# Estimation of Genetic Parameters in Forest Trees Without Raising Progeny1)

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(Received for publication April 29, 1963)

### Introduction

Due to the extremely long period of time generally required for growing forest trees, very few statistico-genetical studies have been made despite their very necessity. WRIGHT, BINGHAM and DORMAN (1958) emphasized the importance of detection and utilization of genetic variability within local populations in forest tree breeding. TODA (1957, 1959, 1961) has succeeded in estimating heritability values for several characters of *Cryptomeria japonica* D. DON by comparing variation in seed propagated populations with that in vegetatively propagated clones on the one hand, and by the analysis of variance of family data, on the other. Genetic and environmental correlations among several characters were also investigated by the same author (1961). BINGHAM, SQUILLACE and WRIGHT (1960) have made a breeding experiment for blister-rust resistance in Pinus monticola. In this experiment, they could estimate heritability in the narrow as well as broad sense by the analysis of variance of family data. The effect of phenotypic selection alone or in combination with progeny testing on the improvement in the resistance of progenies was also investigated by them.

CALLAHAM and HASEL (1961) studied the second year's and the fifteenth year's growth of Pinus ponderosa trees grown in families, in connection with seed size, germination time and elevation of the provenance. They estimated heritability of tree height in the 15th year. They also gave a suggestion for selecting seedlings in the nursery. ZOBEL (1961) gave a general review on studies so far made on heritability in conifers.

CAMPBELL (1961) investigated phenotypic variation in a few characters of Pseudotsuga *menziesii*. He computed repeatability of these characters and regarded it as the uppermost estimate of heritability in broad sense. He found that the estimates for stem interwhorl length, number of branches per whorl or knottiness were generally very low.

In the coconut palm, though it is slightly different from ordinary forest trees, LIYANAGE and SAKAI (1960) and SAKAI (1960a, b) have estimated heritabilities and genetic correlations of several characters by the analysis of variance of family data and constructed selection indices..

The methods of estimation of genetic parameters above described and so far practiced by various authors are in principle of two kinds: (1) Environmental variance is estimated in a clonal population. By subtracting it from the phenotypic variance of a seed-propagated population, genetic variance or covariance is estimated. (2) Under an assumption of random mating, the between-family and within-family variance components are computed by the method of analysis of variance, and genetic variance as well as genetic covariance is therefrom estimated.

These two methods may have some difficulties for general application. In the case of the first method, we are not satisfactorily convinced in taking environmental variations in two separated forests for equal. It is needless to mention that this method can not be adopted to the tree species which can not be propagated vegetatively. For the case of the second method, it is usually difficult to find forests suitable for the study. For instance, it is hardly likely that in the existent forests, members of more than a few families are planted at random in the forest.

In 1938, FAIRFIELD H. SMITH published a paper dealing with the effect of soil heterogeneity in the field on the increase of plot mean variance than theoretically expected. On the basis of this work, V. J. SHRIKHANDE (1957) tried and succeeded to calculate genetic and environmental variances in coconut palm populations. This method is based on an assumption that variation between cluster means consists of one-$x^{th}$ of the genetic variance and one-$x^{b}$ th of the environmental variance, $x$ being number of individuals within each cluster and $b$ being a function of the variation pattern of environmental conditions.

In the present study, we are applying the same method to forest trees for the purpose of estimating heritability values of different characters and further we are expanding the method for the estimation of genetic correlations among characters.

In publishing this paper, the writers wish to express their thanks to Dr. V. G. PANSE, Statistical Adviser, Indian Council of Agricultural Research, for his valuable suggestion and kind information of SHRIKHANDE's work during his short visit to our Institute. Without it, we may have been in a puzzle for a longer period of time.

### Materials and Methods

Materials for this study are data collected from a vegetatively propagated clone of Populus euramericana, C. V. I-476, and two seed-propagated Abies sachalinensis forests. These three forests are grown in Hokkaido. The Populus clone consists of one hundred individuals space-planted at 5 m X 5 m in 1959. The two Abies forests, one called A-population and another I-population, were planted in 1931 in Asahigawa-city and Ikeda-town, respectively. The A-population consisted of 264 trees space-planted at 3 m X 3 m, while the I-population 272 trees space-planted at 2.7 m X 2.7 m. Several trees in each of these three forests have been damaged by some physical or biological accidents, forming vacancies within the forests.

