# Effects of classical silviculture on the genetic quality of the progeny

By W. Wilusz[1]) and M. Giertych[2])

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After a period of fascination with the breeding possibilities in forestry through selection for one chosen character increasingly frequently a need is being felt for thinking in terms of the whole tree, for multiple trait breeding. The traditional silvicultural thinning practiced by Central European forestry for over two centuries, is in fact a process of multiple trait selection. The genetic effects of this selection are difficult to evaluate because of the time factor involved that makes a quick comparison impossible.

A possibility for this has been created by an old experiment established with Scots pine *(Pinus silvestris* L.) in **1914,** in Forest District Trzciel in western Poland, by Busse **(1924).** The aim of the experiment was to compare the value of seeds collected from trees of various age *(table* 1). This experiment is particularily valuable due to care with which it has been established. Even before the variance analysis has been developed (Fisher **1937)** Busse had sufficient intuition to plan the experiment with **4** replicates, in a complete block design with randomization within the blocks. The second value of the experiment lies in the extreme care with which the maternal stands have been selected. They all come from the same forest region and are absolutely certain to be indigenous.

*Table 1.* — **Data on maternal stands.**

| Population | Lat. N | Long. E | Alt. m | Age | Stocking per ha from Schwappach tables for site III |
|---|---|---|---|---|---|
| I | 52$^0$ 36' | 17$^0$ 09' | 90 | 16 | 9000 |
| IIb | 52$^0$ 35' | 17$^0$ 05' | 80 | 47 | 2480 |
| III | 52$^0$ 29' | 17$^0$ 02' | 100 | 74 | 928 |
| IV | 52$^0$ 30' | 17$^0$ 04' | 100 | 112 | 400 |
| V | 52$^0$ 22' | 16$^0$ 04' | 90 | 140 | 289 |
| VI | 52$^0$ 22' | 15$^0$ 38' | 90 | 170 | 210$^+$ |

$^+$ **extrapolated**

Busse was looking for differences in the progeny as a result of the age of maternal trees. Seeds from younger trees were heavier and in the first few years their progeny grew better in the nursery. The differences disappeared after outplanting but reappeared at age **11** and were still significant at age **16** (Busse **1931).** At age **50** years they were substancially in favour of the progeny from the older trees, though not significantly so (Wilusz **1966).** Presently, after **59** years, the progeny of older trees has significantly larger total basal areas per plot *(table* 2). This result indicates that either the compared progenies are distinct provenances or else that they differ as a result of the selection that took place in the maternal stands through natural thinnings and the silvicultural efforts of foresters during the XIX and early XXth century.

The following arguments speak against the separateness of the provenances: $1^0$ There are no doubts about the indigenity of the maternal stands — the older ones were from natural regeneration and the younger ones from sowing or planting using local material. $2^0$ All the maternal stands (except population IIa which has been eliminated from the following discussions) occupied identical sites as regards class (111), soil structure, geological substratum, and phytosociology. $3^0$ The distances between the materna! stands are not great. Most removed, by about **100** km is population VI. Populations I, IIb, III and IV were very close together. They all occupied the same elevation relative to the sea level. $4^0$ Up to **50** years there were no significant differences between the progenies, except those in the early years which it was possible to correlate with the seed weight or the juvenility of the mother trees. $5^0$ The differences now observable have a continuous pattern of DBH increasing from the progeny of the youngest maternal stand to almost the oldest *(tables* 2 *and* **3).**

*Table 2.* — **Total basal area per 0.0433 ha plot in m². Averages underlined together not significantly different.**

| Blocks | Population | | | | | | |
|---|---|---|---|---|---|---|---|
| | I | IIb | III | IV | V | VI | Average |
| A | **1.27** | **1.25** | **1.26** | **1.21** | **1.25** | **1.28** | **1.25** |
| **B** | **1.00** | **1.07** | **1.19** | **1.33** | **1.48** | **1.27** | **1.22** |
| C | **1.07** | **1.18** | **1.22** | **1.08** | **1.28** | **1.24** | **1.18** |
| D | **1.11** | **1.24** | **1.23** | **1.38** | **1.49** | **1.39** | **1.31** |
| Average | **1.11** | **1.19** | **1.23** | **1.25** | **1.37** | **1.30** | **1.24** |

Thus there are good reasons to consider the observed differences as being the result of genetic improvement of the maternal populations caused by natural selection and thinnings. The improvement of progeny following seed collection from older stands can therefore be considered as genetic gain caused by the mass selections made by foresters during thinning operations. Starting from this genetic gain and making some assumptions about selection intensities it should be possible to arrive at some estimate of heritability for the characters that now differentiate the populations.

