions, and in the long run makes it possible to arrange progeny tests with free pollination of the same clones (with pollen from local Hungarian, Finnish or Soviet populations), as well as with controlled pollination using the pollen of known provenances. In consequence, we shall be able to reveal the general characteristics of progenies obtained from distant intraspecific crossings of pine. We will also be able to select those crossing combinations which secure the outcome of a heterosis effect in the hybrid progeny. Before the beginning of seed-bearing in the established experimental plantations, we can make control crossings with the same clones in the USSR, using grafts made in 1964 and Hungarian and Finnish pollen and later raising the obtained hybrids in each of the three countries.

Common research with distant intraspecific hybridization will also be made in larch.

The existing experimental results suggest that a mass production of pine seed from distant intraspecific crossings in forest seed orchards is quite possible and expedient. This is proved by the phenological and genetic compatibility of pine clones with different geographic provenances and also with local populations. Further, valuable seed is obtained as a result of free crossing of different ecotypes. There are also promising results from the progeny tests of the received hybrid progenies.

Seed orchards for a mass production of hybrid pine seed can be established with technology which is quite realizable in conditions of forestry practice. This technology includes: selection of a geographic ecotype used for pollen production (male parent population), which is substantially superior

to the rogued ecotype (female parent population) in its indices; selection of the best stands within the pollen source ecotype; ground preparation for hybrid seed orchards within the bounds of these stands (in strips, 150–200 m in width; with strips of the original stand, 30–40 m in width, between the prepared strips); the selection of pollen-producing trees within the strips (removal of minus trees and a part of normal trees); selection of a large enough number of trees to be used as female parents within the designed female parent population; vegetative propagation of these trees by grafting; establishment of hybrid seed orchards by planting grafted trees of female parent population on the prepared strips within the male parent stand; taking measures contributing to abundant female flowering and delaying male flowering of the grafted trees in seed orchards.

Hybrid orchards established according to this technique will secure a high genetic gain, guarantee the maintenance of polymorphism of natural populations in the hybrid progeny, render good crops of hybrid seed possible and guarantee a high hybrid quality of seed during a sufficient period of time.

Using hybrid seed orchards an increase in the productivity of stands can be achieved, as well as an improvement of quality and resistance to unfavourable environmental factors (diseases, low temperature and so on).

The solution of the second problem is especially urgent in the region of optimal geographic conditions, where the stands are notable for their high productivity.

We have every reason to expect that hybrid orchards, which have been established taking into account the results of genecological research of forest trees and the results of the experiments on intraspecific hybridization will replace the conventional seed orchards in which the offspring of local plus trees is used as parent trees. This will happen since hybrid orchards allow the best use of the geographic genetic variability of forest trees for the production of genetically improved seed. The developing international scientific co-operation renders it possible to establish such orchards on the basis of intergovernmental co-operation and thereby to utilize the whole genetically valuable potential of a given species.

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Metsäpuiden maantieteellisen vaihtelun tutkimisella on suuri merkitys metsänviljelyn ja metsänjalostuksen kannalta. Kun laajassa metsänviljelytoiminnassa paikallista siementä ei aina ole riittävästi käytettävissä, joudutaan siementä tuomaan muualta. Jotta siemensiirroista ei koituisi haittavaikutuksia, täytyy luoda tieteellisesti perusteltu jako siemenvyöhykkeisiin. Siemensiirtoja voidaan pitää myös jalostusmenetelmänä. Kokeissa on todettu, että muualta tuotu alkuperä voi tuottaa paremman metsikön kuin paikallinen siemen. Tämä tutkimusala on erityisen lupaava Neuvostoliitossa, jossa tärkeiden puulajien levinneisyys ulottuu hyvin erilaisille alueille. Käynnissä onkin hyvin laaja tutkimusohjelma, jossa ovat mukana lähes kaikki tutkimuslaitokset ja koeasemat Neuvostoliitossa.

Suurin osa kokeista on männyn provenienssikokeita. Kokeissa on todettu lajin sisäistä vaihtelua

kaikissa tutkituissa biologisissa ja taloudellisissa ominaisuuksissa. Voidaan puhua geneettisesti erilaistuneista maantieteellisistä ekotyypeistä. Vaihtelu on kuitenkin kliinaalista, joten selviä rajoja eri ekotyypin välille ei voida osoittaa. Olemassa olevista provenienssikokeista saatujen tulosten perusteella on siementuottoalueet ja siemensiirtojen rajat määritelty entistä tarkemmin. Tulosten perusteella ei suositella vieraan alueen ekotyypin käyttöä metsänviljelyssä, vaikka viitteitä tällaisen menettelyn hyödyllisyydestä on saatu. Uusia provenienssikokeita varten on laadittu täsmälliset vaatimukset. Kokeita on tarkoitus perustaa yli 2000 ha. Kaukoristetyksiä saman lajin eri ekotyypin välillä pidetään jalostuksen kannalta hyvin lupaavina. Kirjoittaja esittää, että provenienssihybridi-siemenviljelyksiä pitäisi perustaa. Tässä toiminnassa kansainvälisellä yhteistyöllä on suuri merkitys.