Data were collected on an individual tree basis for a few economically important characters such as tree height, stem girth at breast height, crown size, taperingness and clear length in Abies, while for Populus, tree height, stem diameter and crown size only were recorded. In all cases, the accurate location of the investigated trees within the forests were plotted on section paper.

Method of analysis and calculation of genetic and environmental variances followed those of SHRIKHANDE (1957). On the same principle, genetic and environmental covariances betweeen characters were also computed, from which

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genetic correlations were estimated. These methods will be described briefly for the sake of convenience of the reader.

### Method of Statistical Analysis

The method of SHRIKHANDE will be described below in a brief form in order to meet the convenience of the reader. For further details, the reader is referred to the original paper (SHRIKHANDE, 1957).

Let $V_{(x)}$ denote the variance of cluster means, each cluster including x individual trees. Then,

$$V_{(x)} = \frac{G}{x} + \frac{E}{x^b}$$

where G and E stand for genotypic and environmental variances, respectively, and b is a constant lying between zero and unity, if the genotypes are randomly distributed over the field while the field possesses a certain pattern of environmental variation. The formula can be rewritten as

$$x\,V_{(x)} = G + x^{1-b}E = G + x^B E$$

where $B = 1 - b$.

By dividing the population into a number of plots including a given number of trees and making the analysis of variance of the data obtained, we can get a number of pairs of statistics of between- and within-cluster mean squares as seen in *Table 1.* The pooled between-cluster mean squares for plot size 1, 2, ....., x are arranged as follows:

$$\begin{aligned} M.S._{(1)} &= 1\,V_{(1)} = G + 1^B E \\ M.S._{(2)} &= 2\,V_{(2)} = G + 2^B E \\ &\cdot \quad \cdot \quad \cdot \quad \cdot \\ &\cdot \quad \cdot \quad \cdot \quad \cdot \\ M.S._{(x)} &= x\,V_{(x)} = G + x^B E \end{aligned}$$

By the trial and error method, various values between zero and unity are given to B and the set of above formulas are solved for G and E by the least squares method. It is then possible to find out $B_0$ value which gives the best fit between observed and expected between-cluster mean squares. The $G_0$ and $E_0$ values which are obtained with $B_0$ are what we want to get.

The approximate standard errors of calculated $G_0$ and $E_0$ are given, according to SHRIKHANDE, by

$$S.E.(G_0) = \sqrt{\sigma_o^2\left[\frac{1}{n} + \frac{\bar{x}_1^2}{S(x_1^2)}\right]}$$

$$S.E.(E_0) = \sqrt{\sigma_o^2\,\frac{1}{S(x_1^2)}}$$

where

$$\sigma_0^2 = \frac{(R.S.S.)_o}{n-3},\ S(x_1^2) = \Sigma\,(x_i - \bar{x}_1)^2, \text{ and } x_1 = x^B,$$

while n is the number of comparisons. $(R.S.S.)_0$ stands for the corresponding minimum residual sum of squares.

The heritability will then be calculated by

$$h^2 = \frac{G_0}{G_0 + E_0}$$

The heritability obtained here is that in the broad sense.

The method of calculating genetic correlation between characters is quite analogous with the method given above, i. e.

$$x\,W_{(x)} = W_G + x^{1-k}\,W_E = W_G + x^K\,W_E$$

where W stands for covariance, the subscripts G and E denoting genetic and environmental, respectively. By the same procedures as applied for genetic and environmental variances, $W_G$ and $W_E$ are calculated after finding the most reasonable k value instead of b. The genetic and environmental correlations are given by the well known formulas,

$$r_G = \frac{W_G}{\sqrt{G_1 \times G_2}}$$

$$r_E = \frac{W_E}{\sqrt{E_1 \times E_2}}$$

### Result of Study

*I. Test of the Validity of the Method*

The validity of the method is tested by vegetatively propagated clones in which all trees are genotypically the same except for possible mutations of rare occurrence. A 5-year old clone of *Populus euramericana,* C. V. I-476, consisting of 100 trees and growing in Hakodate-district, Hokkaido was investigated individually for tree height, stem diameter and crown size. The location of each tree from which measurement was taken was mapped on section paper. The trees in this forest have not been damaged seriously either artificially or naturally, except for 4 vacancies.