## Materials and Methods

The basic material used in this study are the breast height diameters (DBH) measured on all trees of Busse's experiment in the spring of **1973.** Height of trees has not differentiated the populations at age **50** (Wilusz **1966)** and it is unlikely that at this stage in the development of the trees any differences should now appear, thus the heights were not measured. On the basis of the total basal area per plot it was established with the help of the variance analysis and the Duncan **(1955)** test, which populations differ from which *(table 2).*

The mean DBH is presented in *table* **3** together with the standard deviations for each population made on the basis of individual tree measurements ($\sigma$ DBH).

Assuming that we are dealing with uniform material we can consider the maternal populations as differing only in what has been removed from them during thinning operations. **A** selection conducted in maternal population I during several thinnings over the years **16—47** would then produce population IIb and so on. The selections consider-

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[1]) **Regional Forest Administration, Poznań, Poland.**

[2]) **Institute of Dendrology, 63-120 Kórnik, Poland.**

*Table 3.* — Mean breast height diameter (DBH) per plot in cm. Averages underlined together not significantly different on the basis of within plot variation.

| Blocks | Population I | IIb | III | IV | V | VI | Average |
|---|---|---|---|---|---|---|---|
| A | 15.9 | 15.3 | 16.3 | 17.4 | 16.8 | 16.3 | 16.3 |
| B | 13.4 | 15.1 | 14.5 | 15.4 | 15.7 | 15.0 | 14.9 |
| C | 13.9 | 15.5 | 14.4 | 13.9 | 15.7 | 15.6 | 14.8 |
| D | 14.1 | 13.9 | 14.6 | 14.5 | 14.7 | 14.7 | 14.4 |
| Average | 14.3 | 14.9 | 14.9 | 15.3 | 15.7 | 15.4 | 15.1 |
| Standard deviation on a per tree basis, $\sigma$ DBH | 3.78 | 3.74 | 3.69 | 3.79 | 4.01 | 3.85 | |

ed a phenotypic character of tree suitability P (which consists of a collection of characters either including or not the diameter d). There remained a certain percentage of individuals superior in P. By definition selection intensity $i = \frac{\Delta P}{\sigma P}$, and assuming that P has a normal distribution (which it should have if thinnings are performed properly) i can be obtained from tables as a function of the percentage of individuals left.

Let us assume that q is a measure of the participation of d in P.

Then $\frac{d}{\sigma d} = q \frac{P}{\sigma P}$

Therefore $\frac{\Delta d}{\sigma d} = q \frac{\Delta P}{\sigma P} = qi$

If $P = d$ then $q = \pm 1$ and $\frac{\Delta d}{\sigma d} = \pm i$

If P contains no independent elements of d, then

$$q = 0 \text{ and } \frac{\Delta d}{\sigma d} = 0$$

The genetic gain $\Delta G$ in diameter as a result of selecting within a population depends on the heritability of this character and is given by the formula:

$$\Delta G = h^2 \Delta d = h^2 qi\, \sigma d$$

or in units of standard deviation

$$\Delta G' = h^2 \frac{\Delta d}{\sigma d} = h^2 qi$$

By definition $\Delta G$ is also the difference in DBH measured on the progeny populations:

$$\text{e.g } \Delta G = (DBH)_{IIb} — (DBH)_{I} = \Delta DBH$$

Thus $\Delta G' = \frac{\Delta DBH}{\sigma d} = iqh^2$

Assuming panmixy among the maternal populations the phenotypic variance of diameter in them, $\sigma^2 d$ should be the same as that in the progeny population presently measured. Thus the standard deviation for DBH shown in *table 3* can be used instead of $\sigma d$. This brings us to the relationship:

$$\Delta G' = \frac{\Delta DBH}{\sigma DBH} = iqh^2$$

The differences in average DBH per population were calculated for all comparisons between populations. Having four replicates (blocks) there are four estimates of each difference between populations from which the standard deviation was calculated and each average difference was supplied with its own confidence limits expressed as ±1.96 of its standard deviation (column 4 of *table 4*). The observed differences as well as their confidence limits were expressed in the units of the initial standard deviation for the given comparison (column 5 of *table 4*).

