THE ROLE OF GENETICS AND TREE IMPROVEMENT IN SILVICULTURE*

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Abstract

First part of the paper deals with some of the genetic principles which are related to silviculture. It was discussed the variablity and heritability as well their application to silviculture.

Emphasized was the cytogenetic work with forest tree sprecies. It isdiscussed, the polyploidy, production of haploid material and the problem of interspecific incompatibility.

The second part of the paper deals with two important problems of tree improvement which are closely related to silviculture. In the first one it is discussed what genetic improvement may be expected in natural stands and in the second one what genetic gain may be expected in plantations.

Introduction

This report is aimed at outlining the role of genetics and tree improvement in silviculture. The first part will deal with some of the genetical principles which are related to silviculture.

Many problems which are more theoretical are not mentioned here, because it was wished to outline the importance of genetics in present - day silviculture. In the second part, we wish to present the relationship between tree improvement and silviculture using two examples of growing trees : first in natural stands and the second in plantations.

I. Genetics in silviculture

Most forest trees possess the genetic variability, which is a reflection of the evolution towards their natural environment. In consideration of the specifity of such an object (forest or individual tree) the study of some genetical principles is not practical, but forsome other studies there exist anvantages as, for instance, in the study of migrations, because the trees remain in the population for a long period, and thus it is possible to evaluate in a reliable manner the whole population (LANNER 1966, WRIGHT 1962, LIBBY et al. 1969). In such cases genetic investigations using forest trees may yield experimental proofs or serve as a model. Genetic investigations on forest trees are also useful to us, because

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we become acquainted with genetical principles, as well as with possibilities of their application in tree improvement and silviculture.

For forest tree improvement and through this also for silviculture it is important to know how characters are inherited. The study of heritability gives us an insight as to what extent a certain character is under genetic control. The study of many characters in many species were calculated. HATTEMER (1963) has given a summary of these investigations. On the basis of heritability we may conclude what procedure in tree improvement should be. SCHREINER (1958) has summarized the possible improvement procedure as follows:

Genetical improvement (through selection and breeding):

Minimum number of branches, elimination of forst crackes, elimination of dormant buds, elimination of spiral grain, small fibril angle, fiber length, abnormal grain, other anatomical characteristics, penetrability.

Genetical improvement followed by some degree of silvicultural control:

Straight, single stem, minimum taper, small branch diameter, wide branch angle, stem-deforming agents, elimination of stain in living trees.

Genetical improvement and silvicultural control of equal importance:

Rate of height growth, rate of diameter growth, circular, concentric growth, maximum distance between internodes or branches, no epicormic branching, high or low density, tension wood, chemical composition and properties, mechanical properties, pulp and paper qualities, dimensional stability, machining and working qualities.

Silvicultural control plus genetical research to determine possibilities for genetical improvement:

Uniform height growth, uniform diameter growth, insect damage, uniform density, animal damage.

Silvicultural control:

Early pruning.

The assessment of the components of the population variance in forest tree species, as well as the assessment of the correlations between the characteristics is important not only to understand better the biology of a species, but also for the sake of improvement and eventually the most suitable method of growing. The estimate of the genetic variance and the variance of environment, likewise the estimate of the genotype - environment interaction give a good insight into the variability of a species, as well as into the degree of inheritance of individual characteristics. LIBBY et al. (1969) emphasize the need for understanding the relative importance of the genetic causes and of the environmental causes of the variation within trees, between trees, within stands and between geographical races for many characteristics and many species. Most of the past experiments were designed in the manner to examine only certain parts of this total architecture of the species, while the correlations of separate experiments were not taken into consideration.

Cytogenetic work in forest tree species is of importance in better understanding the particular taxa of tree species, in assessing the growth and other characteristics of polyploid individuals, and in producing artificially polyploids for improvement purposes. Under polyploidy we understand an organism having more than two sets of chromosomes. When an organism has other than an exact multiple of the haploid number of chromosomes it is called aneuploid. In silviculture most aneuploids are of little value, while the polyploids in certain species have a greater significance and may be in the future of great importance.