By the procedures given in the preceding section, the whole population was divided into clusters of various sizes and analysis of variance was conducted to obtain statistics for between-cluster and within-cluster meansquares. Statistics obtained for tree height are presented in *Table 1* by way of example.

In order to test the validity of the method, the first computation was conducted to partition variance into genetic and environmental components on an assumption that the clone were involving genetic variation. If estimates of genetic variance obtained by this way could be regarded as zero, then the method should be considered

*Table 1.* — Between-cluster and within-cluster mean squares for tree height in a clone of *Populus euramericana,* C. V. 1-476.

| Plot size | Shape | Between-cluster M.S. | d. f. | Pooled between-cluster M.S. | Within-cluster M.S. | d.f. | Pooled-within-cluster M.S. |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 0.28299 | 96 | 0.28299 | | | |
| 2 | 2×1 | 0.49447 | 38 | 0.45706 | 0.06788 | 40 | 0.07695 |
| | 1×2 | 0.42681 | 47 | | 0.08468 | 47 | |
| 3 | 3×1 | 0.56663 | 18 | 0.59934 | 0.07474 | 38 | 0.10473 |
| | 1×3 | 0.56318 | 28 | | 0.12345 | 58 | |
| | 2+1* | 0.65271 | 30 | | 0.10559 | 62 | |
| 4 | 4×1 | 0.66389 | 18 | 0.65473 | 0 08535 | 57 | 0.12489 |
| | 1×4 | 0.68240 | 21 | | 0.17102 | 66 | |
| | 2×2 | 0.61085 | 17 | | 0.11023 | 54 | |
| 5 | 5×1 | 0.75229 | 17 | 0.64759 | 0.10356 | 72 | 0.15409 |
| | 1×5 | 0.54481 | 16 | | 0.24176 | 68 | |
| | 2+3* | 0.63965 | 17 | | 0.12183 | 72 | |
| 6 | 6×1 | 0.25629 | 14 | 0.67237 | 0 21198 | 75 | 0.15317 |
| | 3×2 | 0.90555 | 11 | | 0.12390 | 60 | |
| | 2×3 | 0.07990 | 8 | | 0 09452 | 45 | |
| 8 | 8×1 | 0.31606 | 9 | 0.57851 | 0.21854 | 70 | 0.16151 |
| | 4×2 | 0.59569 | 7 | | 0.16806 | 56 | |
| | 2×4 | 0.87625 | 8 | | 0.09232 | 63 | |
| 10 | 10×1 | 0.35467 | 6 | 0.98684 | 0.32555 | 63 | 0.21215 |
| | 5×2 | 1.23733 | 6 | | 0.21182 | 63 | |
| | 2×5 | 1.27312 | 8 | | 0.12420 | 81 | |

*) Neighbouring trees in adjoining rows are grouped.

not invalid. The estimates of G and E thus obtained are presented in the columns designated (I) of *Table 2*.

It is found from this table that none of G's of the investigated characters proved to differ significantly from zero, all G values being smaller than their corresponding standard errors.

Another calculation (II) was conducted by reasonably taking intra-clonal variation wholly as environmental. That is,

$$x V_{(x)} = \frac{E}{x^{b-1}}$$

and

$$\log (x V_{(x)}) = \log E + (1-b) \log x = \log E + B \log x.$$

By the least squares method, E and B were calculated. The obtained values are presented in the columns designated (II) of *Table 2*. It is found in this table that b values obtained by (I) and (II) methods were not significantly different from each other and the same is also true for E values. This result also supports the validity of the method.

In a similar way, covariances were again computed. The results are presented in *Table 3*. It is found that the same still holds for covariances.

*Table 2.* — The b, G and E values obtained in two ways of solution (I and II) from a clonal forest of *Populus euramericana*.

| Character | b |  | G |  | E |  |
|---|---|---|---|---|---|---|
|  | (I) | (II) | (I) | (II) | (I) | (II) |
| Tree height | 0.64 | .57 ± .126 | —.0722 ± .1836 | — | .4038 ± .1054 | .3220 ± .0837 |
| Trunk size | 0.61 | .56 ± .246 | —.0949 ± .1058 | — | .7027 ± .0182 | .5958 ± .1615 |
| Crown size | 0.81 | .78 ± .137 | —.0009 ± .0787 | — | .0710 ± .0071 | .0674 ± .0092 |

*Table 3.* — The k, $W_G$ and $W_E$ values obtained in two ways of solution (I and II) from a clonal forest of *Populus euramericana*.