The age of the maternal stands is given in *table 1*. Making use of the tables of Schwappach (1943) for pine on site class III, which corresponds to the conditions in all the maternal stands, and assuming that Polish foresters working in the Prussian zone of occupied XIX c. Poland have conformed to the norms prevailing in Prussian forestry (on which Schwappach has developed in 1929 his tables) one can read off the number of trees that should have been growing per hectar of the maternal stand. This presumed data on stocking is included in *table 1*. Expressing the stocking as a percentage of that in a younger stand we obtain a measure of the intensity of selection for the given time periods obtained by natural and man-made thinnings (column 2 of *table 4*). Assuming that the thinnings have left populations with normal distributions for the characters considered in the thinnings (which should have been the case if the thinnings were made properly) it is possible to convert the percentage selection intensity into units of standard deviations using the graphs of Namkoong and Snyder (1969) for selections of over 50% and the tables of Nanson (1968) for less intense selections (column 3 of *table 4*).

We have calculated the value of $qh^2$ by dividing the genetic gain $\Delta G'$ (5th column of *table 4*) by the intensity of selection (3rd column of *table 4*) separately for each of the time periods of traditional silviculture in the life of the maternal stands.

## Results and Discussion

The obtained values of $qh^2$ are presented in column 6 of *table 4*. For the time periods in which the gain in DBH was significant *(table 3)* the value of $qh^2$ in *table 4* is provided with an asterisk. The range of values obtained was from —.18 to .23, but for the significant differences it was from .12 to .19. Error of these estimates is rather high, even for significant differences the confidence limits are from ±.13 to ±.20. None the less some conclusions can be drawn from this investigation.

$$\text{Since } 1 \geqslant h^2 \geqslant 0$$
$$\text{and } 1 \geqslant q \geqslant -1$$

both $h^2$ and q must have values above those observed for $qh^2$.

The negative value of $qh^2$ indicates that in the given period, in our case from 140 to 170 years, a negative selection for girth occurred. Since this is a post-felling age period it is difficult to judge what criteria were used when making thinnings. It is not unlikely, that for some specific purpose thickest trees were being felled. Perhaps the thickest trees were removed to facilitate logging. At the time (1885—1914) too large stems may have been a problem in felling and transporting operations, and so they were cut before they grew too big. Perhaps also they were removed for fear of butt rot. Apart from the above it is also possible that the maternal stand for population VI was of a different provenance in view of the fact that it was most removed from the remainder (by about 100 km). In any case the smaller average diameters in population VI than in population V results not only in a negative $qh^2$ for the period 140—170 but also lowers it for all the comparisons including age 170. For the period 112—170, $qh^2 = 0$ indicating that on the average, during that period positive and negative selection for girth have had a zero net effect. Similarily for the other comparisons with age 170 the values of $qh^2$ are generally lower.

*Table 4.* — Gain in DBH at 59 years due to genetic improvement of maternal stands involved in reducing their stocking during normal silvicultural practices in a pine stand on site class III.