An increase in the number of chromosomes means also an increase of the nucleus and thus of the entire cell. The increasing size of the cells in polyploids is very distinctly visible in stomata cells and the pollen grain. Polyploid plants usually possess larger-sized leaves, flowers and fruits. In some cases polyploid plants have better growth than the diploid ones. In forest tree species there occur many examples of polyploidy. In Gymnosperms a much smaller number of polyploids is met with than in Angyosperms. Known are only tree natural polyploid species in Gymnosperms. They are: Sequoia sempervirens, Pseudolarix amabilis, and Juniperus chinensis var. pfitzeriana. In Angyosperms we find a much greater number of natural polyploid species of forest trees. We ought to mention but some genera: Acacia, Acer, Betula, Alnus, Salix, Fraxinus, Tilia, Morus, and others.

The polyploid forms of plants originate spontaneously in nature, but likewise it is possible to produce them artificially, i.e. if plants are treated with colchicine or certain other chemicals.

Similarly, it is possible to induce polyploidy by temperature shocks or by irradiating plants or their parts. Natural polyploids with 4n, 6n, etc. chromosomes are usually inherited, for in such cases each chromosome has its pair in the formation of bivalents in meiosis, while at 3n, 5n, etc. polyploids there is no regularity in the meiotic division, and sterility or heterogenous progeny occur frequently.

The study of polyploidy in forest tree species is very important not only from the theoretical aspect but also from the practical one. There is little chance in Gymnosperms to obtain favourable polyploid forms. Artificially produced tetraploids in the genera of Pinus and Picea are very disappointing from the silvicultural aspect. Somewhat more promising is the work on genus Larix. Very good results have been achieved in Cryptomeria japonica in which artificial tetraploids grow more quickly than diploids. The spontaneous polyploids of the aforementioned species, which were selected in the nursery, likewise exhibited a luxuriant growth (WRIGHT 1962). It should be stressed here that Cryptomeria japonica is very well vegetatively propagated, and there exists a possibility that the polyploid forms of this species be used in the future as clonal material for the cultivation in plantations.

In Angyosperms a well known triploid is Populus tremula f. gigas, which was found in Sweden. Some of the naturally and artificially produced triploids in the genus Populus have proved to be better than their diploid partners in respect to growth, resistance to diseases, and to some properties of their wood. Positive results were obtained in the genus Alnus, Ulmus and Betula.

In recent years special attention has been paid to the production of haploid material in tree species. LIBBY et al. (1969) emphasize that this is of interest not only for tree breeders for the sake of the production if diploid lines, but also for the study of the evolution of somatic mutations in forest tree species.

Many forest tree species can be crossed relatively easely, while others cannot. The problem of incompatibility in species crossing is a field of genetic research on forest tree species, which we consider important forbecoming acquainted with the causes of incompatibility, in order to overcome them. This requires familiarity with physiological and biochemical processes in the development of female and male gametophytes in order to understand the problem of incompatibility. Heretofore much was done in the study of physiological, anatomical and genetic aspects of incompatibility in interspecific crossing of Pines. KRIEBEL (1967) reports that the general pattern of incompatibility in the White Pines differs from that in the Hard Pines. In the White Pines there is no evidence of inhibition after the fertilization until the formation of embryo initials, while in the Hard Pines it seems that the pollen tube inhibition is the critical limiting factor. Irradiated pollen may be useful in overcoming genetic barriers that prevent crossing some species. Pollen given different irradiation treatments sould be used in attempt to cross incompatible species. The physiology of irradiated pollen may be altered sufficiently to overcome or prevent the formation of barriers (17).

The use of serological technic (5) likewise promises a progress in the solution of these problems.

These investigations may be significant for silviculture in that they may enable routine production of interspecific hybrids, which, heretofore, were produced with success only from time to time or found as a rarity in nature.

The geographical variability in forest tree species is of interest to both tree breeders and growers. Older experiments with provenances yielded in many cases valuable results as to which provenances are best suitable for definite regions, and how wide the transfer of seed is recommendable. Recent investigations proceeded in the direction to obtain by such experiments an insight into the variability of the genetic and physiological nature, as well as the variability attributable to the environment. It is understandable that such results have a much greater value for both the breeder and grower. Therefore it is very useful that the study of geographical variability and of provenance tests is carried out under the closest possible cooperation of the breeders and growers.

II. Tree improvement in silviculture

Here we do not wish to describe various different methods of improving forest tree species nor the advantages and drawbacks of individual methods, but to take into consideration only some problems which are of immediate interest for both the breeder and grower.