| Character | k |  | $W_G$ |  | $W_E$ |  |
|---|---|---|---|---|---|---|
|  | (I) | (II) | (I) | (II) | (I) | (II) |
| H × S* | 0.64 | .68 ± .184 | —.1536 ± .2503 | — | .5493 ± .1389 | .6501 ± .1210 |
| H × C* | 0.78 | .77 ± .050 | —.0108 ± .1136 | — | .1211 ± .0822 | .1084 ± .0305 |
| S × C* | 0.71 | .62 ± .075 | —.0529 ± .1265 | — | .1855 ± .0803 | .1268 ± .0499 |

*) H: Tree height; S: Trunk size; C: Crown size.

### *II. Investigation in Seed-propagated Abies Forests*

Forests dealt with here concern those of *Abies sachalinensis* grown in two districts in Hokkaido. The districts are Asahigawa and Ikeda, approximately 130 km. apart on the map. These two forests have been grown from seed randomly and separately collected and are not at all genetically related.

The result of computation of the between-cluster and within-cluster mean squares for tree height in the Asahigawa population is presented in *Table 4* as an example.

*Table 4* reveals that the between-cluster mean squares increase as the plot size becomes bigger while the within-cluster mean squares do slightly or unapparently. The detected b values and culculated G and E for tree height, stem girth, clear length, crown size and taperingness in the two forests, together with their respective heritability values are presented in *Table 5*.

It should be noticed in this table that though b values for the same character were considerably different in the two forests, the heritability values of the same character were approximately the same in both. Of the five characters investigated, taperingness had the highest value of heritability so high as approximating unity, crown size and stem girth coming next, tree height intermediate, while clear length was the lowest in heritability.

Convariances and correlations were computed *(Table 6)*. Of 12 cases, five showed negative value of k which are unexpectable theoretically. The relation between two corresponding genetic correlations for the same pairs of characters of the two forests were rather variable, especially so for the environmental correlations. Whether such inconsistencies found between paired estimates of genetic correlations would be due to genetic differences of the two populations or to some other unknown causes is a question which can not be answered for the present.

### *III. Relation between k and b's*

At present, we are not aware of the mathematical relation, if any, between k and two corresponding b's of the same pair of characters. Now, we shall investigate it by actual data. If k should be a function of two corresponding b's, the simple forms would be that k be an average in some way or other of two b's. Though there may be numberless functions, let us consider four functions of most simple form as given in the first row of *Table 7*.

*Table 4.* — Between-cluster and within-cluster mean squares for tree height in an *Abies sachalinensis* forest grown in Asahigawa. Hokkaido.

| Plot size | Shape | Between-cluster M. S. | d. f. | Pooled between-cluster M. S. | Within-cluster M. S. | d. f. | Pooled within-cluster M. S. |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 1.95127 | 263 | 1.95127 |  |  |  |
| 2 | 2×1 | 1.76721 | 97 | 2.11661 | 1.61242 | 98 | 1.47376 |
|  | 1×2 | 2.41654 | 113 |  | 1.35456 | 114 |  |
| 3 | 3×1 | 2.45568 | 51 | 2.66491 | 1.65971 | 104 | 1.60491 |
|  | 1×3 | 2.81956 | 69 |  | 1.56421 | 140 |  |
| 4 | 4×1 | 2.22471 | 35 | 2.88395 | 1.84424 | 108 | 1.70382 |
|  | 1×4 | 2.85750 | 44 |  | 1.65566 | 135 |  |
|  | 2×2 | 3.47512 | 41 |  | 1.63507 | 126 |  |
| 5 | 5×1 | 3.61772 | 33 | 3.31711 | 1.51044 | 136 | 1.54979 |
|  | 1×5 | 2.90379 | 24 |  | 1.60332 | 100 |  |
| 6 | 6×1 | 4.02036 | 22 | 3.51850 | 1.63780 | 115 | 1.55705 |
|  | 1×6 | 3.67466 | 15 |  | 1.41462 | 80 |  |
|  | 3×2 | 2.49777 | 18 |  | 1.43421 | 95 |  |
|  | 2×3 | 3.76800 | 20 |  | 1.68828 | 105 |  |
| 8 | 8×1 | 4.77337 | 17 | 3.53037 | 1.54263 | 126 | 1.61762 |
|  | 1×8 | 3.55475 | 12 |  | 1.43706 | 91 |  |
|  | 4×2 | 2.06037 | 16 |  | 1.68659 | 119 |  |
|  | 2×4 | 4.22660 | 15 |  | 1.77544 | 112 |  |