| Between years | % stocking left by silviculture | Selection intensity i | $\Delta$ DHB in cm | $\Delta G' = \frac{\Delta \text{DBH}}{\sigma \text{DBH}}$ | $\frac{\Delta G'}{i} = qh^2$ |
|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 5 | 6 |
| 16—47 | 27.6 | 1.21 | .62 ± 2.03 | .16 ± .54 | .13 ± .45 |
| 16—74 | 10.3 | 1.70 | .62 ± .54 | .16 ± .14 | .09 ± .08 |
| 16—112 | 4.4 | 2.11 | .97 ± 1.58 | .26 ± .42 | .12 ± .20* |
| 16—140 | 3.2 | 2.26 | 1.40 ± 1.34 | .37 ± .35 | .16 ± .15* |
| 16—170 | 2.3 | 2.37 | 1.07 ± 1.14 | .28 ± .30 | .12 ± .13* |
| 47—74 | 37.4 | 1.01 | 0 ± 1.72 | 0 ± .46 | 0 ± .46 |
| 47—112 | 16.1 | 1.51 | .35 ± 2.57 | .09 ± .69 | .06 ± .45 |
| 47—140 | 11.7 | 1.68 | .78 ± .92 | .21 ± .25 | .13 ± .15* |
| 47—170 | 8.5 | 1.82 | .45 ± .90 | .12 ± .24 | .07 ± .13 |
| 74—112 | 43.1 | .92 | .35 ± 1.31 | .10 ± .35 | .10 ± .38 |
| 74—140 | 31.1 | 1.13 | .78 ± .84 | .21 ± .23 | .19 ± .20* |
| 74—170 | 22.6 | 1.33 | .45 ± .92 | .12 ± .25 | .09 ± .19 |
| 112—140 | 72.2 | .47 | .42 ± 1.70 | .11 ± .45 | .23 ± .96 |
| 112—170 | 52.5 | .76 | .01 ± 2.02 | 0 ± .53 | 0 ± .70 |
| 140—170 | 72.7 | .45 | —.32 ± .56 | —.08 ± .14 | —.18 ± .31 |

* significant (see *table 3*).

Low values of $qh^2$ are also observed for periods of the early stand development, from 16—74 years of age. In particular for the period 47—74 years the value of $qh^2$ was low, almost zero. This indicates that in that period of time thinnings have been more concerned with other factors than with girth, and that the selection for girth was compensated by selection against girth. This could have been caused by selection thinnings (creaming) or by the policy of removing wolves. In the years 47—74 foresters tend to notice such factors as stem straightness, branchiness, cleaning, spiral grain etc. which could have been the cause of the fact that selection for girth was less effective.

The highest value of $qh^2 = .23$ has been obtained for the period 112—140 years, this value however has also the largest error, thus there are doubts about its significance. However values of the order of .19 (for the period 74—140) suggest that heritability of DBH in mature trees under conditions of normal silviculture is relatively high. Since q has to be smaller than 1, probably substancially smaller, the actual value of $h^2$ must be greater than is usually assumed. The value for the period 74—140 seems to be rather certain thus there are reasons to believe that selection in a mature stand can be genetically very successful in view of the high heritability, well above .19. In the younger stands it is also not insignificant, and considering the probability that q undergoes more fluctuations with time than $h^2$, one can assume that heritability throughout the period from 16 to 170 years is high, of the order of .25 or more. If q were small $h^2$ would be much greater, but since that is unlikely we would have to consider q as being rather large. Thus in general classical silviculture leads to selection of trees with large DBH either directly or through correlation of girth with the characters selected for.

The practical conclusions of these observations are rather important. If in a breeding program we are interested in a particular character, such as specific gravity of wood, figure on wood, or resistance to some disease, we must of course select for this character, but if our aim is to improve the production of volume, a selection of the type practiced by classical thinning operations which considers many characters simultaneously, appears to be very effective.

Reduction of the population to 4.4%, from age 16 to 112 years (within this range there is no question of provenance differences — see *table 1*) gave an increase in average DBH of the progeny from 14.3 cm to 15.3 cm, that is by about 6.9%. On basal area basis calculated per hectar (from *table 2*) this improvement amounts to 3.23 m$^2$ or 12.6%. From the practical point of view this is quite an improvement. Basal area is correlated with volume (Hummel 1955) and thus the observed difference would correspond to a similar improvement in volume.

Thus in forest practice collection of seeds from trees which are as old as possible and therefore underwent severe selection pressures, should be favoured, regardless of the size of the seeds. Selection of seeds by size, which is frequently done by commercial cone extraction plants, eliminates or reduces the utilization of seeds which are genetically best. Collection of cones from juvenile trees should be forbidden.

The results presented here lend support to the doubts voiced by Toda (1972) about the value of early tests. Differences observed between populations in the growth of pines to age 16 underwent a complete about-turn giving at the age of 59 very substancial, statistically and economically significant differences. This last conclusion is independent of the various assumptions made in this paper.