Surely, there exist more such problems than those dealt with here. One such problem which will not be discussed here is, for instance, seed production. We consider seed production to have been rather well discussed by way of published papers and at various consultative conferences. Therefore, it is perhaps better to put to the discussion some other problems, which likewise ought to be understood as well as possible, in order to find the right way for their solution. In my estimation these problems are the following:

1. What genetic improvement may be expected in natural stands?
2. What genetic gain may be expected in plantations?

Views presented here are frequently of general character and do not give experimental proofs. In some cases even we arrived at certain general formulations strictly by deductive reasoning. In addition, we consider that the aforementioned two general concepts should be worked out in details and thus give us a number of research probleme which should be further studied.

What genetic improvement may be expected in natural stands?

From the genetical aspect every natural stand represents a population, i.e. one part of a great population (subpopulation, local population). It is understandable that in such a population there exists genetic variability. If the evolutionary processes, including man, did not act upon the stand, the frequency of genotypes, i.e. its variability from generation to generation would remain the same. If the intraspecific variability is so great that a considerable genetic gain through silvicultural interventions is possible, then there exists likewise the possibiliti for a loss. We are interested in how man should act in order to change the frequency of genotypes in favour of those which are interesting for him, i.e. in order that he would realize the genetic gain. On the basis of the determination of existing variability, we are able to establish:

1. Whether it is a question of clinal or discontinous variability. Whether the races are concerned or not. If there exist a discontinuity of variability it is an indication that the races could exist there. If these variations are spatially delimited in a distinct manner, this is a safe proof of the existance of races.

2. On the basis of the established variability we may get an idea about the heritability of the investigated character. If the variability is of a discontinouns nature then the degree of heritability of this character may either be a high one, or this character is conditioned by a small number of genes. In

so far as the curve of distribution of frequencies of the investigated character is an asymmetrical one, the character is inherited dominantly, or the effect of the environment on the different genotypes is unever. Accordingly, from an analysis of data on the variability much can be concluded.

If we take into consideration that we already know much about the degree of genetic control of individual characters, our conclusions from the analysis of stands will be still safer. On the basis of theoretical formulations and the results obtained, we may conclude what tending interventions ought to be undertaken from the genetic aspect (16).

The thinnings of stands ought to be understood and performed not only as a tending intervention, but also as an intervention which will yield us a genetic improvement of the existing stands and those following. DORMAN (1969) states: ..." the silvicultural practices be developed that apply some of broad principles of intraspecific selection so that pressure will be against undesirable parental and racial stock and in favor of good stock". In this connection we should not deceive ourselves that we know sufficiently the biology of a species and its variability in order to be able to assess safely which individuals ought to be favoured in the stand. A very useful contribution was made in this way by MATTHEWS (1963). His paper explains which trees ought to be selected and favoured in the stand. As a general rule trees are selected for their effective and potential growth, health condition, stem and crown form, and ability to produce wood of the desired quality. Already, from these requirements in the selection of such trees, it is evident that it is difficult to perform a faultless selection because we still have not sufficient information on the basis of which we can proceed.

Exactly for that reason Matthews, work is valuable, for it gives us ideas about what should be like density of foliage, and seed production when we attempt to select the most efficient trees.

By heavy thinnings, in some cases, it is possible to realise also the genetic improvement, while in other cases this is not possible. Let us take, for instance, branchiness. This character is under high genetic control. If in a stand (population) the variability of the number of the branches is high, then by intensive, heavy thinnings, i.e. by selection against undesirable individuals, we shall realise an improvement in this generation and those following.

In the present generation improvement consists in the stand quality, which results after the thinnings, while in the generations following a small genetic improvement will occour. How high the genetic gain will be depends on the selection intensity i.e. on the frequency of desirable genotypes. If, in contrast, we have a stand which does not display a high variability for this character, and the number of branches per tree is great then heavy thinnings will not give a genetic improvement in the following generation, while the improvement of stand quality after thinning will be insignificant. In such a case one should decide oneself in favour of more radical measures, i.e. not to permit that the stand be naturally regenerated, but to perform a reforestation after felling.

It ought to be stressed that the analysis of variability, as well as the deciding upon the silvicultural interventions, which trough natural regeneration should yield a genetic improvement in the next generation, are only feasible in even-aged natural stands. It seems that the only possibility to obtain a genetic gain in the selection forests exist in performing clear cutting on small plots, and in undertaking afterwards a reforestation with a high quality planting stock.