*Table 5.* — Estimated values of genotypic and environmental variances and heritabilities for tree height, stem girth, clear length, crown size and taperingness in *Abies* grown in Asahigawa and Ikeda districts, Hokkaido.

| Character | Asahigawa |  |  |  | Ikeda |  |  |  |
|---|---|---|---|---|---|---|---|---|
|  | b | $\sigma^2_g$ | $\sigma^2_e$ | $h^2$ | b | $\sigma^2_g$ | $\sigma^2_e$ | $h^2$ |
| Tree height | 0.51 | .7569<br>± .1007 | 1.1029<br>± .1007 | 0.41 | 0.09 | 1.7767<br>± .1237 | 1.1337<br>± .0973 | 0.61 |
| Stem girth | 0.61 | 166.59<br>± 27.62 | 45.93<br>± 15.84 | 0.78 | 0.21 | 102.42<br>± 14.07 | 31.64<br>± 1.36 | 0.76 |
| Clear length | 0.38 | .4002<br>± .1229 | 1.5405<br>± .1578 | 0.20 | 0.16 | .1009<br>± .0336 | 1.4483<br>± .0936 | 0.07 |
| Crown size | 0.01 | .3869<br>± .0132 | .0533<br>± .0089 | 0.88 | 0.01 | .1906<br>± .0212 | .0261<br>± .0014 | 0.88 |
| Taperness | —0.28 | .6991<br>± .0860 | .0108<br>± .0011 | 0.98 | 0.31 | .7469<br>± .0258 | .0533<br>± 0093 | 0.95 |

*Table 6.* — Estimated values of genetic and environmental covariances and genetic and environmental correlations among four characters in *Abies*.

| Population | Characters*) | k | $W_P$ | $W_G$ | $W_E$ | $r_P$ | $r_G$ | $r_E$ |
|---|---|---|---|---|---|---|---|---|
| Asahigawa | B × G | 0.71 | 13.854 | 5.3494 ± 0.2321 | 8.5051 ± 1.5469 | 0.697 | 0.476 | 1.130 |
|  | H × C | —0.10 | 0.310 | 0.3104 ± 0.0579 | —0.0009 ± 0.0010 | 0 342 | 0.566 | —0.001 |
|  | H × T | 0.47 | 0.400 | 0.3689 ± 0.0916 | 0 0310 ± 0.0430 | 0 348 | 0.507 | 0.282 |
|  | G × C | 0.02 | 6.638 | 6.3624 ± 0.8831 | 0.2760 ± 0.1935 | 0.699 | 0.782 | 0.179 |
|  | G × T | —0.92 | 7.947 | 7.8295 ± 0.7691 | 0 1177 ± 0.0306 | 0.647 | 0.725 | 0.167 |
|  | T × C | —0.35 | 0.269 | 0.2594 ± 0.0872 | 0.0098 ± 0.0032 | 0.423 | 0.495 | 0.407 |
| Ikeda | H × G | —0.17 | 9.482 | 9.0021 ± 0.3705 | 0.4801 ± 0.0276 | 0.875 | 0.667 | 0.480 |
|  | H × C | 0 38 | 0.100 | —0.7560 ± 0.0943 | 0.1752 ± 0 0382 | 0.125 | —0 130 | 0.981 |
|  | H × T | 0.05 | 0.430 | 0.3689 ± 0.1311 | 0 0614 ± 0.0131 | 0.285 | 0.320 | 0.307 |
|  | G × C | 0.64 | 3.496 | 2.5972 ± 0.1375 | 0 8990 ± 0.0837 | 0.645 | 0.581 | 0.939 |
|  | G × T | —0.90 | 3.472 | 3.4111 ± 0.3900 | 0 0613 ± 0.0079 | 0.339 | 0 390 | 0.061 |
|  | T × C | 0 90 | 0 131 | 0.1890 ± 0.0392 | 0.5824 ± 0.0342 | 0.317 | 0,503 | 0,006 |

*) H: Tree height; G: Stem girth; C: Crown size; T: Taperingness.