## Summary

In 1914 Busse established an experiment in a complete block design aimed at comparing Scots pine progenies differing in the age of maternal stands but otherwise identical as regards provenance, site, indigenity etc. In early years the progeny of younger mother stands grew better, but now at 59 years the opposite is true, indicating that traditional thinning practices have produced a genetic gain, expressed in the progeny as an improvement of tree diameter and basal area per hectar. Heritability of girth appears to be no less than .25 and the character is closely related to those selected for in classical thinning operations. The results indicate that seeds from older stands in spite of

being smaller are genetically superior and that early results can be misleading.

*Key words:* Multiple-trait breeding, progeny tests, early tests, heritability.

## Zusammenfassung

*Auswirkungen klassischen Waldbaus auf die genetische Qualität der Nachkommenschaft.*

Im Jahre 1914 begründete Busse einen vollständigen Blockversuch mit Kiefern-Nachkommenschaften, die von Elternbeständen verschiedener Altersklassen abstammten, die aber hinsichtlich ihrer Provenienz, ihres Standortes usw. identisch gewesen waren. In früheren Jahren wuchsen die Nachkommenschaften junger Mutterbestände besser, doch jetzt nach 59 Jahren ist das Gegenteil der Fall. Dies zeigt, daß die traditionelle Durchforstungspraxis einen genetischen Gewinn gebracht hat, der sich bei der Nachkommenschaft in einer Verbesserung des Stamm-Durchmessers und in der Grundfläche je ha äußert. Die Heritabilität des Umfanges scheint nicht geringer als 0,25 zu sein, und dies Merkmal ist ganz ähnlich dem, das bei den klassischen Durchforstungsmaßnahmen zugrunde gelegt wurde. Diese Ergebnisse zeigen, daß Saatgut von älteren Beständen trotz seiner geringeren Masse genetisch aber besser ist und daß eine zu frühzeitige Beurteilung solcher Versuchsergebnisse zu Mißdeutungen führen können.

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# Hypocotyl Length in Pinus caribaea Seedlings: A Quantitative Genetic Variation Parameter

By C. R. Venator[1]

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## Introduction

Estimation of genetic variability is one of the most urgent needs in subtropical and tropical tree species. Although vast gene pools still exist for many of these species, wild populations are under the constant threat of rapidly being reduced by slash and burn agriculture, selective cutting, etc., with the subsequent loss of genes and combinations that have been built up over the years through mutation and selection (Gomez-Pompa, Vázquez-Yanes, and Guevara, 1972).

Currently, organized International Provenance trials are being under-taken throughout the subtropics, and within a relatively short period tree geneticist will be forced to select from among the provenances those seed sources considered to be best adapted to their country's environments (Kemp, 1973). Although the traditional parameters of height, diameter, stem form, volume, etc. must obviously be taken into consideration when selecting provenances for introduction into a country, these parameters should be considered as final objectives only when no follow-through, long-term breeding program is contemplated. Tree geneticists need accurate estimates of the relative genetic variability between provenances, and perhaps even more important they need to better understand the regulatory mechanisms of multiple inheritance traits.

Determination and classification of genetic variation can be done only if quantitative and/or qualitative differences can be detected among populations or individuals. Detection of genetic variation, of course, can be done at any level of organization in the individuals studied but the geneticist must recognize and compensate for the amount of wobble between the different levels of organization studied.

The nursery stage presents an excellent opportunity to measure genetic differences between provenances since the seedlings are exposed to approximately uniform conditions. Randomization and replication of the nursery plots can help to reduce error resulting from environmental bias.

The occurence of *Pinus caribaea* over a wide range of diverse habitats indicates that this species is highly adaptable and clinal gradations with genetic differences should be detectable among sub-populations. One of the current tenets of populations genetics is that populations with greater amounts of genetic variability are better able to adapt to changing habitats. Thus, it is important that genetic differences be detected for adaptive study.

Several reports have emphasized the general morphological variability of *P. caribaea* and in particular var. *hondurensis*, (Lückhoff, 1962; Nikles, 1971; and Kemp, 1973). However, few quantitative and qualitative genetic parameters have been described for this species. I have reported that seedling hypocotyls are polymorphic for the colors green and purple (in preparation, 1974).

In this report evidence will be given for variation of hypocotyl length among 16 provenances of the 3 varieties of *Pinus caribaea*.

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[1] Present address: Institute of Tropical Forestry, United States Department of Agriculture, Forest Service, P. O. Box AQ, Río Piedras, Puerto Rico 00928.