Even aged stands should be closely observed already from their establishment. Plus variants should be marked and observed as they develop. Minus variants should be eliminated, so that finally the stand includes only plus and normal variants. By comparing several even aged stands of various ages, but which have grown under similar environmental conditions, we should receive more quickly the tentative data about the genetic variability, which can serve us well in planning certain tending interventions. It ought to be stressed that the obtained analysis are valid only for a definite caseand the conclusions should not be generalized.

In addition, it is also important to emphasize an idea, which was expressed by WRIGHT (1962) in his lectures: "Experimental evidence from short lived organisms has shown that response to selection frequently depends on the direction of selection.

Furthermore, most newly mutated genes, chromosomal changes, and recessives, have delaterious effects. Thus, it is reasonable to assume that the beneficial response to positive selection for a period of one or two generations is usually less than the unfavorable response to a similar period of equally intense dysgenic selection. In other words, a forest´s gene pool can be damaged easily than it can be repaired".

Regeneration of even aged natural stands by way of seed trees is not beyond reproach from the genetic aspect. Since the selection differential is low the genetic gain in the next generation will also be small. Therefore, it is recommanded to regenerate natural stands artificially whereever this is possible.

What genetic gain may be expected in plantations?

It is a touism that the hereditary factors and environment determine the growth and wood quality of a tree. Accordingly, for the study of these factors and the application of gained knowledge a close cooperation between tree breeders and growers is needed (RECK 1969, GIORDANO 1969, SHEPHERD and SLEE 1969). The more intensive the silviculture, the more needed is such a cooperation. Such cooperation is especially important whenever plantations are established. The establishment expenses of forest plantations per hectare are much greater than those of natural stands. Because of greater investments into plantations, one also expects greater returns. This is only possible to realize under intensive silvicultural practices, and when a selected and, if possible, improved planting stock is used. In the contrary case the return is lower, and from the silvicultural aspect such plantations are inferior and sometimes completely unsuccessful.

In this connection many problems confront tree breeders and growers which are to be solved jointly. The genetic factors and environment influence differently the tree growth and wood quality.

Besides, their effect on both characteristcs are different as regards the juvenile and nature trees. It is well known that the "wild" forms grow in their youth in plantations more slowly than the improved forms. Such an instructive example represents Cryptomeria japonica in Japan. According to MIYAJIMA (1969) the natural cultivar grows in its youth in plantations more slowly, but retains a constant growth rate for a long period up to maturity, while the growth rate of improved cultivars is excellent in the youth. It is understandable that MIYAJIMA could draw from it many conclusions, about growing improved cultivars in plantations with shorter rotations, fertilizing monoclone cultivation, harmful consequences from biotic and abiotic factors, soil productivity etc.

Here ought to be mentioned also the effect of spacing, i.e. the competition on the genetic potential. Likewise it is necessary to assess the interactions: genotype - site, genotype - fertilizing, and other reciprocal actions. In this connection there are already achieved valuable and interesting results, such as in Pinus silvestris (JOHNSSON 1965, ANDERSSON and TAMM 1968 - after EHRENBERG 1969), and in Larch (KEIDING and OLSEN 1965), and others. It is certain that further studies in this direction will yield results which would be of great importance for the future establishment of plantations.

I think that there is no need again to discuss the harmful conseqences of using genetically por material and applying poor techniques to the establishment and maintenance of plantations.

Therefore adequate measures ought to be undertaken in order to prevent further insufficiently competent establishment of plantations. Scientific and development istitutions as well as groups and individuals in research and practice should to be helped as much as possible in their work on the production of quality seed, hybrid plants and cultivars. It is to be expected that the yield (when taken into account only the genetic gain) from plantations raised from the improved material will be 10-30 % higher than in good natural stands.

References

1. DORMAN K.W. (1969): Positive impacts of silviculture on gene resources. FO - FTB - 69 - 10/3, Washington.

2. EHRENBERG, C. (1969): Breeding for high-yielding characters-stem quality. FO - FTB - 69 - 3/1.

3. GIORDANO, E. (1969): Interaction between breeding and intensive culture. FO - FTB - 69 - 12/1, Washington.

4. HATTEMER, H.H. (1963): Estimates of heritability published in forest tree breeding research. Proc. World Consultation Forest Genet. Tree Improvement, FAO/FORGEN 63 - 2a/3, 14 pp.