*Table 7.* — Relation between k and b's in a clone of *Populus*.

|  |  | $\frac{2}{\frac{1}{b_1}+\frac{1}{b_2}}$ |  |  | $\sqrt{b_1 \times b_2}$ |  |  | $\frac{b_1 + b_2}{2}$ |  |  | $\sqrt{\frac{b^2{}_1 + b^2{}_2}{2}}$ |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | HxT | HxC | TxC | HxT | HxC | TxC | HxT | HxC | TxC | HxT | HxC | TxC |
| I | k computed | .625 | .715 | .696 | .625 | .720 | .703 | .625 | .725 | .710 | .625 | .730 | .717 |
|  | k observed | .64 | .78 | .71 | .64 | .78 | .71 | .64 | .78 | .71 | .64 | .78 | .71 |
|  | Discrepancy | .004403 |  |  | .003673 |  |  | .003050 |  |  | .002582 |  |  |
| II | k computed | .565 | .659 | .652 | .560 | .668 | .661 | .565 | .675 | .670 | .565 | .683 | .679 |
|  | k observed | .68 | .77 | .62 | .68 | .77 | .62 | .68 | .77 | .62 | .68 | .77 | .62 |
|  | Discrepancy | .026643 |  |  | .026356 |  |  | .024750 |  |  | .024263 |  |  |

The b's and k's obtained in two ways of calculation in the *Populus* clone are compared in *Table 7*. This table reveals that of the four calculated averages, the last one, i. e. the square root of average of two squared b's fits the observed k best.

Similar comparison is also made for *Abies* population growing in Ikeda *(Table 8)*. The comparison in the Asahigawa population is not available because as shown in *Table 5*, the b value for taperingness was negative and found unsuitable for calculation of the function.

It is again found from *Table 8* that the square root of average of two squared b's showed the least discrepancy with observed k's.

## Discussion

So far, rather few statistical or population-genetical studies have been made in forest trees. It is needless to mention that the statistico-genetical approach would be of great significance in forest tree breeding.

Toda (1957, 1959, 1961) is, so far as we know, one of the pioneers in the field mentioned, who did determine heritability values of several characters of economic importance in *Cryptomeria japonica*. He made comparison of variances between clonal and sexually propagated populations, on the one hand, and comparison among families, on the other. Toda's estimates of heritability in *Cryptomeria* were as follows:

|  | By the use of clones*) |  | By family analysis**) |
|---|---|---|---|
|  | 1957 | 1961 | 1959 |
| Tree height | 0.68 | 0.89 | 0.265 |
| Stem girth | 0.58 | 0.84 | 0.260 |
| Taperingness | 0.72 | 0.74 |  |
| Crown size | 0.61 | 0.82 |  |
| Bark thickness | 0 68 | 0.44 |  |
| Branch angle | 0.72 |  |  |

*Remarks:* The three groups of estimates were obtained from three different populations.

*) The heritability in the broad sense.

**) The heritability in the narrow sense.

Toda (1961) also determined genetic correlations among different characters in *Cryptomeria*.

Similar studies have also been conducted in other tree species by Bingham, Squillace and Wright (1960), Callaham

*Table 8.* — Relation between k and b's in an *Abies* population in Ikeda.

| | | k computed | k observed | Discrepancy |
|---|---|---|---|---|
| $\frac{2}{\frac{1}{b_1}+\frac{1}{b_2}}$ | H × G | .126 | —.17 | 2.7111 |
| | H × C | .018 | .38 | |
| | H × T | .140 | .05 | |
| | G × C | .019 | .64 | |
| | G × T | .250 | —.90 | |
| | T × C | .019 | .90 | |
| $\sqrt{b_1 \times b_2}$ | H × G | .137 | —.17 | 2.6310 |
| | H × C | .030 | .38 | |
| | H × T | .167 | .05 | |
| | G × C | .046 | .64 | |
| | G × T | .255 | — 90 | |
| | T × C | .056 | .90 | |
| $\frac{b_1+b_2}{2}$ | H × G | .150 | —.17 | 2.4696 |
| | H × C | .050 | .38 | |
| | H × T | .200 | .05 | |
| | G × C | .110 | .64 | |
| | G × T | .260 | —.90 | |
| | T × C | 160 | .90 | |
| $\sqrt{\frac{b^2_1+b^2_2}{2}}$ | H × G | .162 | —.17 | 2.3025 |
| | H × C | .065 | .38 | |
| | H × T | .228 | .05 | |
| | G × C | .149 | .64 | |
| | G × T | .265 | —.90 | |
| | T × C | .219 | .90 | |

and Hasel (1961), Campbell (1961) and Zobel (1961), though their methods of estimation of genetic parameters were more or less different from Toda's. Most of these estimations were made by the method of family analysis, an exception being the investigation made by Campbell on *Pseudotsuga menziesii*. The latter author investigated phenotypic variation in populations of the species and computed the repeatability of characters by the method of analysis of variance. He regarded the repeatability as the maximum estimate of heritability.

Liyanage and Sakai (1960) and Sakai (1960 a, b) have investigated heritabilities and genetic correlations among several characters of the coconut palm. The method of study adopted by them was also of family analysis.

These methods, i. e. the use of the clonal population or the analysis of within- and between-families variance components are orthodox which have repeatedly been practiced in other species of plants and animals. However, the former method of comparing intra-clonal variance with population variance may not be useful for those tree species where vegetative propagation can not be practiced. Furthermore, there might be some difficulties in taking it for granted that the environmental variance measured in one location could be applied to other locations.

Estimation of genetic parameters by family breeding, be it made by the regression of offspring on parents or by the analysis of variance, is one of the soundest methods. However, this can be done correctly only in forests in which members of not few families grown from mother trees selected at random from a population are planted at random in the field. This seems in our present forests rather difficult to be realized except for an exceptional case where the forest has been especially planted for genetical purpose. We shall have to wait until the next few decades to grow up new available families for the study.

The method of analysis presented in this paper, that is, by making use of variation patterns of environmental conditions in the field appears useful for partition of genotypic and environmental components of variance and covariance of characters and estimation of heritability and genetic correlation in any standing forest of any species so far as the following requirements are met: (1) The forest should have been planted at the same time, that is, the trees in the forest should be of the same age. (2) The planting distance within the forest should be more than moderately uniform. (3) The forest should have been damaged neither artificially nor naturally. (4) The forest should not have been thinned heavily.

Theoretically speaking, value of heritability should depend on the genetic constitution of the population and the environmental conditions of the location where the population stands at the time when the measurement is taken. In the perennial plants like forest trees, the year or season effect may not be so important as other two factors. In this respect, it is very interesting to find from *Table 5* that the estimates of heritability for the same character in two unrelated *Abies* forests growing in different locations were very similar either for tree height, stem girth, clear length, crown size or taperingness.

The estimates of genetic correlation were rather inconsistent in the two forests. Whether genetic correlations obtained in different populations are naturally very variable or not is a question of interest and importance in planning forest tree breeding.

## Conclusion

Surmounting hardships involved in dealing with forest trees, an effective method of estimation of genetic parameters in standing forests requiring neither breeding experiment nor existence of isogenic clones has been described in this paper. The requirements for the successful estimation by this method are as follows: (1) The forest should consist of trees of the same age. (2) Inter-tree spacing should not be very far from equidistant. (3) The forest should have been damaged neither artificially nor naturally. (4) The forest should not have been thinned heavily. The method is considered useful, because genetic variance estimated by it in a clonal forest proved to be so small as regarded as zero. Furthermore, it was found that in two genetically unrelated *Abies* populations, the heritability values estimated by this method for the same characters were very similar. Though a few points may have to be solved by further investigations, the method may be usable in the study of forest tree genetics.

## Summary

1. Based on the works of Fairfield Smith (1938) and Shrikhande (1957), the method of estimating heritability and genetic correlations in forest trees was investigated. The underlying assumption of the method is that genetic components of the variance or covariance of cluster means in a hybrid forest or a forest grown from open-pollinated seed is inversely proportional to the number of individuals included in each cluster, while environmental component to the b-power of the number, b being a constant determined by the character and the variation pattern of environmental conditions in the forest.

2. By repeated grouping of individual measurements into various cluster sizes, calculation is performed to obtain between-cluster mean squares or mean products. By the procedures as given in the text, b, G (genetic variance) or $W_G$ (genetic covariance) and E (environmental variance) or $W_E$ (environmental covariance) are calculated, from which heritability or genetic correlation is estimated.

3. This method thus requires neither isogenic clonal forest nor families grown from randomly selected mother-trees for investigation.