5. HAGMAN, M. (1967): Serological studies of pollen, and the incompati-

bility in forest trees. Proc. XIV Congr. I.U.F.R.O., Vol. 3, Sec. 22: 60-70.

6. KEIDING, H. and OLSEN, H.C. (1965): Assessment of stem form in clones and progenies of larch. Silvae Genet., 14 (4): 115-122.

7. KRIEBEL, H.B. (1967): The timing of the incompatibility reaction in interspecific crosses in Pinus strobus. Proc. XIV Congr. I.U.F.R.O., Vol. 3, Sec. 22: 77-87.

8. LANNER, R.M. (1966): Needed: a new approach to the study of pollen dispersion. Silvae Genet., 15: 50-52.

9. LIBBY, W.J., STETTLER, R.F., and SEITZ, F.W. (1969): Forest genetics and forest-tree breeding, Ann. Rev. Genet., 3: 469 - 494.

10. MATTHEWS, J.D. (1963): Some applications of genetics and physiology in thinning. Forestry 36(2): 172-180.

11. MIYAJIMA, H. (1969): Approach to intensive culture and forest-tree breeding of Cryptomeria in Japan. FO - FTB - - 69 - 12/2, Washington.

12. RECK, S. (1969): Controlling growth rate and wood density within conifer species by means of genetical selection and intensive culture. FO - FTB - 69 - 12/2, Washington.

13. STETTLER, R.F. (1968): Irradiated mentor pollen: Its use in remote hybridization of black cottonwood. Nature 2/9: 746 - 47.

14. SCHREINER, E.J. (1958): Possibilities for genetic improvement in the utilization of forest trees. Silvae Genet., 7 (4): 122 - 128.

15. SHEPHERD, K.R. and SLEE, M.U. (1969): Tree breeding programmes and silvicultural practice. FO - FTB - 69 - 9/9, Washington.

16. VIDAKOVIC, M. (1967): Genetics in silviculture. Pak. J. For. 17 (3): 325 - 335.

17. VIDAKOVIC, M. and JURKOVIC-BEVILACQUA, B. (1970): Observations on the ovule development following cross pollination between Austrian and Scots pines using irradiated and non-irradiated pollen.

I. U. F. RO., Sec. 22, Meeting of the working group on reproduction of forest trees, Varparanta, 8 pp.

18. WRIGHT, J. W. (1962): Genetics of forest tree improvement. F. A. O., Roma, 399 pp.

19. WRIGHT, J. W. (1966): Genetics of forest tree improvement, (Lectures).

Résumé

La première partie de cette communication traite les principes fondamentales de la génétique et de leur importance pour la sylviculture. L'auteur discute surtout la variabilité et l'héritabilité, ainsi que leur application dans le domaine de la sylviculture. On tire l'attention sur les recherches cytogénétiques dont les arbres forestiers ont été l'objet. L'auteur parle plus spécialement de de la polyploidie, de la production de matériel haploid et du problème de l'incompatibilité interspécifique.

La seconde partie de la communication est consacrée à deux importants problèmes de l'amélioration des arbres, qui sont en relation directe avec la pratique de la sylviculture. L'auteur discute ainsi l'amélioration génétique qui peut être obtenue dans des peuplements naturels et le gain génétique qui peut être réalisé dans les plantations.

Zusammenfassung

DIE ROLLE DER GENETIK UND DER FORSTPFLANZENZÜCHTUNG IM WALDBAU

Im ersten Abschnitt des Berichtes werden die Grundzüge der Genetik und ihre Bedeutung für den Waldbau behandelt. Der Autor erörtert namentlich die Variabilität und die Vererblichkeit. Hingewiesen wird auf die zytogenetischen Arbeiten mit den Waldbaumarten. Der Autor bespricht die Plyploidie, die Erzeugung von Haploidmaterial sowie das Problem der zwischenartigen Inkompatibilität.

Der zweite Abschnitt des Berichtes behandelt zwei wichtige Probleme der Forstpflanzenzüchtung, die mit dem Waldbau eng verbunden sind. Im ersten Problem wird die genetische Verbesserung besprochen, welche zu erwarten ist und im zweiten der genetische Gewinn, der in den Plantagen vorauszusehen ist.