4. This method proved to be usable by a study of a vegetatively propagated clone because estimates of genetic variance in it could undoubtedly be regarded as zero.

5. The heritabilities of taperingness, crown size and stem girth in *Abies sachalinensis* populations were high, while the tree height was intermediate, and clear length was low in heritability. These characters were generally positively correlated genetically with each other.

## Zusammenfassung

Titel der Arbeit: *Schätzung genetischer Parameter bei Waldbäumen ohne Herstellung von Nachkommenschaften.*

(1) Die Methode der Schätzung der Heritabilität und genetischer Korrelationen wurde auf der Grundlage der Arbeiten von Fairfield Smith (1938) und Shrikhande (1957) untersucht. Der Methode liegt die Annahme zugrunde, daß die genetische Komponente der Varianz oder Kovarianz von Baumgruppenmitteln in einem Hybridenbestand oder in einem mit Saatgut aus Windbestäubung begründeten Bestand umgekehrt proportional der Anzahl von Bäumen in jeder Baumgruppe ist, und daß andererseits die Umweltkomponente umgekehrt proportional der b-ten Potenz dieser Zahl ist (b ist eine Konstante, die abhängig ist vom Merkmal und der Art der Verteilung der Standortsunterschiede in dem Bestand).

(2) Durch wiederholte Umgruppierung der Meßwerte von Einzelbäumen zu Baumgruppen verschiedener Größe werden die mittleren Abweichungsquadrate und -produkte „zwischen Baumgruppen" errechnet. Nach den im Text beschriebenen Verfahren werden b, G (genetische Varianz) oder $W_G$ (genetische Kovarianz) und E (Umweltvarianz) oder $W_E$ (Umweltkovarianz) errechnet, mit denen wiederum Heritabilität oder genetische Merkmalskorrelation geschätzt werden.

(3) Diese Untersuchungsmethode setzt weder einen genotypisch uniformen Klonbestand noch Familien aus Nachkommen ausgewählter Mutterbäume voraus.

(4) Diese Methode erwies sich als brauchbar in einer Untersuchung an einem vegetativ vermehrten Klon, da die genetische Varianz innerhalb eines solchen zweifellos als gleich Null angesehen werden konnte.

(5) In Populationen von *Abies sachalinensis* waren die Heritabilitäten der Abformigkeit des Schafts, der Kronengröße und des Schaftumfangs hoch, während die der Baumhöhe mittelhoch und die der Länge des astreinen Schafts niedrig waren. Diese Merkmale waren im allgemeinen positiv miteinander korreliert.

## Résumé

Titre de l'article: *Estimation de paramètres génétiques chez les arbres forestiers sans test de descendance.*

(1) On a étudié une méthode d'estimation de l'héritabilité et des corrélations génétiques chez les arbres forestiers, basée sur les travaux de Fairfield Smith (1938) et Shrikhande (1957). L'hypothèse de base de la méthode est que les composants génétiques de la variance ou de la covariance de moyenne de bouquets d'arbres dans une forêt composée d'hybrides ou issue de graines librement fécondées sont inversement proportionnels au nombre d'individus compris dans chaque bouquet, alors que la variance due au milieu l'est à la puissance b-de ce nombre, b- étant une constante déterminée par le caractère et le type de variation des conditions du milieu dans la forêt.

(2) En répétant des groupements de mesures individuelles en bouquets de différentes importances, le calcul permet d'obtenir les carrés moyens ou les produits moyens entre bouquets. On calcule ainsi, par les méthodes exposées dans le texte, b, G (variance génétique) ou $W_G$ (covariance génétique) et E (variance due au milieu) ou $W_E$ (covariance due au milieu); à partir de ces valeurs, on estime l'héritabilité ou la corrélation génétique.

(3) Cette méthode permet d'éviter l'emploi de clones ou de familles constitués à partir d'arbres-mères choisis au hasard.

(4) On a vérifié que cette méthode pouvait être utilisable par l'étude d'un clone, à la suite de laquelle on a trouvé que l'estimation de la variance génétique pouvait sans aucun doute être considérée comme nulle.

(5) Pour *Abies sachalinensis,* les héritabilités de la décroissance, de la largeur de la couronne et de la circonférence du tronc sont élevées, tandis que celle de la hauteur totale est de valeur moyenne et celle de la hauteur élaguée de valeur faible. En général, ces caractères présentent entre eux des corrélations génétiques positives.

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